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Influence of foliar application of silicon on chlorophyll fluorescence, photosynthetic pigments, and growth in water-stressed wheat cultivars differing in drought tolerance

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Abstract: The influence of foliar application of silicon (Si) on chlorophyll contents, chlorophyll fluorescence, and growth of four wheat cultivars differing in drought tolerance (Sirvan and Chamran, as relatively drought tolerant, and Shiraz and Marvdasht, as drought sensitive) was examined under water deficit (100% and 40% F.C.) created in a greenhouse. The results showed that water deficit decreased shoot and root lengths, shoot dry weight, root dry weight, water utilization efficiency, chlorophyll a and b, and chlorophyll stability index. In contrast, foliar application of Si improved plant growth parameters and chlorophyll pigment concentration under water deficit; however, it did not significantly affect wheat growth under control conditions. Limited water supply reduced the values of minimal fluorescence from dark-adapted leaf (F_0), maximal fluorescence from dark-adapted leaf (F_m), maximum quantum yield of PSII (F_v/F_m), effective quantum yield of PSII (ΦPSII), photochemical quenching (q_P), and apparent photosynthetic electron transport rate (ETR). However, under water deficit, foliar application of Si application increased the earlier mentioned parameters. In contrast, nonphotochemical quenching (q_N) and F_0/F_m increased under water deficit, and application of Si further improved these parameters. Chlorophyll fluorescence analysis suggested that Si alleviated water deficit-induced adverse effects by reducing nonphotochemical quenching, while increasing F_v/F_m and q_P, so that it improved the light use efficiency in the four wheat cultivars under stress. Overall, we concluded that drought-sensitive cultivars (Shiraz and Marvdasht) could resemble resistant cultivars upon foliar application of silicon.

Key words: Silicon, *Triticum aestivum* L., nonphotochemical quenching coefficient, photosystem II, water deficiency

Abbreviations: PSII: photosystem II; F_0: Minimal fluorescence from dark-adapted leaf (level of fluorescence when primary quinone electron acceptors of PSII are maximally oxidized (PSII centers are open)); F_0': Minimal fluorescence from light-adapted leaf; F_s: steady state value of fluorescence; F_m: Maximal fluorescence from dark-adapted leaf (level of fluorescence when PSII is maximally reduced (PSII centers are closed)); F_m': Maximal fluorescence from light-adapted leaf; F_v: Variable fluorescence from dark-adapted leaf (demonstrates the ability of PSII to perform primary photochemistry); F_v': Variable fluorescence from light-adapted leaf; F_v/F_m: Maximum quantum efficiency of PSII photochemistry; F_v'/F_m': PSII maximum efficiency (provides an estimate of the maximum efficiency of PSII photochemistry at a given light intensity, which is the PSII operating efficiency if all the PSII centers were open); φ_{PSII}: quantum yield of PSII electron transport; q_N: nonphotochemical quenching coefficient (Estimates the nonphotochemical quenching from F_m to F_m': Monitors the apparent rate constant for nonradiative decay (heat loss) from PSII and its antennae); q_P: photochemical quenching coefficient; **ETR**: Apparent photosynthetic electron transport rate.

1. Introduction

Despite the fact that silicon (Si) is the second most abundant element in soils, it is not considered an essential element for plants (Ma and Takahashi, 2002; Ashraf et al., 2009). However, this element is beneficial for higher plants, especially under stressful environments (Li et al., 2009). For example, Si is known to alleviate the adverse effects of salt stress, high temperature, and heavy metal toxicity on plants (Shi et al., 2005; Parveen and Ashraf, 2010). Moreover, there are some studies that show the beneficial role of Si in plants exposed to drought stress, mainly with respect to water relations, photosynthesis, and some other key physiological traits (Hattori et al., 2005; Liang et al., 2007). However, the mechanism of Si-induced mitigation of the adverse effects of drought stress on plants remains unclear.

Although wheat (*Triticum aestivum* L.) is grown in many countries around the world, its productivity is hampered due to a variety of abiotic stresses such as drought, salinity, and heat, particularly in arid and

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semiarid regions of the world (Emam, 2011). Of these, drought is the major abiotic stress that is regarded as highly deleterious to growth and productivity of the wheat crop. Although drought stress inhibits a variety of physiological processes in plants, its most significant inhibitory effect can be observed on photosynthesis (Chen et al., 2011). In particular, PSII photochemistry has been shown to be sensitive to water deficit conditions (Baker and Rosenqvist, 2004; Naumann et al., 2010). For example, water deficit conditions considerably damage the oxygen evolving complex of PSII and the PSII reaction centers in most plants (Naumann et al., 2010). Such drought-induced damage to PSII reaction centers has been ascribed to the degradation of structural proteins (Ohashi et al., 2006). However, it is thought that drought-induced reduction in photosynthesis could be due to perturbation in the mechanism of chlorophyll fluorescence. It is now evident that drought-induced decline in photosynthesis occurs primarily due to closure of stomata. Drought-induced stomatal closure decreases intercellular CO_2 concentration in leaves, which in turn reduces the rate of CO_2 assimilation, hence causing an imbalance between the PSII photochemical activity and electron requirement for photosynthesis (DeEll and Toivonen, 2003).

The activity of PSII helps to sustain leaf photosynthesis in plants exposed to abiotic stresses and this pigment system is the primary target of damage caused by photoinhibition (Perks et al., 2001), although some controversies exist concerning this notion (Souza et al., 2004). Addition of inorganic nutrients to the root growing medium of plants subjected to drought stress causes protection of different cellular organelles (Aiken, 1996). Silicon is among the known inorganic nutrients that really may play a role in some physiological processes in plants subjected to drought stress (Habibi and Hajiboland, 2013). For example, Si is thought to improve the efficiency of light absorption by bringing about the conduction of light to the mesophyll tissue. However, this hypothesis is not be supported by sound evidence (Ma and Takahashi, 2002). In some studies, a marked Si-induced enhancement in photosynthesis and chlorophyll fluorescence has been reported in sorghum (Hattori et al., 2005) plants under water deficit conditions. Although previous studies have shown that application of silicon can improve the drought tolerance of plants, in most of these studies silicon had been introduced through the roots, while little work has been done on the effects of foliar application (Liang et al., 2005; Guével et al., 2007; Hellal et al., 2012). Therefore, in this research, the effects of foliar Si application (in the form of Na_2SiO_3) on chlorophyll fluorescence and wheat growth under water-deficit conditions were examined. The results could help us to achieve a better understanding of the physiological mechanisms of Si-induced drought tolerance in wheat plants.

2. Materials and methods

To evaluate the effect of foliar application of silicon on chlorophyll fluorescence, chlorophyll pigments, and growth of four wheat cultivars under water-deficit conditions, an experiment was carried out at the greenhouse of the College of Agriculture Shiraz University, Shiraz, Iran, in 2013. Two wheat cultivars were relatively drought tolerant (Sirvan and Chamran) while the other two (cvs. Shiraz and Marvdasht) were drought sensitive.

This study was carried out as a factorial experiment based on a completely randomized design (CRD) with four replicates. There were four treatments for each wheat cultivar: no water deficit and no foliar application of silicon (wet, Si –), no water deficit and 6 mM silicon application (wet, Si +), water deficit and no foliar application of silicon (dry, Si –), and water deficit and 6 mM silicon application (dry, Si +).

Before sowing all seeds were surface sterilized in 1% sodium hypochlorite solution for 10 min, and rinsed thoroughly with distilled water. The seeds were germinated on moist filter paper placed in petri dishes for 48 h. Ten-day-old seedlings were transplanted into plastic pots each of 5 L volume (five seedlings per pot). The pots were filled with soil + sand in 2:1 ratio (soil classification: fine, mixed, mesic, Cacixerollic Xerochrepts). Electrical conductivity (EC), pH, available N, available P, and available K of the experimental soil were 0.60 dS m^{-1}, 7.09, 0.15%, 12 mg kg^{-1}, and 720 mg kg^{-1}, respectively. Each pot was considered an experimental unit. Plants were fertilized with urea at a rate of 150 kg ha^{-1} on the day of transplanting. Minimum and maximum temperatures in the greenhouse were 14 and 28 °C, respectively, and relative humidity was 55%–60%. The wheat plants were grown under 14-h photoperiod.

The pots were watered regularly to maintain soil moisture at 100% field capacity (F.C.) before starting irrigation treatments. Water deficit treatment (40% F.C.) was imposed 25 days after sowing and continued for a period of 20 days. The control pots were regularly watered to maintain 100% F.C. The silicon concentration (6 mM) was applied as sodium silicate. Foliar application of silicon was carried out at 30 days after sowing.

Si was applied (with a hand sprayer until the solution began to drip off leaves) at sunset to ensure its complete uptake by the leaves. It was applied on three consecutive days. The pots not receiving Si treatment were similarly sprayed with an equivalent amount of distilled water.

2.1. Measurements of chlorophyll fluorescence of leaves in dark- and light-adapted states

Chlorophyll fluorescence was measured on the youngest fully expanded leaf at room temperature (25 °C) using a portable fluorimeter (PAM-2000, Walz, Germany) on 45-day-old plants following Genty et al.'s (1989) method. After sunset, the pots were kept in the dark for 2 h or 2 h after the automated supplemental light was shut off, whichever occurred last. The fluorimeter was connected to a leaf-clip holder with a trifurcated fiberoptic and to a computer equipped with data acquisition software (DA-2000, Walz).

The minimal fluorescence level (F_0) with all PSII reaction centers open and the maximal fluorescence level (F_m) with all PSII reaction centers closed were determined on dark-adapted leaves. Then the leaves were continuously illuminated with a white actinic light at an irradiance of 180 µmol m^{-2} s^{-1} to measure the steady-state value of fluorescence (F_s), which occurred at about 6 min after the initiation of white actinic light. The maximal fluorescence level in the light-adapted state ($F_m{}'$) was recorded after subjecting the leaf to a second saturating pulse at 8000 µmol m^{-2} s^{-1}.

The minimal fluorescence level in the light-adapted state ($F_0{}'$) was determined by exposing the leaf to far-red light for 3 s. Using both light and dark fluorescence data, the following parameters were calculated:

- **F_v** (maximum variable chlorophyll fluorescence yield in a dark-adapted state) was calculated following Maxwell and Johnson (2000): $F_v = F_m - F_0$
- **F_v/F_m** (the maximal efficiency of PSII photochemistry in the dark-adapted state) was calculated following Krause and Weis (1991): $F_v/F_m = (F_m - F_0)/F_m$
- **q_P** (the photochemical quenching coefficient): $q_P = (F_m{}' - F_s)/(F_m{}' - F_0{}')$
- **q_N** (nonphotochemical quenching coefficient): $q_N = 1 - (F_m{}' - F_0{}')/(F_m - F_0)$.
- **φPSII** (the actual quantum yield of PSII electron transport in the light-adapted state): $\varphi PSII = (F_m{}' - F_s)/F_m{}'$, which was equal to the product of q_P and $F_v{}'/F_m{}'$ (Genty et al., 1989). Thus, φPSII depends on the degree of closure of PSII reaction centers and the efficiency of excitation energy capture in PSII.
- **ETR** (Apparent photosynthetic electron transport rate):
  $ETR = \Delta F/F_m{}' \times PPFD \times 0.5 \times 0.84$

2.2. Measurements of growth parameters

Plants were harvested at 45 days after transplanting to determine shoot and root length, shoot and root dry weight, and water utilization efficiency. Water utilization efficiency was calculated as the plant dry weight divided by total water used (Chen et al., 2011). Three plants were randomly selected from each pot, and their average dry weight considered as the mean for that treatment. The plants were separated into root and shoot to determine their dry weight. The samples were oven-dried at 70 °C for 48 h before weighing.

Chlorophyll a and b as well as carotenoids were determined according to Lichtenthaler and Wellburn (1983). One hundred milligrams of fresh leaf material were taken from the youngest fully expanded leaves and extracted with 95% methanol. Absorption was read using a spectrophotometer at wavelengths of 653 and 666 nm for chlorophyll a and b, respectively. The chlorophyll contents were calculated using the following equations:

$$\text{Chl a} = (12.25\ A_{663} - 2.79\ A_{646})$$

$$\text{Chl b} = (21.21\ A_{646} - 5.1\ A_{663})$$

The chlorophyll stability index (CSI) was worked out according to Sairam et al. (1997):

$$\text{CSI} = \frac{\text{Total Chl under stress}}{\text{Total Chl under control}} \times 100$$

2.3. Data analysis

The collected data for each attribute were subjected to analysis of variance using SAS v.9.1 software. Duncan's multiple range test ($P \leq 0.05$) was used to determine significant differences between treatment means.

3. Results

3.1. Effect of water deficit and silicon on plant growth

Growth of all four wheat cultivars was significantly affected by silicon and water deficit. Exogenously applied Si did not affect shoot dry weight of the wheat cultivars under normal watering regimes, whereas under water deficit conditions exogenously applied 6 mM silicon significantly improved all these growth attributes (Table).

Shoot dry weight was also similarly affected by Si and water deficit. There were significant differences among the wheat cultivars in shoot dry weight: the drought tolerant cultivars (Sirvan and Chamran) showed significantly greater shoot dry weight compared to Shiraz and Marvdasht (intolerant cultivars) under water deficit conditions. Furthermore, Si application improved shoot dry weight by 40% in cv. Sirvan, 32% in Chamran, 20% in Shiraz, and 24% in Marvdasht. Indeed, the response of the four cultivars to Si varied for shoot dry weight; cultivar Sirvan was found more responsive than the other cultivars to foliar-applied Si (Table).

The present study also showed that water deficit (40% F.C.) significantly inhibited root growth (Table). There was a significant difference among the cultivars with respect to root dry weight: Sirvan and Chamran (drought tolerant) showed significantly higher root dry weight than Shiraz and Marvdasht (drought sensitive) under water-deficit conditions. However, Si application had no significant effect on the root dry weight of the wheat cultivars. In contrast, sodium silicate application improved shoot length in the four wheat cultivars, with no significant effect on root growth (Table).

Table. Effect of silicon application on growth parameters of wheat cultivars under different moisture conditions (100% F.C. as normal and 40% F.C. as water deficit).

Moisture conditions	Silicon application	Cultivar	Shoot dry weight (g/pot)	Root dry weight (g/pot)	Shoot length (cm)	Root length (cm)	Water utilization efficiency (g cm^3)	Chlorophyll a (mg/g FW)	Chlorophyll b (mg/g FW)
100% F.C.	-	Chamran	2.09b	1.20a	30.30b	20.32bc	0.30c	6.85a	3.65ab
	+		2.20b	1.22a	30.00b	21.36b	0.45a	6.80a	3.92a
40% F.C.	-		1.24e	1.00c	23.50e	15.23e	0.21e	4.39e	2.65c
	+		2.08b	1.00c	26.32c	16.50e	0.26d	5.02de	3.23b
100% F.C.	-	Sirvan	2.34a	1.25a	29.5b	24.32a	0.31c	7.11a	3.68a
	+		2.40a	1.28a	29.5b	23.00ab	0.48a	7.00a	3.77a
40% F.C.	-		1.61d	1.12b	25.50d	21.00b	0.25d	5.47d	3.00bc
	+		2.35a	1.15b	27.00c	21.50b	0.31c	6.31bc	3.56b
100% F.C.	-	Shiraz	2.04c	1.26a	31.26a	20.85c	0.29c	6.43b	3.62ab
	+		2.10b	1.23a	32.00a	19.89cd	0.35b	6.22c	3.84a
40% F.C.	-		0.84g	0.86d	19.32f	11.63f	0.16f	2.65g	1.08e
	+		1.05f	0.85d	20.50f	11.00f	0.19e	3.87f	1.54d
100% F.C.	-	Marvdasht	2.05c	1.19ab	29.00b	21.36b	0.28cd	6.75ab	3.64ab
	+		2.10b	1.19ab	30.00b	20.10b	0.34b	6.60b	3.55b
40% F.C.	-		0.87g	0.75e	17.50h	11.50f	0.15f	2.71g	1.15e
	+		1.13e	0.79e	19.00g	11.00f	0.17ef	3.32fg	1.76d

Means followed by the same letters within each column do not differ significantly at P ≤ 0.05.

Water-deficit stress reduced water utilization efficiency in all cultivars (Table). There was a significant difference among the wheat cultivars in water use efficiency; the reduction in this attribute was higher in Shiraz (45%) and Marvdasht (47%) (drought sensitive) as compared to that in Sirvan (20%) and Chamran (30%) (drought tolerant). Exogenous application of silicon improved water utilization efficiency in all cultivars under both well-watered and water-deficit conditions, but the Si-induced effect was more pronounced under water-deficit conditions (Table).

Water deficit caused a significant decrease in chlorophyll a and chlorophyll b in all four cultivars (Table). Si application also significantly changed the concentrations of chlorophyll pigments. Si improved chlorophyll a and chlorophyll b in all cultivars under water-deficit conditions, but there were significant differences among the wheat cultivars in chlorophyll pigment concentration: Sirvan and Chamran (drought tolerant) showed significantly more chlorophyll a and chlorophyll b than did Shiraz and Marvdasht (drought sensitive) under water-deficit conditions (Table). The chlorophyll stability index decreased in all cultivars under water-deficit conditions. However, the silicon-treated plants had a higher chlorophyll stability index under water-deficit conditions (Figure 1).

3.2. Effects of water deficit and silicon on chlorophyll fluorescence parameters

Water deficit significantly reduced the F_0 parameter in all wheat cultivars (Figure 2). There was a significant difference between cultivars in F_0, the minimum fluorescence yield, in dark-adapted state. Sirvan and Chamran (drought-tolerant cultivars) showed significantly higher F_0 levels than did Shiraz and Marvdasht (drought-sensitive cultivars) under water-deficit stress. Additionally, in water-deficit conditions, the supply of 6 mM sodium silicate

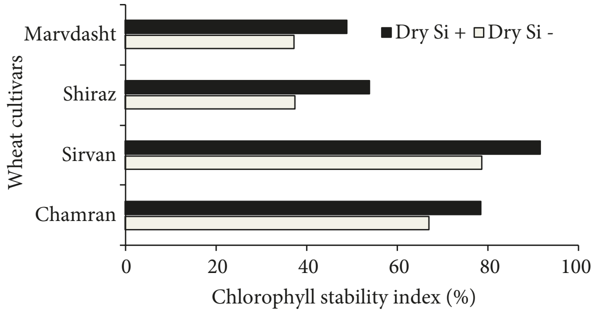

Figure 1. Effect of Si application on chlorophyll stability index (CSI) of wheat cultivars underwater deficit conditions.

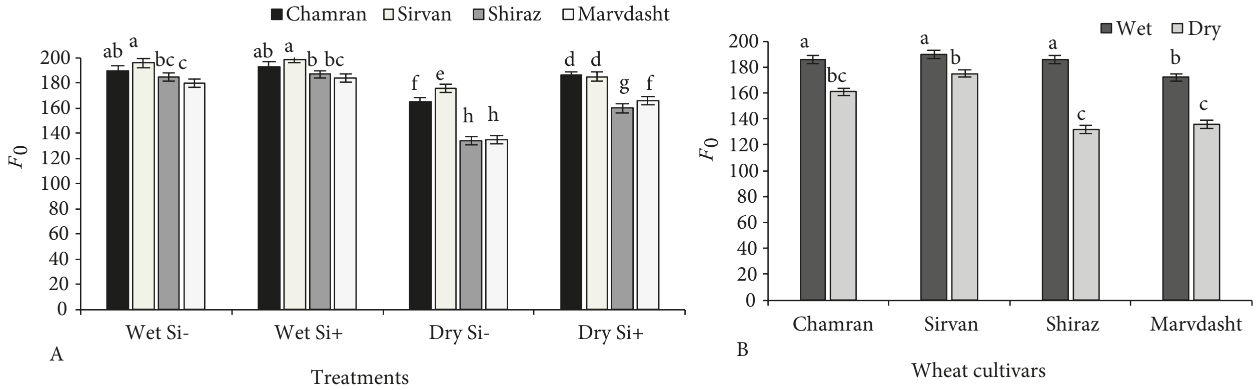

Figure 2. Effects of water deficit stress and Si application on F_0 (minimal fluorescence) (A) and responses of wheat cultivars to water deficit conditions with respect to F_0 (B). In each figure columns with the same letters are not significantly different (Duncan's multiple range test, $P \leq 0.05$). Vertical bars represent the standard errors (n = 4 in A and n = 8 in B).

resulted in improved F_0 in the four wheat cultivars (Figure 2). Furthermore, water-deficit stress (F.C. 40%) reduced F_m (Figure 3) and the maximum quantum yield of PSII (F_v/F_m) in all wheat cultivars (Figure 4). Si application increased these parameters of water-stressed plants compared to the water-stressed plants without Si treatment. There was a significant difference in F_m and F_v/F_m among the wheat cultivars: F_m (Figure 3) and F_v/F_m (Figure 4) were higher in the leaves of Sirvan and Chamran than in the other wheat cultivars in water-deficit conditions.

Water-deficit stress also decreased the effective quantum yield of PSII (ΦPSII) (Figure 5) and photochemical

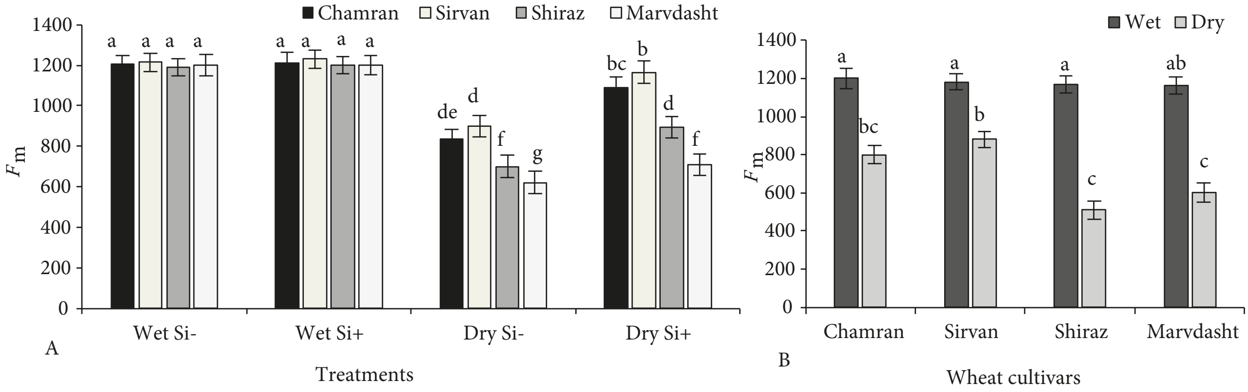

Figure 3. Effects of water deficit stress and Si application on F_m (maximal fluorescence) (A) and responses of wheat cultivars to water deficit conditions with respect to F_m (B). In each figure columns with the same letters are not significantly different (Duncan's multiple range test, $P \leq 0.05$). Vertical bars represent the standard errors (n = 4 in A and n = 8 in B).

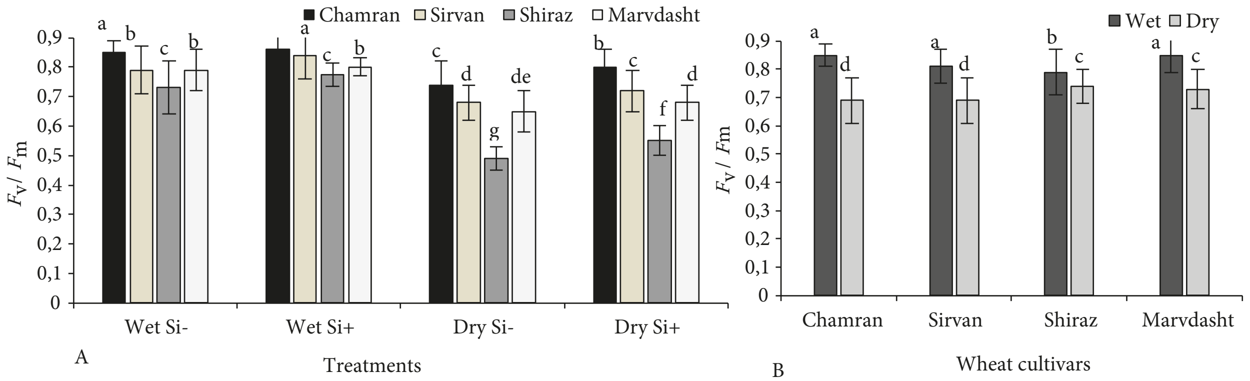

Figure 4. Effects of water deficit stress and Si application on F_v/F_m (maximum quantum efficiency of PSII photochemistry) (A) and responses of wheat cultivars to water deficit conditions with respect to F_v/F_m (B). In each figure columns with the same letters are not significantly different (Duncan's multiple range test, $P \leq 0.05$). Vertical bars represent the standard errors (n = 4 in A and n = 8 in B).

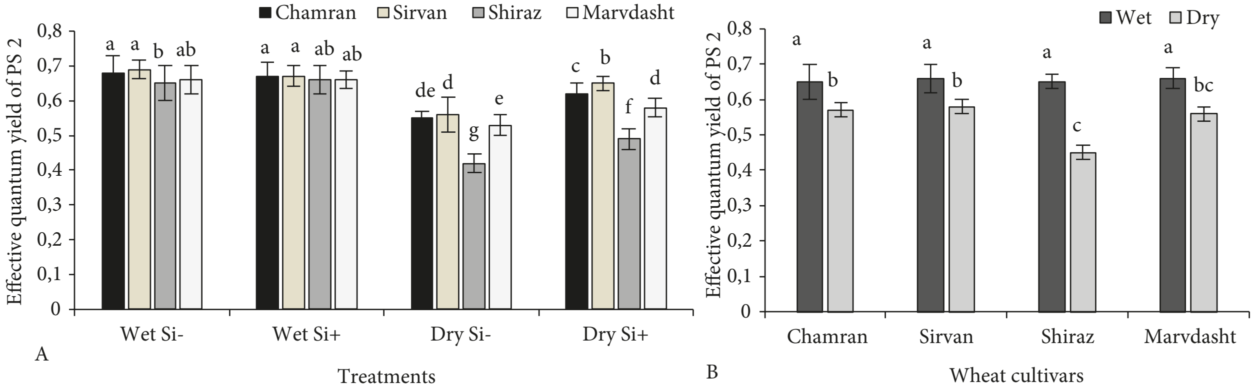

Figure 5. Effects of water deficit stress and Si application on effective quantum yield of PS2 (A) and responses of wheat cultivars to water deficit conditions with respect to effective quantum yield of PS2 (B). In each figure columns with the same letters are not significantly different (Duncan's multiple range test, $P \leq 0.05$). Vertical bars represent the standard errors (n = 4 in A and n = 8 in B).

quenching (q_P) in all cultivars (Figure 6). In contrast, nonphotochemical quenching (q_N) increased under water-deficit conditions (Figure 7). Similar to plant growth data, Si supplementation did not affect the photochemical parameters in well-watered plants (Figure 6); however, it improved ΦPSII (Figure 5) and decreased q_N (Figure 7) of the four wheat cultivars under water-deficit conditions. Furthermore, in water-stressed plants of all four cultivars, application of 6 mM Si induced a significant increase in q_P (Figure 6).

A significant reduction in apparent photosynthetic electron transport rate (ETR) was observed under water-deficit conditions. However, Si application improved ETR in all four wheat cultivars under water-deficit conditions (Figure 8). The results also showed that water-deficit stress significantly increased F_0/F_m (Figure 9).

There was significant difference in F_0/F_m ratio, which might be termed the basal quantum yield of nonphotochemical processes in PSII in dark-adapted state among wheat cultivars. It was higher in the leaves of Shiraz and Marvdasht in both control and water-deficit conditions. Application of 6 mM sodium silicate resulted in reduced F_0/F_m values in water-stressed plants. In the four wheat cultivars, Si application significantly reduced the F_0/F_m of drought-stressed plants (Figure 9). Drought-tolerant cultivars (Sirvan and Chamran) showed significantly greater values of F_0 (Figure 2), F_m (Figure 3), F_v/F_m (Figure 4), φ_{PSII} (Figure 5), qp (Figure 6), and ETR (Figure 8) than those in Shiraz and Marvdasht (intolerant cultivars) under water-deficit conditions. Sirvan and Chamran also showed a lower q_N under water-deficit conditions (Figure 7).

4. Discussion

Water-deficit conditions are thought to affect the growth and physiological processes of almost all crops including cereals (Yao et al., 2009; Emam, 2011). However, many

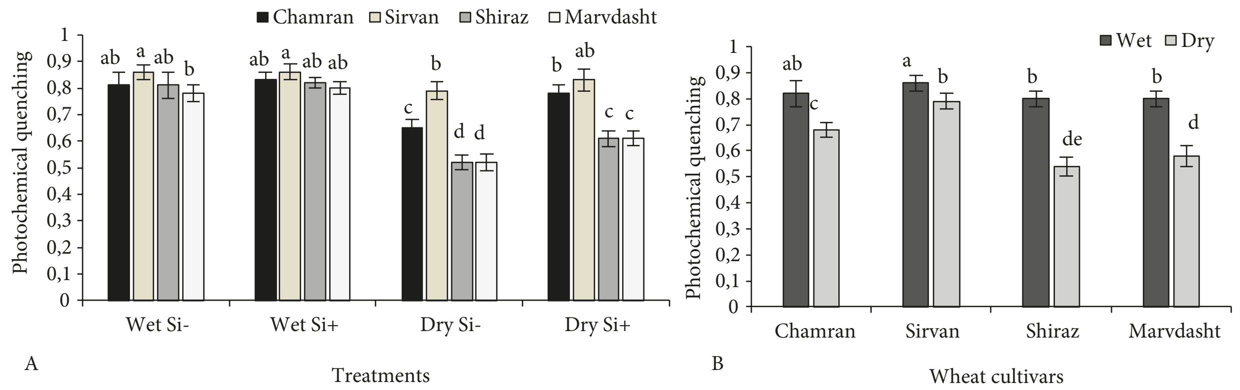

Figure 6. Effects of water deficit stress and Si application on photochemical quenching (A) and responses of wheat cultivars to water deficit conditions with respect to photochemical quenching (B). In each figure columns with the same letters are not significantly different (Duncan's multiple range test, P ≤ 0.05). Vertical bars represent the standard errors (n = 4 in A and n = 8 in B).

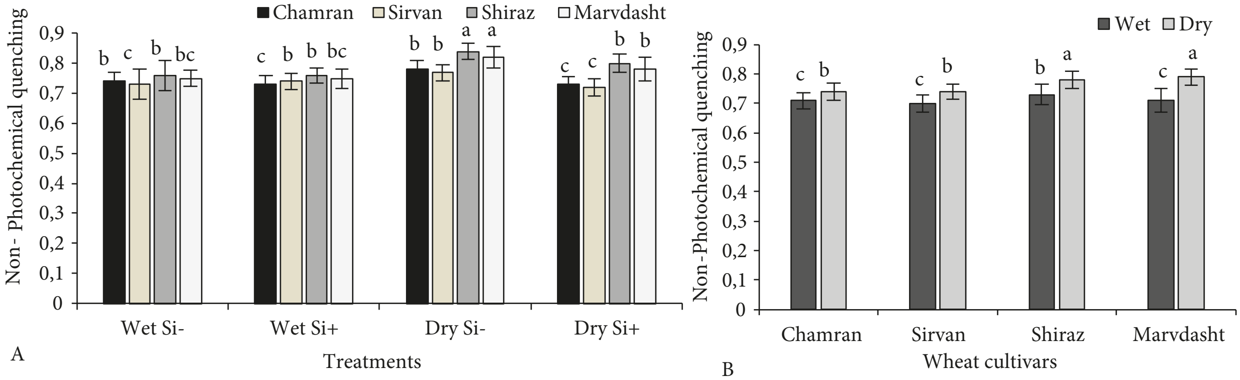

Figure 7. Effects of water deficit stress and Si application on nonphotochemical quenching (A) and responses of wheat cultivars to water deficit conditions with respect to nonphotochemical quenching (B). In each figure columns with the same letters are not significantly different (Duncan's multiple range test, P ≤ 0.05). Vertical bars represent the standard errors (n = 4 in A and n = 8 in B).

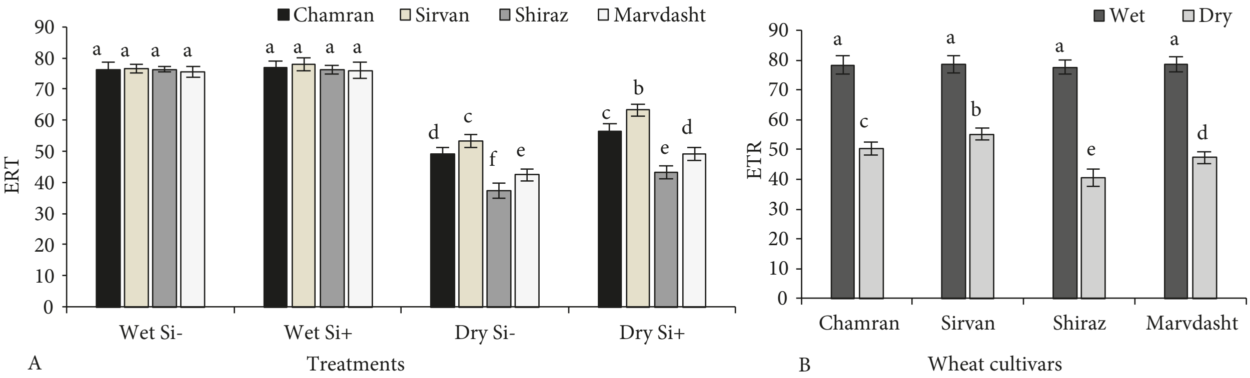

Figure 8. Effects of water deficit stress and Si application on ETR (apparent photosynthetic electron transport rate) (A) and responses of wheat cultivars to water deficit conditions with respect to ETR (B). In each figure columns with the same letters are not significantly different (Duncan's multiple range test, P ≤ 0.05). Vertical bars represent the standard errors (n = 4 in A and n = 8 in B).

researchers have already shown that silicon could increase the tolerance of plants exposed to stressful environments (Kaya et al., 2006; Liang et al., 2008). Si-induced growth improvement under water-deficit conditions has been observed in different species such as wheat (Gong and Chen, 2012), rice (Chen et al., 2011), and soybean (Shen et al., 2010). Indeed, comprehensive studies have been carried out to uncover the possible mechanisms for Si-enhanced tolerance of plants to abiotic stresses (Liang et al., 2007; Chen et al., 2011).

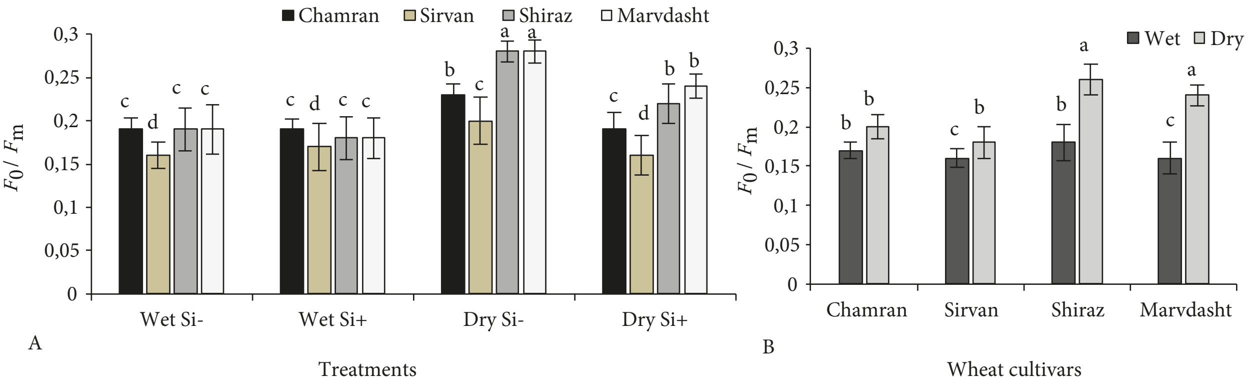

Figure 9. Effects of water deficit stress and Si application on F_0/F_m (A) and responses of wheat cultivars to water deficit conditions with respect to F_0/F_m (B). In each figure columns with the same letters are not significantly different (Duncan's multiple range test, P ≤ 0.05). Vertical bars represent the standard errors (n = 4 in A and n = 8 in B).

In the present study, water-deficit treatments caused significant decreases in shoot and root lengths, shoot dry weight, root dry weight, water utilization efficiency, and chlorophyll pigment concentrations of the four wheat cultivars examined. However, Si improved all these parameters only under water-deficit conditions (Table). Roots, despite playing an important role in uptake of ions and water, have a vital role in assimilation, synthesis, and transportation of many solutes. Therefore, root traits can directly affect the growth and development of wheat plants under stress conditions (Aiken, 1996). Water deficit not only significantly decreased root growth of the four wheat cultivars, but also inhibited their biomass accumulation (Table).

It is now widely accepted that chlorophyll fluorescence parameters provide useful information on PSII activity and photosynthetic metabolism in stressed plants (Kastori et al., 2000; Nedbal et al., 2000). Maximum quantum efficiency of PSII (F_v/F_m) is known to be related to leaf photosynthetic efficiency (Shangguan et al., 2000). Thus, F_v/F_m is widely used to appraise stress-induced impairment in the photosynthetic apparatus. The results of this research showed that water deficit resulted in reduced F_v/F_m (Figure 4), which may have been linked to decreased efficiency of energy transfer from the antennae to the reaction centers and/or inhibition in the activity of PSII reaction centers (Rosenqvist and van Kooten, 2003).

The decline in F_v/F_m indicates serious damage to PSII (Maxwell and Johnson, 2000). Baker and Rosenqvist (2004) were of the view that the decline in F_v/F_m might hinder the rate of photosynthesis, thereby affecting plant growth and development.

It is imperative to note that Si supply enhanced F_v/F_m under water-deficit conditions in our study (Figure 4). This suggests that Si supply was able to alleviate the harmful effects of drought on the photochemical reactions in the plants of all four wheat cultivars. In contrast, Souza et al. (2004) reported that despite a considerable reduction in photochemistry in drought-stressed cowpea plants, the overall photosynthetic process remained unaffected. Although water stress-induced suppression in apparent photosynthetic electron transport rate (ETR) (Figure 8) may suggest low tolerance of plants to drought stress, an increase in q_N (Figure 7) may be an important adaptive component to counteract excessive light energy when plants show a low photosynthetic rate. Moreover, it is thought that the stress-induced reduction in ETR may also be caused by photochemical down-regulation (Yordanov et al., 2000).

In this study, water deficit increased nonphotochemical quenching (q_N) (Figure 7). Ohashi et al. (2006) showed that drought-induced damage to the photosynthetic apparatus may occur due to photoinhibition. Photoinhibition may also cause a slow and reversible reduction in photosynthetic efficiency that partially impairs transformation of radiation energy into net assimilates production. Excessive light energy could be dissipated as heat through q_N (Yordanov et al., 2000) as has been observed in water deficit-stressed plants in this study. Toivonen and DeEll (2001) suggested that adequate supply of CO_2 for carbon reactions may prevent photoinhibition, which has been reflected in the significantly higher F_v/F_m value in the plants of all four wheat cultivars. In the present study, although water deficit reduced the F_v/F_m values, they were significantly higher in Si-treated plants under water-deficit conditions (Figure 4).

Studies have shown that changes in F_0 could be interpreted in different ways. F_0 represents an estimate of the relative size of the antenna pigments of the PSII complex (Huang et al., 2004). Baker and Rosenqvist (2004) also suggested that an increase in F_0 has been shown to be a symptom of damage to the PSII reaction center, resulting in a reduction in absorbed light and a subsequent increase in unused emitted light. The results of our research showed that water deficit reduced F_m (Figure 2) but increased F_0/F_m (Figure 9). Atal et al. (1991) also showed a reduction in F_m and an increase in F_0/F_m in wheat seedlings treated with low concentrations of Cd. Additionally, Rohacek (2002) reported that a reduction in F_v/F_m ratio, under stress conditions, is often an indicator of photoinhibition or injury to PSII components. Therefore, an increase in nonphotochemical quenching would be expected under drought stress as a result of a decrease in the utilization of light energy due to a drought-induced reduction in PSII efficiency (F_v/F_m) (Figure 4). This might explain the increase in the value of F_0/F_m in Si-treated plants under water-deficit conditions (Figure 9). Several studies have reported stress-induced increases in the values of F_0/F_m and q_N and decreases in F_v/F_m, q_P, F_0, and φPSII (Yordanov et al., 2000; Baker and Rosenqvist, 2004; Ohashi et al., 2006; Habibi and Hajiboland, 2013).

However, in plants under water-deficit stress, supply of 0.6 mM Si significantly increased the value of F_v/F_m (Figure 4), as well as that of q_P (Figure 6). Si-induced reductions in the values of F_0/F_m and q_N and increases in F_v/F_m, q_P, F_0, and φPSII have been reported in plants under abiotic stress conditions (Ohashi et al., 2006; Chen et al., 2011; Habibi and Hajiboland, 2013). In another study, Al-aghabary et al. (2004) reported that addition of Si to the root growing medium of salt-stressed tomato plants enhanced F_v/F_m as well as improved the photochemical efficiency of PSII. In the view of Kaufman et al. (1979), Si deposited in leaf epidermal cells as silica could enhance light-use efficiency by helping to transmit light to the photosynthetically active mesophyll tissue.

I conclusion the results presented here showed that under water-deficit conditions foliar application of Si could improve plant growth and increase maximum quantum yield of PSII and photochemical quenching in all wheat cultivars. The beneficial effects of foliar application of Si on chlorophyll fluorescence and photosynthetic pigments suggest enhanced drought tolerance in wheat plants. Foliar application of Si alleviated the adverse effects of water deficit on all wheat plants examined in the present study. Indeed, it has been demonstrated that the responses of two susceptible (Shiraz and Marvdasht) wheat cultivars to water stress could be altered upon silicon application: susceptible plants applied with silicon resembled resistant plants. Furthermore, chlorophyll fluorescence analysis suggested that foliar application of Si alleviates the adverse effects of water deficit by increasing F_v/F_m and q_P while reducing nonphotochemical quenching, thereby improving light use efficiency.

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