

Silicon (Si) ameliorates the gas exchange and reduces negative impacts on photosynthetic pigments in maize plants under Zinc (Zn) toxicity

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Abstract

This research aimed to (i) measure oxidative stress, (ii) evaluate the responses on gas exchange, (iii) determinate the repercussion on photosynthetic pigments, and (iv) respond if application of exogenous silicon (Si) is efficient to attenuate negative impact on maize plants exposed to Zn toxicity. The experiment employed an entirely randomized design with four treatments (0, 2 mM Zn; 2 mM Zn + 2 mM Si; and 2 mM Si). Hydrogen peroxide and electrolyte leakage were evaluated in root and leaves of maize plants. The gas exchange, net photosynthetic rate, stomatal conductance, transpiration rate, water use efficiency were measured. The pigments such as chlorophylls and carotenoids were measured in leaf. Zn application produced increases in hydrogen peroxide and electrolyte leakage to both tissues, confirming the effects of toxicity. The Zn toxicity + Si presented significant increases of 33.3, 25.2, 15 and 9.8% to stomatal conductance, net photosynthetic rate, transpiration rate, and water use efficiency, respectively, compared to Zn-only treatment. The total, *a* and *b* chlorophyll and carotenoids presented non-significant increases, when compared to plants exposed to Zn toxicity. This study revealed the positive contribution of the Si on gas exchange and reduction of the negative effects provoked on chlorophylls and carotenoids in maize plants under Zn toxicity.

Keywords: Chlorophylls, hydrogen peroxide, net photosynthetic rate, silicon, toxicity, *Zea mays* L., zinc.

Abbreviations: CAR_carotenoids, CHL *a*_chlorophyll *a*, CHL *b*_chlorophyll *b*, CO₂_carbon dioxide, *E*_transpiration rate, EL_electrolyte leakage, *g_s*_stomatal conductance, H₂O₂_hydrogen peroxide, H₄SiO₄_monosilicic acid, LHCII_light-harvesting complex, Mg_magnesium, NADPH_nicotinamide adenine dinucleotide phosphate-oxidase, *P_N*_net photosynthetic rate, ROS_reactive oxygen species, Si_silicon, TOTAL CHL_total chlorophyll, Zn_zinc, WUE_water use efficiency.

Introduction

Currently, Brazil is the third largest worldwide producer of maize, being overcome only by United States of America and China. In 2013, the Brazil presented the production of 80.5 million tons and yield of 5.25 tons ha⁻¹ (FAO, 2014), by which the economical and nutritional importance of this grain is justified. This country also is one of the highest exporter of this grain having large cultivated areas (Araújo et al., 2004), with the maize being used to human and animal food (Deuner et al., 2008). Additionally, this grain also can be used as base to fabrication of industrial products, such as corn starch and in fermentation and distillation industries (Rakshit et al., 2010; Souza et al., 2012).

Zinc (Zn) is the second more frequent transition metal detected in organisms (Barber 1995; Broadley et al., 2007), being the only presents in all enzymes classes (Vallee and Auld, 1990). It exercises several roles in metabolic processes in plants, such as cofactor of enzyme (Henriques et al., 2012), synthesis and interactions of proteins (Klug, 1999; Engbrecht et al., 2004), besides of carbohydrate and lipid

compositions (Rout and Das, 2003). Despite the Zn is required as micronutrient in higher plants, it is toxic in higher concentrations and provokes negative effects (Garbisu and Alkorta, 2003), as reduction in photosynthetic pigments (Radic et al., 2010), minor integrity and permeability of membranes (Stoyanova and Doncheva, 2002), increase of the oxidative stress related with production and accumulation of reactive oxygen species (ROS), besides to increase the activities of antioxidant enzymes (Jain et al., 2010), and in extreme levels may induce cell death (Chang et al., 2005).

The silicon (Si) is the second more abundant chemical element on the earth crust and soil (Wedepohl, 1995; Liang et al., 2006), being frequently found in solid phase as amorphous and crystalline forms (Sauer et al., 2006). However, under specific conditions, such as dissolution of primary minerals and biogenic through of interaction with organic matter can be dissolved in soil (Saccone et al., 2008; Cornelis et al., 2011). The soluble form of Si in soil is monosilicic acid (H₄SiO₄), in which must be easily

assimilated, transported and accumulated by the plants (Ma et al., 2007; Keller et al., 2012). The concentration of this element in soil normally is oscillating between 0.1 and 0.6 mM (Epstein, 1999).

Beneficial uses of Silicon (Si) in higher plants are intensively found (Lobato et al., 2009; Pereira et al., 2013; Marques et al., 2014). Isa et al. (2010) reported that Si is largely accumulated in leaves. Silva et al. (2012) described increases in chlorophylls produced by exogenous Si application. Si also induces higher mechanical resistance in cell wall (Kim et al., 2002). Chen et al. (2011) found better light reception and increasing net photosynthesis rate and CO₂ capitation after Si treatment.

Different mechanisms has been proposed to explain the tolerance of plants to toxicity induced by heavy metals, as specific transporters, metal ion homeostasis and compartmentalization of metals into the vacuole (Verkleij et al., 1998; Williams et al., 2000). However, responses linked to contribution of Si in plants subjected to Zn excess are unknown, especially on gas exchanges and photosynthetic pigments. Based in this overview, this research had objectives to (i) measure oxidative stress, (ii) evaluate the responses on gas exchange, (iii) determinate the repercussion on photosynthetic pigments, and (iv) respond, if application of exogenous silicon (Si) is efficient to attenuate negative impact on maize plants exposed to Zn toxicity.

Results

Si and Zn concentrations in leaf

The plants submitted to Si application presented an increase of ~12% (Table 1) in Si concentrations, compared to control treatment (without Si), while Zn toxicity + Si treatment induced a reduction of 20%, if compared with plants treated only with Si. The Zn toxicity increased the Zn concentrations in leaf (87%) (Table 1), compared to control plants. On the other hand, the Zn toxicity + Si treatment presented decrease of 1.8%, when compared to Zn toxicity.

Interferences produced by Zn toxicity on oxidative stress

The hydrogen peroxide (H₂O₂) level presented in leaf in plants subjected to Zn or Si applications suffered increases (Fig 1A), being showed values of 27.1 and 11.6%, respectively, when compared to control treatment. In addition, plants exposed to Zn toxicity + Si exhibited a significant decrease of 19.8% in (H₂O₂) level, compared to treatment with Zn. In root, the H₂O₂ levels of plants under individual application of Zn or Si presented significant increase of 84.8 and 68.7% (Fig 1 B), respectively, compared to control treatment. Plants exposed to Zn toxicity + Si showed a reduction of 6.4%, when compared with Zn treatment. When plants exposed to Zn treatment the electrolyte leakage (EL) in leaf presented a significant increase of 21.33%, while a non-significant increase of 7% observed under Si treatment, compared to control (Fig 1 C). The treatment Zn toxicity + Si promoted a decrease of 12.7%, compared to Zn treatment. The EL in root of plants treated with Zn presented significant increase of 15.4% and Si treatment resulted in non-significant increase of 2.8%, compared to control treatment (Fig 1 D). Plants exposed to Zn toxicity + Si presented reduction of 2.8%, when compared with plants treated only with Zn.

Si attenuates Zn toxicity on gas exchange

The net photosynthetic rate (P_N) after Zn application produced significant decrease of 22.1%, while in Si treated plants a not significant increase of 2.8% observed, both compared to control treatment (Fig 2 A). The stomatal conductance (g_s) of plants exposed to Zn or Si applications suffered significant reduction (Fig 2 B) of 50% in both the treatments, compared to control. In addition, the Zn toxicity + Si treatment significantly promoted the stomatal conductance (g_s) with increase of 33.3%, when copared to treatment under Zn application. The treatment Zn toxicity + Si had significant increase of 25.2%, compared to Zn-only treatment. For transpiration rate (E), the treatment under application of Si or Zn suffered reduction (Fig 2 C) of 23.1 and 9.6%, respectively, compared to control treatment. Plants exposed to Zn toxicity + Si presented significant increase of 15%, when compared to plants under Zn treatment. The water use efficiency (WUE) was maintained in plants treated with Zn. However, the Si induced a significant increase of 13.2%, related to control treatment (Fig 2 D). Plants subjected to Zn toxicity + Si presented significant increase of 9.8%, compared to Zn treated plants.

Effects promoted by Si on photosynthetic pigments

The chlorophyll *a* (CHL *a*) in treatment under Zn application suffered significant reduction of 34.3% (Fig 3 A). In treatment with Si, an increase of 15.2% was occurred, when compared to control treatment. Plants exposed to Zn toxicity + Si presented an increase of 11%, compared to treatment with Zn. In plants subjected to Zn application a significant decrease of 35.1% was observed in chlorophyll *b* (CHL *b*). The Si treatment promoted the chlorophyll *b* (CHL *b*) production with an increase of 19.7%, when compared to control treatment (Fig 3 B). The chlorophyll *b* (CHL *b*) of exogenously Si treated plants exposed to Zn toxicity showed an increase of 8.2%, compared to Zn-only treated plants. The total chlorophyll (TOTAL CHL) in Zn treated plants showed a significant reduction of 34.4%. The exogenous application of Si increased the total chlorophyll by 16%, compared to control treatment (Fig 3 C). The Si application in plants exposed to Zn toxicity induced an increase of 7.3%, when compared with Zn treatment. The carotenoids (CAR) levels in Zn treated plants presented a significant reduction of 27.4% (Fig 3 D). However, addition of Si caused a non-significant increase of 11.4%, compared to control treatment (Fig 3 D). Treatment with Zn toxicity + Si caused an increase of 20.1% in carotenoids (CAR) levels, when associated to treatment with Zn application.

Discussion

The Si application caused accumulation of this nutrient in plant tissues, indicating an efficient assimilation of this nutrient by the plants. This result was explained by Ma et al. (2004), by which activation of SIT 1 and SIT 2 transporters, located in plasmatic membranes of the root cells and plasmatic membranes of xylem cells, respectively, are responsible for the Si transportation to the root and consequent liberation to xylem.

The plants exposed to Zn toxicity + Si showed a slight reduction in Zn concentrations in leaf. This behavior reveals that Si inhibited the Zn assimilation, as described by Gu et al.

Table 1. Concentrations of Si and Zn in leaf (dry matter) of *Zea mays* plants subjected to silicon and zinc toxicity. Different letters to treatments indicate significant differences in the Skott-Knott test ($P \leq 0.05$). Columns represent the mean values from four repetitions, and bars represent the standard deviations.

Treatments	Concentrations in leaf					
	Si (mg g^{-1} DM)		Zn ($\mu\text{g g}^{-1}$ DM)			
Control	5.4	± 0.44	c	11.8	± 0.81	a
Zn toxicity	3.6	± 0.16	c	103.1	± 6.01	b
Zn toxicity + Si	39.4	± 3.08	b	101.2	± 0.64	b
Si	49.3	± 3.25	a	13.2	± 2.96	a

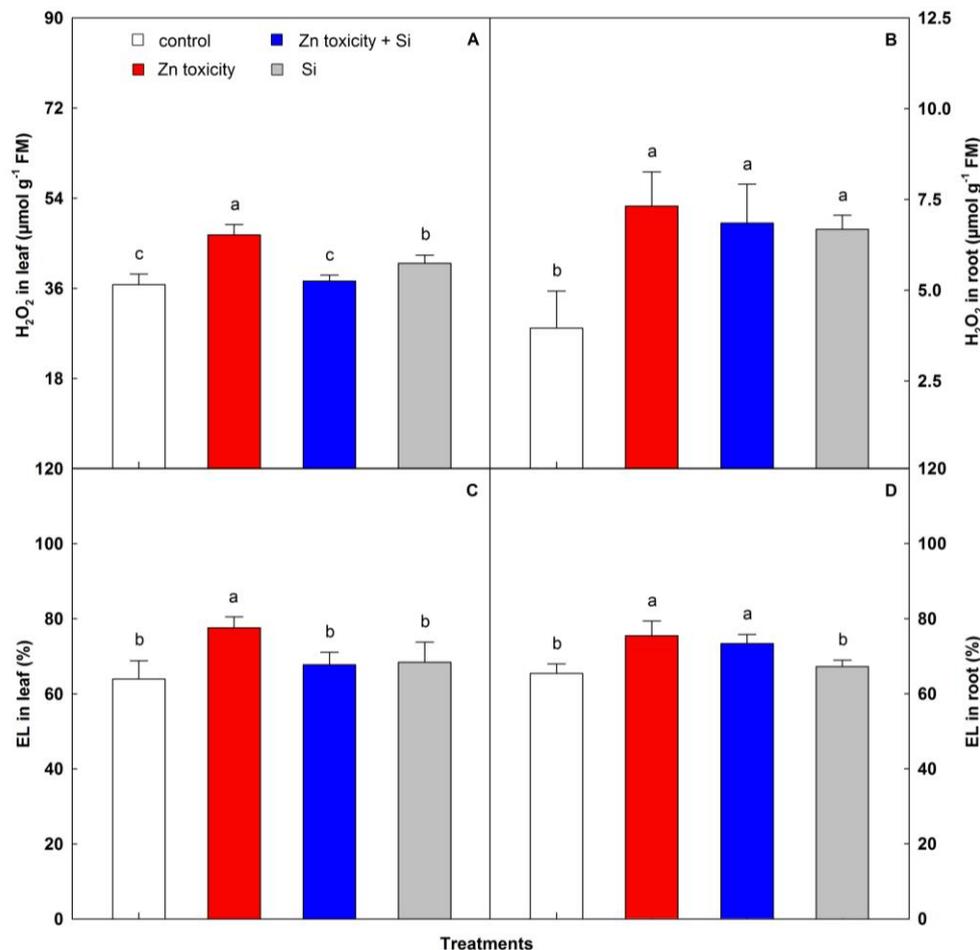


Fig 1. Hydrogen peroxide in leaf and root (A - B), and electrolyte leakage (C - D) in *Zea mays* plants subjected to silicon and zinc toxicity. Different letters indicate significant differences in the Skott-Knott test ($P \leq 0.05$). Columns represent the mean values from four repetitions, and bars represent the standard deviations.

(2012), explained by the interference of the Zn translocation from root to shoot using xylem, in which this effect was occasioned by the Si application. Similar results were reported by Song et al. (2011) that showed decrease in Zn concentrations after Si addition in *Oryza sativa* plants.

The plants subjected to Zn toxicity presented an increase in hydrogen peroxide (H_2O_2) levels in leaf and root. This increase is related to occurrence of oxidative stress, that is one of the conditions, in which reactive oxygen species (ROS) are generated, and the superoxide is quickly converted to H_2O_2 by the action of the superoxide dismutase enzyme (Apel and Hirt, 2004; Farouk et al., 2013; Lozano, 2003). Gupta et al. (2011) worked on *Vigna mungo* plants under Zn toxicity and reported increases in concentrations of H_2O_2 in

leaf. Li et al. (2012) investigated the Zn toxicity in *Triticum aestivum* and reported the increase of element in root, corroborating with the results described in this research.

The increases in EL of both tissues of plants subjected to Zn toxicity can be attributed to accumulation of hydrogen peroxide (H_2O_2). The excess of H_2O_2 in cells will produce the oxidative stress, conducting increase in intracellular levels of ROS, occasioning significant damages in proprieties of the cell membrane such as membrane breakdown and consequently electrolytes liberation (Bhattachrjee, 2005). Hosseini and Poorakbar (2013) also related increase in EL of *Zea mays* when plant exposed to Zn stress.

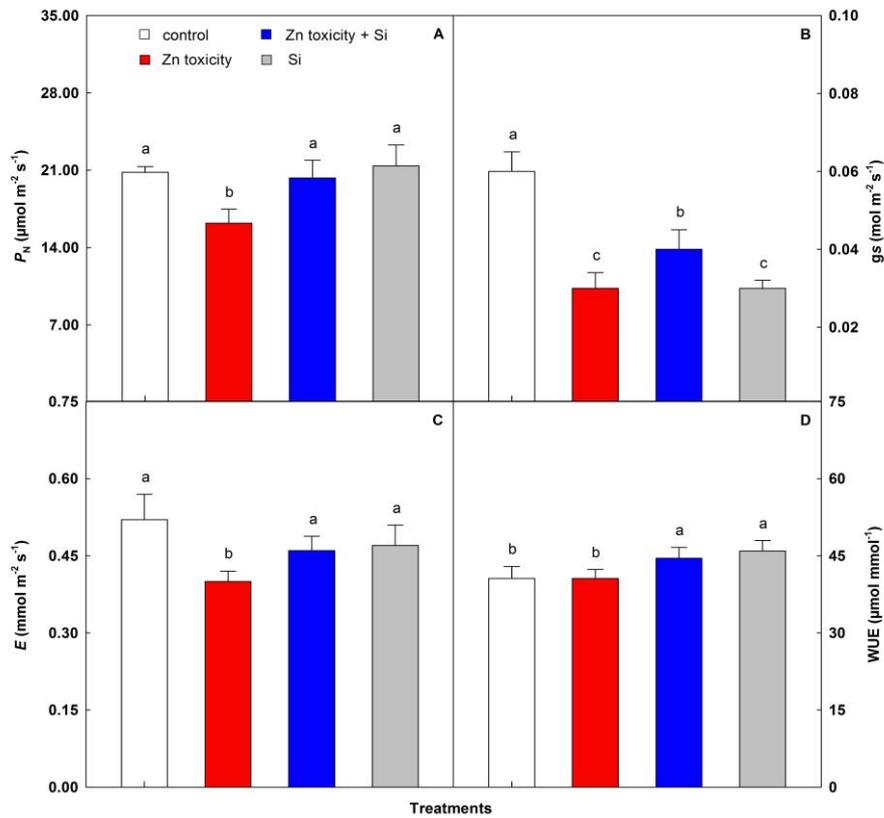


Fig 2. Photosynthesis rate (A), stomatal conductance (B), transpiration rate (C) and water use efficiency (D) in *Zea mays* plants subjected to silicon and zinc toxicity. Different letters of treatments indicate significant differences from the Skott-Knott test ($P \leq 0.05$). Columns represent the mean values from four repetitions, and bars represent the standard deviations.

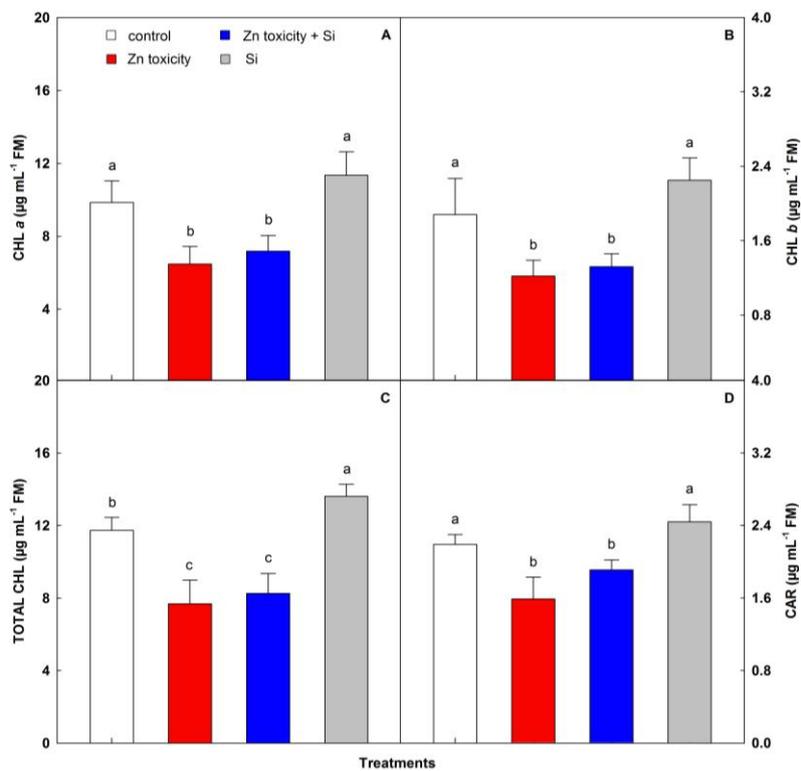


Fig 3. Chlorophyll a (A), chlorophyll b (B), total chlorophyll (C) and carotenoids (D) in *Zea mays* plants subjected to silicon and zinc toxicity. Different letters of treatments indicate significant differences from the Skott-Knott test ($P \leq 0.05$). Columns represent the mean values from four repetitions, and bars represent the standard deviations

The plants under Zn toxicity presented a reduction in net photosynthetic rate. This effect explained by the stomatal limitation, arising minor stomatal conductance and consequent decrease of the CO₂ assimilation to photosynthetic process (Ripley et al., 2007; Flexas et al., 2006). Similar results were found by Shi and Cai (2009) on *Arachis hypogaea* plants exposed to Zn stress, corroborating with results obtained in this research.

The Zn toxicity produced a negative interaction promoting stomatal closing, and consequently reduction in stomatal conductance. This effect can be attributed to Zn excess, in which it will induce a minor density and size of these structures, with structural differences in adaxial and abaxial sides, besides minor stomatal aperture sizes (Sagardoy et al., 2010). Similar results were obtained by Pavlíková et al. (2014) in *Nicotiana tabacum* plants subjected to Zn stress. The reduction of the transpiration in plants under high application of Zn can possibly be attributed to decrease in stomatal conductance. This stomatal limitation reduces the transpiration rate, promoting minor water loss from plant to atmosphere, and consequently limited nutrients reposition in form of adsorbed ions into substrate with water, through the root system (Mott and Franks, 2001). In other words, the transpiration is responsible for the dynamic of nutrient transportation from substrate into the root and leaf (Ronda et al., 2001), besides to avoid the cavitation in xylem (Sperry, 2000). Fernández et al. (2012) also described reduction in transpiration rate in *Populus deltoides* plants subjected to high Zn concentrations.

The exogenous application of Si promoted an increase in water use efficiency (WUE). This result can be explained due to increase in net photosynthetic rate (P_N) and reduction in transpiration rate (E). The ratio between photosynthesis and transpiration will result in WUE (Ma et al., 2004), a physiological parameter that quantitatively describes the behavior momentaneous of the gas exchanges in leaf and must reveal the efficiency, by with the plant utilizes the water resource (Silva et al., 2008). Our results are corroborated with Moussa (2006) which was done on *Zea mays* seedlings under exogenous application of Si.

The decrease in CHL *a* occurred due to Zn toxicity, probably related to minor biosynthesis rate of CHL *a* (Manivasagaperumal et al., 2011). The Zn excess negatively interferes with NADPH availability in chloroplasts (Mousavi, 2011), because the NADPH is one of the substrates of the divinyl chlorophyllide *a* 8-vinyl-reductase enzyme, that is responsible for CHL *a* synthesis (Parham and Rebeiz, 1995). The Zn excess promoted a decrease in CHL *b* level. This result can be explained by the oxidative stress induced by the overproduction of reactive species oxygen (ROS), such as H₂O₂ (Madhava and Sresty, 2000; López et al., 2005). Besides, the H₂O₂ is toxic to chloroplasts and considered as an inhibitor of the carbon metabolism (Hung et al., 2005), resulting in acceleration of leaf senescence through the lipid peroxidation and oxidative damages (Sairam and Srivastava, 2000). Similar results were reported by Bettaieb (2008) that evaluated *Solanum tuberosum* cultivars.

The total CHL level was reduced after Zn toxicity. This fact is related to substitution of magnesium (Mg) by the Zn in chlorophyll molecule, which cause an inadequate work of the light-harvesting complex (LHCII), and consequently the photosynthesis limitation (Kowalewska et al., 1992; Wettstein et al., 1995; Küpper et al., 1996). Our results on reduction in CHL total were corroborated with Bassi and Sarma (1993) in *Triticum aestivum* seedlings.

In treatment under Zn toxicity, a reduction in carotenoids production was occurred. This effect can be explained probably by the minor availability of lycopene. The lycopene is the substrate of the lycopene cyclase enzyme, in which this reaction is responsible by the cyclization and carotenoids production of carotenoids (Beyer et al., 1991; Cardoso, 1997), such as α and β -carotenes (Cunningham et al., 1996). Similar results were reported by Sagardoy et al. (2008) evaluating *Beta vulgaris* plants cultivated under high concentrations of Zn, producing decrease in carotenoids.

Materials and Methods

Location and growth conditions

The experiment was performed on the Campus of Paragominas of the Universidade Federal Rural da Amazônia, Paragominas, Brazil (2°55'S and 47°34'W). The study was conducted in a greenhouse without control of humidity, temperature and luminosity. Minimum, maximum, and median temperatures were 21°C, 35°C, and 25°C, respectively. The relative humidity during the experimental period varied between 45% and 72%, and the photoperiod was set to 12 h of light. During the measurement period (12:00 h), the amount of photosynthetically active radiation varied between 466 and 1,492 $\mu\text{mol m}^{-2} \text{s}^{-1}$.

Plants, substrate and containers

Seeds of *Zea mays* L. hybrid 30F53YH PioneerTM were germinated and grew in 1.2-L pots (0.15 m in height and 0.10 m in diameter) in mixed substrate composed by sand and vermiculite in proportion 3:1, respectively. For semi hydroponic cultivation, the pots (described previously) were equipped with one hole in bottom side and covered with mesh to keep the substrate and root aeration, and solution absorption by capillarity, by placing into other containers (0.15 m in height and 0.15 m in diameter) containing 500 mL of distilled water during four days, and after the nutritive solution of Hoagland and Arnon (1950) modified.

Experimental design

The experiment was set up as a completely randomized design with four treatments (0, 2 mM Zn; 2 mM Zn + 2 mM Si; and 2 mM Si; being described as control, Zn toxicity, Zn toxicity + Si and Si, respectively). The experiment was assembled with five replicates for a total of 20 experimental units, with one plant in each unit.

Plant conduction and Zn and Si treatments

Five seeds were placed in each pot, and each pot was limited to one seedling in 7th day after seed emergency. All plants during seven days received only distilled water. After this period, nutritive solution, was increased to cause ionic forces of 25, 50 and 100% at 8th, 9th and 10th day, respectively (after experiment implementation). The treatments received macronutrients and micronutrients from the nutritive solution described by 8.75 mmol KNO₃, 7.5 mmol Ca(NO₃)₂·4H₂O, 3.25 mmol NH₄H₂PO₄, 1.5 mmol MgSO₄·7 H₂O, 31.25 μmol KCl, 15.68 μmol H₃BO₃, 1.25 μmol MnSO₄·H₂O, 1.25 μmol ZnSO₄·7H₂O, 0.32 μmol CuSO₄·5H₂O, 0.32 μmol NaMoO₄·5H₂O, and 200.0 μmol NaEDTAFE·3H₂O in a total volume of 0.4 L without silicon and zinc additions. To simulate the Zn toxicity, 2 mM ZnCl₂ was added in treatment

to act as Zn toxicity. For Si treatments 2 mM Na₂SiO₃·9H₂O was used, and for Zn toxicity + Si treatment 2 mM Zn + 2 mM Si were added. All reagents used in this study were Sigma-Aldrich™. Treatments were applied to plants for 20 days, and regularly changed at 07:00 h over 3-day intervals and with their pH adjusted to 5.5 ± 0.1 with the addition of HCl or NaOH. On the 20th day, all plants were physiologically measured and harvested for biochemical evaluations.

Extraction and Si determination

Samples containing 100 mg of dry leaf matter were placed in muffle furnace and kept for 3 h at 500°C. The material was removed and mixed in 10 mL 1% NaOH. For Si determination, 200 µL of supernatant and 1,720 µL of reaction mixture (0.078 N HCl, 3.45 mM NH₄Mo₇O₂₄, 54 mM tartaric acid) were mixed to 80 µL reducing agent. The reducing agent was prepared with 40 mM Na₂SO₃, 10.5 mM 1-amino-2-naphthol-4-sulfonic acid, and 1.45 mM NaHSO₃. The absorbance was measured at 600 nm (Ma et al., 2004).

Extraction and Zn determination in leaf

Samples containing 100 mg of dry leaf matter were pre-digested with 2 mL of concentrated HNO₃ (sub-boiling) for 48 h in 50 mL conic tubes (BD, model Falcon). Afterwards, 4 mL of H₂O₂ (30% v/v, Fluka) + 4 mL of ultra-pure water (Milli-Q) were added and the mixture was transferred to a PFA digestion vessel and digested in a microwave system (Milestone, model ETHOS 1600), according to the following heating regimes: (i) 100 °C for 20 min; (ii) 150 °C for 20 min; (iii) 230 °C for 10 min; and (iv) left to cool. The volume was then filled up to 50 mL with ultra-pure water and rhodium was added as an internal standard (10 µg L⁻¹). The analyses were performed by using an inductively coupled plasma mass spectrometer (ICP-MS Perkin Elmer, model ELAN DRC II).

Leaf gas exchange

Net photosynthetic rate (P_N), stomatal conductance (g_s) and transpiration rate (E) were evaluated using an infrared gas analyser (ADC Bioscientific, model LCPro+, England). These parameters were measured at the adaxial surface of fully expanded leaves, localised in the middle region of the plant. The instantaneous water-use efficiency (WUE), being expressed by formula P_N / E , and it estimated according to Ma et al. (2004). Gas exchange was evaluated in all plants between 9:00 and 12:00 h. The irradiance was maintained at 800 µmol m⁻² s⁻¹ during the measurements.

Extraction of oxidant compound

Oxidant compounds (H₂O₂) were extracted from leaf and root tissues as described by Wu et al. (2006). Briefly, an extraction mixture was prepared by homogenising 500 mg of fresh matter in 5 mL of 5% (w/v) trichloroacetic acid. Subsequently, the samples were centrifuged at 15,000 × g for 15 min at 3°C, and the supernatant was collected.

Hydrogen peroxide determination

For H₂O₂ detection, 200 µL of supernatant and 1,800 µL of reaction mixture (2.5 mM potassium phosphate buffer [pH

7.0] and 500 mM potassium iodide) were mixed, and the absorbance was measured at 390 nm (Velikova et al., 2000).

Electrolyte leakage (EL)

Electrolyte leakage was measured according to the method described by Gong et al. (1998) with minor modifications. Fresh tissues (200 mg) were cut into pieces with a length of 1 cm and were placed in containers containing 8 mL of distilled deionised water. The containers were incubated in a water bath at 35°C for 30 min, and the initial electrical conductivity of the medium (EC₁) was measured. The samples were boiled at 95 °C for 20 min to release the electrolytes. After the samples were cooled, the final electrical conductivity (EC₂) was measured (Gong et al., 1998). The percentage of electrolyte leakage was calculated using the formula EL (%) = EC₁ / EC₂ × 100.

Determination of chlorophyll content

The determination of the photosynthetic pigments was carried out with 40 mg of leaf tissue. The samples were homogenised in the dark and in the presence of 8 mL of methanol (90%) (Nuclear). Subsequently the homogenate was centrifuged at 6,000 g by 10 minutes in the temperature of 5°C. The supernatant was removed and the chlorophyll *a* and *b*, carotenoids and total chlorophylls were quantified using spectrophotometer Bel Photonics (UV-M51), according to the methodology of Lichtenthaler and Buschmann (2001).

Data analysis

The data were subjected to an analysis of variance, and significant differences between the means were determined using the Skott-Knott at a probability level of 5% (Steel et al., 2006). Standard deviations were calculated for each treatment. The statistical analyses were performed using Assistat software.

Conclusion

Zn application produced increases in hydrogen peroxide and electrolyte leakage to both tissues confirming the toxicity of Zn. The treatment of Zn toxicity + Si presented significant increases of 33.3, 25.2, 15 and 9.8% to stomatal conductance, net photosynthetic rate, transpiration rate, and water use efficiency, respectively, compared with Zn-only treatment. With regard to chlorophylls *a*, *b* and *total* and carotenoids non-significant increases were observed, when compared with plants exposed to Zn toxicity. This study revealed the positive contribution of the Si on gas exchange and reduction of the negative effects provoked on chlorophylls and carotenoids in maize plants under Zn toxicity.

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