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Alleviation of field water stress in wheat cultivars by using silicon and salicylic acid applied separately or in combination

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Abstract. The role of exogenous individual or combined application of silicon (Si) and salicylic acid (SA) (control, 6 mM Si, 1 mM SA, and 6 mM Si + 1 mM SA) on grain yield and some key physiological characteristics of wheat (*Triticum aestivum* L.) cvv. Shiraz (drought-sensitive) and Sirvan (drought-tolerant) was investigated under field water-stress conditions (100% and 40% field capacity). Drought stress caused a considerable reduction in biological yield, yield and yield components, relative water content and leaf water potential of both cultivars. Application of Si and SA effectively improved these parameters in water-deficit treatments. Moreover, water-limited conditions markedly promoted the activities of key antioxidant enzymes including peroxidase, ascorbate peroxidase, catalase and superoxide dismutase as well as the levels of malondialdehyde (MDA) and hydrogen peroxide (H_2O_2), while enhancing the accumulation of soluble sugars, potassium, magnesium and calcium in leaf tissues. Application of Si and SA further enhanced the activities of the key antioxidant enzymes and accumulation of osmolytes, and decreased the levels of H_2O_2 and MDA in drought-stressed plants; the positive effects of Si were greatest when it was applied with SA. Synergistic effects of Si + SA application on yield and physiological parameters were apparent compared with Si or SA applied separately. Water-stress alleviation and yield improvement in the wheat cultivars by Si and SA application was attributable to partly improved osmotic adjustment and antioxidant activity as well as to more favourable water status under stress conditions. Overall, Si and SA application proved to have great potential in promoting grain yield of wheat in drought-prone areas.

Additional keywords: membrane stability, osmoregulation, osmotic stress, plant growth regulator.

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Introduction

Wheat (*Triticum aestivum* L.) is a vital food crop around the world, but often its yield potential cannot be achieved because of the presence of environmental stresses such as heat, salinity and drought (Emam 2011). Although all abiotic stresses adversely affect the wheat growth and production, water scarcity imposes the most severe effects on this crop (González *et al*. 2010). Water scarcity adversely affects all phases of growth, most strikingly noted at the reproductive phase and grain filling, leading to fewer grains and smaller grain size in cereal crops including wheat. Impairment of assimilate partitioning and of activities of vital enzymes taking part in the synthetic processes of key carbohydrates including starch and sucrose reduces grain filling (Guttieri *et al*. 2001; Erocli *et al*. 2007). Drought stress is also believed to affect the uptake, transport and accumulation of key inorganic nutrients in plants (Sinclair 2011).

Silicon (Si) occurs abundantly in soils, but it is not as important as other known inorganic elements such as nitrogen (N), potassium (K), phosphorus (P), calcium (Ca) and magnesium (Mg) for plant growth (Ashraf *et al*. 2009; Zhang *et al*. 2017). However, Si is believed to play a beneficial role in plants subjected to stressful cues (Li *et al*. 2009; Maghsoudi *et al*. 2015; Maghsoudi *et al*. 2016). For example, Si has been reported to be effective in mitigating the harmful effects of salinity, drought, high temperature and metal stress on plants (Ma and Takahashi 2002; Parveen and Ashraf 2010; Maghsoudi *et al*. 2016). Furthermore, beneficial effects of Si have been reported in plants subjected to water-deficit treatments, with respect to drought-induced regulation of metabolic processes and water relations (Liang *et al*. 2007; Ashraf 2009; Zhang *et al*. 2017). However, the mechanism by which Si can effectively alleviate drought-induced harmful effects remains unknown.

Various plant growth regulators (PGRs) are currently used to achieve enhanced growth and production of different crops worldwide (Hayat *et al*. 2000; Tuna *et al*. 2007; Arora *et al*. 2008). Of several PGRs, salicylic acid (SA) is believed to be very effective in masking the adverse effects of different abiotic and biotic stresses on crops as well as being an essential component of the signal-transduction pathways operating in plants exposed to environmental cues including drought stress (Hayat *et al*. 2010). Ashraf and Foolad (2007) reported that SA also has a crucial function in the mechanism of plant water-stress tolerance. Exogenously applied SA has been reported to influence uptake and transport of nutrients (Kaydan *et al*. 2007), stomatal regulation (Morris *et al*. 2000), growth and photosynthetic rate (Khan *et al*. 2003), chlorophyll synthesis (Misra and Saxena 2009) and transpiration (Morris *et al*. 2000).

Furthermore, both Si (Gong *et al*. 2008; Ashraf 2009) and SA (Senaratna *et al*. 2000; Khodary 2004) can increase the antioxidative defence systems, both enzymatic and non-enzymatic, and thereby alleviate damage from reactive oxygen species (ROS) induced by stresses. Application of Si (Isa *et al*. 2010) and SA (Misra and Saxena 2009) also increases synthesis of osmolytes, improving plant tolerance against stresses. The positive role of osmolytes in osmoregulation has been reported (Sonobe *et al*. 2010; Murmu *et al*. 2017). Szabados and Savoure (2010) suggested that the accumulation of osmolytes in leaves might be involved in one or more of the above processes and contribute to drought tolerance.

Although, it has been shown that exogenous supplementation of Si or SA can effectively promote the endurance of plants against a variety of stresses (Senaratna *et al*. 2000; Ashraf *et al*. 2009; Hayat *et al*. 2010; Zhang *et al*. 2017), the literature has little information on the role of Si and SA applied in combination in alleviating drought-induced injurious effects on plants. Therefore, in the present study, we appraised the effects of exogenous Si and SA applied individually or in combination on wheat growth and grain yield under water-deficit conditions.

Materials and methods

Plant materials and growth conditions

Two wheat cultivars, Shiraz (relatively drought-sensitive) and Sirvan (drought-tolerant), were selected. Seeds of uniform size of both cultivars were sown in a field at the Research Farm of the College of Agriculture (altitude 1810 m a.m.s.l.), Shiraz University, Iran, during the 2013–14 growing season. The crop was irrigated with good-quality irrigation water. The soil texture is loam, pH(H_2O) 7.7 and electrical conductivity (EC) 2.55 dS m^{-1}.

Experimental design and treatments

The experiment was set up in a split-split-plot complete randomised block design with three replicates. Watering treatments (100% and 40% field capacity (FC)) were considered as main plots; foliar application of Si and SA (control (nil), 6 mM Si, 1 mM SA, and 6 mM Si + 1 mM SA) as subplots; and the two wheat cultivars as sub-subplots. The seeds were hand-sown (150 kg ha^{-1}) during the first week of November in 2013. Each plot was 3 m wide and 2 m long. The soil was fertilised with 150 kg ha^{-1} of urea before sowing, and at mid-tillering and anthesis stages. Until the anthesis stage, all plots were irrigated to maintain 100% FC. From anthesis to ripening, water-stress treatment was initiated to maintain 40% FC, while the control plots were maintained at 100% FC. Silicon (as $Na_2Si_3O_7$) and SA were sprayed onto the leaves of the appropriate plants at tillering and anthesis. These chemicals were sprayed for three consecutive days to ensure their uptake by the plants.

Measurements

All measurements based on fresh plant samples were done before the grain-filling stage. The fully expanded flag leaves were used for all biochemical analysis. Measurements included relative water content (RWC) (Castillo 1996), soluble sugars (Zhang *et al*. 2006) and soluble proteins (Bradford 1976); activities of peroxidase (POD) (Cakmak *et al*. 1993), ascorbate peroxidase (APX) (Nakano and Asada 1981), catalase (CAT) (Aebi 1984) and superoxide dismutase (SOD) (Dhindsa and Matow 1981); levels of hydrogen peroxide (H_2O_2) (Veljovic-Jovanovic *et al*. 2002) and malondialdehyde (MDA) (Hodges *et al*. 1999); concentrations of Ca, K and Mg by flame photometer (model 410; Corning Inc., Corning, NY, USA); and leaf water potential (Ψ_w) (PMS Instrument Company, Albany, OR, USA).

At maturity, grain yield, number of grains per spike, 1000-grain weight and harvest index were measured.

Statistical analyses

Analysis of variance was performed on data for each parameter by using SAS version 9.1 software (SAS Institute, Cary, NC, USA). Significant differences among mean values were compared using Duncan's multiple range test (at $P \leq 0.05$).

Results

Yield and yield components

Water stress (40% FC) significantly reduced grain number per spike by 24.65% in cv. Sirvan and 38.77% in cv. Shiraz. The negative impact of water stress on number of grains per spike was alleviated by application of Si and SA. Under water stress, foliar application of Si, SA and Si + SA caused an increase of 11.32%, 11.64% and 18.19%, respectively, in grain number per spike in cv. Sirvan, and 8.44%, 10.91% and 13.97% in cv. Shiraz (Table 1). Furthermore, in both wheat cultivars, 1000-grain weight decreased significantly under water stress. The drought-tolerant cultivar Sirvan had higher 1000-grain weight than drought-sensitive Shiraz under water stress (Table 1). The decline in 1000-grain weight was considerably less in plants supplied with Si, SA or Si + SA than that when these treatments were not applied. Therefore, foliar application of these treatments can significantly improve 1000-grain weight under field water-deficit conditions; maximum benefit was recorded with Si + SA when applied under water-stress conditions to cv. Sirvan, increasing 1000-grain weight by 22.90% (Table 1).

Grain yield decreased significantly under water-stress conditions, by 35.55% in drought-tolerant cv. Sirvan and 63.00% in drought-sensitive cv. Shiraz. However, foliar application of SA, Si and Si + SA caused a significant increase in grain yield under water-limited conditions. The effect of Si + SA was greater than of Si or SA applied separately (Table 1). With applications of Si, SA and Si + SA, grain yield was 18.31%, 19.71% and 31.96% higher, respectively, for cv. Sirvan, and 11.03%, 18.61% and 23.36% higher for cv. Shiraz than with no foliar application under water stress (Table 1). In both cultivars, the biological yield decreased significantly under water-stress conditions; however, Si- and SA-treated plants had higher biological yield than untreated plants under water stress alone. The effect of Si + SA application on biological yield was greater than of Si or SA applied separately (Table 1). Water stress decreased harvest index of drought-sensitive Shiraz only. Foliar application of Si + SA significantly promoted harvest index of both wheat varieties under water-limited conditions (Table 1).

Organic substances (soluble sugars and soluble proteins) and inorganic ions

Soluble sugar concentration in the flag leaf increased significantly under water-stress conditions, by 19.09% in cv. Shiraz and 43.83% in cv. Sirvan (Table 2). Plants treated with Si and SA had significantly higher soluble sugar content than untreated plants under water stress alone. The influence of Si + SA on soluble sugars in plants under water stress tended to be greater than of Si or SA applied separately. The response of cultivars to Si and SA varied significantly, with cv. Sirvan more responsive; in Si, SA and Si + SA treatments and under water stress, soluble sugar content was 21.75%, 15.20% and 29.57% higher, respectively, in cv. Sirvan, and 13.70%, 15.71% and 21.10% higher in cv. Shiraz than with no foliar application (Table 2).

In both cultivars the levels of soluble proteins decreased markedly under water-limited conditions. Application of Si and SA improved the soluble protein levels of water-stressed plants of both cultivars compared with plants exposed to drought stress without Si and SA application, and the effect of Si + SA on soluble protein content was greater than of Si or SA applied separately. Foliar application of Si + SA also significantly increased soluble protein content by 6.96% and 17.61%, respectively in cv. Shiraz and cv. Sirvan under non-stress conditions (Table 2).

Concentrations of K, Mg and Ca increased significantly under water stress, by 38.06%, 76.19% and 62.20%, respectively, in cv. Sirvan, and 15.62%, 25.21% and 12.36% in cv. Shiraz (Table 2). Drought-stressed plants fed with Si and SA accumulated a greater concentration of K than control plants. Supplementation with SA and Si + SA caused a marked increase in Mg concentration in water-stressed plants compared with those receiving no foliar treatment (Table 2). Calcium concentration increased significantly in both cultivars under water stress; foliar application of Si, SA and Si + SA caused a further increase in this nutrient only in cv. Sirvan. The concentrations of the three mineral nutrients K, Mg and Ca were greater in cv. Sirvan than in cv. Shiraz under water-stress conditions (Table 2).

Antioxidant enzyme activities, H_2O_2 and MDA

The activity of POD was significantly increased due to water stress, by 75.06% in cv. Sirvan and 5.49% in cv. Shiraz. In both

Table 1. Influence of separate or combined application of silicon (Si, 6 mM) and salicylic acid (SA, 1 mM) on yield, yield components, biological yield and harvest index of two wheat cultivars (Shiraz and Sirvan) under field water-stress and non-stress conditions

For each parameter, means followed by the same letter are not significantly different at $P = 0.05$

Irrigation treatment	Chemical treatment	No. of grains per spike		1000-grain weight (g)		Grain yield (g m^{-2})		Biological yield (g m^{-2})		Harvest index	
		Shiraz	Sirvan	Shiraz	Sirvan	Shiraz	Sirvan	Shiraz	Sirvan	Shiraz	Sirvan
100% field capacity	0	41.01b	40.56b	42.00a	42.13a	570.00a	570.87a	1354.62a	1300.52b	42.18b	43.53b
	Si	41.61b	43.12a	42.32a	42.23a	570.65a	575.32a	1342.00a	1310.23ab	42.45b	43.71b
	SA	41.54b	41.32b	42.81a	42.58a	580.23a	578.32a	1336.23a	1315.02ab	43.50b	43.58b
	Si + SA	43.52a	43.63a	43.15a	43.54a	584.47a	582.23a	1380.23a	1364.02a	42.38b	42.30b
40% field capacity	0	25.11g	30.56e	22.52f	31.00d	210.87g	367.87d	600.68 g	853.32e	35.00d	43.19b
	Si	27.23f	34.02d	25.05e	34.23c	234.15f	435.23c	650.10f	970.50d	35.84d	44.23ab
	SA	27.85f	34.12d	25.00e	35.26c	250.12e	440.40c	653.14f	970.25d	38.02c	45.12ab
	Si + SA	28.62f	36.12c	26.01e	38.10b	260.13e	485.45b	668.12f	1000.88c	38.45c	48.12a

Table 2. Influence of separate or combined application of silicon (Si, 6 mM) and salicylic acid (SA, 1 mM) on concentrations (mg g^{-1}) of soluble sugars, soluble proteins and mineral nutrients in the leaves of two wheat cultivars (Shiraz and Sirvan) under field water-stress and non-stress conditions

Measures of sugars and minerals by dry weight, protein by fresh weight. For each parameter, means followed by the same letter are not significantly different at $P = 0.05$

Irrigation treatment	Chemical treatment	Soluble sugars		Soluble proteins		Potassium		Magnesium		Calcium	
		Shiraz	Sirvan	Shiraz	Sirvan	Shiraz	Sirvan	Shiraz	Sirvan	Shiraz	Sirvan
100% field capacity	0	43.00g	43.12g	16.50b	15.50bc	48.63h	47.08hi	2.30e	2.31e	8.33d	7.25de
	Si	46.32fg	47.32f	15.85bc	15.32bc	48.52h	48.10h	2.31e	2.28e	8.10d	7.26de
	SA	47.00f	47.86f	16.00b	15.69bc	52.00gh	52.01gh	2.30e	2.29e	8.21d	7.15de
	Si + SA	47.08f	50.00f	17.65a	18.23a	53.00g	52.11gh	2.29e	2.31e	8.15d	7.28de
40% field capacity	0	51.21f	62.02d	10.52f	12.36e	56.23g	65.00e	2.88d	4.07b	9.36c	11.76b
	Si	58.23de	75.51ab	14.02d	14.36d	61.85f	73.10c	2.85d	4.10b	9.45c	12.95a
	SA	59.26d	71.45bc	14.00d	14.32d	63.15d	78.00a	3.02c	4.65a	9.27c	12.64a
	Si + SA	62.02d	80.36a	16.43b	16.32b	63.96d	80.12a	3.10c	4.71a	9.36c	13.00a

Table 3. Influence of separate or combined application of silicon (Si, 6 mM) and salicylic acid (SA, 1 mM) on activities of peroxidase (POD), superoxide dismutase (SOD), ascorbate peroxidase (APX) and catalase (CAT), as well as levels of hydrogen peroxide (H_2O_2) and malondialdehyde (MDA) of two wheat cultivars (Shiraz and Sirvan) under field water-stress and non-stress conditions

For each parameter, means followed by the same letter are not significantly different at $P = 0.05$

Irrigation treatment	Chemical treatment	POD		SOD		APX		CAT		H_2O_2 (µmol g^{-1} FW)		MDA (nmol g^{-1} FW)	
		(U mg^{-1} protein)											
		Shiraz	Sirvan	Shiraz	Sirvan	Shiraz	Sirvan	Shiraz	Sirvan	Shiraz	Sirvan	Shiraz	Sirvan
100% field capacity	0	25.68f	38.02d	5.20f	5.12f	1.65ef	1.18g	3.15gh	3.12gh	11.71g	11.23g	5.42g	5.54g
	Si	23.36f	40.32d	5.18f	5.15f	1.64ef	1.22g	3.16gh	3.10gh	11.02g	11.00g	4.00h	4.14gh
	SA	23.52f	37.25d	6.00e	5.97ef	1.75e	1.86e	3.15gh	3.13gh	11.00g	11.12g	3.47h	3.23h
	Si + SA	25.48f	40.98d	6.50de	6.02e	1.77e	1.83e	3.57g	3.89g	10.81g	10.00g	3.20h	3.14h
40% field capacity	0	27.09ef	66.56c	7.00d	8.32c	2.24cd	2.87c	5.11ef	7.21cd	56.62a	42.71b	17.20a	12.36c
	Si	30.36e	76.32ab	7.50cd	9.12b	2.85c	3.62ab	5.41e	7.84c	38.01c	22.23e	14.35b	9.23e
	SA	29.39e	71.65b	7.50cd	9.32b	2.92c	3.88a	5.55e	8.02b	33.58d	25.34e	11.63c	6.32f
	Si + SA	33.87e	82.36a	8.01c	10.54a	2.87c	3.86a	5.84e	8.87a	28.78e	15.34f	11.23cd	6.42f

cultivars, application of Si, SA and Si + SA significantly increased POD activity of water-stressed plants; the influence of Si + SA was greater than of Si or SA applied separately. POD was much higher in cv. Sirvan than in cv. Shiraz under water-stress conditions, especially with foliar-applied Si + SA (Table 3).

Activity of SOD rose significantly under water-stress conditions, by 34.61% in cv. Shiraz and 62.50% in cv. Sirvan. Plants treated with Si or SA had greater SOD activity than those grown solely under water limitation. The effect of Si + SA was greater than of Si or SA applied separately. Varietal response to Si and SA varied significantly for SOD activity; cv. Sirvan was more responsive. In addition, under normal water conditions, combined application of Si + SA significantly promoted SOD activity relative to no foliar application in both wheat varieties (Table 3).

Activity of APX also increased in both wheat varieties under water stress, and this increase was more pronounced in cv. Sirvan. Application of Si and/or SA had no significant effect on APX activity in cv. Shiraz under either water regime, whereas in cv. Sirvan, APX significantly increased with application of SA and Si + SA under normal water conditions and with application of Si, SA and Si + SA under water stress (Table 3).

In both cultivars, water stress increased the CAT activity. Application of Si or SA supplementation had no significant effect on CAT activity in cv. Shiraz under either water-limited and normal watering conditions, whereas in cv. Sirvan, CAT activity increased with application of SA and Si + SA under drought-stress conditions (Table 3).

Levels of H_2O_2 increased markedly under water-limited conditions. Plants treated with Si and/or SA had lower H_2O_2 levels than plants under water stress alone. Furthermore, the influence of Si + SA application on H_2O_2 content was greater than with either Si or SA applied separately. With application of Si, SA and Si + SA and under water stress, H_2O_2 content was lower than with no foliar application, in both cultivars (Table 3).

In addition, drought stress caused a significant increase in the levels of MDA in both wheat cultivars. Although the cultivars did not differ significantly from each other under normal watering, cv. Shiraz (drought-sensitive) had considerably higher levels of MDA than cv. Sirvan (drought-tolerant) under water-limited conditions. Treatment with Si, SA and Si + SA decreased MDA levels under both non-stress and water-limited regimes in both cultivars, but the influence was more evident under water deficit (Table 3).

Table 4. Influence of separate or combined application of silicon (Si, 6 mM) and salicylic acid (SA, 1 mM) on relative water content and leaf water potential of two wheat cultivars (Shiraz and Sirvan) under field water-stress and non-stress conditions

For each parameter, means followed by the same letter are not significantly different at $P = 0.05$

Irrigation treatment	Chemical treatment	Relative water content (%)		Leaf water potential (–MPa)	
		Shiraz	Sirvan	Shiraz	Sirvan
100% field capacity	0	82.32b	83.01b	1.79e	1.80e
	Si	82.21b	84.09b	1.78e	1.78e
	SA	82.00b	84.10b	1.75e	1.78e
	Si + SA	82.00b	84.00b	1.73e	1.68ef
40% field capacity	0	40.13f	57.02c	2.99a	2.43bc
	Si	45.15e	82.32b	2.50b	1.96d
	SA	45.20e	82.23b	2.51b	1.97d
	Si + SA	49.40d	88.20a	2.21c	1.85d

Relative water content and leaf water potential (Ψ_w)

Water-deficit treatments caused a marked suppression in RWC and Ψ_w in both wheat varieties. However, cv. Sirvan had higher RWC and Ψ_w than cv. Shiraz under drought stress. Application of Si, SA and Si + SA significantly improved the RWC and Ψ_w of water-stressed plants in both cultivars (Table 4).

Discussion

Water stress (40% FC) imposed from anthesis to grain ripening strongly reduced the yield of two wheat cultivars of differing drought tolerance in the present study. Indeed, the importance of water availability during grain filling for yield formation of bread wheat was demonstrated here. Generally, drought imposed during anthesis and grain filling leads to small-sized and fewer grains (Guttieri *et al*. 2001; Erocli *et al*. 2007; Sinclair 2011). Impaired grain filling was reported to be attributable to reduced partitioning of assimilates and reduced activities of key enzymes involved in sucrose and starch synthesis (Sinclair 2011). However, reduction of grain yield, yield components and biological yield in both wheat cultivars was lower in the presence of externally applied Si, SA, and especially combined Si + SA. Therefore, application of Si and SA could improve grain yield under water-stress conditions. Similarly, Tahir *et al*. (2006) observed that exogenous application of Si promoted grain yield in a wheat crop (by 50%) under stressful environmental conditions. A marked improvement was observed in biomass under drought stress, showing a promising effect of exogenous application of Si in counteracting the injurious effects of drought (Parveen and Ashraf 2010; Maghsoudi *et al*. 2016; Zhang *et al*. 2017). These results are similar to reports for sorghum (*Sorghum bicolor*) (Sonobe *et al*. 2010; Ahmed *et al*. 2011). Furthermore, foliar application of SA was previously reported to result in a significant increase in yield of wheat under water-stress conditions (Ahmad *et al*. 2014; Zamaninejad *et al*. 2013).

Water-stress conditions are believed to affect physiological responses and growth of several cereal crops (Maghsoudi and Maghsoudi Moud 2008; Yao *et al*. 2009), and several studies suggest that Si could improve endurance of plants under stressful conditions (Hattori *et al*. 2007; Liang *et al*. 2008; Maghsoudi *et al*. 2015; Mauad *et al*. 2016). Si-induced growth promotion under water-starved regimes has been reported in different crops, e.g. wheat (Gong *et al*. 2005; Gong and Chen 2012; Maghsoudi *et al*. 2016), rice (*Oryza sativa*) (Chen *et al*. 2011; Mauad *et al*. 2016) and soybean (*Glycine max*) (Shen *et al*. 2010).

Silicon is indispensable for promoting growth of several crops including cereals (Broadley *et al*. 2012), and SA, like several other known plant growth regulators, plays a key role in promoting plant resistance against drought stress (Ashraf and Foolad 2007). Some reports show the vital role of exogenous supply of SA in counteracting injurious effects of stressful environments in different plants (Hayat *et al*. 2010). Both SA, as a plant growth regulator, and Si, as a mineral, are believed to regulate different physio-biochemical processes in plants including photosynthesis, stomatal regulation and ion uptake. Thus, Si and SA have potential roles in activating plant growth and productivity (Ashraf *et al*. 2009; Hayat *et al*. 2010; Mauad *et al*. 2016; Ali and Hassan 2017).

Application of Si can effectively mitigate drought-induced injury in different plants (Gong *et al*. 2005; Hattori *et al*. 2005; Liang *et al*. 2007; Parveen and Ashraf 2010; Ahmed *et al*. 2011; Cooke and Leishman 2011; Broadley *et al*. 2012; Mauad *et al*. 2016; Ali and Hassan 2017). The benefits of soil-applied Si in counteracting both abiotic and biotic stresses have been reported by several researchers (e.g. Gong *et al*. 2005; Hattori *et al*. 2005; Li *et al*. 2009); however, beneficial effects of foliar-applied Si for counteracting these stresses have received less attention (Guével *et al*. 2007; Hellal *et al*. 2012).

The present investigation showed that increased activity of antioxidant enzymes such as CAT, POD, APX and SOD occurred to alleviate water-stress-induced adverse effects on wheat plants. Similar findings have been reported by Tari *et al*. (2004) and Ashraf (2009). Molassiotis *et al*. (2006) found that ROS-induced oxidative damage may cause oxidation of lipids and proteins. However, in the view of Møller *et al*. (2007), a balance between ROS generation and the activities of antioxidant enzymes may ensure the extent to which oxidative damage and signalling will take place. In fact, capacity to scavenge ROS may promote drought tolerance in plants (Tsugane *et al*. 1999).

In the present research, application of Si and SA enhanced the activity of some important enzymes taking part in the oxidative defence system and decreased the levels of H_2O_2 and MDA in water-stressed plants. Furthermore, in cv. Sirvan, the synergistic effects of Si + SA on activity of antioxidant enzymes were greater than effects of Si or SA applied separately, under water-stress conditions.

Our results are similar to findings reported by other workers demonstrating that Si application to soil is very effective in mitigating the harmful effects of environmental stresses including drought (Ashraf *et al*. 2009; Li *et al*. 2009; Parveen and Ashraf 2010; Zhang *et al*. 2017). A similar mechanism of Si and SA in reducing drought stress is the improvement of antioxidant activity in plants under abiotic stresses (Senaratna *et al*. 2000; Liang *et al*. 2007). Our findings also show that exogenously applied Si (e.g. Liang *et al*. 2007) and SA (e.g. Khodary 2004; Shakirova 2007) modulate the activities of vital antioxidant enzymes such as SOD and POD, and improve plant tolerance to drought stress.

An increase in mineral nutrient ions (K^+, Mg^{2+}, Ca^{2+} and Na^+) is believed to be another critical mechanism for plants to resist to stress (Zhu *et al*. 2005). In the present investigation, accumulation of K^+, Ca^{2+} and Mg^{2+} took place in the leaves of plants subjected to water-limited conditions, and foliar-applied Si, similar to SA, caused a further enhancement in K^+ levels in the leaves of water-stressed wheat plants.

Soluble sugars also generally increase in plant tissues exposed to water-limited conditions and they are potential contributors to osmoregulation (Shao *et al*. 2006). In our study, soluble sugars (as osmolytes) were considerably enhanced in the wheat leaves exposed to low water supply, more markedly in cv. Sirvan (drought-tolerant), than in cv. Shiraz. Foliar application of SA and Si further increased soluble sugar content and in cv. Sirvan, and the synergistic effect of Si + SA application was greater than of Si or SA alone. Enhanced levels of soluble sugars are believed to have a role in stress tolerance, because soluble sugars are actively involved in protection of enzyme structure, osmoregulation, biological membrane stabilisation and protection against hydroxyl radicals (Shao *et al*. 2006). Nayyar and Walia (2003) found that stress-resistant plants usually accumulate greater amounts of soluble sugars than stress-sensitive plants.

Leaf water potential is a potential indicator for determining plant water status, and it plays an important role in enhancing plant photosynthetic rate (Endres *et al*. 2010). In the present investigation, drought-tolerant cv. Sirvan maintained significantly higher Ψ_w and RWC than drought-sensitive cv. Shiraz under water-limited conditions.

Zhu *et al*. (2004) believed that Si considerably improves the water status of plant leaves, which in turn helps the plant to mitigate cellular dehydration, and hence lower oxidative stress. Moreover, Gong *et al*. (2005, 2008) reported that addition of Si to soil can improve leaf Ψ_w in plants subjected to water-limited regimens. Si-induced improvement in Ψ_w may be associated with enhanced stomatal conductance and higher RWC. Thus, Si plays an effective role in maintaining water balance in plant tissues, most probably through higher water uptake. Isa *et al*. (2010) reported that Si supply may improve the rigidity and strength of cell walls, thereby helping to reduce the solute leakage and stabilise the ultrastructure of biological membranes.

Silicon deposition in the cytoplasm of cells is a unique mechanism of Si in reducing abiotic stress in plants.

Nonetheless, the functions of Si and SA in water uptake and osmoregulation in plants under drought are not yet well defined. The results of this research show that osmolyte accumulation in leaves of plants treated with Si and SA under drought stress was more prominent in drought-stressed plants receiving no Si or SA treatment. Thus, supply of Si (Zhang *et al*. 2017) and SA (Hayat *et al*. 2010) can enhance the ability of plants to adjust themselves osmotically so as to maintain high water content and leaf water potential.

Conclusion

Foliar application of Si, SA and especially the combination Si + SA, markedly improved grain yield and yield components of the two wheat cultivars under water-deficit. In Si, SA and Si + SA treatments, grain yield was 15.63%, 16.60% and 24.32% higher respectively, than with no foliar application under water stress in cv. Sirvan, and 10.25%, 16.02% and 19.25% higher in cv. Shiraz. The results of the study highlight the role of Si and SA application in regulating water-stress response of wheat, suggesting that Si and SA are involved in physiological activities. These results showed positive effects of Si and SA in terms of increased antioxidant activity as well as relative water content and leaf water potential. In addition, Si and SA stimulated the active accumulation of some osmolytes in leaves of water-stressed wheat plants, which suggests enhanced osmoregulation ability. The synergistic effects of Si + SA application on yield and physiological parameters were greater than of Si or SA applied separately. Therefore, proper application of Si and SA might result in increased production of wheat, particularly in dryland areas.

Conflicts of interest

The authors declare no conflicts of interest.

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