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Silicon (Si) Application Improved the Antioxidant Response and Grain Yield Formation in rice Under High Temperature Conditions

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Abstract

Purpose The present study was conducted to investigate the silicon (Si) induced modulations in the antioxidant response and yield formation of rice under high temperature conditions.

Methods Four rice genotypes i.e., wild-type flower 11 (WT), nitrate reductase gene interference material (NR-RNAi), nitric oxide synthase interference material (NO-RNAi), and nitric oxide synthase overexpression material (NO-OR) were applied with two Si fertilizer treatments i.e., Si0: 0 g/pot and Si12: 12 g/pot. All genotypes were grown in early season (April to July) with mean maximum temperature ranged from 29.32℃ to 36.13 ℃ (higher than critical temperature range).

Results Compared with Si0, the Si12 increased the grain number per panicle, effective panicle number, and seed setting rate as well as rice yield of all rice genotypes under high temperature conditions. The yields of NR- RNAi and NO-OR was increased by 95.11% and 103.40%, respectively in Si12 than Si0. Moreover, Si application also improved the dry biomass of all rice genotypes whereas the stem and leaf weight of WT and leaf weight of NO-OR was increased by 36.70%, 166.67% and 36.63%, respectively, in Si12 as compared with Si0. In addition, the Si12 increased the catalase (CAT) activity and decreased the malondialdehyde (MDA) contents, which markedly reflected in NO-RNAi CAT activity (67.10%) at heading stage and NO-RNAi MDA content (53.61%) at maturity stage.

Conclusions Overall, Si application tend to increase the rice yield, improved dry matter accumulation and enhanced the stress tolerance of rice under high temperature conditions.

Keywords High temperature · Silicon · Rice · Yield · Antioxidant physiology

1 Introduction

Rice (*Oryza sativa* L.) is one of the major food crops and is a primary source of food for 50% of the world's population [1, 2]. According to the Intergovernmental Panel on Climate Change (IPCC, 2014), the global mean temperature will rise up to 4–5 °C till the end of this century. Global warming leads to the significant impact of high temperature on cereals yields, which are one of the important issues in agricultural production [3, 4]. Peng et al. [5] reported that rice grain

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yield declined under high night temperatures. Therefore, it is imperative to investigate the response of rice to high temperature stress and to develop possible mitigation strategies to overcome its adverse effects.

Generally, high temperature stress affects the enzymes involved in the metabolism of nucleic acids, proteins and sugar, and regulates lipid peroxidation in rice [6, 7]. Besides, the high temperature stress led to the over-production of reactive oxygen species (ROS) and alterations in enzymes activity of antioxidant system [8–10]. It also causes substantial reductions in photosynthetic rate owing to inhibition in photosynthetic efficiency and photochemical activity [11]. Therefore, the growth and dry matter accumulation would be influenced, leading to a significant reduction in the grain yield and related attributes [12]. The high temperature stress tolerance in rice can be improved by regulating the physio-biochemical mechanisms, antioxidant defense system, and morphological attributes in rice [13].

Heat tolerance is one of the key requirements for improving global food security and addressing crop production challenges under high temperature conditions in cereals [14]. As a beneficial element, silicon (Si) involves in promoting plant growth and yield by improving plant stress tolerance [15]. Interestingly, Si has a positive effect on the growth and development of rice, and can alleviate the biological and abiotic stress in rice. Si also reduces leaf temperature under high temperature stress, stable thylakoid membrane of chloroplast, and improves the heat resistance in rice The application of Si can regulate the antioxidant system and transcription of key genes related to thermal stress response, thus assisting plants to encounter heat-induced oxidative stress [16–18]. Si application improved the grain yield in rice owing to enhanced effective panicle number and grain number per panicle under high night temperatures [19]. Exogenous Si application can improve the high temperature stress tolerance in rice [20, 21]. Si application not only enhance the antioxidant defense system, but also increased the content of proline and soluble sugar in rice and improved the temperature stress tolerance in rice [22, 23]. In addition, applying Si fertilizer is also considered as an ecologically compatible strategy to improve the crop stress tolerance under changing climate scenario [24, 25].

In general, the Si not only can improve plant antioxidant defense ability [26, 27], but also may contribute to the biosynthesis of endogenous nitric oxide (especially under stress conditions), thus regulates the plant defense system [28–30]. On the other hand, Si-induced accumulation of nitric oxide (NO) can further enhance the stress tolerance in plants [31, 32]. Moreover, increasing endogenous NO in crops genetically, is a major biotechnological application to improve crop productivity under stress conditions [33]. In plants, the NO can be produced through the nitrate reductase (NR) pathway, nitric oxide synthase pathway, or non-enzymatic pathway [34–36]. For instance, the NR is able to induce NO synthesis, and enhance the degree of strawberry tolerance to iron deficiency by upregulating the ascorbate–glutathione cycle [37] whereas Si can also improve the viability of nitrate reductase in plants [38]. In addition, the mechanism of how proteins with nitric oxide synthase (NOS) activity in plants synthesizing NO has been widely concerned [39–41]. Interestingly, Si might promote the expression of NOS-like activity to nitric oxide metabolism in rice under arsenic stress [42]. Based on the indispensable role of NR and NO in plant physiology, it would be of great interest to explore the Si-induced modulations in morpho-physiological and yield traits of rice under high temperature conditions. However, little is known about Si-induced heat stress responses (HSRs) and tolerance mechanisms in certain rice genotypes. Therefore, the present study was conducted to explore the Si induced regulations in morpho-physiological and yield attributes as well as anti-oxidant defense response of different rice genotypes under high temperature stress conditions. The finding of the present study would provide the theoretical basis for the high temperature stress tolerance in new rice genotype with Si application to improve the rice productivity.

2 Materials and Methods

2.1 Experimental Details

Four different rice genotypes i.e., wild-type flower 11 (WT), nitrate reductase gene interference material (NR-RNAi), nitric oxide synthase interference material (NO-RNAi), and nitric oxide synthase overexpression material (NO-OR), were obtained from the College of Agriculture, South China Agricultural University, Guangzhou, China. The test fertilizer was "rice silicon power", containing 72% mineral silicon, and was provided by JiangsuYancheng Xinhe Plant Nutrition Technology Co., Ltd.

The pot experiment was conducted in the greenhouse of South China Agricultural University, Guangzhou, China from April to July 2018 (early season). The temperature of the experimental period has shown in Table 1. The experimental soil (0–20 cm) was collected from rice fields, dried and sieved

Table 1 The temperature of the experimental period

Month	Maximum temperature	Minimum temperature	Daily mean temperature
April	29.32℃	22.51℃	25.06℃
May	33.38℃	23.83℃	27.64℃
June	35.90℃	26.21℃	29.93℃
July	36.13℃	26.02℃	30.02℃

(2 mm mesh size). The soil samples were analyzed to determine the physical and chemical properties and available silica. Samples were extracted with the citric acid solution, and the soil immersion solution was determined for "available silica" by 600 nm colorimetric molybdenum blue. The experimental soil was sandy loam containing 23.34 g/kg organic matter, 6.14 pH, total nitrogen 1.139 g/kg, total phosphorus 1.136 g/kg, total potassium 24.41 g/kg, alkali-hydrolyzable nitrogen 114.27 mg/kg, available potassium 61.34 mg/kg, available phosphate 127.03 mg/kg and available silica (water-soluble) 51.30 g/kg.

2.2 Silicon Treatments

Two different basal applications of silicon fertilizer were applied i.e., Si0 (0 g/pot) and Si12 (12 g/pot). Each treatment was repeated in triplicate, and a total of 24 pots were filled with 12.5 kg air-dried rice soil after 10 days, the seedlings of 4 rice varieties were manually transplanted into plastic pots filled with the soil (5 hills per pot and 3 seedlings per hill). Compound fertilizer (N:P:K = 15%:15%:15%) was applied as basal dose to all the pots and flooding conditions (3-4 cm soil layer) were maintained during whole crop growth period.

2.3 Sampling and Measurement

2.3.1 Determination of Yield and Yield Components

At maturity stage, 36 representative rice samples were selected for each treatment, threshed manually, sun-dried and filled grains were separated by a separator adjusted with fan for air blowing. Grain numbers per spike, total number of grains and effective panicles per hill of each treatment were recorded to calculate rice yield and seed setting rate. Filled grains were counted and weighed to record 1000- grain weight. The harvest index was calculated with the following formula:

$$\text{Harvest Index} = \text{Grain Yield}/\text{Total dry weight} \times 100\%$$

2.3.2 Determination of Dry Weight

At maturity stage, nine representative rice samples were selected for each treatment to measure plant height. For dry weight, the rice samples washed with water and separated into stem, leaf, and spike, and oven-dried at 105℃ for 30 min and at 80℃ to constant weight.

2.3.3 Physio-biochemical Assays

At the rice heading and maturity stage, 12 representative sword leaves were taken and frozen in liquid nitrogen for 3 min and kept at −80 °C till biochemical analyses. The crude enzyme solution was extracted as follows:

Fresh leaves (0.3 g) were ground with liquid nitrogen, added 5 ml pH7.8 phosphate buffer solution to make homogenate, and centrifuged at 8000 rpm at 4℃ for 15 min.

2.3.4 Determination of Antioxidants

The superoxide dismutase (SOD) activity was determined by nitro-blue tetrazolium (NBT) method [43]. Crude enzyme extract (50 µl) was added to 1.50 ml of sodium phosphate (50 mM), 0.3 ml Met (130 mM), 0.3 ml EDTA-Na (100 µM), 0.3 ml of riboflavin (20 µM) and 0.25 ml of distilled water and the absorbance was read at 560 nm. One unit (U) was defined as the amount of enzyme required to inhibit the 50% NBT photoreduction reaction, with activity units expressed as U/(g·FW).

The peroxidase (POD) activity was estimated by measuring the oxidation of guaiacol [44]. The assay solution contained 50 µl of crude enzyme extract, 1 ml of 0.3% H_2O_2, 0.95 ml of 0.2% guaiacol, and 1 ml sodium phosphate buffer (50 mM), and the absorbance was read at 470 nm. One unit (U) was set to increase the light absorption value by 0.01 per minute, with activity units expressed as U/(g·FW).

The catalase (CAT) activity was measures according to Zhang et al. [45]. The reaction mixture was comprised of 1.95 ml distilled water, 1.0 ml of 0.3% hydrogen peroxide solution, and 0.05 ml of enzyme extract and the absorbance was read at 240 nm once at 30 s intervals for 2 min. One unit (U) was defined as an absorbance reduction of 0.01 per min with activity units expressed as U/(g·FW).

The malondialdehyde (MDA) content was estimated according to Hao et al. [46]. Crude enzyme extract (1.5 ml) was added with 2 ml of 0.5% thiobarbituric acid (TBA), centrifuged at 3000 rpm for 15 min and absorbance of the supernatant was measured at 450 nm, 532 nm and 600 nm and expressed as µmol/(g·FW).

2.4 Statistical Analyses

The experimental data were analyzed by Statistix version 8 (Analytical Software, Tallahassee, Florida, USA) and Microsoft Excel 2010 (Microsoft Corporation, New Mexico, USA). Comparisons of means among different treatments were assessed by the least significant difference (LSD) test at 0.05 significance level ($P < 0.05$).

3 Results

3.1 Yield Components

For both WT and gene interference materials, the Si0 treatment was found statistically similar ($P > 0.05$) to Si12 treatment regarding grain numbers per spike, 1000-grain weight,

and effective panicles per hill. However, compared with Si0 treatment, the Si12 treatment significantly improved the seed setting rate of NR-RNAi and NO-OR by 61.20%, 55.11%, respectively, whereas the WT remained substantially different from NO-RNAi and NO-OR under Si0 treatment, respectively. In addition, significant differences were observed between both WT and other rice genotypes under Si12 treatment. Meanwhile, the genotype difference and Si application significantly affected the seed setting rate and effective panicles per hill, respectively (Table 2).

3.2 Yield, Biomass and Plant Height

Compared with Si0, the Si12 treatment significantly increased the yield of NR-RNAi and NO-OR by 95.11%, 103.55%, respectively, as well as improved the yield of WT and NO-RNAi. Moreover, the Si12 treatment significantly increased the total weight of WT, and plant height of NO-RNAi, as compared with Si0. Moreover, the plant height of WT significantly remained lower than NO-RNAi under Si12 treatment. For grain yield, no significant difference was found among the three genotypes (gene interference materials) and WT under Si0 treatment, but the yield increasement of NR-RNAi was substantially higher than WT under Si12 treatment. Regarding harvest index and the total dry weight, no significant difference between WT and gene interference materials were noticed. Meanwhile, the Si application improved yield, harvest index, total dry weight and plant height of all rice genotypes (Table 3).

3.3 Dry Matter Accumulation and Proportions

Compared with Si0, the Si12 treatment significantly increased the leaf dry weight of WT and NO-OR by 166.67%, 36.63%, respectively. The leaf dry weight of WT was obviously lower than NR-RNAi within Si0 treatment and higher than NO-RNAi for Si12 treatment. The Si12 treatment also significantly increased the stem sheath dry weight of WT by 36.70%. In addition, slight increments were detected in panicle dry weight for all four genotypes of rice. Moreover, the genotype differences have significant effects on the panicle dry weight of rice, the Si treatment on stem sheath dry weight and leaf dry weight as well. Moreover, genotype and Si interaction (G × T) also affected the leaf dry weight substantially (Table 4).

Compared with Si0 treatment, the Si12 treatment significantly increased the leaf proportion of WT by 93.67%. Under Si0 treatment, the leaf proportion of WT was substantially lower than NR-RNAi, while the panicle of WT was higher than NO-RNAi. On the other hand, four rice genotypes were remained statistically similar (P˃0.05) regarding the leaf proportion, the stem proportion, and the panicle proportion under Si12 treatment. However, the genotype differences have a significant impact on the proportion of panicle, the Si treatment on the leaf proportion as well, while the leaf proportion and the panicle proportion were notably affected by genotype interaction with silicon (G × T) (Table 4).

3.4 Antioxidant Enzyme Activities

The SOD activity was overall reduced in four different genotypes after Si12 treatment at high temperatures. The decrease of SOD activity in the rice heading stage was 12.67%-37.72%, but the SOD activity was marginally increased in Si12 treatment for WT and NR-RNAi at maturity stage. Compared with Si0, no significant difference was observed between WT and other genotypes in Si12. Moreover, the

Table 2 Effects of Si application on yield components of rice genotypes under high temperature conditions

Genotype	Treatment	Grain numbers per spike	1000- grain weight	Seed setting rate	Effective panicles per hill
WT	Si0	127.89 a	23.81 a	18.92 e	5.17 a
	Si12	136.14 a	24.14 a	32.90 de	5.50 a
NR-RNAi	Si0	113.07 a	24.35 a	41.03 cde	5.33 a
	Si12	135.24 a	24.07 a	66.14 ab	5.67 a
NO-RNAi	Si0	104.02 a	23.87 a	60.82 abc	4.17 a
	Si12	120.13 a	24.27 a	61.14 abc	5.50 a
NO-OR	Si0	112.78 a	24.26 a	44.00 bcd	4.17 a
	Si12	121.93 a	23.83 a	68.25 a	5.50 a
F-value	G	ns	ns	**	*
	T	ns	ns	*	**
	G × T	ns	ns	ns	ns

Different lowercase letters in the same column mean significant difference ($P < 0.05$);* indicates significant difference($P < 0.05$);** indicates extremely significant difference ($P < 0.01$); ns indicates no significant difference ($P > 0.05$) level

Table 3 Effects of Si application on yield, harvest index, total dry weight and plant height of rice genotypes under high temperature conditions

Genotype	Treatment	Grain yield	Harvest index	Total dry weight	Plant height
WT	Si0	14.81 d	16.82 b	88.08 c	75.73 b
	Si12	31.62 bcd	26.39 ab	119.81 ab	78.28 b
NR-RNAi	Si0	30.90 bcd	26.66 ab	115.91 abc	75.60 b
	Si12	60.29 a	43.91 a	137.28 a	77.50 b
NO-RNAi	Si0	32.17 bcd	31.84 ab	101.05 c	76.73 b
	Si12	47.03 abc	45.97 a	102.31 bc	84.53 a
NO-OR	Si0	25.92 cd	25.93 ab	99.95 bc	76.97 b
	Si12	52.76 ab	47.57 a	110.90 abc	77.98 b
F-value	G	ns	ns	ns	ns
	T	**	*	**	**
	G×T	ns	ns	ns	ns

Different lowercase letters in the same column mean significant difference ($P<0.05$);* indicates significant difference($P<0.05$);** indicates extremely significant difference ($P<0.01$); ns indicates no significant difference ($P>0.05$) level

SOD activity in different genotypes was markedly different at heading stage (Fig. 1).

Compared with Si0 treatment, the POD activity of NO-OR during the heading stage decreased by 27.28% under Si12 treatment. However, the POD activity of NR-RNAi and NO-RNAi increased, where the POD activity of NO-RNAi during the maturity stage was increased by 29.66% under Si12 treatment. Moreover, no significant difference between WT and NR-RNAi under different silicon fertilizer treatments was noticed, while the POD activity of WT under Si12 treatment was significantly higher than NO-OR at heading stage. At the maturity stage, the POD activity of WT was significantly higher than NO-RNAi under Si0 treatment but opposite under Si12 treatment. Furthermore, genotype interaction with silicon (G×T) showed a significant effect on POD activity in the rice maturity stage (Fig. 2).

Furthermore, Si12 treatment overall improved the CAT activity in all rice genotypes as compared with Si0 treatment. At heading stage, the Si12 treatment significantly increased the CAT activity of WT and NO-RNAi by 23.19%, 67.10%, respectively. Furthermore, the Si12 treatment significantly increased the CAT activity of NO-OR during the maturity stage by 62.64%. The CAT activities of WT were significantly higher than NR-RNAi and NO-OR under Si12 treatment at heading stage. However, the CAT activities of WT were significantly lower than other rice genotypes under different Si fertilizer treatments at maturity stage. Additionally, the genotype differences were apparent regarding CAT activity during the rice maturity stage, while the Si treatment, as well as genotype interaction with silicon (G×T), all had a significant effect on the CAT activity at heading and maturity stage (Fig. 3).

Table 4 Effects of Si application on dry matter accumulation of rice genotypes under high temperature conditions

Genotype	Treatment	Stem sheath dry weight	Leaf dry weight	Panicle dry weight	Proportion of stem	Proportion of leaf	Proportion of panicle
WT	Si0	9.89 c	1.08 d	6.65 abc	55.92 abc	6.32 b	37.76 a
	Si12	13.52 ab	2.88 a	7.57 ab	56.69 abc	12.24 a	31.07 ab
NR- RNAi	Si0	13.41 abc	2.34 abc	7.44 ab	57.52 abc	10.40 a	32.03 ab
	Si12	16.90 c	2.73 a	7.82 ab	62.08 ab	10.37 ab	27.55 b
NO-RNAi	Si0	10.85 bc	1.52 d	4.72 c	63.85 a	8.88 ab	27.26 b
	Si12	12.80 abc	1.73 bcd	5.93 bc	60.50 ab	8.75 ab	30.75 ab
NO-OR	Si0	11.16 bc	1.72 cd	7.11 abc	54.88 bc	9.01 ab	36.10 ab
	Si12	10.99 bc	2.35 ab	8.84 a	49.31 c	10.66 a	40.04 a
F-value	G	ns	ns	*	ns	ns	*
	T	*	**	ns	ns	*	ns
	G×T	ns	**	ns	ns	*	*

Different lowercase letters in the same column mean significant difference ($P<0.05$);* indicates significant difference($P<0.05$);** indicates extremely significant difference ($P<0.01$); ns indicates no significant difference ($P>0.05$) level

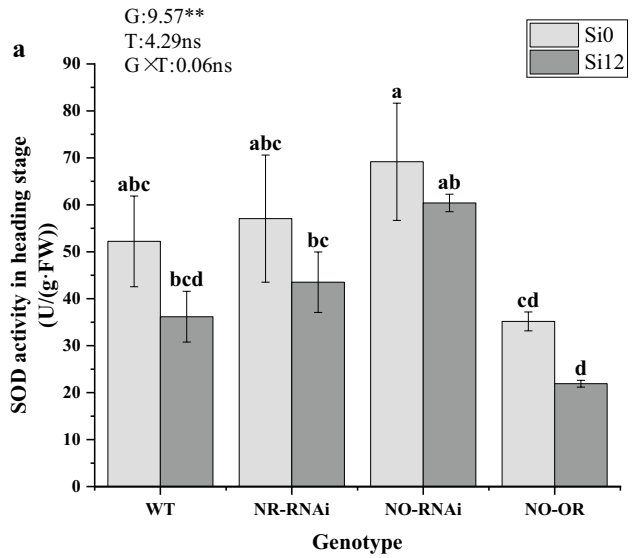

Fig. 1 Effects of Si application on SOD activity of different rice genotypes at (**a**) heading stage, and (**b**) at maturity stage under high temperature conditions. Si0 represents the silicon application as 0 g/pot, Si12 represents the silicon application as 12 g/pot. The capped bars represent the SDs. Columns with different lowercase letter(s) differ statistically at $P < 0.05$

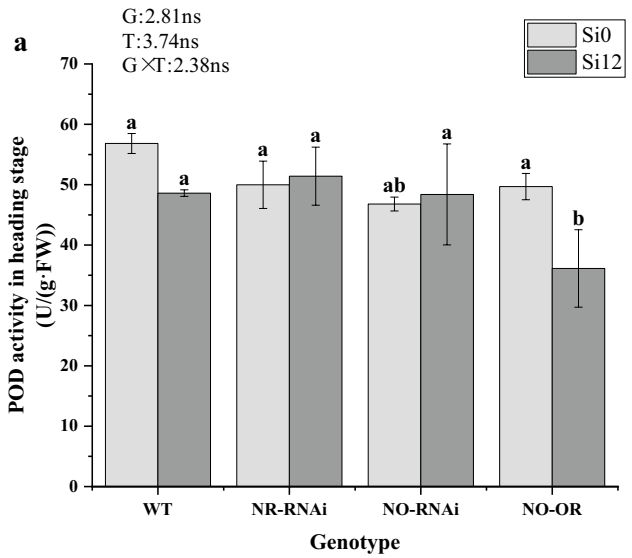

Fig. 2 Effects of Si application on POD activity of different rice genotypes at (**a**) heading stage, and (**b**) at maturity stage under high temperature conditions**.** Si0 represents the silicon application as 0 g/pot, Si12 represents the silicon application as 12 g/pot. The capped bars represent the SDs. Columns with different lowercase letter(s) differ statistically at $P < 0.05$

3.5 Malondialdehyde (MDA) Contents

Compared with Si0 treatment, the Si12 treatment significantly decreased the MDA content of WT (25.03%) at heading stage, as well as for NO-RNAi (53.61%) at maturity stage. At heading stage, it was noticed that the WT was significantly higher than NR-RNAi in both Si treatments as well as than NO-OR under Si0 treatment. At maturity stage, the MDA content of WT was significantly higher than NO-RNAi under Si12 treatment. Furthermore, the genotype differences and Si treatment substantially reduced the MDA content of the rice at heading stage, respectively, whereas the genotype interaction with silicon (G × T) was found significant regarding MDA contents for all rice cultivars at both heading and maturity stages (Fig. 4).

3.6 Correlation Analysis

Correlation analysis was performed by using yield and yield components, dry material accumulation and physiological

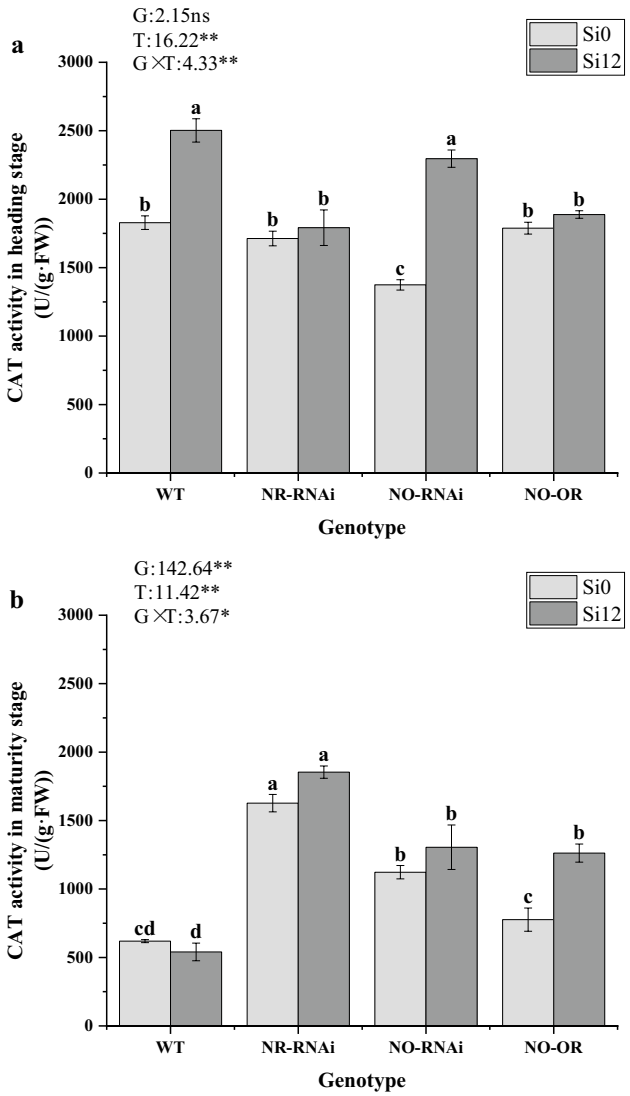

Fig. 3 Effects of Si application on CAT activity of different rice genotypes at (**a**) heading stage, and (**b**) at maturity stage under high temperature conditions. Si0 represents the silicon application as 0 g/pot, Si12 represents the silicon application as 12 g/pot. The capped bars represent the SDs. Columns with different lowercase letter(s) differ statistically at $P < 0.05$

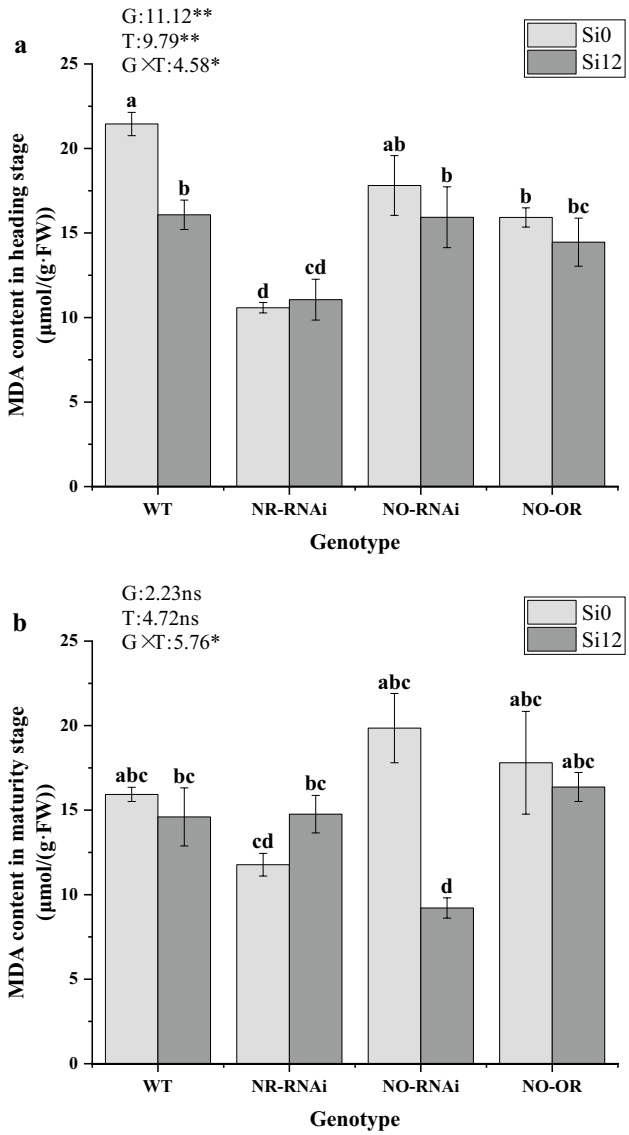

Fig. 4 Effects of Si application on MDA contents of different rice genotypes at (**a**) heading stage, and (**b**) at maturity stage under high temperature conditions. Si0 represents the silicon application as 0 g/pot, Si12 represents the silicon application as 12 g/pot. The capped bars represent the SDs. Columns with different lowercase letter(s) differ statistically at $P < 0.05$

indices, which indicated that harvest index, seed setting rate, and CAT activity in leaf at maturity stage showed a significant positive correlation with yield, respectively (Table 5).

4 Discussion

Climate change poses a threat to productivity of staple heat-sensitive crops [47], for likely every 1℃ increase in the global mean temperature, rice yield decreased by an average of 3.2% [48] and the local climatic conditions also affecting the rice productivity of South China [49]. Si element has been recognized by the international soil community as the fourth plant nutrient element after nitrogen, phosphorus and potassium [50]. Applying Si fertilizer can increase the number of effective ears per unit area, grain number per panicle and seed setting rate, thus increasing the yield [51]. The objective of the current study was to explore the response of different rice genotypes to Si application under high temperature. Previously, Liu et al. [52] reported that Si fertilizer had a positive effect on nitrogen, phosphorus and

Table 5 Correlation relationship between yield and yield components, dry matter accumulation, and physiological attributes of rice genotypes

Index	Correlation coefficient	P-value	Index	Correlation coefficient	P-value
Harvest index	0.9456	0.0004	Panicle dry weight	0.3703	0.3666
Total dry weight	0.7048	0.0509	SOD activity in leaf at heading stage	-0.2653	0.5254
Plant height	0.4481	0.2656	SOD activity in leaf at maturity stage	-0.3900	0.3396
Grain numbers per panicle	0.2713	0.5157	POD activity in leaf at heading stage	-0.5324	0.1743
1000- grain weight	0.0339	0.9365	POD activity in leaf at maturity stage	0.0622	0.8837
Seed setting rate	0.8667	0.0053	CAT activity in leaf at heading stage	0.1873	0.6569
Effective panicles per hill	0.5181	0.1884	CAT activity in leaf at maturity stage	0.7258	0.0425
Stem sheath dry weight	0.6413	0.0866	MDA content in leaf at heading stage	-0.6191	0.1017
Leaf dry weight	0.5857	0.1271	MDA content in leaf at maturity stage	-0.2696	0.5185

potassium translocation efficiencies by rice under high temperature. Moreover, adequate Si fertilization substantially increased rice yield and improved stress tolerance [53]. Our results showed that the yield, harvest index, dry total weight, and plant height all responded significantly to Si treatments, whilst Si12 treatment had significant effects on the grain yield of NR-RNAi and NO-OR, the total weight of WT, as well as the plant height of NO-RNAi (Table 3). Although no marked difference was found in the harvest index of four rice genotypes, it showed a significant positive correlation with yield (Table 5). These analyses are consistent with previous literature [54–56], which demonstrated that the Si application may have substantial effects on rice yield especially when reproductive phase suffers high-temperature stress conditions.

Regarding yield components, the seed setting rate and effective panicles substantially improved in all genotype under Si treatment whereas the seed setting rate of NR-RNAi and NO-OR were substantially higher than other genotypes (Table 2). Furthermore, the seed setting rate also showed a significant positive correlation with yield (Table 5). These findings corroborate with Dorairaj et al. [57] and Tamai et al. [58] who reported that Si application significantly improved the grain filling percentage and yield formation in rice. However, Si might have different implications for rice yield components. For example, Deren et al. [59] reported that the increase in yield was mainly due to Si induced improvement in grains per panicle. In this study, Si12 treatment slightly improved the grain per panicle. Moreover, application of Si fertilizer enhanced the 1000-grain weight and tiller number in rice [60, 61]. Overall, Si was found effective to improve the yield traits of rice possibly due to better coordinating the source and sink relationships.

The accumulation and distribution of aboveground dry biomass in rice are the determinants of rice yield, but high temperature stress negatively affects the dry matter allocation in leaf, leaf sheath, culm, and panicles [62]. Guo et al. [63] reported that Si application can improve the growth and development characteristics of rice, increase the accumulation of dry matter of rice, and improve the quality of rice population. Previous literature shown that Si improves the yield of rice by improving physiological mechanism, leaf and stem sheath morphology, while modulating the allocation of resources within rice plants [64, 65]. In this study, Si12 treatment overall increased the stem, leaf and panicle weight of different genotypes of rice, in which obvious enhancements were detected in the stem weight of WT, and the leaf weight of WT and NO-OR (Table 4). However, the proportion of stem, leaf, and panicle of rice varied differently, in which the leaf proportion of WT significantly increased after Si12 treatment (Table 4).

At reproductive stage, heat tolerance might be realized by protecting structural proteins, enzymes and membranes from thermal damage [66]. Plant cells typically respond to ROS by deploying antioxidant enzymes, including SOD, POD, and CAT [67–71], while exogenous Si can inhibit the production of ROS and lipid peroxidation, thus enhance the plant stress tolerance [72, 73]. Our results showed that different stress indicators responded differently to rice genotypes (Figs. 1, 2, 3, 4). For instance, the Si12 treatment overall reduced the SOD activity as compared with Si0 treatment, but the inter-treatment changes were not significant. The Si12 treatment also decreased the POD activities in WT and NO-OR and increased in NR-RNAi and NO-RNAi as compared with Si0 treatment. However, Si12 treatment generally improved the CAT activities of the four rice genotypes as compared with Si0 treatment. In addition, Si12 treatment overall decreased the MDA content of the four rice genotypes as compared with Si0 treatment. Moreover, genotypes difference had shown a significant effect on SOD activity and MDA content at heading stage, as well as CAT activity at maturity stage. Similar to our results, Rahman et al. [74] and Dufey et al. [75] reported that the response of plants to Si is genotype specific. In addition, application of Si fertilizer can improve the rice yield, quality and lodging resistance to some extent [76]. Liu et al. [77] reported that Se-Si co-application improved the yield and lodging resistance in rice. Hence, these analyses indicated that further investigation are needed to understand the physiological mechanism triggered by Si application to improve the rice yield under high temperature stress conditions.

5 Conclusion

In summary, the Si application improved the plant height, panicle weight, leaf weight, dry matter accumulation and yield components of the four genotypes of rice under high temperature conditions. Moreover, the antioxidant enzyme activities was improved whereas the MDA contents were reduced in all rice genotypes in Si treatment under high temperature stress conditions. Overall, Si application could improve the morpho-physiological, biochemical and yield attributes of rice under high temperature conditions, however, insights into the understanding Si-induced heat stress resistance mechanisms in rice genotypes would open novel perspectives regarding high temperature stress management through Si fertilization.

Author Contribution Zhaowen Mo designed and supervised the experiments, Long Zhang performed the traits investigation, Huizi Deng, Xinyi Wang, Umair Ashraf, and Siying Deng analyzed the data and wrote the manuscript. Hua Tian, Muhammad Imran, and Xiangru Tang revised and edited the manuscript. All of the authors approved the final version of the manuscript.

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Code Availability No code.

Declarations

Competing Interests The authors declare no competing interests.

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