

Silicon induces changes in the antioxidant system of millet cultivated in drought and salinity

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ABSTRACT

In recent years, benefits of silicon in plants grown under stress conditions have been reported. The objective of the research was to evaluate the response at a physiological and biochemical level of millet (*Panicum miliaceum* L.) to fertilization with Si under controlled stress conditions during vegetative stage, drought, salinity and the control (without stress). After stress, shoot and root length, DM content, peroxidase (POD) and catalase (CAT) activity, proline, H₂O₂ and Si content, seed yield and germination percentage were measured. Drought and salinity significantly decreased shoot (24%, 21%) and root (30% in drought) development, weight (36%, 29%) and seed number (30%, 21%) per plant. Application of Si significantly increased seed number (289) and seed weight (1.20 g) in the control plants, increased seed weight (0.83 g) in plants under drought and germination percentage (99%) in plants under salinity. Silicon increased 2.1 times POD activity in drought, 1.4 times in salinity and control plants; CAT activity increased 10.6 times in salinity and 1.7 times in control plants. Silicon decreased 10 times proline levels in plants under drought; in salinity and control, proline content increased 1.3 times with Si and H₂O₂ levels decreased in these treatments. The Si content in plants fertilized with Si under drought, salinity and control was 6%, 3.54% and 5.45% respectively. In conclusion, Si can improve plant stress tolerance by stimulating POD and CAT activity, and regulating proline levels, allowing it to improve the production and physiological seed.

Key words: Catalase, Panicum miliaceum, peroxidase, proline, seed.

INTRODUCTION

Millets are C₄ type photosynthesis cereals, they have high water use efficiency, capable of growing under low fertility soils: saline soils and arid areas (Kumar et al., 2018). Proso millet (*Panicum miliaceum* L.) produces high nutritional small grains; it contains 54 mg Fe kg⁻¹, 36 mg Zn kg⁻¹, 165 mg Ca kg⁻¹ and 14% protein, on average (Vetriventhan and Upadhyaya, 2018). It is a source of phenolic acids, insoluble dietary fiber, and unsaturated fatty acids (linoleic, oleic, and α -linolenic acids). Millets have a low glycemic index equal to or less than 55 and gluten-free, a timely food source for diabetics and celiacs (Bora et al., 2019).

Under climate change current trend, it is predicted that two thirds of world population will experience increasingly long and frequent droughts during next 100 years, in order to reach mega droughts that will directly impact groundwater and surface water reserves (Naumann et al., 2018). Salinity destroys 1.5 million arable hectares each year (Hossain, 2019). Drought and salinity affect growth and performance plant attributes, it hinders physiological and biochemical processes,

such as gas exchange and photosynthesis. Plants cope to stress by modifying their morphology, synthesizing molecules for osmoregulation or with antioxidant activity (Hussain et al., 2019). In search for alternatives for higher food production with the current edaphoclimatic conditions, Si is being included in crops fertilization such as beans (Phaseolus vulgaris L.) (Rady et al., 2019), sorghum (Sorghum bicolor (L.) Moench) and sunflower (Helianthus annuus L.) (Hurtado et al., 2019). Si has been shown to have benefits to mitigate salinity and drought negative effects, Abdel-Rahman et al. (2018) reported better growth and yield in cowpea (Vigna unguiculata (L.) Walp.) with Si (2 mM) fertilization under drought conditions. Si fertilization (2 mM) through roots in sorghum seedlings improved tolerance to salinity through better efficiency in nutrients absorption and less Na⁺ accumulation (Hurtado et al., 2019). Pepper (Capsicum annuum L.) is not considered Si accumulator; however, Si inclusion (1.8 mM) prevented oxidative damage through the improvement of the antioxidant system, in addition to improving photosynthesis and maintaining nutrients balance under salinity conditions (Manivannan et al., 2016). Si helps to mitigate drought and salinity through increase in osmolytes such as proline and modulation of antioxidant activity enzymes, peroxidase (POD), catalase (CAT) and superoxide dismutase; these molecules are considered among first response of defense against stress (Hasanuzzaman et al., 2018; Maghsoudi et al., 2019). Shortage on water resources availability, degraded soils, millets are a promising alternative for food security and will contribute to food diversity. The objective of this research was to evaluate millet response to Si fertilization under drought and salinity conditions at a physiological and biochemical levels.

MATERIALS AND METHODS

The experiment was carried out in the Departmento de Estudios de Postgrado e Investigación of Tecnológico Nacional de México/IT Roque, Celaya, Guanajuato, Mexico, in 2019 spring-summer season. Millet (Panicum miliaceum L.) seeds were obtained from local market; six treatments were evaluated: drought + Si $(1.8 \text{ mM Na}_2\text{SiO}_3)$, drought, salinity (350 mM NaCl) + Si, salinity, millet + Si, and control. Sodium metasilicate (Na₂SiO₃·5H₂O, Sigma Aldrich, Saint Louis, Missouri, USA) was used as Si source. Different Si doses (1, 2, 3 and 4 mM) have been evaluated in millet; 2 mM dosis showed better results for millet growth, based on the preliminary experiment and reports of Manivannan et al. (2016); 1.8 mM Si dose was selected. A randomized complete block design with a factorial arrangement and four replicates were used. Seeds were planted directly in polyethylene bags for greenhouse (40 cm hight \times 40 cm wide \times 22 cm long) filled with Pellic Vertisol type soil (IUSS Working Group WRB, 2015) and were fertilized with commercial NPK (17-17-17); recommended dose by manufacturer was used (10 g per pot), each pot had five plants. Temperature was 30 °C/23 °C (day/night). Eight days after planting, seedlings were pretreated with or without Si (1.8 mM), supplying a solution (pH 5.8) via roots; stress started 15 d after planting (DAP). Drought was simulated with irrigation suspension of 15-30 DAP (vegetative stage) and for salinity treatment, plants were watered field capacity with a (NaCl 350 mM) saline solution at 15 and 22 DAP, and control plants were watered fiel capacity with tap water each 8 d. After stress treatment (30 DAP) whole plants were collected for further analysis; and recovery irrigation was applied to the rest of plants with tap water at field capacity, and other three irrigations were applied at 38, 46 and 54 d. Shoot and root length (cm) were measured; DM content (%) was determined by drying samples at 65 °C for 72 h in oven. The peroxidase, catalase antivities, proline content, H₂O₂ content and silicon content were determined. At 60 DAP, seeds were harvested, seed number and seed weight per plant and seed germination percentage were recorded.

Peroxidase and catalase activity

Peroxidase (EC.1.11.1.7; POD) and catalase activity (EC.1.11.1.6; CAT) were determined according to the method of Balois-Morales et al. (2018). For POD, 1 g matter plant was ground in 7 mL cold solution containing 100 mM Tris-HCl pH 7 and 1% polyvinylpyrrolidone (PVP40), centrifuged at 18510 g for 20 min at 4 °C with microcentrifuge (Micro 21R, Sorvall Legend, Thermo Scientific, Waltham, Massachusetts, USA) and the supernatant was recovered. Reaction mixture contained 2.5 mL Tris-HCl at 100 mM pH 7, 0.25 mL guaiacol at 100 mM, 0.1 mL 0.25% H₂O₂ and 0.15 mL supernatant; absorbance change at 460 nm was recorded. To measure CAT activity, 1 g plant matter was ground in 7 mL cold solution containing 100 mM Tris-HCl pH 8.5 and 0.1% PVP40, centrifuged under the same conditions as POD and recovered the supernatant. Mixture reaction consisted of 2.8 mL Tris-HCl at 10 mM pH 8.5, 0.1 mL H₂O₂ at 0.88% and 0.1 mL supernatant; absorbance change was recorded for 5 min at 240 nm in a microplate absorbance spectrophotometer (xMark,

Bio-Rad Laboratories, Hercules, California, USA). Results were reported as units of enzyme activity per milligram of protein (U mg⁻¹ Prot). One unit was defined as 0.001 absorbance change in 1 min. Protein content was quantified by method of Bradford (1976).

Proline and H₂O₂ content

Proline content was quantified by method of Bates et al. (1973). Three grams of plant tissue were ground in 30 mL 3% sulfosalicylic acid and centrifuged at 5000 rpm for 5 min. For reaction, 0.6 mL supernatant was taken, 0.6 mL 3% sulfosalicylic acid, 0.4 mL acid ninhydrin, 0.4 mL glacial acetic acid were added and incubated at 97 °C for 1 h. Reaction was stopped in thermal shock for 5 min, once at room temperature 1 mL toluene was added and it was vortexed for 1 min. The organic phase was taken and absorbance at 520 nm was read. The H_2O_2 content was determined according to Singh et al. (2006), 0.3 g plant tissue were homogenized in 2 mL 0.1% trichloroacetic acid and centrifuged at 8000 rpm for 15 min. For the reaction, an aliquot of 0.5 mL supernatant was taken, 0.5 mL potassium phosphate buffer was added at 100 mM pH 7 and 1 mL 1 M KI; absorbance was read at 390 nm.

Si content

Si content was determined according to the method of Kurabachew and Wydra (2014). Samples were dried at 80 °C for 72 h and finely ground. A sample of 10 mg was digested in 0.5 mL of a solution containing 1 M HCl:2.3 M HF (1:2); it was left stirring overnight, then it was centrifuged at 10000 g for 10 min. An aliquot of 20 μ L supernatant was taken and 0.25 mL 3.2% boric acid was added and left stirring overnight. Then 250 μ L colorimetric reagent containing 0.08 M H₂SO₄:20 g L⁻¹ (NH₄)₆M₇O₂·4H₂O (1:1) was added and incubated for 30 min; for color development 0.25 mL tartaric acid (33 g L⁻¹) and 0.25 mL ascorbic acid (4 g L⁻¹) were added and absorbance was read at 811 nm. Si content was calculated using a standard Si curve. ANOVA was performed and means comparison was carried out by Tukey's test using SAS software version 9.4 (SAS Institute, Cary, North Carolina, USA).

RESULTS AND DISCUSSION

Stem development, root and DM content

Drought significantly decreased shoot and root length of proso millet plants, while significantly increased shoot DM content, panicle and total weight (Table 1). Biomass accumulation is essential since it acts as a reserve in later events such as spikelets formation, which consequently relies on the number of fertilized flowers and grain formation. In pearl and proso millet, drought on early stage caused losses in shoot and panicle length and biomass content (Debieu et al., 2018). Chlorophyll content (a, b, and total) was affected by stress; reduced cell number and growth are effects of water scarcity (Mir et al., 2019). Salinity induced by 350 mM NaCl only modified shoot length (Table 1). Osmotic stress induced by salinity and drought decreases absorption of water; cells water depletion causes a loss of turgor, shrinkage of tissues and affects structure of the canopy; sum of these effects can lead to altered mitosis (Mir et al., 2019), in addition to alter phytohormone production that control cell elongation and division. As an adaptive response, leaf area diminution avoids loss of water through a smaller number of active stomata and a lower transpiration rate (Bhaskaran et al., 2013).

Factors interaction (Si × Environment) was nonsignificant, a significant response of Si was not observed with respect to the sprout development, root and DM content in the three evaluated environments (Table 1). In contrast with Alzahrani et al. (2018), who reported that Si applied to wheat under salinity and drought conditions decreased losses in shoot length, leaf area, fresh and dry weight; reductions were 31%, 33%, 35% and 37% respectively, compared to control. Si affects plants in many ways: there were no noticeable effects on millet evaluated physiological attributes. Zhu et al. (2019) reported that Si fertilization in cucumber improved DM content, photosynthetic rate and stomatal conductance in plants under saline stress; under irrigation conditions an obvious effect of Si was not observed. Si mode supply can influence plants performance; wheat improved development when supply Si through roots, while sunflower improved through foliar Si applications (Hurtado et al., 2019). This indicates that plants response to Si fertilization depends on several factors, mode application and crop genetics.

Table 1. Means comparison for growth variables in proso millet evaluated in three environments and Si fertilization.

Factors	Levels	SL	RL	SDM	PC	TDC
		cm	cm	%	%	%
Si	1.8 mM	30.78a	8.39a	14.62a	23.83a	17.50a
	0 mM	29.43a	8.88a	12.83b	20.23b	15.30b
Environment	Drought	26.15c	6.31b	15.14a	24.35a	17.99a
	Salinity	29.69b	10.63a	14.04ab	22.11b	16.70a
	Control	34.46a	8.97a	11.99b	19.61c	14.52b
Interaction						
Si	Environment					
1.8 mM	Drought	28.43ab	6.75b	27.05a	72.94b	18.96a
0 mM	Drought	23.88b	5.87b	24.81a	75.19b	18.92a
1.8 mM	Salinity	29.63ab	9.25ab	19.63b	80.39a	14.64b
0 mM	Salinity	29.75ab	12.00a	21.65b	78.35a	17.01ab
1.8 mM	Millet	34.28a	9.18ab	19.42b	80.58a	14.49b
0 mM	Control	34.65a	8.76ab	19.61b	80.39a	14.40b

Variables with same letters are significantly equal according to Tukey's test ($P \le 0.05$).

SL: Stem length; RL: root length; SDM: stem DM; PC: panicle content; TDC: total DM.

Seed yield and germination

Drought and salinity application in vegetative stage of millet significantly decreased seeds number and seeds weight per plant (Table 2), in 1000 seeds weight there were nonsignificant differences (data not shown), so that stress it directly affected fertilized flowers number and therefore, grains number produced. Debieu et al. (2018) also reported losses in plant grains number produced in pearl millet due to a drought in the early stage; there were even plants that did not produce seeds; this means that the impact of drought at vegetative stage is decisive in grain yield. Yield losses and germination percentage of millet seeds are due to low biomass production and low photosynthesis caused by stress (Anatala et al., 2015).

Si fertilization in control plants significantly increased seeds number and seeds weight per plant (Table 2); under drought conditions there were nonsignificant differences with or without Si fertilization in seeds number and seeds weight. Seeds germination percentage produced under salinity and control improved significantly; Si significantly improves seeds productivity and seeds physiological quality under well-irrigated conditions.

Si application in cowpea under drought conditions increased pod number per plant (33%), seed weight per plant (31%) and 100 seed weight (18%) as compared to control; researchers point out that the best performance of experimental plants was due to the better absorption and use of nutrients, N, P and K, which significantly increased their content (Abdel-Rahman et al., 2018). Significant increase in rapeseed yield with Si fertilization + 160 kg N ha⁻¹ was due to higher number of siliques per plant, based on the fact that there were no differences in 1000 seed weight between experiments and control (Lainé et al., 2019).

Peroxidase and catalase activity

Drought significantly decreased POD and CAT activity in leaves, while a drastic increase in POD and a decrease in CAT activity were observed in roots (Table 3); Mir et al. (2019) reported increases in POD and CAT activity in both, roots and leaves of millet in a way dependent on the time of exposure to water deficit. Antioxidant enzymes activity could be an indication of genotypes efficiency to cope with drought; wheat genotypes CAT and POD activity fluctuated between 2.13-2.36 U mg⁻¹ Prot and between 24.42-35.17 U mg⁻¹ Prot under irrigation conditions, and in water deficit activities it increased between 6.15-7.68 U mg⁻¹ Prot and between 30.12-44.12 U mg⁻¹ Prot, respectively (Maghsoudi et al., 2019).

Saline stress significantly decreased POD activity in millet leaves and roots; but the significant increase in CAT activity in leaves could compensate lack of POD activity to decrease the concentration of reactive oxygen species (ROS) (Table 3); in the roots, CAT activity decreased significantly. It is possible that salt stress intensity (350 mM NaCl) has caused a partial or total inhibition of the antioxidant system and consequently a limitation in the elimination of excesses of induced ROS (Alzahrani et al., 2018). Physiological drought induced by salinity leads to overproduction of ROS such as H₂O₂, peroxide anion and singlet oxygen; O⁻² and H₂O₂ (2-3 μ mol g⁻¹ PF) high concentration in alfalfa was correlated with high malondialdehyde (MDA) content, as a result of lipid peroxidation; stimulation of POD activity and flavonoid metabolism showed a high antioxidant capacity that contributes to tolerance to saline-alkaline stress (Meng et al., 2020).

Factors	Levels	Seed number	Seed weight	Germination
			g	%
Si	1.8 mM	207.17a	0.93a	98.50a
	0 mM	152.58b	0.70b	96.83b
Environment	Drought	147.38b	0.69b	97.00b
	Salinity	162.25b	0.78ab	97.25b
	Control	230.00a	0.99a	98.75a
Interaction				
Si	Environment			
1.8 mM	Drought	176.75b	0.83ab	97.00bc
0 mM	Drought	118.00b	0.55b	97.00bc
1.8 mM	Salinity	155.75b	0.77ab	99.00ab
0 mM	Salinity	168.75b	0.79ab	95.50c
1.8 mM	Millet	289.00a	1.20a	99.50a
0 mM	Control	171.00b	0.77ab	98.00ab

Table 2. Means comparison for seeds number and seeds weight per plant and germination percentage of proso millet seeds grown in three environments and Si fertilization.

Variables with same letters are significantly equal according to Tukey's test ($P \le 0.05$).

In factors interaction (Si × Environment) (Table 3), treatment with Si significantly increased POD activity in millet leaves in the three environments, while in the roots, POD activity only increased under salinity; under drought condition and in control, POD activity decreased. However, in plant roots subjected to salinity, a decrease in CAT activity was observed, as well as in control plants. Significant increase in roots CAT activity of plants with drought could well maintain balance of ROS against low POD activity. Leaves CAT activity increased significantly with Si presence under salinity and in control (Table 3). These results are comparable with those reported in cowpea (Abdel-Rahman et al., 2018), Si significantly favored POD and CAT activity under drought conditions. Low stomatal conductance and transpiration low rate induced by the water deficit falls on photosynthesis and electron transport chain processes causing excessive ROS accumulation; in response to this, the antioxidant system is activated (Mohanabharathi et al., 2019); Si role increase POD activity and may be part of millet's strategies to tolerate stress and function as a pretreatment in environments with irrigation availability.

Liu et al. (2015) found out that Si fertilization in sorghum plants subjected to salinity caused a decrease in POD activity, but increased CAT activity in roots. In alfalfa (Meng et al., 2020), wheat (Alzahrani et al., 2018) and beans (Rady et al., 2019), Si significantly increased CAT and POD activity in leaves under salinity conditions. Modulation antioxidant enzymes activity could be an adaptive response to cope the damaging effects of stress; POD and CAT reduce ROS levels through H₂O₂ consumption in physiological processes (Alzahrani et al., 2018; Hasanuzzaman et al., 2018).

Table 3. Means comparison for POD and CAT activities and proline content in leaves and roots of proso millet cultivated under three environments and Si fertilization.

Factors	Levels	POD leaf	POD root	CAT leaf	CAT root	Pro leaf	Pro root
Si	1.8 mM	50.84a	94.46b	10.87a	1.23b	2.08b	0.42a
	0 mM	36.61b	153.47a	3.07b	2.74a	2.82a	0.41a
Environment	Drought	20.51c	158.32a	3.74c	1.49b	2.21b	0.15b
	Salinity	35.41b	86.67c	11.39a	1.25c	3.19a	1.01a
	Control	75.26a	126.90b	5.79b	3.22a	1.96c	0.09c
Interaction							
Si	Environment						
1.8 mM	Drought	28.00c	100.65c	4.48c	1.79b	0.39f	0.10de
0 mM	Drought	13.01d	216.00a	3.01c	1.20c	4.02a	0.21c
1.8 mM	Salinity	37.75c	93.33cd	20.93a	0.91d	3.61b	1.14a
0 mM	Salinity	33.08c	80.00e	1.88d	1.58b	2.77c	0.89b
1.8 mM	Millet	86.77a	89.40de	7.21b	0.98cd	2.25d	0.04e
0 mM	Control	63.75b	164.40b	4.37c	5.46a	1.68e	0.14cd

Variables with same letters are significantly equal according to Tukey's test ($P \le 0.05$). POD: Peroxidase; CAT: catalase; Pro: proline.

Proline content

Drought and salinity caused a high proline accumulation in proso millet leaves and roots, proline synthesis increases as a defense response of the cellular system, especially in plants that grow in water deficit (Mohanabharathi et al., 2019). Drought-tolerant wheat genotype leaves and another susceptible, proline content was 5 and 3 mg g⁻¹ FW after a water deficit as compared to control, which was 2 mg g⁻¹ FW (Maghsoudi et al., 2018). Increased expression levels of *P5CS* gene have been positively correlated with high proline levels; P5CS (Δ^1 pyrroline-5-carboxylate synthetase) is the main catalyst for proline biosynthesis (Bandurska et al., 2017; Maghsoudi et al., 2018). Proline can act in the maintenance of the osmotic gradient in the roots to minimize water loss and recover the low potential caused by drought and saline stress or as a singlet oxygen scavenger, as a source of N and C in recovery processes (Ali et al., 2018; Rady et al., 2019).

Si fertilization in plants under drought treatment significantly decreased proline content (Table 3), it is possible that drough impact is less in plants with Si or that proline is being used as a source of N and C in metabolic processes. Proline loss due to degradation or synthesis reduction indicates a recovery (Verma et al., 2020). Similar results have been reported in rapeseed (*Brassica napus* L.); damage mitigation caused by drought was accompanied by a decrease in proline content in plants that were Si fertilized (Hasanuzzaman et al., 2018). However, such performance varied widely. Si fertilization in a sorghum genotype (Alzahrani et al., 2018), in cowpea (Abdel-Rahman et al., 2018) and in tomato (Ali et al., 2018) subjected to drought further stimulated proline accumulation with respect to drought only. In millet plants under salinity, Si significantly increased proline content in both leaves and roots, while in control plants it only increased in leaves. Similar results were reported in wheat (Alzahrani et al., 2018) and beans (Rady et al., 2019), Si fertilization in plants cultivated under salinity increased proline content. Hasanuzzaman et al. (2018) agree that Si stimulates proline accumulation even under stress-free conditions.

H₂O₂ and Si content

Stress conditions promoted high H_2O_2 accumulation, especially drought; there was a higher concentration in leaves than in roots, regardless of type of environment (Table 4). Liu et al. (2020) pointed that H_2O_2 accumulation is dependent on NADPH oxidase in cell wall and in the apoplast acts as a signaling intermediate in the regulation of proline accumulation in wheat plants exposed to salinity.

Si fertilization significantly decreased H_2O_2 levels in salinity-grown millet leaves and in control plants (Table 4); this result could be due to POD and CAT activity and proline high content stimulated by Si. Liu et al. (2015) mentioned that Si contributed to the low H_2O_2 content in sorghum. CAT activity stimulated by Si in *Glycyrrhiza uralensis* Fisch. ex DC. was correlated with H_2O_2 low content, low MDA content and a low membrane permeability (Abdel-Rahman et al., 2018). Si can affect H_2O_2 excess either by limiting its generation or neutralizing its activity through the antioxidant system (Khan et al., 2020).

Factors	Levels	Leaf H ₂ O ₂	Root H ₂ O ₂	Panicle Si	Leaf Si	Root Si	Total Si
		—— nmol g	g ⁻¹ FW ——		— mg 100 r	ng-1 DW —	
Si	1.8 mM	0.38b	0.14a	2.39a	1.87a	1.92a	6.18a
	0 mM	0.42a	0.13b	1.84b	1.34b	0.76b	3.94b
Environment	Drought	0.47a	0.15a	2.70a	1.58b	1.91a	6.19a
	Salinity	0.35c	0.13b	0.96b	1.03c	1.55a	3.54b
	Control	0.40b	0.12c	2.69a	2.21a	0.55b	5.45b
Interaction							
Si	Environment						
1.8 mM	Drought	0.56a	0.70a	3.43a	1.68ab	2.85a	7.96a
0 mM	Drought	0.37c	0.14b	1.95c	1.49b	0.97c	4.42bc
1.8 mM	Salinity	0.32d	0.14b	0.85d	1.52b	2.00b	4.37bc
0 mM	Salinity	0.37c	0.12c	1.07d	0.54c	1.11c	2.71c
1.8 mM	Millet	0.26e	0.11c	2.89ab	2.43a	0.90cd	6.21ab
0 mM	Control	0.53b	0.12c	2.49bc	1.99ab	0.21d	4.68b

Table 4. Means comparison for hydrogen peroxide (H_2O_2) content in leaf and root and Si content in proso millet cultivative statements of the second statement of the seco	ed
under three conditions and Si fertilization.	

Variables with same letters are significantly equal according to Tukey's test ($P \le 0.05$).

Si fertilization further increased Si content in plants; it should be noted that presence of saline ions affected Si levels in millet, while the drought condition promoted a higher Si content. The environment factor affected the internal Si distribution; under drought conditions, Si was distributed mainly in panicle, followed by roots and leaves; under a saline environment Si accumulated mostly in roots, followed by leaves and panicle. In control plants, Si was distributed mainly in panicle and leaves. In rice, Si total content ranged between 6% and 10%; distribution in leaves varied from 3% to 5% and in the husk, it becomes between 5% and 8% depending on varieties (Schaller et al., 2019). Ali et al. (2012) agree that salinity limits the accumulation of Si, wheat Si content fertilized with 75 and 150 mg kg⁻¹ Si was 16.51 and 20.56 mg g⁻¹ DW, as compared to those cultivated under non-saline soils; these increased significantly to 18.6 and 24.6 mg g⁻¹ DW, respectively. Root Si deposition can influence absorption, transport and distribution of mineral elements and root hydraulic conductance (Verma et al., 2020).

CONCLUSIONS

According to the results of this study, the stress due to water deficit and saline stress imposed in the vegetative stage is critical for the final yield of proso millet. Silicon fertilization significantly increased number and percentage of seed germination in control plants, increased the percentage of seed germination in plants under salinity and the weight of seeds in plants under drought. Silicon improved the tolerance of plants to drought and salinity stress by stimulating peroxidase and catalase activity. The high content of proline in proso millet leaves under salinity and fertilized with Si could participate in the osmotic adjustment, as an antioxidant or source of C and N. The low content of proline in plants with drought could indicate a low impact of stress due to the effect of Si. The yield of different species or even varieties to fertilization with Si is highly variable, but provides benefits to mitigate the damage induced by abiotic stress, such as salinity and drought, and even improve productivity when the plants are grown in good conditions irrigation. Current studies provide information on the benefits of Si in agricultural crops, which will allow recommending fertilization with Si to improve the behavior and yield of crops, however, more studies are needed at the molecular level to unravel the mechanisms of action of Si in plants cultivated in different environments.

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