



Silicon improves rice grain yield and photosynthesis specifically when supplied during the reproductive growth stage



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ABSTRACT

Silicon (Si) has been recognized as a beneficial element to improve rice (*Oryza sativa* L.) grain yield. Despite some evidence suggesting that this positive effect is observed when Si is supplied along the reproductive growth stage (from panicle initiation to heading), it remains unclear whether its supplementation during distinct growth phases can differentially impact physiological aspects of rice and its yield and the underlying mechanisms. Here, we investigated the effects of additions/removals of Si at different growth stages and their impacts on rice yield components, photosynthetic performance, and expression of genes (*Lsi1*, *Lsi2* and *Lsi6*) involved in Si distribution within rice shoots. Positive effects of Si on rice production and photosynthesis were manifested when it was specifically supplied during the reproductive growth stage, as demonstrated by: (1) a high crop yield associated with higher grain number and higher 1000-grain weight, whereas the leaf area and whole-plant biomass remained unchanged; (2) an increased sink strength which, in turn, exerted a feed-forward effect on photosynthesis that was coupled with increases in both stomatal conductance and biochemical capacity to fix CO₂; (3) higher Si amounts in the developing panicles (and grain husks) in good agreement with a remarkable up-regulation of *Lsi6* (and to a lesser extent *Lsi1*). We suggest that proper levels of Si in these reproductive structures seem to play an as yet unidentified role culminating with higher grain number and size.

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1. Introduction

Silicon (Si), the second most abundant element both on the Earth's crust and in the soil, is not considered an essential element for higher plants. However, the positive effects of Si on plant growth have remarkably been recognized, particularly when the plant faces some form of imposed stress (Epstein, 2009). Indeed, Si is the only known mineral element that effectively mitigates the negative impacts of multiple environmental stresses, including both biotic (e.g., pathogens and insects) and abiotic (e.g., salt, heavy metals, light and drought) stresses in many plant species (Epstein, 2009; Keeping and Reynolds, 2009; Farooq and Dietz, 2015).

Rice (*Oryza sativa*), a typical Si accumulating species, is able to accumulate Si at concentrations as high as 10% of shoot dry weight (Ma and Takahashi, 2002). This accumulating ability has been associated with presence of specific Si transporters: in roots, Si is transported via *Lsi1* and *Lsi2* from the root epidermis into the root steles and then travels to the shoot with the transpirational water flow via the xylem sap (Ma et al., 2006). In the xylem, Si is presented in the form of monosilicic acid and is unloaded by *Lsi6*, a homolog of *Lsi1* in rice (Yamaji et al., 2008). However, different from *Lsi1* and *Lsi2*, *Lsi6* is also expressed in the leaf sheaths and leaf blades in addition to the root tips in rice (Ma et al., 2011). Recent evidence suggests that distribution of Si to panicles and husk is associated with three Si transporters (*Lsi2*, *Lsi3* and *Lsi6*) located at the node; knockout of these transporters seems to decrease Si distribution to the panicles and increased Si levels in the flag leaf (Yamaji et al., 2015).

Si has been recognized as a beneficial element to improve rice grain yields (Ishibashi, 1936; Okuda and Takahashi, 1961). Si fer-

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tilization has therefore widely been used in many countries to guarantee high and sustainable rice crop yields (Guntzer et al., 2012; Ma and Yamagagi, 2015). Improvements in rice grain production associated with Si fertilization have also been demonstrated in rice mutants defective in Si uptake, which produce much less sealable crops than their wild-type counterparts (Tamai and Ma, 2008; Detmann et al., 2012). These positive effects of Si have traditionally been associated with the Si's role in alleviating abiotic and biotic stresses in addition to improving resistance to lodging and increasing the erectness of leaves, which allows better light transmittance through rice canopies and thereby potentially enhancing whole-plant photosynthesis (Tamai and Ma, 2008). Furthermore, Si fertilization seems to have a direct and positive effect on grain production in rice. It was previously demonstrated that Si supply improves rice grain yields by enhancing straw biomass, the number of spikelets per panicle, and particularly the percentage of filled spikelets, with no significant effect on the panicle number or the 1000-grain weight (Ma et al., 1989; Tamai and Ma, 2008). We have recently also observed an increased number of spikelets in Si-treated plants (Detmann et al., 2012); however, in sharp contrast with the results of Ma and colleagues, increased grain weight was associated with no significant effect of Si on both straw biomass and the percentage of filled spikelets (Detmann et al., 2012). We reasoned that higher crop yields in Si-treated rice plants brought about an increased sink strength that, in turn, exerted a feed-forward effect on photosynthesis that was fundamentally associated with increased mesophyll conductance.

Ma et al. (1989) demonstrated, by adding or removing Si during the vegetative, reproductive and ripening stages of the rice growth cycle, that Si led to increases in dry weights of straw and grains when this element is specifically supplied during the reproductive stage. Of the yield components of rice, the percentage of filled spikelets was by far the most affected by presence of Si during this stage, whereas the 1000-grain weight was unaffected and the panicle number and spikelet number per panicle were only marginally increased (although significantly) by Si supplied during the reproductive phase. In any case, in the study of Ma et al. (1989), heading was unexpectedly delayed regardless of Si addition/removal at different growth stages. Such a delay affected the fertility of the spikelets, thus ultimately rendering a low index harvest. Therefore, caution must be taken when considering the effects of Si, supplied or removed at varying growth stages, on rice production as solely based on the results of Ma et al. (1989). In addition, there is no further information whether and to what extent the photosynthetic capacity is adjusted to support the anticipated increased grain production as promoted by Si application during the reproductive growth stage. Given these facts, we decided (1) to confirm the functional importance of Si on rice yield when supplied at different growth phases, (2) to examine the adjustments in photosynthesis in response to varying sink demand, and (3) whether Si may act as a player affecting developmental processes that result in increased grain production. To reach these goals, we conducted an in-depth analysis of both the agronomic components of rice crop yield and the photosynthetic performance. We additionally investigated how the imposed Si treatments could affect the expression of key genes (*Lsi1*, *Lsi2* and *Lsi6*) associated with Si distribution in rice shoots. Our results demonstrated that Si is present at higher amounts in the developing panicles in good agreement with a remarkable up-regulation of *Lsi6* (and to a lesser extent *Lsi1*) when Si is specifically supplied at the reproductive growth stage. We linked these results with alterations in developmental processes that culminated with increased grain number and size, which in turn exerted a feed-forward effect of photosynthesis via enhanced stomatal conductance and higher biochemical capacity to fix CO₂.

2. Materials and methods

2.1. Plant material, growth conditions and experimental design

The experiments were carried out in Viçosa (20°45'S, 42°54'W, 650 m altitude) in south-eastern Brazil. Rice plants from cv. 'Oochikara' were grown in non-aerated culture solutions (in plastic pots with 5 L volume) in a greenhouse with controlled air temperature (30/25 ± 2 °C (day/night)) and naturally fluctuating photosynthetic photon flux density (PPFD) (maximum PPFD was approx. 1500 μmol photons m⁻² s⁻¹ inside the greenhouse at mid-day). Si was supplied as monosilicic acid, which was prepared by passing potassium silicate through cation-exchange resin (Amberlite IR-120B, H⁺ form; Sigma-Aldrich, São Paulo, Brazil). Further details of the applied methodology (e.g., seed germination, composition of the nutrient solutions, pH control, etc.) have been described by Dallagnol et al. (2011).

Unless otherwise indicated, Si was supplied (2 mM) or not (0 mM) to the culture solutions during three specific periods of the rice growth cycle: (i) the vegetative growth stage (V), from transplanting to panicle initiation (that occurred at 60 days after transplanting; panicle initiation was periodically monitored using a stereoscopic microscope in an extra group of plants); (ii) the reproductive stage (R1), from panicle initiation to heading (90 days after transplanting); and (iii) the ripening stage (R2), from heading to maturity. Specifically, Si was supplied (+Si) or not (-Si) during V, R1 and R2 growth stages, as follows: -Si/-Si/-Si, -Si/-Si/+Si, -Si/+Si/-Si, -Si/+Si/+Si, +Si/-Si/-Si, +Si/-Si/+Si, +Si/+Si/-Si, and +Si/+Si/+Si (Fig. 1). Therefore, eight treatment combinations were applied over the course of the experiment. Essentially, this experimental design is the same previously used by Ma et al. (1989).

The experiment had a completely randomized design, with six plants in individual pots per treatment combination serving as conditional replicates (six per treatment combinations).

2.2. Si concentration

At the end of the experiment, flag leaves and grain hulls were collected, and their Si concentrations were colourimetrically determined using 100 mg of dried and alkali-digested material according to Dallagnol et al. (2011). Additionally, Si levels were quantified in panicles (using an extra group of plants) in their early development stages (panicle developmental stage 3, characterized by small and sleazy tissues, according to Wang et al. (2010)). Due to the reduced panicle biomass to perform the above-quoted colourimetric assay, Si concentrations were determined using scanning electron microscopy (SEM) coupled to energy dispersive X-ray spectrometry (EDS) (Hayasaka et al., 2008). In brief, panicle tissues were dehydrated in an alcoholic series and subsequently dried in a "critical point dryer" (CPD 030 model, Bal-Tec, Balzers, Liechtenstein). The tissues were mounted on aluminium metal supports covered with double-sided adhesive tape, and then vaporized in carbon. Electron micrographs were obtained using a SEM (model 1450 VP, Carl Zeiss AG, Cambridge, England) operated at 10 kV, equipped with an EDS detector; the micrometric scale was projected onto the same optical conditions using rhodium (Rh) as an internal standard.

2.3. Photosynthetic gas exchange measurements

Photosynthetic parameters were assessed in flag leaves at approximately 100 days after transplanting. The net CO₂ assimilation rate (*A*), stomatal conductance to water vapour (*g_s*), and internal CO₂ concentrations (*C_i*) were measured simultaneously with chlorophyll *a* fluorescence parameters on the attached flag leaves using two cross-calibrated portable open-flow gas exchange

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