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# Effect on soil water availability, rather than silicon uptake by plants, explains the beneficial effect of silicon on rice during

# drought

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#### Abstract

Various studies showed a decrease of drought stress specific parameters of plants after silicon (Si) fertilization. But all studies differed in soil Si concentration between the control and Si treatments. As amorphous silica (ASi) was recently found to cause a strong increase of water holding capacity and plant available water in soils, a combined effect of soil moisture and plant response due to Si addition was assumed. In this study, the influence of the soil Si content was excluded by using the same Si enriched soil for treatments of two rice lines, *lsi1* mutant defective in Si uptake and its wild-type rice. Most plant parameters, such as nutrient contents, biomass, specific leaf area, specific root length, leaf water content and C allocation did not differ significantly between the genotypes neither under flooded conditions, nor under drought conditions. Only photosynthesis and stomatal conductance were slightly higher for the wild type in both drought and flooded treatments. Overall, our data showed that Si accumulation within the plant tissues has only a minor effect on plant performance under drought stress. Hence, existing studies should be reinterpreted in light of the fact that Si additions may increase soil water availability.

#### KEYWORDS

carbon allocation, drought, photosynthesis, plant performance, silicon

#### 1 | INTRODUCTION

Climate change is predicted to cause a shift in frequency and severity of droughts in the future threatening terrestrial ecosystems and especially agroecosystems in dryland regions (Jia et al., 2019). As a limiting factor for plant growth, water is essential for the survival of plants, which makes a sufficient water supply fundamental for crop production. With freshwater resources becoming scarcer, the security of food production will become a major problem in the years ahead (Dubey, Singh, & Abhilash, 2020; Gupta, Rico-Medina, & Caño-Delgado, 2020). Yield losses of up to 25% (compared with 1961– 1990) are expected for Europe (Ciscar et al., 2011) with drought as a large factor for this decline (Webber et al., 2018).

Plants have developed strategies to cope with water scarcity, such as avoidance of water loss through transpiration (e.g., by stomatal closure, reduction of stomata size and number, decrease of leaf size, number and branching, xeromorphic traits, sclerophylly), increase of water uptake from the soil by morphological changes in root architecture, osmotic adjustment (accumulation of solutes in dividing cells under reduced water potential) and hormonal regulation as a response of plant organs to dehydration for an optimized water usage (Basu, Ramegowda, Kumar, & Pereira, 2016; Gupta et al., 2020).

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There are several measures discussed to adapt or mitigate the upcoming challenges of intensifying droughts. One approach is the development of more drought-tolerant crops using traditional breeding or transgenic technologies, but also bioengineering at molecular level (Basu et al., 2016; Dubey et al., 2020; Gupta et al., 2020; Pray et al., 2011). Another option are adaptive soil and water management techniques, for example, mulching, minimum tillage, input of organic matter or alternate wetting and drying (Bodner, Nakhforoosh, & Kaul, 2015; Dharmappa et al., 2019), as well as the innovation of new cultivation methods, for instance foliar application of film-forming anti-transparent or the usage of growth-promoting rhizobacteria (Dubey et al., 2020). A more recent idea is the fertilization with silicon (Si).

Si is the second most abundant element in the earth's crust with approximately 28% by weight. The Si availability in soils varies strongly with soil type (Schaller, Puppe, Kaczorek, Ellerbrock, & Sommer, 2021) and composition of a solid phase (primary and secondary minerals and amorphous form) and a liquid phase (monosilicic acid. polysilicic acid and complexed forms) (Schaller et al., 2021). Plants take up Si either actively or passively (Takahashi, Ma, & Miyake, 1990) in form of monosilicic acid (H<sub>4</sub>SiO<sub>4</sub>), which typically occurs in a range of 0.1-0.6 mM in soil solution (Epstein, 1994). The *lsi1* transporter allows the influx of silicic acid from soil solution into root cells of exodermis and endodermis (Ma et al., 2006) and the *lsi2* transporter is responsible for the efflux from root cells into the xylem (Ma et al., 2007). In the xylem, silicic acid is translocated into the shoot by the transpiration stream and unloaded via the Lsi6 transporter into parenchyma cells (Yamaji, Mitatni, & Ma, 2008). Silicic acid polymerizes there and is deposited in form of silica cells (dumb-bellshaped cells on vascular bundle) or silica bodies (on bulliform or motor cells in epidermis) (Currie & Perry, 2007; J. F. Ma & Takahashi, 2002; Prychid, Rudall, & Gregory, 2003). Depending on the species, plants accumulate Si between 0.1 and 10% of dry weight, with rice as a strong Si accumulator (J. F. Ma & Takahashi, 2002). However, Si was not considered to be essential for growth of higher plants for a long time, because it is not involved in the plant metabolism. In 2005 Epstein and Bloom (2005) stated new criteria for essentiality, whereupon Si is essential for higher plants, because it is a component of phytoliths, that are incorporated into plant structure cells, and plants under Si deficiency performed less resistant against stresses like pests, salt or drought (E. Epstein, 1999; J. F. Ma et al., 2004; J. F. Ma & Yamaji, 2006).

Multiple studies detected an enhanced plant performance with Si fertilization under drought conditions compared to non-fertilized plants. This enhancement found expression in a higher biomass production reported as an increase in dry weights or straw yields (Chen, Yao, Cai, & Chen, 2011; H. j. Gong, Chen, Chen, Wang, & Zhang, 2003; Hattori et al., 2005; Ibrahim, Merwad, & Elnaka, 2018). For the aboveground biomass, this became apparent particularly by a bigger leaf area (Alzahrani, Kuşvuran, Alharby, Kuşvuran, & Rady, 2018; H. j. Gong et al., 2003). Elevation of root length and root to shoot (R/S) ratio showed that especially belowground biomass was improved by Si addition under drought (Chen et al., 2011; Hattori et al., 2005; Ibrahim et al., 2018). Investigations of nutrient uptake were ambivalent, as Chen et al. (2011) found a decrease under drought with Si fertilization, while Ibrahim et al. (2018) detected an increase in plant nutrient status. On the other hand, studies clearly determined Si addition to increase photosynthetic rate and, in most cases, also stomatal conductance of drought-stressed plants (Chen et al., 2011; Hattori et al., 2005; Ibrahim et al., 2018).

The improved root formation is seen as the basis for a better water supply for plants, which also tends to enhance nutrient uptake. The higher water absorption through increased root length and surface also ameliorates the nutrient and water transport into the shoot, increases growth and reduces the closure of stomata (Chen et al., 2011; Hattori et al., 2005; Ibrahim et al., 2018), Furthermore, leaf water status is improved by a decrease in transpirational water loss due to formation of thicker leaves (H. j. Gong et al., 2003). Silicon was also found to prevent deterioration of cell membrane structures and functions, maintaining an intact cell membrane in stressed plants and thus promoting growth and productivity (Agarie, Uchida, Agata, Kubota, & Kaufman, 1998). A larger leaf area due to increased growth combined with a reduced degradation of chlorophyll by Si application results in enhanced assimilation through higher photosynthetic activity, which again leads to a higher dry matter production (Agarie, Agata, Kubota, & Kaufman, 1992; H. j. Gong et al., 2003). However, all those studies showed effects of Si fertilization on plant performance during drought in systems with Si addition to soil which may have altered the water availability in the soils. So far, changes in soil water availability after Si addition were not considered.

Most recently, silicon addition to soils (using amorphous silica, ASi) was found to strongly increase the water holding capacity and the plant available water of soils (Schaller, Cramer, Carminati, & Zarebanadkouki, 2020). An increase of ASi by 1% or 5% (weight) increased the water content at any water potential and the plant available water increased by up to >40% or >60%, respectively. If the water availability in the soil is changed by the addition of silicon, experiments fertilizing soils with Si may show not only the response of plant physiology to Si addition during drought but also an effect of Si addition altering the water availability of soil. Therefore, we wanted to determine the extent to which the positive effect of Si on plant performance during drought is via increased Si uptake and effects on physiological processes or simply via an increase in soil water availability.

To examine the effects of plant Si accumulation on plant performance during drought, while excluding potential effects of Si addition to soil, we cultivated wild type rice (*Oryza sativa* cv. Oochikara) and compared it with the mutant low silicon rice 1 (*Isi1*) defective in Si uptake (Ma et al., 2006) under the same soil conditions (e.g., same soil Si content and soil water content) during the whole experiment to exclude soil Si concentration as factor affecting plant performance. Soil was fertilized with Si, because root uptake of Si is scientifically proven by the discovery of the special transporters by Ma et al. (2006). We used the rice plant subspecies *japonica*, which is a paddy rice with reported negative plant performance during drought and a cultivar for which a deficiency mutant with knock out Si uptake WII FY\_Plant, Cell &

transport system is existing. Using the wild type and the *lsi1* mutant of rice is a good choice excluding effects from different phylogeny (Ma et al., 2006). The identical genetic background would allow assessing the influence of silicon in the plant, decoupled from the effects in the soil.

If the plant Si content is the main factor influencing plant performance and the soil Si content can be neglected, we would expect plants with elevated Si content to be less responsive to drought and result in (I) improved plant performance, that is, enhanced total nutrient uptake, higher biomass production, root length and leaf area as well as an increased leaf water content and rates of photosynthesis and stomatal conductance, and (II) a higher assimilation and allocation of recently incorporated C to roots relative to plants with low Si. Plants under drought were found to invest more C in root development to improve water uptake as well as exudation and respiration (Bouman & Tuong, 2001; Kim et al., 2020). Hence, we assume that under drought, a high Si content in biomass will allow the plant to maintain higher assimilation and to increase investments of newly assimilated C into root development for improved water uptake. The comparison of the Si-uptake-defective mutant with the wild type rice provides us with a unique opportunity to investigate the importance of Si-accumulation in plant tissue for drought resistance of rice. excluding possible changes in soil processes caused by Si-fertilization.

#### 2 | MATERIAL AND METHODS

### 2.1 | Plant material, growth conditions and experimental treatments

The soil used in this experiment was a sandy loam collected from the Ap horizon (0-20 cm) from an arable field of the Landwirtschaftliche Lehranstalten Bayreuth. After sieving it at 2 mm, the soil was mixed with 15 g hydrophilic pyrogenic silicon dioxide (SiO<sub>2</sub>) per 1 kg soil in form of Aerosil 300 (Evonik Industries AG, Essen, Germany). This mixture was filled into PP-pots of 7 cm diameter and a height of 30 cm with an in and outlet for gas sampling. One fitting was located 7 cm from the bottom and the other was located 5 cm from the top. The bottom of each pot was filled with 50 plastic balls to guarantee enough air volume for the soil CO<sub>2</sub> measurements (Figure S1). The wild-type rice (Oryza sativa cv. Oochikara) and a mutant defective in Si uptake, Isi1 were used in this study (Ma et al., 2006). The seeds were germinated in the pots, flooded with water about 2 cm above the soil surface (paddy conditions), and grown in a climate chamber (Conviron Adaptis A 1000, Controlled Environments Ltd., Winnipeg, MB, Canada) under a 14 hr/25°C day and 10 hr/20°C night regime (270  $\mu$ mol m<sup>-2</sup> s<sup>-1</sup> light intensity) and daily watering with deionized water. Five replicates of each rice type (WT and Isi1) were treated with drought after 48 days for 2 weeks by a reduction of watering to achieve 20% (vol) soil moisture. Another five pots of WT and Isi1 remained flooded (paddy) all the time. The volumetric soil moisture was measured frequently over the duration of the experiment by a TDR sensor (EasyTest, Institute of Agrophysics, Polish Academy of

Science, Poland) with three technical replications at different positions within the pot in a minimum of three pots per treatment. To maintain proper nutrient availability the soil was fertilized with 0.2 g  $NH_4NO_3$  per pot on day 31 after sowing and with 0.5 mL Wuxal<sup>®</sup> Super (AGLUKON Spezialdünger GmbH & Co. KG, Düsseldorf, Germany) per pot on day 33. A mycotic infection (not differing between the treatments) was detected on the leaves on day 48 after sowing, therefore the plants were treated with Folicur 1% (Bayer AG, Leverkusen, Germany).

#### 2.2 | Assessment of physio-biochemical attributes

Photosynthesis and stomatal conductance were determined with the portable photosynthesis system LI-6400XT (LI-COR Bioscience Inc., Lincoln, NE) using the standard leaf chamber combined with the 6400-02B Red/Blue LED Light Source. Measurements were done in the middle of the youngest fully developed leaf of every pot at two-daily intervals during the drought period, with a replication of five and a technical replication of 10. Light intensity of 300 µmol m<sup>-2</sup> s<sup>-1</sup>, CO<sub>2</sub> concentration of 400 µmol mol<sup>-1</sup> and temperature of 25°C were adjusted to the conditions in the climate chamber.

#### 2.3 | <sup>13</sup>C pulse labelling

To study the allocation of recently assimilated C in the plant-soil-systems, the paddy pots were sealed with silicone rubber (Tacosil 171 and Vernetzer 28, Thauer & Co. KG, Dresden, Germany) on day 59 after sowing and labelled in a two-compartment Plexiglas chamber on the next day. For this, 5 M H<sub>2</sub>SO<sub>4</sub> was dripped into a bottle with Na<sup>13</sup>CO<sub>3</sub> (sodium carbonate-<sup>13</sup>C 99 atom % <sup>13</sup>C, Sigma-Aldrich Chemie GmbH, Taufkirchen, Germany) dissolved in deionized water and 1 M NaOH. The outgassing <sup>13</sup>CO<sub>2</sub> was released into the chamber. Plants remained in the enriched atmosphere for 4 hr to guarantee a sufficient uptake and metabolization of the tracer. Afterwards, they were connected to CO<sub>2</sub> trapping systems (Figure S2) for 2 days to determine the soil CO<sub>2</sub> production and its isotopic composition. These traps consisted of a flask filled with 15 mL 1 M NaOH, an empty flask as a water trap and a pump. At the end of the 2 days the air in the closed-circuit trapping systems was pumped through the NaOH for 1 hr. Afterwards, plants and soil were harvested. The same procedure was done with the drought pots (sealing with silicone paste on day 60, labelling on day 61, pumping and harvest on day 63). Additional four pots of each rice type and watering treatment (i.e., drought and paddy) were used for natural isotope abundance measurements.

#### 2.4 | Harvest

At harvest, the shoots were cut off from the roots and separated into single leaves and stems to determine the leaf area with the LI-3000A (LI-COR Bioscience Inc., Lincoln, NE) and subsequently dried at 60°C. The roots were separated from the soil by handpicking, washed and stored fresh in tubes with deionized water for further analyses of root length and diameter at the EPSON PERFECTION V800 PHOTO scanner with the program winRHIZO<sup>™</sup> (Regent Instruments Inc., Québec, Canada) and dried afterwards at 60°C. The soil was dried at 105°C. Fresh and dry weight were determined for all samples and they were pulverized in a ball mill (Schwingmühle, Retsch, Haan, Germany) for further analysis. For ash free dry weight, the samples were burned in a laboratory muffle furnace M110 (Heraeus Holding GmbH, Hanau, Germany).

#### 2.5 | Sample analysis

The natural abundance of <sup>13</sup>C of soil CO<sub>2</sub> before <sup>13</sup>C-labelling of the plants was measured in 12 mL vacuum gas vials (exetainer, Labco Ltd., Lampeter, UK) taken just before the labelling of the plants. Measurements were performed using a gas chromatograph (GC-Box, Thermo Fischer Scientific Bremen, Germany) coupled to a Delta plus XP (Thermo Fischer Scientific Bremen, Germany) isotope ratio mass spectrometer via a combustion interface (Conflo IV, Thermo Fischer Scientific Bremen, Germany) at Centre for Stable Isotope Research and Analysis at the Georg-August-University of Göttingen.  $\delta^{13}$ C values were expressed relative to Vienna Pee Dee Belemnite (VPDB, <sup>13</sup>C/<sup>12</sup>C = 0.0112372).

The C content in the NaOH from the CO<sub>2</sub>-traps was measured at the multi N/C 2100 S (Analytik Jena, Germany). For <sup>13</sup>C-analysis, SrCO<sub>3</sub> was precipitated from the NaOH by addition of 1 M SrCl<sub>2</sub>, then centrifuged and freeze-dried (Harris, Porter, & Paul, 1997). The resulting powder as well as the ground soil, root and shoot samples were analysed for total C, total N content and <sup>13</sup>C value (VPDB, <sup>13</sup>C/<sup>12</sup>C = 0.0112372) with an EA-IRMS coupling (NC 2500, CE Instruments, Mailand, Italy and delta plus, Thermo Fisher Scientific, Bremen, Germany) at the Keylab of Isotope-Biogeochemistry of the University of Bayreuth. Si and P were measured at an ICP-OES (Varian, Vista-Pro radial, Palo Alto, California, USA). For this, Si was extracted from 0.03 g shoot material with 30 ml Na<sub>2</sub>CO<sub>3</sub> at 85°C and filtrated at pore-size of 0.2 mm. For P, 0.1–0.2 g shoot material was digested in a microwave digestion system (CEM-Mars5, CEM Corporation, Matthews, NC) at 180°C with 3 ml HNO<sub>3</sub> and 2 ml H<sub>2</sub>O<sub>2</sub>.

#### 2.6 | Statistical analysis and calculations

The received data was statistically analysed using IBM<sup>®</sup> SPSS<sup>®</sup> Statistics (Version 21.0, IBM, Armonk, NY, USA) and RStudio (Version 1.1.419 – © 2009–2018 RStudio Inc., Boston, MA). An ANOVA was carried out to prove the statistical differences between the two factors. As the reference treatment (the wild type under well-watered conditions, WT paddy) was used. Between the wild type (WT) and the mutant (*Isi1*) the differences were tested for normality using the shapiro–wilk test at first and afterwards with a Welch *t*-test or a one factor ANOVA (type one). The correlation between Si:N and Si:C was tested with the cor.test function (Pearson method). The ash free dry weight (AFDW) was calculated by multiplying the dry weight (DW) with the quotient of 100 minus the percentage of ash (PA) divided by 100.

$$\mathsf{AFDW} = \mathsf{DW} \times (100 - \mathsf{PA}) \times 100^{-1}. \tag{1}$$

The elemental contents were calculated using the concentrations (c) in mg  $g^{-1}$  divided by the percentage of ash (PA).

Elemental contents = 
$$c \times (PA)^{-1}$$
. (2)

The specific leaf area (SLA) was calculated by taking the leaf area (A) of the plants and dividing it by the dry weight (DW) of the shoots (Pérez-Harguindeguy et al., 2013).

$$SLA = A \times (DW_{shoots})^{-1}$$
. (3)

The specific root length (SRL) equals the root length (RL) divided by the dry weight (DW) of the roots (Pérez-Harguindeguy et al., 2013).

$$SRL = RL \times (DW_{roots})^{-1}.$$
 (4)

The leaf water content (LWC) is the difference between fresh weight (FW) and DW of the shoot divided by the FW of the shoot.

$$LWC = (FW - DW) \times FW^{-1}.$$
 (5)

Values for photosynthesis and stomatal conductance were output directly from the LI-6400XT. The plants always needed some time to acclimate to the conditions in the leaf chamber. Hence, only the last three measurement points of each pot, when the values had already stabilized, were averaged and used for further calculations.

For carbon allocation to the different pools and fluxes (shoot, root, soil and CO<sub>2</sub>) in the plant-soil-system, the <sup>13</sup>C excess of each pool was calculated as the difference between the amount of <sup>13</sup>C of the respective pool after labelling (<sup>13</sup>C<sub>L</sub>) and the natural abundance of <sup>13</sup>C in the same pool before labelling (<sup>13</sup>C<sub>NA</sub>) in atomic percentage (AT%).

$$\delta^{13} Cex_{pool}(AT\%) = {}^{13}C_{L}(AT\%) - {}^{13}C_{NA}(AT\%).$$
(6)

The total <sup>13</sup>C content of shoot, root, and soil, respectively, was obtained by Equation (7), where C is the relative amount of C in the particular pool and DW the dry weight of this pool.

$$\label{eq:choot_root_soil} \begin{split} ^{13}C_{\text{shoot,root,soil}}(\text{mg/pot}) &= {}^{13}\text{C}\,\text{ex}_{\text{shoot,root,soil}}(\text{AT}\%) \times 100 \times \text{C}(\%) \\ &\times 100^{-1} \times \text{DW}\,(\text{mg/pot}). \end{split} \tag{7}$$

To calculate the amount of  $CO_2$  trapped in NaOH, the measured mass concentration of inorganic C in the NaOH (IC) was multiplied with the volume of the NaOH ( $V_{NaOH}$ ).

$$CO_2(mg) = IC(mg/L) \times V_{NaOH}(L).$$
(8)

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The total <sup>13</sup>C content of the  $CO_2$ -pool was received according to Equation (9) where  $CO_2$  (mg/pot) is the cumulative  $CO_2$  efflux over 2 days:

$$^{13}C_{CO_{2}}(\textit{mg/pot}^{-1}) = {}^{13}C~\textit{ex}_{CO_{2}}(\textit{AT}\%) \times 100^{-1} \times CO_{2}(\textit{mg/pot}^{-1})~(9)$$

#### 3 | RESULTS

#### 3.1 | Leaf elemental content

The C content of the shoots decreased significantly (p = .001; F = 17.737, df = 1) under drought (WT drought 0.43 and *lsi1* drought 0.53 g g<sup>-1</sup> dry weight) to nearly half of the plants under continuously flooding (WT paddy 0.76 and *lsi1* paddy 0.74 g g<sup>-1</sup> dry weight) (-Figure S3A). Within the drought treatment, the *lsi1* type showed a slightly higher C content than the wild type (p = .076, *t*-test). However, the root C content did not significantly differ between the genotypes and water levels. The averages varied between 0.034 g g<sup>-1</sup> (WT drought) and 0.051 g/g dry weight (WT paddy) (Figure S3B).

For the N content of the shoots, a similar pattern as for C became apparent. The continuously flooded treatments (WT paddy 0.064 and *lsi1* paddy 0.060 g/g dry weight) had significantly (p = .005; F = 11.505, df = 1) higher N content as the plants under drought conditions (0.037 (WT drought) and 0.042 g/g dry weight (*lsi1* drought)) (Figure S4A). There was no significant effect between WT and *lsi1* for none of the water treatments. Again, for the root N content no significant difference between the two genotypes and two water levels could be detected (Figure S4B).

The shoot P contents were between 6.0 (lsi1 drought) and 7.2 mg/g dry weight (WT paddy). They did not differ significantly neither between genotypes nor between water levels (Table S1).

We found a significant difference in Si content of the aboveground biomass between the wild type (WT paddy 38.41 and WT drought 46.73 mg/g dry weight) and the *lsi1* mutant (*lsi1* paddy 16.31 and *lsi1* drought 11.81 mg/g dry weight) (p < .001; F = 82.741, df = 1) (Figure 1). The defect in Si uptake of the lsi1 was proven by this 2 (paddy) to 4 (drought) times lower Si content compared to the wild type. No differences were found between the two watering treatments.

#### 3.2 | Root and shoot biomass

The shoot biomass showed a clear difference (p < .001; F = 26.467, df = 1) in dry weight between plants under drought and under flooded conditions (Figure 2a). Between the two genotypes there was no significant effect within the treatments (p = .455; F = 0.585, df = 1). The same pattern occurred for the ash free dry weight of the shoots but with an overall lower weight (Figure 2b).

In contrast, for the root biomass no significant difference in dry weight between the treatments appeared. Only the WT drought



**FIGURE 1** Silicon content of the aboveground biomass for control (*lsi1*) and wild type (WT) under paddy and drought conditions, n = 5. The letters a and b indicate significant differences (p < .001) between the treatments

treatment showed a lower root biomass, but this was also not significant (p = .09, *t*-test) (Figure 2c). Ash free dry weight was again lower, but not in the same order of magnitude as for the shoots (Figure 2d).

#### 3.3 | SLA and specific root length

Regarding the specific leaf area (SLA), the four treatments did not differ significantly. The drought treatments were slightly, but not significantly, lower (p = .087; F = 3.484, df = 1) than the continuously flooded ones (Figure 3a).

Contrary to this, a significant (p = .01; F = 15.452; df = 1) decrease of the specific root length (SRL) was detected under drought, but no significant difference between wild type and *lsi1* mutant within this treatment (Figure 3b).

#### 3.4 | Leaf water content

The water content of the aboveground biomass was significantly (p < .001; F = 22.725; df = 1) lower under drought (WT drought 76.56% and *lsi1* drought 77.33%) than under flooded conditions (WT paddy 80.69% and *lsi1* paddy 81.83%) (Figure 4). For both water levels, the *lsi1* type was not significantly higher than the wild type (p = .308; F = 1.106; df = 1).

## 3.5 | Photosynthesis, stomatal conductance and related soil moisture

The continuously flooded treatments showed relatively stable rates of ~12 to ~15 µmol CO<sub>2</sub> m<sup>-2</sup>/s for photosynthesis and 0.3–0.5 mol H<sub>2</sub>O m<sup>-2</sup>/s for stomatal conductance over the measurement period. We found significantly higher values of photosynthesis (p = .007; F = 7.293; df = 1) and stomatal conductance (p < .001; F = 15.730;



FIGURE 2 Aboveground and belowground biomass expressed as dry weight (a) and ash free dry weight (b) of shoots and dry weight (c) and ash free dry weight (d) of roots for control (lsi1) and wild type (WT) under paddy and drought conditions, each replication of five. The letters a and b indicate significant differences (p < .001) between the treatments [Colour figure can be viewed at wileyonlinelibrary.com]

df = 1) for the WT treatment (wild type) compared to the mutant (*lsi1*) (Figure 5). After inducing drought, photosynthesis (p < .001; F = 140.842; df = 1) and stomatal conductance (p < .001; F = 330.311; df = 1) rates of the drought treatments decreased especially after day four. On day eight the largest difference between WT and Isi1 was detected, with higher rates for WT. This effect disappeared on the next measurement day 10.

The soil moisture of the continuously flooded treatments showed relatively stable values of  $\sim$ 60 to  $\sim$ 65 vol% water (Figure 6). We found no significant differences in soil moisture between the WT treatment (wild type) compared to the mutant (Isi1) for the continuously flooded treatments (p = .382; F = 0.916; df = 1). After inducing drought, the soil moisture of the drought treatments decreased significantly to less than 30% (p = .001; F = 39.594; df = 1). During drought we found no significant differences in soil moisture between the WT treatment (wild type) and to the mutant (lsi1) (p = .132; *F* = 3.278; *df* = 1) (Figure 6).

#### 3.6 Carbon allocation to various pools and fluxes within the plant-soil-system

Most of the C assimilated by plants remained aboveground. This accounted for about 90% and there were no significant differences between the four treatments (Table S2). The allocation of recently assimilated <sup>13</sup>C to belowground pools, consisting of roots, soil and CO<sub>2</sub>, varied between 7 and 10%. The percentages of <sup>13</sup>C in the soil were similar among the water levels and genotypes (2.2-3.0%), but roots and CO<sub>2</sub> showed contrary pattern. Under drought, the percentage of <sup>13</sup>C in CO<sub>2</sub> was twice as high as for the flooded treatments. In contrast, under continuously flooded conditions 3 (Isi1) to 8 (WT) times more C was allocated to the roots compared to the drought-stressed plants (Table S2).

The overall highest amount of <sup>13</sup>C was detected for the WT paddy group with 7.34 mg, in descending order followed by Isi1 paddy (6.77 mg), Isi1 drought (4.72 mg) and WT drought (3.58 mg). The



**FIGURE 3** Specific leaf area (a) and specific root length (b) for control (*lsi1*) and wild type (WT) under paddy and drought conditions, n = 5. The letters a and b indicate significant differences (p < .001) between the treatments [Colour figure can be viewed at wileyonlinelibrary.com]



**FIGURE 4** Water content of the aboveground biomass for control (*lsi1*) and wild type (WT) under paddy and drought conditions, n = 5. The letters a and b indicate significant differences (p < .001) between the treatments [Colour figure can be viewed at wileyonlinelibrary.com]

amount of <sup>13</sup>C in the aboveground biomass was about 10 times higher than in the belowground pools for all treatments (Figure 7a). The <sup>13</sup>C content in the shoots decreased significantly (p = .001; F = 18.789, df = 1) under drought (WT drought 3.31 and *lsi1* drought 4.33 mg) versus flooded conditions (WT paddy 6.62 and *lsi1* paddy 6.21 mg), but within the drought treatment no significant difference occurred between wild type and mutant. A similar distribution was observed for the roots with <sup>13</sup>C amounts in decreasing order: WT paddy (0.45 mg) > *lsi1* paddy (0.25 mg) > *lsi1* drought (0.06 mg) > WT drought (0.03 mg). The <sup>13</sup>C allocation to roots in drought treatments was significantly (p < .001; F = 37.827, df = 1) lower than in continuously flooded treatments. Under flooded conditions, the wild type showed a higher <sup>13</sup>C content than the *lsi1* type, but not significant. In



**FIGURE 5** Photosynthetic rate (a) and conductance to H<sub>2</sub>O (b) over the drought period. Data points are means of the last three logging points of the measured pots, when the curves had stabilized. Errors bars represent standard errors (the number of measured pots per treatment [*n*] varied between 3 and 6) for control (*lsi1*) and wild type (WT) under paddy and drought conditions, each treatment with a replication of five [Colour figure can be viewed at wileyonlinelibrary.com]



**FIGURE 6** Volumetric soil moisture over the drought period (%). Data were obtained by a TDR sensor. Errors bars represent standard errors (n = 3-5). The letters a and b indicate significant differences (p < 0.001) between the treatments [Colour figure can be viewed at wileyonlinelibrary.com]



**FIGURE 7** <sup>13</sup>C content of the aboveground biomass (a) and the belowground compartments roots, soil and  $CO_2$  (b) for control (*lsi1*) and wild type (WT) under paddy and drought conditions. Bars are means and error bars are standard errors, n = 5 [Colour figure can be viewed at wileyonlinelibrary.com]

comparison to that, the amounts in  $CO_2$  and soil were in the same range for all treatments (Figure 7b).

#### 4 | DISCUSSION

In contrast to existing literature our data showed that Si accumulation in rice plants has only minor effects on plant performance under drought stress. Only photosynthesis and stomatal conductance were slightly higher for the wild type in both drought and flooded treatments. All other plant parameters, such as nutrient contents, biomass, SLA, specific root length, leaf water content and C allocation did not differ between the genotypes neither under flooded conditions, nor under drought conditions. Therefore, we suggest an improved water availability in soil after Si fertilization to be responsible for the improved plant performance under drought in older studies.

Both the *lsi1* mutant and its wild type rice showed significant drought effects on aboveground biomass, SRL, LWC, photosynthetic rate, stomatal conductance, total C allocation and C allocation into shoots and roots. The drought treatment also caused a shift in C allocation ratio from predominating allocation to roots in relation to CO<sub>2</sub> under flooded conditions to a clearly higher allocation in CO<sub>2</sub> compared to roots under drought.

The Si effect between the two different rice genotypes could be proven for photosynthesis and stomatal conductance with significantly higher values of the wild type with regular Si uptake under

both, flooded and drought conditions. All other parameters (root biomass, LWC and C allocation into shoots, roots, soil and CO<sub>2</sub>) did not differ significantly between the *lsi1* and the wild type.

The current experiment showed only a small effect of the plant Si accumulation on plant performance parameters of rice plants under drought as soon as the soil Si content is excluded as an influencing variable. A comparison of other studies with the present study is difficult since no other research with similar experimental setup is known.

Several studies showed increased plant performance during drought after Si application to soils. Increased values of dry weights, leaf area and relative water content with Si fertilization under drought were found in the experiment of H. j. Gong et al. (2003). Hattori et al. (2005) and Chen et al. (2011) also showed that plants performed better with than without Si in the soil under water stress. Another study found increased growth, gas exchange and tissue water of wheat plants grown on Si enriched soil compared to plants grown on soil without additional Si (Alzahrani et al., 2018). Enhanced rates of photosynthesis, stomatal conductance, relative water content and water potential of leaves under drought stress with Si addition were observed by H. Gong and Chen (2012) in the field. Recently, however, it was found that Si addition to soil has a strong effect on the water holding capacity and the plant available water in soils (Schaller et al., 2020). Therefore, it is not clear whether the improved plant performance under drought shown in several studies was caused by Si in planta or is just referable to a higher soil water availability, which may be assumed due to Si addition. It is also known that the higher plant performance during drought after Si fertilization may be explained by factors like higher nitrogen use efficiency and altered primary metabolism due to Si accumulation (Detmann et al., 2012). However, the data from the current experiment did not show differences in nitrogen accumulation pattern.

The influence of Si on drought resistance of plants was not only investigated in pot experiments, but also in hydroponics. Here, water is never a limiting factor, which is why other substances must be added to simulate drought stress. Therefore, polyethylene glycol (PEG) 6,000 can be used to modify the osmotic potential of a nutrient solution in a way that is comparable to water deficiency (Kaufmann & Eckard, 1971). Using this method, Meunier et al. (2017) observed an increase of fresh weights and relative water content by Si addition under drought simulation with PEG, but also a considerable decrease of plant Si concentration. Ming, Pei, Naeem, Gong, and Zhou (2012) also detected an inhibition of Si uptake in their PEG-treatment compared to the control. They assumed this effect due to the high viscosity of PEG solution, which is effective to inhibit water uptake by roots (Chazen, Hartung, & Neumann, 1995; Slama et al., 2007). Since the interaction of PEG with Si in hydroponic nutrient solutions has not yet been investigated, possible reasons for this effect can only be assumed. It cannot be excluded that Si may alter the effect of PEG on water availability for plants and may mitigate the inhibition of water uptake by roots, which again would generate a better plant performance. That could happen as a result of a reaction or interaction of Si and PEG in the solution. However, this could also imply a change in Si availability for plants from the nutrient solution in presence of PEG. It

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is also conceivable, that PEG is not only inhibiting the uptake of water molecules, but rather that of Si.

To overcome the discussed issue, continuous measurements of plant available water would be required in order to keep soils with and without Si at the same level. A simpler way is to use the same Si enriched soil in combination with a plant and its variety with defective Si uptake mechanism, like in the present study. In the present study, photosynthesis and stomatal conductance showed a significant genotype effect and thus an effect of Si on gas exchange of plants under drought and flooded conditions. This is in line with similar findings according to these parameters of other studies (Alzahrani et al., 2018; Chen et al., 2011; Hattori et al., 2005). In contrast to the other studies, no other parameters of plant performance were enhanced by Si fertilization under drought. If Si in the plant was the reason for positive effects on plant growth, water and nutrient status, we should have seen these effects, too. However, our rice plants were relatively young when exposed to drought stress. The Si concentration of rice plants was found to increase over time (Ma. Goto, Tamai, & Ichii, 2001; Ma, Miyake, & Takahashi, 2001). Hence, the Si content of the wild type plants might not have been high enough at the examined growing stage. This could be a reason for the minor differences compared to the mutant. Like discussed earlier. Si addition also plays an important role in increasing plant available water, which in turn facilitates a better plant performance. In our experiment, only gas exchange was influenced by Si in the plant. In view of the fact, that Si maintains chlorophyll content in plants under water stress (Kaya, Tuna, & Higgs, 2006; Pei et al., 2010), it seems to prevent the destruction of chlorophyll and causes higher photosynthetic rates (Agarie et al., 1992) and act as stress reliever for plants (Markovich et al., 2017). Hence, a part of the improved plant performance in other research at later stages of rice growth (e.g., heading or grain filling) might be explained by consistently higher gas exchange and photosynthetic rates, but not exclusively. The present results suggest that Si in the soil, that potentially increases plant available water, may have a stronger influence on plant performance than Si in planta that preserves assimilation processes.

This was also evident for the <sup>13</sup>C allocation data. The enhanced assimilation due to Si fertilization under drought did not cause the expected increase of C investment into roots. Drought was the only factor with a significant impact on both genotypes by reducing total <sup>13</sup>C incorporation and in particular the <sup>13</sup>C contents of shoots and roots. These findings fit the data of reduced photosynthesis and shoot DW under drought stress (Figures 2 and 5), since less aboveground biomass is associated with a lower photosynthetically active surface leading to decreased assimilation rates and this in turn to a lower C incorporation. Interestingly, a shift in allocation ratio from flooded to drought conditions was detected between roots and CO<sub>2</sub>. While the values of CO<sub>2</sub> did not change among the watering treatments, the absolute <sup>13</sup>C amounts in roots were distinctly higher relative to those of CO<sub>2</sub> in the submerged soils and dropped considerably below values of CO<sub>2</sub> under water stress. This effect can also be seen in the SRL data (Figure 3), which decreased significantly under drought. The decrease originates not only from a lower total <sup>13</sup>C assimilation but

also from a decline of root length because root dry weights were similar in both watering treatments (Figure 2). Moreover, mineralization is not only limited by aeration, but also by soil moisture (Barros, Gomez-Orellana, Feijóo, & Balsa, 1995; Liu et al., 2019; Tate & Terry, 1980). This could explain why total <sup>13</sup>C in soil respiration did not increase under drought compared to flooded conditions in the present study.

Comparable to our observations, Tian et al. (2013) found lower <sup>14</sup>C recovery in roots as well as higher <sup>14</sup>C recovery of cumulated respiration (roots and microbial) under non-flooded versus flooded conditions in their labelling experiment with rice (cf. Table S2). These patterns are explained by lower rhizodeposition (as one energy source for microorganisms) and production of toxic substances (such as lactate and ethanol), that inhibit activity of roots and microbial activities under anaerobic conditions (Tian et al., 2013). Therefore, respiration and thus CO<sub>2</sub> efflux decrease, and more C is kept in the roots. In contrast, non-flooded soils provide aerobic conditions that enhance rhizodeposition and root respiration, which means that more C is released from the roots to the soil. Increase of soil C in an aerobic environment stimulates microbes to quickly mineralise these organic compounds, which again contributes to a higher  $CO_2$  efflux.

Overall, the observed <sup>13</sup>C allocation pattern fits the 112 datasets reviewed by Liu et al. (2019), that reported major incorporation into shoot by about 79%, followed by belowground pools (roots 13.4%, soil 5.5%, microbial biomass 2.1%). Furthermore, the fact that we found no differences in the plants phosphorus status between the wild type and the *lsi1* deficiency mutant may also be explained by the fact the soil did not differ in Si availability and Si availability is the main driver for phosphorus availability (Schaller et al., 2019) and plant uptake.

Former research assumed better plant performance under Si fertilization mainly due to molecular processes in planta but neglected the effect of Si on soil water by using different Si levels in culture mediums (Alzahrani et al., 2018; Chen et al., 2011; Gong et al., 2003; Hattori et al., 2005; Ibrahim et al., 2018; Meunier et al., 2017). In our study we have grown two types of genetically identic rice plants, of which one was not able to take up Si because of a mutation, in the same soil. The results showed the effect of Si on drought relevant plant parameters like photosynthesis and stomatal conductance, but C allocation to different pools was not affected by Si accumulation under drought either. We cannot rule out that our study may be also affected by the short duration of drought and the use of relatively young plants.

In the light of proceeding climate change with more frequent and more intense drought events in the future (IPCC, 2019), Si might be potential way to meet this challenge besides other measures (Basu et al., 2016; Dharmappa et al., 2019; Dubey et al., 2020; Gupta et al., 2020; Pray et al., 2011). Si fertilization of soils can contribute to a better drought resistance of plants by (i) maintaining photosynthetic assimilation and (ii) and other suggests that Si improves soil water status, especially water holding capacity and plant available water. More research is needed to investigate the precise effects of Si on plant physiology, especially in terms of long-term response and depending on severity and intensity of the drought. For this different plants

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growth stages (with potentially larger difference in plant Si accumulation) or plants commonly cultivated on drier soils (not like rice being cultivated mostly under paddy conditions) should be considered.

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#### CONFLICT OF INTEREST

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be a potential conflict of interest.

#### AUTHOR CONTRIBUTION

Jörg Schaller and Johanna Pausch: Designed the study. Jana Kuhla: Conducted the experiments and did the measurements. Jana Kuhla, Jörg Schaller and Johanna Pausch: Wrote the manuscript.

#### DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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#### SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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