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[Short report]

Effects of Silicon on Stomatal Blue-Light Response in Rice (*Oryza sativa* L.)

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Many studies have clearly shown that silicon has positive effects on the growth of rice plants (*Oryza sativa* L.) (Agarie et al., 1992 ; Elawad et al., 1979 ; Lewin et al., 1969 ; Ma et al., 1989), however, its physiological function is still unclear. It is well known that transpiration from leaves of rice plants is considerably reduced by the application of silicon (Elawad et al., 1979 ; Lewin et al., 1969), and in Si-deficient plants, wilting and necrosis of the leaves, which are often observed as typical symptoms, are pronounced under conditions of high temperatures with low humidity (Lewin et al., 1969). These observations suggested that transpiration-induced water stress occurs in rice leaves with Si-deficiency. We showed previously that the reduction in transpiration following the application of silicon was largely attributable to a reduction in the rate of transpiration through stomatal pores, indicating that silicon influences stomatal movement (Agarie et al.,1998a).

Stomatal movement is stimulated by many environmental stimuli. Light is a dominant environmental stimulus that regulates stomatal apertures. Previously we showed that the stomata of the Si-treated leaves respond to light to reduce excessive water loss from the leaves (Agarie et al., 1998a). Photocontrol of stomata is governed by at least two photoreceptor systems. Red and blue light (BL) effects both stimulating the opening via their specific photoreceptors. In particular, light absorbed by the blue light photoreceptor is effective in inducing stomatal opening (Zeiger, 1983).

To characterize the effect of silicon on stomatal light responses, we compared changes in stomatal opening, evaluated by leaf conductance, in response to blue light between Si-treated and non-treated leaves.

Materials and Methods

Rice plants (*Oryza sativa* L. cv. Koshihikari) were grown hydroponically in nutrient solution with (100 ppm SiO_2) and without silicon. The procedure for hydroponic culture has been described previously (Agarie et al., 1992). The uppermost, fully expanded leaves on the main culms that had been grown with (+Si) or without Si (−Si) for 50 days were used for the present study. BL-induced stomatal opening was measured as the changes in leaf conductance. Blue light was provided from a tungsten lamp (Philips, 150 W) through a glass filter (Corning 5-61). Red light was obtained by filtering the light from the tungsten lamp through two layers of cellophane paper (Nakagawa Chemical, 222C). The procedure for measuring the gas exchange rate has been described previously (Agarie et al.,1998a). The gas exchange system and the plants were placed in a dark box (2 m×2 m×2 m) covered with a black cloth to exclude any illumination by light from the room during the measurement process.

Results and Discussion

Fig. 1 shows a typical pattern of stomatal BL response of +Si and −Si leaves. The application of BL pulses (20s) resulted in an increase in the leaf conductance in both +Si and −Si leaves, peaking at approximately 2-3 min after the application, followed by a decrease with time, reaching steady-state levels 10-15 min after the application. The response pattern was similar between +Si and −Si leaves, but the maximal value of the leaf conductance was higher in the −Si leaves than in the +Si leaves. In the −Si leaves, the time required for reaching the peak and the steady-state level were longer than those in +Si leaves. The difference in the leaf conductance at the peaks between +Si and -S leaves was greater than that at the steady-state level. The value of the leaf conductance at the steady-state level indicated the degree of cuticular conductance ; therefore, the higher leaf conductance of −Si leaves may reflect a greater stomatal aperture. To our knowledge, this is the first report showing that silicon influences the stomatal BL response.

Stomatal opening is driven by an increase in the turgor of guard cells and depends on the uptake of K^+ and

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Abbreviations : BL, blue light ; RH, relative humidity.

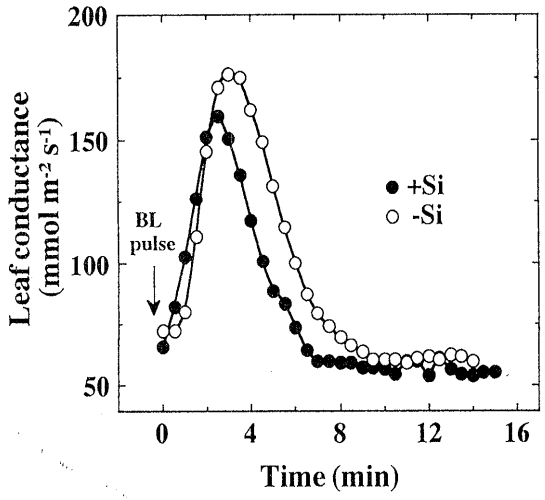

Fig. 1. Stomatal blue-light response of the leaves of rice plants grown in nutrient solutions with supplemented SiO_2 (100 ppm; ● +Si) or without SiO_2 (○ −Si). Red-light irradiation (34 mol m^{-2} s^{-1}) was applied throughout the experiment as background light. Blue light (50 mol m^{-2} s^{-1}) was applied as a short pulse (20 s) 90 min after the onset of the red-light irradiation. Measurements were made using the uppermost fully expanded leaves at a leaf temperature of 26.8±0.5°C and a vapor pressure difference of 2.0±0.1 kPa.

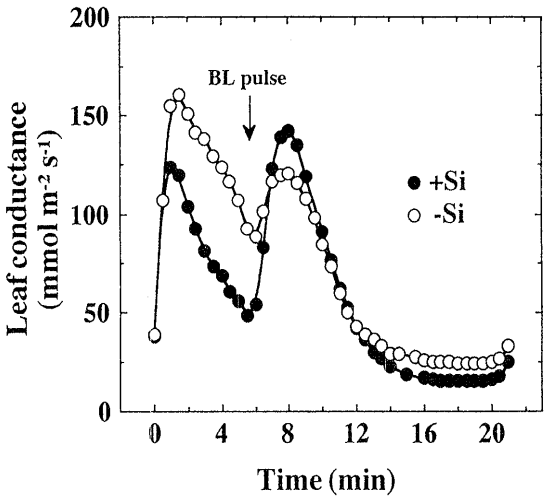

Fig. 2. Changes in stomatal blue-light response of the leaves of rice plants grown in nutrient solutions supplemented with SiO_2 (100 ppm; ● +Si) or without SiO_2 (○) as affected by decreased humidity. Red-light irradiation (34 mol m^{-2} s^{-1}) was applied through the experiment as background light. Relative humidity was changed from 65.2% (vapor pressure difference of 1.15±0.28 kPa) to 11.1% (vapor pressure difference of 2.39±0.28 kPa) 85 min after the onset of the red-light irradiation. A short pulse (20 s) at blue light of 50 mol m^{-2} s^{-1} was applied at 5 min after the onset of the decrease in humidity change. Measurements were made using the uppermost fully expanded leaves at a leaf temperature of 25.9±1.8°C.

anions and the production of malate in guard cells (Raschke, 1975). BL activates proton pump which generates an inside-negative electron potential across the plasma membranes, sustaining passive influx of K^+ (Zeiger, 1983). Our findings in this study suggest that silicon influences the stomatal BL response via some of these processes. However, silicon as H_4SiO_4 is readily absorbed by plants, and the form in which silicon is ultimately deposited is mainly amorphous SiO_2-nH_2O, or "opal" (Epstein, 1994). Therefore, judging from the chemical form of silicon in plant tissues, it is difficult to consider that silicon influenced the stomatal BL response via some biochemical reactions in the guard cells.

Our previous ultrastructural observations revealed that the hydrated, amorphous silica was predominant in the epidermal cells, and in particular in the outer cell walls of the cells (Agarie et al., 1998b). In addition, we found that the +Si leaves contained higher levels of polysaccharides of cell walls than −Si leaves, suggesting the involvement of silicon in the biosynthesis of cell wall components. Reportedly, silicon is crosslinked with the constituents of cell walls and participates in the biosynthesis and deposition of lignin (Adatia et al., 1986; Schwarz, 1973). These facts suggest that silicon affects the mechanical properties of the cell walls, such as their rigidity (Adatia et al., 1986), architecture, resilience (Schwarz, 1973) and elasticity (Emadian et al., 1989). The geometry and viscoelastic properties of cell walls of guard cells has been suggested to be important factors responsible for stomatal movements (Jinno et al., 1982). Therefore, silicon is considered to influence the stomatal BL response via the mechanical and physical properties of cell walls, such as elasticity of the guard cells. The interrelations among the content of silicon and the cell wall components, and changes in water potential of leaves as affected by air humidity remain to be investigated to validate this hypothesis.

Our previous investigations on the effects of silicon on the stomatal response to several environmental stimuli, such as light (Agarie et al., 1998a), CO_2 (unpublished data), and humidity (Agarie et al., 1998a), revealed that silicon clearly influenced stomatal movement in rice leaves; and the effect was striking under dry conditions. To test the effect of silicon on the stomatal BL-response as affected by humidity, we examined the changes in the leaf conductance in response to a BL pulse under a lower humidity in the +Si and −Si leaves (Fig. 2). The leaf conductance of both +Si and −Si leaves increased rapidly within 1 min after the onset of the decrease in humidity, but it gradually decreased thereafter. This rapid increase of leaf conductance in response to the decreased humidity may be due to the opening of stomata resulting from the generation of a gradient of water potential between the guard cells and the epidermal cells and the entry of water from the epidermal cells into the guard cells. The pattern of the decrease of the leaf conductance was similar in +Si and −Si leaves; but, the values of the leaf conductance in −Si leaves were always higher than those in +Si leaves. A BL pulse given 5 min after the onset of decrease in humidity resulted in an increase in leaf conductance, peaking at

around 3 min after the application of the BL pulse. The leaf conductance was increased by 180% in +Si leaves and 71.4% in −Si leaves (Fig. 2).

The leaf conductance at around 16 min, after the onset of the humidity change, when stomata might be almost completely closed, represents the differences in the cuticular conductance between +Si and −Si leaves (Fig. 2). The transpiration rate of both +Si and −Si leaves was in parallel with those of the leaf conductance (data not shown). Therefore, the higher leaf conductance in −Si leaves before the BL pulse reflects the higher transpiration through both stomatal pores and cuticular layers in −Si leaves. The excessive transpiration in −Si leaves might cause decrease of the water potential in epidermal cells surrounding the stomata under the dry condition (Agarie et al., 1998a). Stomata are opened following an increase in the turgor pressure in guard cells resulting from the entry of water into the guard cells from surrounding epidermal cells. Therefore, the differences in the increase of leaf conductance in response to the BL pulse between the +Si and −Si leaves (Fig. 2) may reflect the differences in the water potential of epidermal systems at the onset of the application of the BL pulse. Namely, in +Si leaves, the water potential in epidermal cells surrounding the stomata was maintained high under the dry conditions, and the water flux into guard cells was facilitated, with generation of greater swelling of the guard cells, after the application of the BL pulse. This phenomena also indicates that the stomata opening in response to changes in environmental stimuli is not desirable for the Si-deficient leaves due to water loss caused by the excessive transpiration (Agarie et al., 1998a).

In some species, stoma respond directly to the humidity of the ambient air (Maier-Maerker, 1983), even when the bulk leaf water potential is unchanged. In this case the cuticular layer plays an important role in the regulation of stomatal movement via limiting the water transport from xylem vessels to the sites thier transpiration occurred and the amount of water transpired from guard cells to ambient air (Nonami et al., 1991). As mentioned above, in rice, silica is mainly deposited in the epidermal tissues of the leaf (Agarie et al., 1998b), and forms double cuticular-silica layers at the surface of epidermal cells beneath the cuticle (Clarkson et al., 1980; Yoshida et al., 1962), reduction of cuticular transpiration (Fig. 1 and Fig. 2; Agarie et al., 1998a). Therefore, silica, in combination with the cuticle, may influence stomatal movement in response to environmental stimuli by regulating the water potential in the epidermal cells of rice leaves.

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