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REGULAR ARTICLE

Effects of silicon on maize photosynthesis and grain yield in black soils

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ABSTRACT

This study aimed at elucidating the role of silicon on photosynthetic parameters, enzymatic activities and yield of maize (*Zea mays* L.) grown on the black soils of North Eastern China. The effects of silicon on chlorophyll fluorescence, photosynthetic parameters, non-structural carbohydrates, antioxidant enzyme activity and grain yield of maize were studied at five different concentrations: 0, 45, 90, 150 and 225 kg· ha^{-1}. Silicon fertilizer boosted the grain yield by increasing photosynthesis and antioxidant enzyme activity. Significant increases in the maximum quantum yield (Fv/Fm) of photosystem II (PS II), effective quantum efficiency of PS-II (ΦPS-II = Fm′-Fs/Fm′) and photochemical quenching of PSII (qP) were detected at 225 kg· ha^{-1} level. No significant differences in intercellular CO_2 concentration (Ci) were found at different silicon levels, indicating that the enhanced photosynthetic rate (Pn) might due to the regulation of combined stomatal and non-stomatal factors. Increases in total soluble sugar (TSS) and starch were observed, contributing to the synthesis and accumulation of dry matter. The results showed that silicon enhanced the net photosynthetic rate (Pn) and grain yield in maize by maintaining the integrity of the photosynthetic machinery as well as increasing pigmentation and absorption of nutrients.

Keywords: Chlorophyll fluorescence; Antioxidant enzymes; Dry matter accumulation; Total soluble sugar; Starch

INTRODUCTION

Silicon (Si) is the second most abundant element both on the surface of the Earth's crust and in soils (Liang et al., 2007; Gottardi et al., 2012; Ali et al., 2013; Shi et al., 2014). Silicon has been proved to be beneficial for the healthy growth and development of many plant species, particularly graminaceous plants such as rice and sugarcane and some cyperaceous plants (Liang et al., 2007). Dissolved silicon within the soil environment is easily absorbed by plants. It plays an important role in plant growth and mineral nutrition (Hobara et al., 2016; He et al., 2015; Song et al., 2012). The beneficial effects of silicon are particularly distinct in plants subject to both abiotic and biotic stresses (Epstein, 1999; Ma, 2004). Silicon is an essential element for higher plants based on newly described criteria (Epstein and Bloom, 2005).

Photosynthesis plays an important physiological role in terms of growth and development in plants (Qiu et al., 2013). It plays a crucial role in the interaction between internal metabolism and external environment. Initial symptoms of environmental stress can be traced to variation in photosynthesis (Zhang et al., 2014). Chlorophyll fluorescence in higher plants may reflect photosynthetic performance (Hussain and Reigosa, 2011). It is widely used to analyze photosynthesis and related mechanisms in plants under different conditions (Guo et al., 2005). The chlorophyll fluorescence parameters including initial fluorescence intensity (Fo), maximal fluorescence (Fm), maximum quantum yield of photosystem II (PSII) (Fv/Fm), photochemical quenching of PSII (qP), nonphotochemical quenching of PSII (NPQ) and quantum yield of PS II (ΦPS II) are widely used in studies on the effects of environmental stress on plants (Abdeshahian et al., 2010; VanDorst et al., 2010). Studying the changes in chlorophyll fluorescence in photosynthesis might help elucidate photosynthetic mechanisms in maize (Asmar et al., 2013).

Silicon supplementation might increase photosynthetic rate (Pn) and boost the production of chlorophyll

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a and b. It is also associated with positive effects on stomatal conductance and transpiration under isolated and multiple stress conditions (Yao et al., 2011). Although research involving effects of silicon on photosynthesis and chlorophyll fluorescence in plant are well documented under stress conditions, studies under natural field conditions are limited. Therefore, in order to analyze the effect of silicon on changes in chlorophyll fluorescence and photosynthesis, we selected the ZD 958 variety of maize grown in black soils of Northeast China to investigate the underlying physiological and biochemical mechanisms.

MATERIALS AND METHODS

Experimental setup

The study was carried out at the experimental station of Jilin Agricultural University, Changchun city, Jilin Province, P.R. of China (125.10E Longitude, 43.53N Latitude). The study site involved black fertile soils (Udolls, US Soil Taxonomy) with abundant water resource. The soil physical and chemical properties are listed in Table 1.

Experimental design

A randomized complete block design in triplicate with a plot size of 5 m × 10 m was used. The popular maize variety, ZD 958 was cultivated at a density of 65 000 plants· ha^{-1}. A uniform dose of basal fertilizer was applied to all experimental plots prior to seed sowing with N 200 $kg.ha^{-1}$ as urea, P_2O_5 100 $kg.ha^{-1}$ as single super phosphate, and K_2O 80 $kg.ha^{-1}$ as potassium sulphate. The experiments included treatment at four levels T2, T3, T4 and T5 corresponding to SiO_2 concentrations of 45 kg· ha^{-1}, 90 kg· ha^{-1}, 150 kg· ha^{-1} and 225 kg· ha^{-1}, respectively. A T1 level with SiO_2 at 0 kg· ha^{-1} served as the control. Potassium metasilicate (K_2SiO_3) was used as the silicon fertilizer, with a soluble SiO_2 content of 30%. Increased K concentration due to additional potassium metasilicate would be deducted from potassium sulphate. All the silicon fertilizers were applied as basal applications. Soil pH was 6.9 after fertilization, and no significant difference was found among all soil samples.

Measurement of soil nutrient

All the physiological characteristics were tested in the grain-filling period. Potassium dichromate-volumetric analysis was used to determine the organic content in the soil. The alkaline hydrolysis diffusion method was used to measure the available nitrogen (N). The available phosphorus (P) was determined using the sodium bicarbonate method (Li et al., 2008). Available potassium (K) was measured by the atomic absorption spectrometry. The soil pH was measured in H_2O at a soil/solution ratio of 1:2.5 using a glass electrode.

Measurement of photosynthesis and chlorophyll fluorescence

Net photosynthetic rate (Pn), transpiration rate (E), stomatal conductance (g_s) and intercellular CO_2 concentration (Ci) were measured using a portable, open flow gas exchange system LI-6400 (Li-cor Inc., USA) between 9:00 am and 11:00 am in the field. Measurements were conducted on attached and fully expanded leaves of maize plants using, the photosynthetically active radiation of 2000 $\mu mol \cdot m^{-2} \cdot s^{-1}$, CO_2 concentration of 350 $\mu mol \cdot mol^{-1}$ and at a temperature of 25°C.

Chlorophyll fluorescence was measured using a portable chlorophyll fluorometer (OS-30P Inc., USA). The minimal (Fo) and maximal (Fm) fluorescence yield were determined with weak modulated light (0.04 $\mu mol \cdot m^{-2} \cdot s^{-1}$), followed by a 3-s saturating pulse of radiation (3000 $\mu mol \cdot m^{-2} \cdot s^{-1}$). The ratio of Fv/Fm served as a measure of the maximum photochemical efficiency of PS II. Photochemical quenching of PSII (qP) and non-photochemical quenching of PS II (NPQ) were calculated according to Schreiber et al (1986). The efficiency of energy conversion in PS II (ΦPS II) was calculated as (Fm'-Fs)/Fm' (Fs = stationary level of fluorescence emission, Fm' = maximum fluorescence during illumination).

Determination of total soluble sugar and starch content

Leaves (0.1 g) were pulverized with a mortar and pestle using 5 mL distilled water, immersed in boiling water for 30 min, and centrifuged at 4000 rpm for 10 min. The TSS was determined by reacting 1 mL of the diethyl ether extract and 5.0 mL freshly prepared anthrone (150 mg anthrone along with 100 mL 76% (v/v) H_2SO_4) in a 90°C water bath for 15 min. The cooled samples were read at 625 nm in a 752-C spectrophotometer (Gao et al., 2006). Starch content was measured according to the method of Zeng et al (2014).

Enzyme activity assays

Fresh maize leaves were homogenized in 5 mL phosphate buffer (0.1 mol/L, pH 7.8), 1% (w/v) polyvinyl polypyrrolidone, and centrifuged at 10,000×g for 20 min at 4°C. The supernatant was collected for superoxide dismutase (SOD), catalase (CAT), and peroxidase (POD) assays. SOD activity was determined by the

Table 1: Black soil physico-chemical profile

Parameter	Organic matter (g/kg)	Avail. N (mg/kg)	Avail. P (mg/kg)	Avail. K (mg/kg)	Avail. Silicon (mg/kg)	pH
Mean	27.2	153.60	29.50	119.86	268.33	6.80

inhibition of reduced nitroblue tetrazolium (NBT) by superoxide radicals generated photochemically (Beyer and Fridovich 1987). POD activity was determined using guaiacol oxidation in a reaction mixture containing 50 mM phosphate buffer (pH 6.0), 20.1 mM guaiacol, 12.3 mM H_2O_2, and enzyme extract (Bai et al., 1996). CAT activity was measured by the disappearance of H_2O_2 (Samantary 2002). MDA was measured according to the thiobarbituric acid (TBA) reaction as described by Zhang and Qu (2003).

Statistical analysis

Data were analyzed with SPSS for Windows (version 16.0, SPSS, Inc., Chicago, IL, USA) using one-way analysis of variance (ANOVA) to determine significant differences. Group comparisons were made using Fisher's protected least significant difference (LSD) tests. Statistical significance was set at $p < 0.05$.

RESULTS

Chlorophyll fluorescence and photosynthesis

As shown in Fig. 1, no significant changes in the Fv/Fm, ΦPS II, qP and NPQ were apparent at T1 to T4 levels. Fv/Fm showed a sharp increase at T5 level, which was consistent with the changes in ΦPS II and qP. Conversely, the NPQ remained higher from T1 to T4 levels, followed by a sudden drop at T5.

No significant differences in P_n were observed from T1 to T4 (Fig. 2). A sharp increase occurred at T5, and a similar trend was found in g_s, although a slight reduction occurred at T3. Both E and Ci of maize increased first and then decreased. The E values attained a peak at T3 level, and Ci was the highest at T2. No significant difference in Ci was found at different silicon levels (p>0.05).

Total soluble sugar and starch content

The non-structural carbohydrate content of maize leaves at different silicon levels revealed increased TSS and starch levels with a peak value at T5 (Fig. 3). Whose concentrations increased by 1.29 and 1.19 times from T1 to T5, respectively.

Antioxidant enzyme activities

As shown in Table 2, silicon application enhanced the SOD and POD activities of maize significantly (p<0.05) while decreasing the MDA content markedly (p<0.01). With increasing silicon concentrations, no significant changes were seen in CAT activities (p>0.05), however, SOD and POD activities of maize markedly increased and MDA content declined with T4 and T5 treatments. At a concentration of 150 kg· ha^{-1}, the silicon fertilizer significantly improved enzyme activity and decreased MDA content.

Grain yield

Ear length, kernels per ear and 100-kernel weight of maize were significantly increased with silicon levels at 150 kg· ha^{-1}

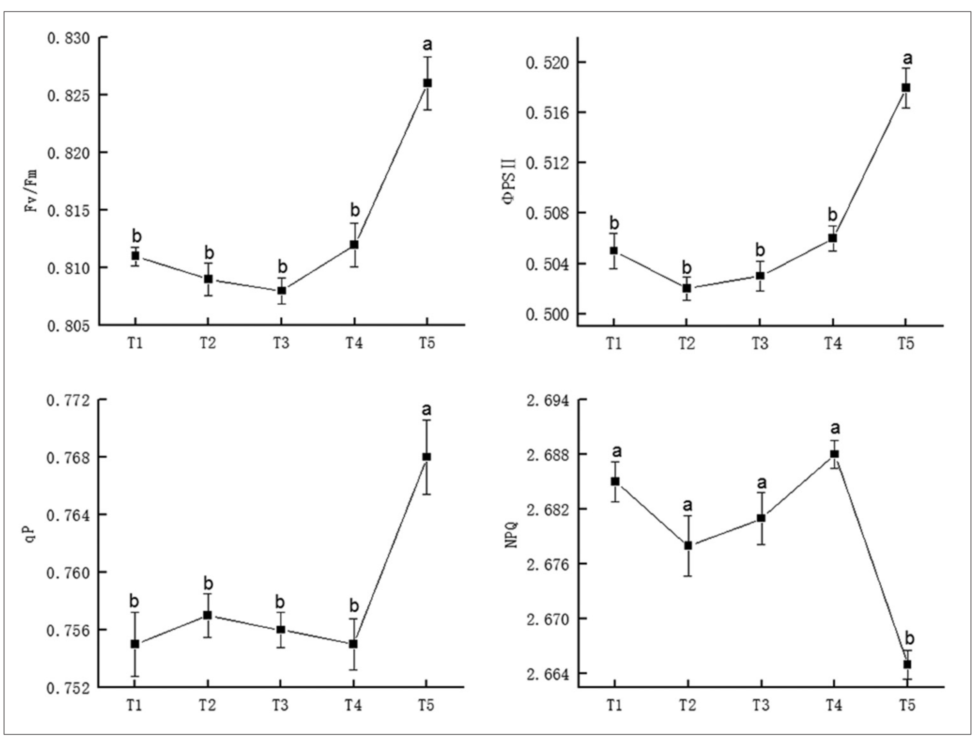

Fig 1. Effects of silicon on chlorophyll fluorescence in maize. Means followed by different letters are significantly different (p < 0.05) by Duncan's test, n = 10.

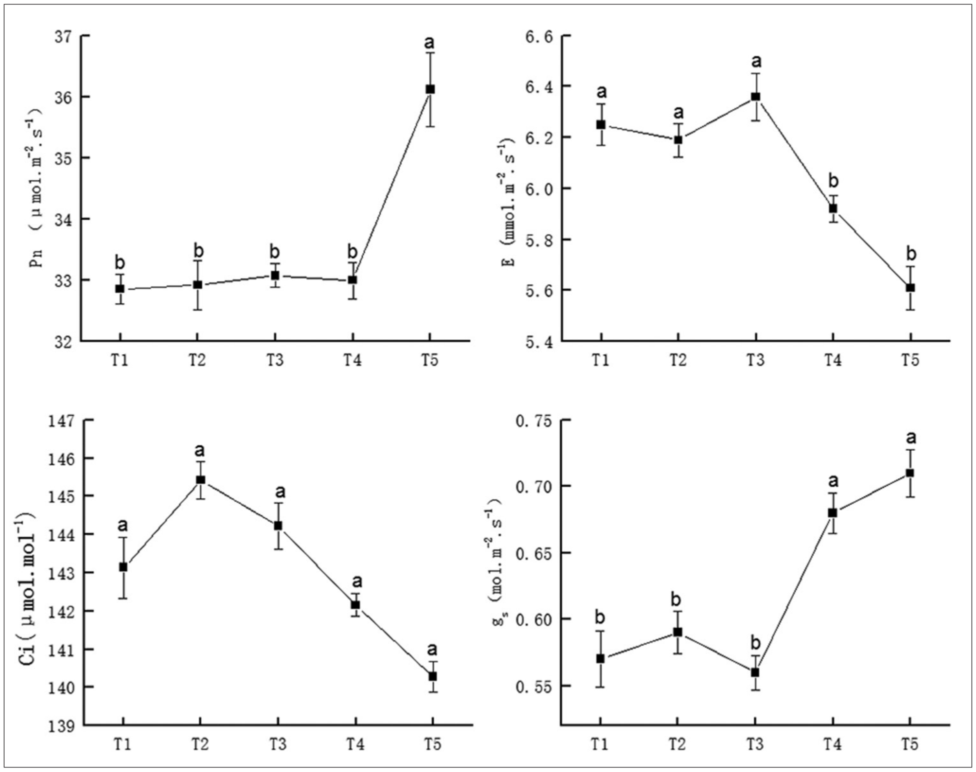

Fig 2. Effects of silicon on maize photosynthesis. Means followed by different letters are significantly different (p < 0.05) by Duncan's test, n = 10.

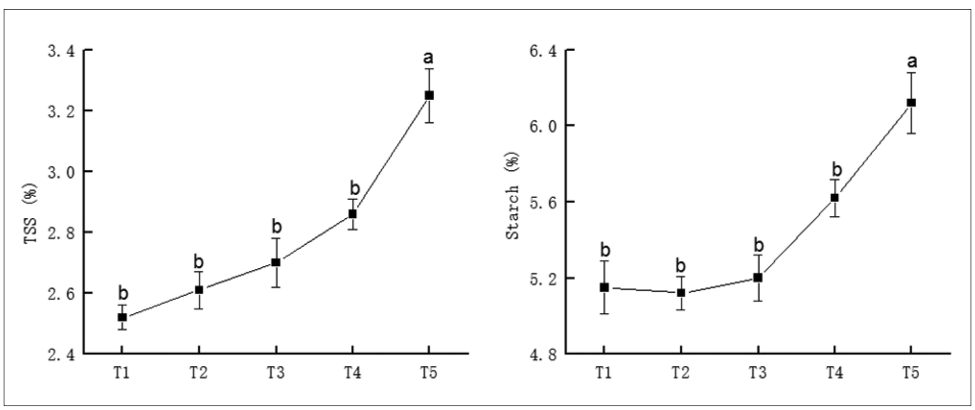

Fig 3. Effects of silicon on total soluble sugar (TSS) and starch content in maize. Means followed by different letters are significantly different (p < 0.05) by Duncan's test, n = 10.

Table 2: Effects of silicon on antioxidant enzyme activities and MDA content

Silicon level (kg/ha)	SOD activity (U/gFW)	POD activity ΔOD_{470}/ (gFW·min .g)	CAT activity [H_2O_2mg/(g·min)]	MDA content (μmol/g)
T1	309.24^{c}	174.22^{c}	65.09^{a}	43.89^{a}
T2	322.37^{c}	178.40^{c}	65.21^{a}	41.34^{a}
T3	329.65^{c}	182.13^{c}	67.89^{a}	38.97^{a}
T4	398.77^{a}	217.23^{a}	69.30^{a}	26.90^{c}
T5	410.06^{a}	208.09^{a}	70.01^{a}	24.22^{c}

Mean labeled with different letters within each column are significantly different (p<0.05) by Duncan's test, n=10

and 225 kg· ha^{-1} (Table 3), which contributed to the high grain yield. Ear barren tip significantly decreased with silicon addition (p<0.05), especially, with silicon levels at 150 kg· ha^{-1} and 225 kg· ha^{-1}.

DISCUSSION

Silicon plays an important role in the improvement of plant resistance under various stresses, thus providing a

Table 3: Effects of silicon on grain yield

Silicon level(kg/ha)	Ear length (cm)	Barren tip (cm)	Kernel per ear (cm)	100 kernel weight (g)	Yield (kg/hm^2)
T1	19.81^b	2.32^a	536^c	29.32^b	11225^c
T2	19.62^b	2.21^a	540^c	29.81^b	11257^c
T3	20.10^b	2.10^a	533^c	30.56^b	11232^c
T4	22.36^a	1.50^b	560^b	33.12^a	13776^a
T5	22.90^a	1.43^b	577^a	33.43^a	13979^a

Mean labeled with different letters within each column are significantly different ($p<0.05$) by Duncan's test, n=10

rationale for agricultural application. Silicates increased the growth and yields of field crops, such as rice, sugarcane, wheat, cotton and sorghum (Hossain et al., 2002; Gong and Chen, 2012; Farooq et al., 2013; Sonobe et al., 2011). Similar beneficial effects were observed in this study. However, no such effects of silicon fertilization on the yields of tomato and other vegetables have been reported (Lewin and Reimann, 1969). Complex physiological and biochemical mechanisms may therefore, be associated with the effects of silicon on plant metabolism.

Silicon may increase plant yield via increased photosynthesis. Fv/Fm and ΦPS II represent the conversion and capture efficiency of primary light energy (Guidi et al., 2007). A small decrease in Fv/Fm and ΦPS II might be the result of a down-regulation of PSII in the light-adapted state, leading to an increase in the proportion of closed PSII centers, and decreased qP (Lu et al., 2002). NPQ is a sensitive marker of thermal dissipation (Maxwell and Johnson, 2000). An increase of ΦPS II was associated with decreased energy dissipation as measured by NPQ (Sui et al., 2012). Our results show a gradual increase of ΦPS II accompanied by an increase in Pn. However, whether photosynthesis was associated with increased heat dissipation or accretion of chlorophyll needs further investigation (Meng et al., 2012). The availability of CO_2 was one of the most limiting environmental factors in photosynthesis. Silicon addition promoted an increase in the Pn in our study, which is probably related to mechanisms maintaining the structural integrity of the photosynthetic apparatus (Bauer et al., 2011; Feng et al., 2010).

Silicon application significantly reduced the E of maize, explaining the reduction in stomatal transpiration. Furthermore, changes in cellular morphology, decreased lumen size, atrophy and thickening of cell wall were observed (Kang et al., 2016). Diminished moisture penetration in plants may also reduce insignificant transpiration, the decline in E favored the maintenance of high water potential and reduced water loss, Such conditions potentially lead to improved and efficient water usage in agriculture in drought-prone regions. And this can be explained that silicon not only inhibited transpiration of plants through the deposition on the cytoderm, but also effectively regulated kinds of metabolic activities of plants, thus providing favorable metabolic conditions (Guo et al., 2006). Insignificant effect of silicon on Ci in our study suggested that silicon increased net photosynthesis via a combination of stomatal and non-stomatal factors (Herrera et al., 2006).

Antioxidant protective enzymes exist in higher plants under different growth conditions. The metabolism of ROS depends on several, functionally interrelated antioxidant enzymes (Mittler, 2002). In this experiment, no significant changes in the activity of CAT were observed in maize following silicon supplementation compared with the control. However, it was found that silicon application enhanced the activities of SOD and POD (Shen et al., 2010; Masoumi et al., 2011). It indicated that the antioxidant activities were triggered by the increased production of ROS or the increased activity might be a protective mechanism adopted by maize against oxidative damage. SOD is probably the key enzyme to defense against toxic ROS (Wang et al., 2010). SOD repaired injured plant cells by catalyzing the dismutation of O^{2-} to H_2O_2 and O_2 (Wu et al., 2014; Liu et al., 2010). POD, which catalyzed the reaction between H_2O_2 and ROOH to H_2O and R-OH, ameliorates cell damage (Zhang et al., 2014; Monk et al., 1989). Furthermore, our findings also suggested relatively lower lipid peroxidation resulting from elevated antioxidant enzyme activities following silicon addition. The results are consistent with the reports of Gong et al (2005), indicating that the addition of silicon increased the antioxidant activity in wheat under drought conditions. Thus, our results suggested that silicon supplementation alleviated the oxidative damage in the leaves of maize via prevention of the structural and functional deterioration of cell membranes.

CONCLUSION

Our results suggest that silicon application improves maize photosynthesis in black soils. Our field study confirmed that silicon addition increased the chlorophyll fluorescence and some photosynthetic parameters as well as antioxidant enzymes and grain yield in maize. However, unexpected reduction in certain photosynthetic parameters suggests complex underlying physiological and biochemical mechanisms. Further morphological and physiological investigations are therefore, needed to confirm the effects of silicon on photosynthesis.

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Authors' contribution

H. X. wrote the article and corrected it. Y. L. and Z. X. designed the study. H. X. and F. S. conducted the experimental work.

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