Journal of Soil Science and Plant Nutrition (2023) 23:220–237
https://doi.org/10.1007/s42729-021-00712-9

ORIGINAL PAPER

Morpho-physiological Responses of Tropical Rice to Potassium and Silicon Fertilization Under Water-Deficit Stress

Debesh Das[1,2] · Hayat Ullah[1] · Rujira Tisarum[3] · Suriyan Cha-um[3] · Avishek Datta[1]

Received: 17 August 2021 / Accepted: 23 November 2021 / Published online: 29 November 2021

Abstract

A factorial experiment consisting of three factors, namely six fertilizer doses including different combinations of potassium (K) and silicon (Si) along with nitrogen (N) and phosphorus (P) and the control (NP_{100} [control], $NP_{100}+K_{100}$, $NP_{100}+Si_{100}$, $NP_{100}+K_{75}+Si_{25}$, $NP_{100}+K_{50}+Si_{50}$, $NP_{100}+K_{25}+Si_{75}$), three soil water potential levels (0, –15, –30 kPa), and two cultivation methods (wet direct seeding, transplanting), was conducted to evaluate the response of rice in terms of growth, physiological traits, yield, and water productivity. The experiment was laid out in a completely randomized design with three replications and the data were collected on selective growth parameters, physiological traits, yield components, and grain yield of rice. Supplementing N and P with only K ($NP_{100}+K_{100}$) helped in alleviating the harmful effect of water-deficit stress, and resulted in 11%, 8%, 47%, 40%, 40%, and 42% higher leaf greenness, leaf relative water content, net photosynthetic rate, free proline content (wet direct-seeded plants), grain yield (wet direct-seeded plants), and water productivity, respectively, than NP_{100} at – 30 kPa, while transpiration rate was reduced by 22% for the same treatment combinations. Silicon supplementation either with NP_{100} alone or in combination with different proportions of K also promoted rice growth, physiological traits, and grain yield; however, the response of rice was largely similar among different K and Si combinations, except for $NP_{100}+K_{25}+Si_{75}$. Inclusion of K and Si with N and P in a fertilizer management program where the share of K is at least 50% could be a promising approach to minimize the harmful impact of water-deficit stress in rice cultivated through either wet direct seeding or transplanting method.

Keywords Drought · *Oryza sativa* L. · Photosynthesis · Plant nutrition · Water productivity

1 Introduction

Drought is a severe environmental stress threatening global food security by adversely impacting sustainable crop production (Ullah et al. 2017; Ilyas et al. 2021). Rice (*Oryza sativa* L.) is the leading cereal crop and the largest consumer of freshwater in the agricultural sector. However, decreasing freshwater availability due to enormous population growth, climate change, industrialization, and unproductive water loss is the main challenge to its sustainable production (Chareesri et al. 2020; Das et al. 2021a). Drought induces down-regulation of different physiological and biochemical processes in which signal transmitted through several messengers that modulate the production of reactive oxygen species (ROS) in rice causing severe oxidative damage to cellular activities resulting in a significant yield loss (Farooq et al. 2009; Ullah et al. 2019b; Panda et al. 2021). Drought response is also developed at molecular level where changes in gene expression (up- and down-regulation) take place (Farooq et al. 2009). Different genes are induced in response to drought at the transcriptional level, and these gene products are thought to function in tolerance to drought (Farooq et al. 2009). Future climate projection indicates more uncertainties on irrigation water availability and frequent episodes of drought, which will further disturb

✉ Avishek Datta
datta@ait.ac.th; avishek.ait@gmail.com

1 Agricultural Systems and Engineering, Department of Food, Agriculture and Bioresources, School of Environment, Resources and Development, Asian Institute of Technology, Klong Luang, Pathum Thani 12120, Thailand

2 Agrotechnology Discipline, Khulna University, Khulna 9208, Bangladesh

3 National Centre for Genetic Engineering and Biotechnology (BIOTEC), National Science and Technology Development Agency (NSTDA), Klong Luang, Pathum Thani 12120, Thailand

the widely prevailing rice production systems under inundated conditions where fields are kept flooded during most part of the growth period (Ullah et al. 2017). Conventional rice cultivation system under continuous flooding is water intensive overexploiting freshwater resources and should be replaced with water-saving rice production systems to maintain productivity and to conserve environment without compromising grain yield (Ruiz-Sanchez et al. 2011). Alternate wetting and drying (AWD) is a highly efficient water-saving and environment-friendly irrigation technique for lowland irrigated rice, which reduces irrigation water input by as high as 38% and greenhouse gas emissions by as high as 78% compared with the traditional method of rice cultivation without compromising yield (Maneepitak et al. 2019a; Santiago-Arenas et al. 2021; Das et al. 2021b). Despite visible benefits, adoption of AWD at larger scale is still a challenge largely due to the associated fear of yield loss, which warrants for agronomic management options to maintain yield. In addition, proper implementation of AWD where soil drying does not go beyond the so-called safe level (field water level is not allowed to drop more than 15 cm below the soil surface [soil water potential ≥ –20 kPa]) is also critical for better results (Carrijo et al. 2017). Another constraint, specifically associated with Thailand, regarding the implementation of AWD in the wet season is continuous rainfall, which makes the maintenance of the dry phase of the AWD cycle difficult; therefore, the adoption of this technique is substantially higher in the dry season rice compared with the wet season rice (Ruensuk et al. 2021). Proper implementation of AWD coupled with better nutrient management option would help boost the confidence of rice-growing farmers inclined to adopt this technique. In this regard, potassium (K) or silicon (Si) when applied in conjugation with optimum nitrogen (N) and phosphorus (P) fertilization has been found effective in enhancing growth, yield, and irrigation water productivity of rice under water-deficit stress (Guntzer et al. 2012; Ullah et al. 2018b, 2019a). Therefore, exogenous soil application of K or Si is a promising approach for sustainable rice production in the context of decreasing irrigation water availability.

Potassium is an indispensable macronutrient and chemical constituent of various crucial biomolecules that regulate many physiological and biochemical functions in plants including enzyme activation, protein synthesis, and carbohydrate metabolism (Sardans and Peñuelas 2021). The direct role of K in regulating stomatal movements, photosynthetic carbon reduction, antioxidant-mediated defense, ion homeostasis, and ROS detoxification in plants is well documented that confers tolerance to plants against drought stress (Waraich et al. 2012). Potassium-induced stomatal regulation helps reduce water loss through transpiration improving water use efficiency of plants (Chaves et al. 2002; Miao et al. 2010). Potassium mediates plant-water relations regulating ionic balance and osmotic adjustment by maintaining lower osmotic potential with higher turgor pressure in plant cell under drought stress (Römheld and Kirkby 2010; Ullah et al. 2019a). High concentration of K in cytosol of root tissues promotes root hair elongation, which in turn accelerates water and nutrient uptake potential of roots resulting in better utilization of soil moisture under limited water supply (Zain and Ismail 2016; Wang et al. 2017). Scavenging ROS through enzymatic and non-enzymatic antioxidant mechanisms is closely associated with the level of cellular K concentration for improved tolerance when cell encounters dehydration (Farooq et al. 2010). Potassium fertilization facilitates proline biosynthesis in plants, which is a well-known osmolyte playing a significant protective role through osmotic adjustment and enhanced antioxidant enzyme activities protecting cells against dehydration (Teixeira and Pereira 2007; Ellouzi et al. 2017). Different metabolic reactions are catalyzed by cellular K, which also controls repairing of tissue damage through scavenging toxic molecules in plant cells (Kanai et al. 2011). It has been reported that K fertilization facilitates various physiological and biochemical mechanisms, such as an enhancement of aquaporins activity, water use efficiency, root growth, and cell membrane stability, resulting in an improved drought tolerance (Jatav et al. 2014; Wang et al. 2017).

In plant nutrition, Si is considered an "anomaly" as it is apparently not essential for plant growth and development, but an increasing evidence in the literature shows that soluble Si is beneficial to plants, especially in alleviating the adverse effect of drought stress on most of the cereal crops (Cuong et al. 2017; Hoseinian et al. 2020). Silicon improves soil water holding capacity to ensure an increase in plant available water for maintaining photosynthetic carbon assimilation inducing drought tolerance in plants (Kuhla et al. 2021). The functional role of Si has been well documented in rice, which minimizes cell damage either by deposition in the cell wall and intercellular spaces or inducing lignin biosynthesis for regulating plant metabolism (Ullah et al. 2018b; Sirisuntornlak et al. 2019; Sathe et al. 2021). Plants uptake Si in the form of monosilicic acid and rice being a hyper-accumulator of Si has a greater capability of Si acquisition in culm/stem and leaf, which help enhance mechanical strength with improved light harvesting and distribution capacity (Zargar et al. 2019). Silicon is highly effective in mitigating abiotic stress-mediated cellular damage and in improving crop yield (Yan et al. 2018). Exogenous soil application of Si and microbial inoculation has been reported to minimize drought stress-induced damage on growth, yield, and water productivity of rice (Das et al. 2021a). Silicon in soil produces organic acid, phytohormone, biosurfactant, allelochemicals, and exopolymer in plant root, which help protect plant from heavy metal stress and nutrient deficiency (Ahmed et al. 2011; Etesami 2018). Exogenous soil application of Si alleviates drought stress by (i) improving photochemical efficiency with better chlorophyll integrity, enhancement of CO_2 assimilation rate, and activation of antioxidant defense capacity (Rizwan et al. 2015), (ii) enhancing hydraulic conductance of roots and water use efficiency, nutrient acquisition, and osmotic adjustment (Tripathi et al. 2015; Chen et al. 2018; Zargar et al. 2019; Schaller et al. 2021), and (iii) reducing stomatal conductance (Vandegeer et al. 2021). The role of Si in reducing stomatal conductance is not well established in rice. In contrast, Liu et al. (2014) reported that Si enhanced transpiration rate under water-deficit stress through up-regulating aquaporin gene expression. Similarly, Ming et al. (2012) reported higher root hydraulic conductance, stomatal conductance, and leaf transpiration rate of Si-supplemented rice plants with improved water uptake to induce tolerance against water-deficit stress. It has been well documented that Si is highly beneficial in enhancing growth and yield of various agronomic and horticultural crops under water-deficit stress (Guntzer et al. 2012; Ullah et al. 2018b; Sirisuntornlak et al. 2019; Alam et al. 2021; Chakma et al. 2021).

Drought-driven yield loss could be minimized by using various approaches, but judicious management of K and Si nutrition synchronized with efficient water management might be a promising strategy for optimizing growth and yield of rice under water-deficit stress. Moreover, the popular establishment method of rice through transplanting seedlings from nursery to well-puddled soil is also a water-intensive approach associated with a high amount of unproductive water loss along with a high demand of labor (Ullah et al. 2017). In contrast, direct seeding (wet) is increasingly gaining popularity for its water- and labor-saving potential where three basic field operations, such as puddling, transplanting, and maintaining a 3–5 cm of standing water throughout the growing season, are avoided (Ullah et al. 2017). A handful of published work evaluating the individual effect of K or Si on rice is available, but to the best of our knowledge, no published literature is available dealing with a synchronized use of K and/or Si under various levels of AWD and cultivation methods to optimize yield and water productivity of rice. It was hypothesized that proper combination of K and Si fertilizer would improve growth, yield, and water productivity of rice cultivated through wet direct seeding method by using the "safe" AWD irrigation. Therefore, the objective of this study was to evaluate the impact of K and Si fertilizer applied alone or in combination on growth, yield, and water productivity of rice cultivated through wet direct seeding or transplanting method subjected to water-deficit stress.

2 Materials and Methods

2.1 Experimental Set-up

A polyhouse experiment was conducted at the Asian Institute of Technology (14.0791° N, 100.6114° E), Bangkok, Thailand, during 2020. Black plastic pot (height: 30 cm, bottom diameter: 28 cm, and top diameter: 36 cm) was filled with 10 kg dry soil collected from the research farm of the Asian Institute of Technology consisting of 12% sand, 30% silt, 58% clay, and 2.6% organic matter. The soil is slightly acidic (pH of 6.0) with an inherent Si content of 0.0056% along with exchangeable P, K, Ca, and Mg contents of 0.0044%, 0.0304%, 0.33%, and 0.0359%, respectively. Field capacity of the soil was calculated following Datta et al. (2009) where 39.6% soil moisture content was determined at 100% field capacity corresponding to 0 kPa soil water potential. Temperature inside the polyhouse ranged from 22 to 36 °C, while relative humidity fluctuated between 70 and 85% throughout the growing period.

2.2 Experimental Treatment and Design

The factorial experiment consisted of three factors: six fertilizer doses including different combinations of K and Si applied along with N and P and the control (NP_{100} [control], $NP_{100}+K_{100}$, $NP_{100}+Si_{100}$, $NP_{100}+K_{75}+Si_{25}$, $NP_{100}+K_{50}+Si_{50}$, and $NP_{100}+K_{25}+Si_{75}$), three soil water potential levels maintained through AWD irrigation (0, –15, and –30 kPa), and two cultivation methods (wet direct seeding and transplanting). The subscript values of 100, 75, 50, and 25 under a specific nutrient represent 100%, 75%, 50%, and 25% of the recommended field application dose of that particular nutrient. The experiment was arranged in a completely randomized design with three replications in which each pot containing one single plant was considered as an experimental unit for an individual treatment combination.

2.3 Crop Husbandry and Nutrient Management

Seeds of Pathumthani 1 rice variety (*Oryza sativa* L. ssp. *indica*) were procured from the Pathum Thani Rice Research Center, Pathum Thani, Thailand. Pathumthani 1 is a photoperiod-insensitive, drought-susceptible variety (Cha-um et al. 2010), and its maturity period ranges from 110 to 120 days cultivated through broadcasting (direct seeding) method and 115 to 125 days cultivated through transplanting method (Ullah et al. 2018a; Santiago-Arenas et al. 2019, 2020). The required commercial fertilizers, such as urea (46% N), triple superphosphate (46% P_2O_5), potassium chloride (60% K_2O), and monosilicic acid (20% Si), were collected from a local market. Each pot was fertilized with 0.71 g of NP (16:20; 156 kg ha^{-1}) as a basal dose at 1 day before sowing or transplanting along with 0.43 g of urea (94 kg ha^{-1}) during panicle initiation stage (80 days after seeding/sowing or 65 days after transplanting). These N and P doses were treated as the 100% recommended field application dose of N and P (Maneepitak et al. 2019b). For K and Si fertilization, potassium chloride at 200 kg ha^{-1}

(120 kg K ha^{-1}) (Ullah et al. 2019a) and monosilicic acid at 300 kg ha^{-1} (60 kg ha^{-1} soluble Si) (Ullah et al. 2018b) were applied as a basal dose in which each respective pot received 0.91 g potassium chloride and 1.36 g monosilicic acid. These K and Si doses were used for the baseline calculation of 100% K and 100% Si. Other doses of K and Si (75%, 50%, and 25%) were calculated based on the doses of 100% K and 100% Si. Seeds were surface sterilized with 10% H_2O_2 for 10 min for disinfection and breaking of dormancy, rinsed thoroughly with distilled water, and then soaked in distilled water for 24 h before sowing (Ullah et al. 2017). Pre-germinated seeds were sown in plastic pots (three pre-germinated seeds in each pot) for the wet direct seeding method, while three healthy seedlings were transplanted into each pot from the nursery tray at 15 days after sowing for the transplanting method. Finally, one seedling was kept in each pot for both cultivation methods.

2.4 Establishment of Different Soil Water Potential Levels

Tensiometer (Model 2725ARL Jet Fill Tensiometer, Soil moisture Equipment Corp., CA, USA) was permanently installed into the pot for the whole growing season to monitor soil water potential. The tensiometer was set at 15 cm soil depth as most of the rice roots proliferate within this range of soil depth (Ullah et al. 2019b). Sufficient soil moisture was maintained until 30 day of seedling growth followed by establishment of desired soil water potential levels (0, –15, and –30 kPa) maintained through AWD irrigation. Soil water potential levels of 0, –15, and –30 kPa corresponded to approximately 100%, 80%, and 60% field capacity, respectively. Irrigation water was applied when soil water potential reached at the desired level. Soil water potential of –15 and –30 kPa indicates a 20% and 40% depletion of the maximum amount of water held in the soil, respectively, whereas 0 kPa refers to the maximum amount of water held in the soil after gravitational water drainage stops.

2.5 Data Collection

Data on plant height (cm), flag leaf length (FLL) (cm), root dry matter (RDM) (g $plant^{-1}$), shoot dry matter (SDM) (g $plant^{-1}$), leaf greenness (SPAD value), leaf relative water content (LRWC) (%), net photosynthetic rate (P_n) (μmol CO_2 m^{-2} s^{-1}), stomatal conductance (g_s) (mmol H_2O m^{-2} s^{-1}), transpiration rate (E) (mmol H_2O m^{-2} s^{-1}), free proline (μg g^{-1} fresh weight), tiller number $plant^{-1}$, panicle number $plant^{-1}$, spikelet number $panicle^{-1}$, filled grain (%), 1000-grain weight (g), grain yield (g $plant^{-1}$), harvest index (%), water productivity (kg m^{-3}), and shoot K and Si content (mg g^{-1} dry weight) were collected. Data on plant height, FLL, SPAD value, LRWC, tiller number $plant^{-1}$, and panicle number $plant^{-1}$ were measured before harvest.

Plant height was measured from the ground level to the tip of the topmost leaf/panicle using a meter scale 1 day before harvest. Flag leaf length was measured as the distance from the base to the tip of the uppermost leaf blade of three rice tillers and the mean value is presented as FLL. Root dry matter and SDM were determined by measuring the oven-dried (80 °C) weight of rice root and shoot (excluding panicles) until constant weight was obtained.

SPAD value (leaf greenness) was recorded from the fully expanded three leaves at panicle initiation stage using a handheld chlorophyll meter (SPAD-502 plus, Minolta Corporation, Ltd., Osaka, Japan) and the mean value is presented for each treatment as described by Hussain et al. (2000). At panicle initiation stage, LRWC was determined using the method as outlined by Dasgupta et al. (2015). For determination of LRWC, leaf samples were collected from the fully expanded second leaf from the top of the plant. Leaves were weighed for their fresh weight (FW) immediately after sampling. After collecting FW, leaves were cut into small segments of 2 cm, immersed into distilled water in test tubes, kept overnight in the laboratory, and turgid weight (TW) of the samples measured. The fully turgid leaf samples were then dried in an oven at 80 °C until dry weight was constant followed by the measurement of dry weight (DW) of the samples. The following formula was used for determining LRWC:

$$LRWC\% = \frac{(FW - DW)}{(TW - DW)} \times 100$$

Photosynthesis-related parameters, such as P_n, E, and g_s of the flag leaf, were measured between 09.30 am and 11.30 am using a portable photosynthesis system (LI-6400XT, Li-COR, Lincoln, NE, USA) at panicle initiation stage. Measurements were started at a concentration of CO_2 in air of approximately 370 ± 20 μmol mol^{-1} in the assimilation chamber. The ambient temperature was 28 ± 1 °C. Artificial illumination from a red-blue 6400-02B LED light source that could release continuous light at 1000 μmol m^{-2} s^{-1} photosynthetic photon flux density was used during the measurements (Cha-um et al. 2006). Free proline content was measured from the second fully expanded leaf starting from the top at panicle initiation stage following the method of Bates et al. (1973). For free proline determination, fresh leaf sample was cut into small pieces, ground in the mortar with liquid nitrogen into a powder, and 0.05 g of the sample was homogenized in 1.0 mL of 3% aqueous sulfosalicylic acid followed by centrifugation at 10,000 rpm for 10 min. Then, 200 μL of the extract was put into a test tube with the addition of 200 μL acid ninhydrin and 200 μL glacial acetic acid followed by heating in boiling water for 1 h, and finally the reaction was terminated in an ice bath. After cooling, 200 μL of mixture solution was extracted with 400 μL toluene, mixed vigorously at 6000 rpm for 5 min, kept for complete precipitation, and the upper layer was separated for measuring the value of absorbance at 520 nm. The final concentration of free proline in fresh leaf was calculated from standard curve with absorbance value of different concentrations of standard proline solutions.

Yield components, such as tiller number plant^{-1}, panicle number plant^{-1}, spikelet number panicle^{-1}, filled grain (%), and 1000-grain weight, were determined at harvest. Grain yield was measured and adjusted to 14% grain moisture content. Harvest index was calculated by the ratio of grain yield to biological yield (total biomass). Water productivity was calculated by the ratio of grain yield (kg) to total water input (m^3) per pot as described by Maneepitak et al. (2019b).

For measuring shoot K and Si content, shoot sample (consisted of leaf and culm) from each treatment was collected, rinsed thoroughly with deionized water, and oven dried at 72 °C until constant weight. Then, the sample was cut into small pieces, ground to fine powder, and digested with nitric acid via modified USEPA method 3050B using the Hot Block Digestion System (Tarantino et al. 2017). After that, 50 mg of each sample was suspended in 1 mL of 1:1 of nitric acid:deionized water followed by heating at 105 °C for 15 min. After cooling, 2 mL of concentrated nitric acid was added and again digested for 2 h followed by the addition of deionized water for preparing 10 mL solution. This digested solution was filtered through 0.45 μm pore size PTFE filter and filtered samples were diluted with 2.5% nitric acid before the determination of K and Si content via an inductively coupled plasma-optical emission spectroscopy (ICP-OES; Perkin Elmer Avio 200) following Phukunkamkaew et al. (2021). The content of K and Si standard was calibrated on ICP-OES using 1.0 g L^{-1} of K and Si standard each (Perkin Elmer, 5% nitric acid).

2.6 Statistical Analysis

The data were subjected to a three-way analysis of variance (ANOVA) and were analyzed using Statistix 10 software program (Analytical Software, Tallahassee, FL, USA). Means of significant treatment effects were separated by conducting post hoc analysis using Tukey's honest significant difference test. In all analyses, differences were considered significant at $P \leq 0.05$. Data for significant treatment effect are presented based on the highest order of factorial combination that was significant in the ANOVA.

3 Results

3.1 Shoot K and Si Content

The two-way interaction between fertilizer dose and soil water potential had a significant effect on shoot K and Si content (Table 1). Both nutrients were better accumulated in shoots when NP_{100} was supplemented with different combinations of K and Si, while accumulation was significantly lower at NP_{100} fertilizer dose irrespective of soil water potential levels (Fig. 1A,B). Similarly, both K and Si accumulation in shoot was drastically reduced when soil water potential dropped from 0 to –30 kPa. $NP_{100} + K_{100}$ fertilizer dose had 9%, 10%, and 10% higher shoot K content than NP_{100} at 0, –15, and –30 kPa, respectively (Fig. 1A). Shoot K content exhibited a reduction in the range of 10% ($NP_{100} + K_{75} + Si_{25}$) to 16% ($NP_{100} + K_{50} + Si_{50}$) when soil water potential dropped from 0 to –30 kPa. Shoot Si content was not affected by different splits of Si, and $NP_{100} + Si_{100}$ fertilizer dose had 24% higher accumulation of Si in shoot than NP_{100} at 0 kPa (Fig. 1B). Shoot Si content was reduced by 13–21% for different fertilizer doses upon decreasing soil water potential from 0 to –30 kPa.

3.2 Growth Parameters

All growth parameters (plant height, FLL, RDM, and SDM) were significantly affected by the main effect of fertilizer dose, soil water potential, and cultivation method, but the two-way and three-way interactions were not significant (Table 1). Plants were the tallest at $NP_{100} + Si_{100}$ fertilizer combination, which were 7% longer than the plants at NP_{100} (Table 2). Plant height progressively decreased with increasing water-deficit stress, while wet direct-seeded plants were significantly longer than transplanted plants. All combinations of K and Si with NP_{100} had similar FLL, which was maximized at $NP_{100} + K_{75} + Si_{25}$ with a 17% increase from NP_{100} alone (Table 2). There was no difference in FLL between –15 and –30 kPa, while wet direct-seeded plants had significantly higher FLL than transplanted plants. Plants fertilized with $NP_{100} + K_{75} + Si_{25}$ had 44% higher RDM than those fertilized with NP_{100} alone (Table 2). Decreasing soil water potential up to –15 kPa had no effect on RDM, which was reduced by 20% at –30 kPa compared with 0 kPa. Root dry matter of transplanted plants was 39% higher than wet direct-seeded plants. Shoot dry matter exhibited a different trend where no difference was observed among all fertilizer combinations, except for $NP_{100} + K_{50} + Si_{50}$ where SDM was 21% higher than NP_{100}

Table 1 Significance level in the three-way ANOVA of the effect of fertilizer dose, soil water potential, and cultivation method on growth, physiological and biochemical traits, yield components, grain yield, harvest index, water productivity, and nutrient content of rice

Items	Fertilizer dose (F)	Soil water potential (SW)	Cultivation method (C)	F×SW	F×C	SW×C	F×SW×C
Growth parameters							
Plant height (cm)	*	**	**	ns	ns	ns	ns
Flag leaf length (cm)	**	**	**	ns	ns	ns	ns
Root dry matter (g plant^{-1})	*	*	*	ns	ns	ns	ns
Shoot dry matter (g plant^{-1})	*	*	*	ns	ns	ns	ns
Physiological and biochemical traits							
Leaf greenness (SPAD value)	*	*	ns	*	ns	ns	ns
Leaf relative water content (%)	**	*	*	**	ns	ns	ns
Net photosynthetic rate (μmol CO_2 m^{-2} s^{-1})	*	*	ns	*	*	*	ns
Stomatal conductance (mmol H_2O m^{-2} s^{-1})	*	**	*	*	*	**	*
Transpiration rate (mmol H_2O m^{-2} s^{-1})	*	*	ns	*	ns	ns	ns
Proline content (μg g^{-1} fresh weight)	**	**	**	*	*	*	*
Yield and yield components							
Tiller number plant^{-1}	*	*	*	ns	ns	ns	ns
Panicle number plant^{-1}	**	*	**	ns	ns	ns	ns
Spikelet number panicle^{-1}	**	**	**	ns	ns	ns	ns
Filled grain (%)	*	*	**	ns	ns	ns	ns
1000-grain weight (g)	*	*	**	*	ns	ns	ns
Grain yield (g plant^{-1})	*	*	ns	*	*	*	*
Harvest index (%)	**	**	ns	ns	*	*	*
Water productivity and shoot nutrient content							
Water productivity (kg m^{-3})	**	**	ns	*	ns	ns	ns
Shoot K content (mg g^{-1} dry weight)	*	*	*	*	ns	ns	ns
Shoot Si content (mg g^{-1} dry weight)	*	**	*	*	ns	ns	ns

**, *, and ns indicate $P \leq 0.01$, $P \leq 0.05$, and not significant, respectively

alone (Table 2). Shoot dry matter progressively decreased with decreasing soil moisture regime (8% and 11% at –15 and –30 kPa, respectively, compared with 0 kPa), while wet direct-seeded plants had significantly higher SDM than transplanted plants.

3.3 Physiological and Biochemical Traits

Leaf greenness (SPAD value), LRWC, P_n, and E were significantly affected by the interactive effect between fertilizer dose and soil water potential (Table 1). SPAD value largely remained similar across fertilizer doses under a particular soil water potential level, while decreasing soil water potential up to –15 kPa had no effect on SPAD value regardless of fertilizer doses (Fig. 2A). At –30 kPa, a significant reduction in SPAD value was evident for all fertilizer doses, except for $NP_{100}+K_{100}$ combination where decreasing soil water potential did not affect SPAD value. Fertilizer dose of $NP_{100}+K_{100}$ had an overall higher LRWC regardless of soil water potential levels, which was reduced by 10% for NP_{100} at 0 kPa and by 9% and 10% for $NP_{100}+K_{25}+Si_{75}$ at –15 and –30 kPa, respectively (Fig. 2B). Leaf relative water content was significantly reduced with decreasing soil water potential irrespective of fertilizer doses where a maximum reduction of 12% was recorded at –30 kPa compared with 0 kPa for $NP_{100}+K_{25}+Si_{75}$ fertilizer dose. Fertilizers application with no K or Si supplementation (NP_{100}) had an overall lower P_n followed by $NP_{100}+K_{25}+Si_{75}$ fertilizer dose regardless of soil water potential levels (Fig. 3A). There was no significant difference in P_n among other fertilizer doses across soil water potential levels. A significant reduction in P_n ranging from 36% ($NP_{100}+K_{100}$) to 45% ($NP_{100}+K_{25}+Si_{75}$) was recorded when soil water potential was reduced from 0 to –30 kPa. Transpiration rate remained lower for $NP_{100}+K_{100}$ fertilizer dose at all soil water potential levels, while the other fertilizer doses had largely similar E across soil water potential levels (Fig. 3B). The effect of decreasing soil water potential was evident on E of plants at all fertilizer doses with more profound impact at NP_{100} where E was reduced by 28% when soil water potential was reduced from 0 to –30 kPa. The three-way interaction among fertilizer dose, cultivation method, and soil water potential

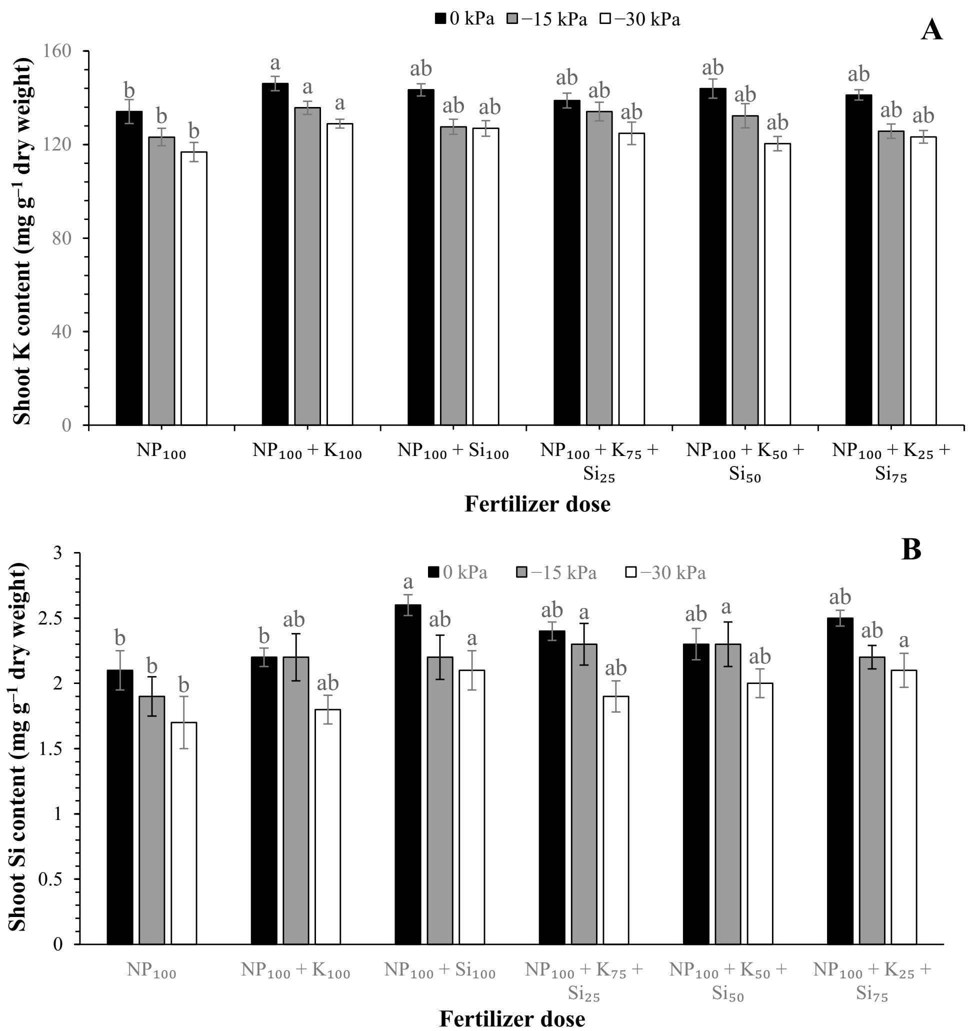

Fig. 1 Interaction effect of fertilizer dose and soil water potential on shoot K content (A) and shoot Si content (B) of rice. Means followed by the same letters are statistically similar among fertilizer doses within a particular soil water potential based on Tukey's honest significant difference test at $P \leq 0.05$. Bars show means ± standard errors of three replications

Table 2 Individual effect of fertilizer dose, soil water potential, and cultivation method on plant height, flag leaf length, root dry matter, and shoot dry matter of rice

Factor	Plant height (cm)	Flag leaf length (cm)	Root dry matter (g plant^{-1})	Shoot dry matter (g plant^{-1})
Fertilizer dose				
NP_{100}	71.1 ± 0.86b	22.8 ± 0.59b	14.3 ± 0.48c	56.1 ± 1.4b
$NP_{100} + K_{100}$	74.5 ± 0.95ab	26.6 ± 0.75a	17.1 ± 0.53b	56.6 ± 1.7b
$NP_{100} + Si_{100}$	76.2 ± 0.92a	25.1 ± 0.73ab	20.1 ± 0.39a	61.1 ± 1.9ab
$NP_{100} + K_{75} + Si_{25}$	73.7 ± 0.84ab	26.7 ± 0.81a	20.6 ± 0.85a	59.7 ± 2.3b
$NP_{100} + K_{50} + Si_{50}$	75.1 ± 0.92a	25.9 ± 0.72ab	19.8 ± 0.64ab	68.1 ± 1.9a
$NP_{100} + K_{25} + Si_{75}$	72.9 ± 0.83b	24.1 ± 0.9ab	21.7 ± 0.57a	61.6 ± 1.5ab
Soil water potential				
0 kPa	75.9 ± 0.44a	27.7 ± 0.58a	20.7 ± 0.98a	63.8 ± 1.7a
− 15 kPa	74.1 ± 0.59b	24.4 ± 0.47b	19.4 ± 0.56a	58.4 ± 1.3b
− 30 kPa	71.6 ± 0.72c	23.2 ± 0.44b	16.6 ± 0.35b	56.9 ± 1.2b
Cultivation method				
Wet direct seeding	76.1 ± 0.35a	25.7 ± 0.44a	16.8 ± 0.76b	62.7 ± 1.5a
Transplanting	71.2 ± 0.51b	24.4 ± 0.39b	23.4 ± 0.94a	59.5 ± 1.1b

Means followed by the same letters within a column are statistically similar based on Tukey's honest significant difference test at $P \leq 0.05$; data are means of three replications ± standard errors

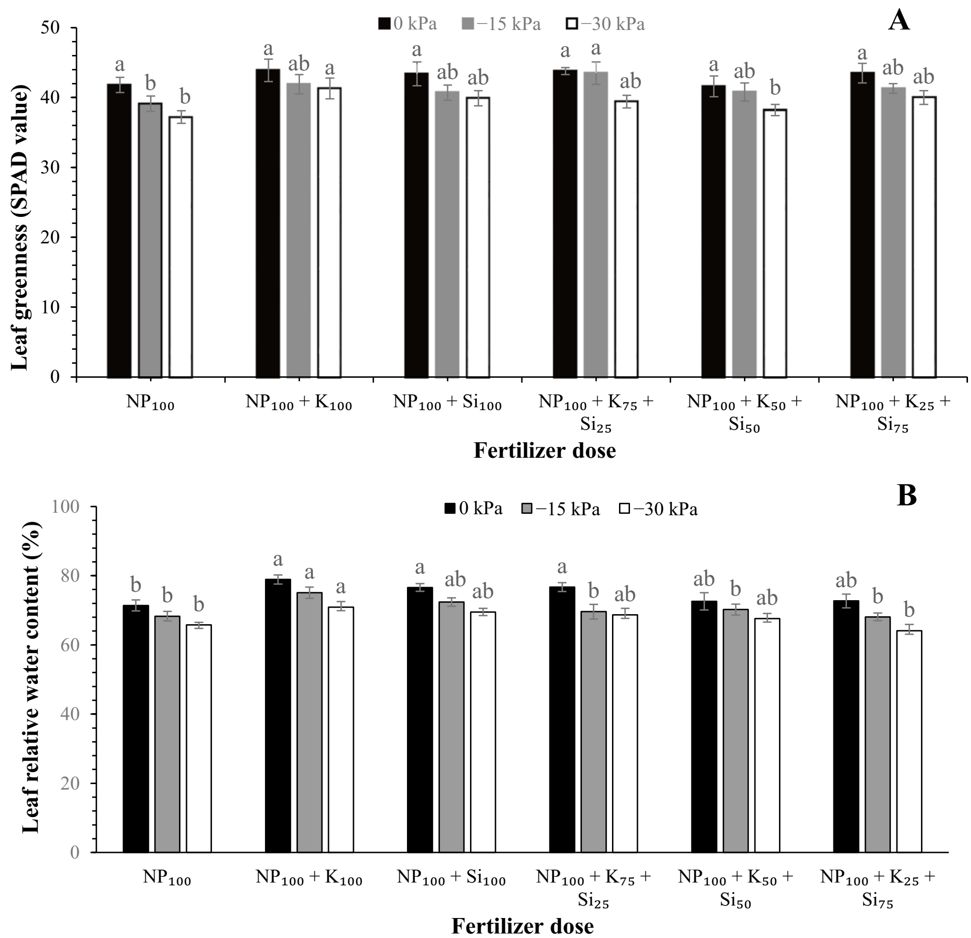

Fig. 2 Interaction effect of fertilizer dose and soil water potential on leaf greenness (A) and leaf relative water content (B) of rice. Means followed by the same letters are statistically similar among fertilizer doses within a particular soil water potential based on Tukey's honest significant difference test at $P \leq 0.05$. Bars show means ± standard errors of three replications

had a significant effect on g_s and proline content (Table 1). Different fertilizer doses had largely similar g_s for wet direct seeding method of cultivation at all soil water potential levels and the same was also true for the two cultivation methods within a particular fertilizer dose and soil water potential (Table 3). Transplanted plants had 37% higher g_s at NP_{100} fertilizer dose than $NP_{100} + K_{100}$ and $NP_{100} + K_{75} + Si_{25}$ fertilizer doses at 0 kPa, while the same difference was 35% and 53% compared with $NP_{100} + Si_{100}$ and $NP_{100} + K_{25} + Si_{75}$ fertilizer doses, respectively, at –15 kPa. Stomatal conductance significantly reduced with decreasing soil water potential regardless of cultivation methods or fertilizer doses, and a maximum decrease of 50% in g_s of wet direct-seeded plants was evident at $NP_{100} + K_{100}$ fertilizer dose when soil water potential was reduced from 0 to –30 kPa.

The three-way interaction among fertilizer dose, cultivation method, and soil water potential indicated that plants cultivated through wet direct seeding method had more proline content than transplanted plants across soil water potential levels and fertilizer doses (Table 3). Proline content ranged from 84.6 μg g^{-1} (NP_{100}) to 103.3 μg g^{-1} ($NP_{100} + K_{75} + Si_{25}$) at 0 kPa for wet direct-seeded plants, the corresponding range for transplanted plants was 64.0 μg g^{-1} ($NP_{100} + K_{25} + Si_{75}$) to 86.1 μg g^{-1} ($NP_{100} + K_{75} + Si_{25}$). Proline content showed a maximum increase of 27% at $NP_{100} + K_{50} + Si_{50}$ fertilizer dose compared with NP_{100} for wet direct-seeded plants at –15 kPa and 40% increase at $NP_{100} + K_{100}$ compared with NP_{100} for the same cultivation method at –30 kPa. $NP_{100} + Si_{100}$ had 25% and 48% higher proline content than $NP_{100} + K_{25} + Si_{75}$ fertilizer dose for transplanted plants at –15 and –30 kPa, respectively. A significant increase in proline content was observed with decreasing soil water potential across fertilizer doses and cultivation methods. A maximum increase of 58% in proline content of wet direct-seeded plants was evident at $NP_{100} + K_{100}$ fertilizer dose when soil water potential decreased from 0 to –30 kPa.

3.4 Yield Components, Yield, and Water Productivity

Tiller number $plant^{-1}$, panicle number $plant^{-1}$, spikelet number $panicle^{-1}$, and filled grain percentage were only significantly affected by the main effect of fertilizer dose, soil water potential, and cultivation method (Table 1). The performance of NP_{100} fertilizer dose was poor for all these

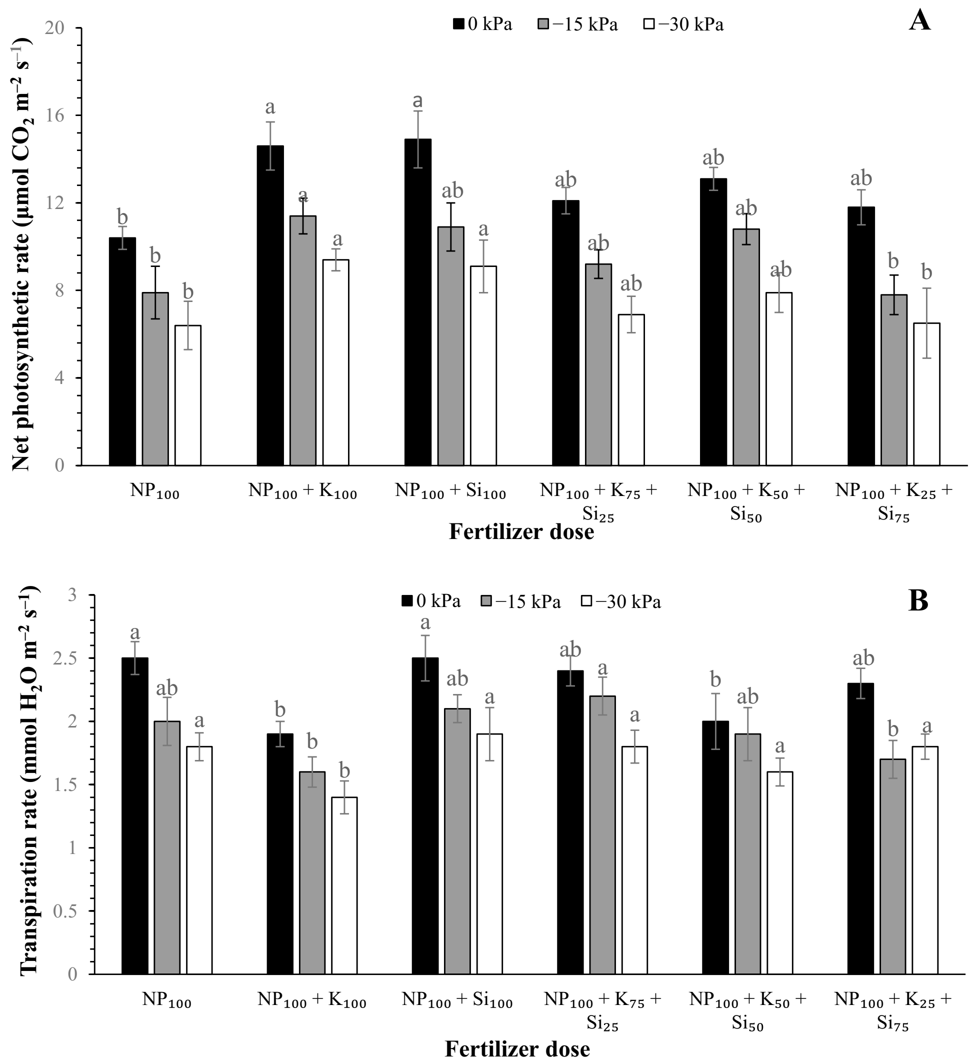

Fig. 3 Interaction effect of fertilizer dose and soil water potential on net photosynthetic rate (A) and transpiration rate (B) of rice. Means followed by the same letters are statistically similar among fertilizer doses within a particular soil water potential based on Tukey's honest significant difference test at $P \leq 0.05$. Bars show means ± standard errors of three replications

yield components, while other fertilizer doses had up to 19% higher tiller number plant^{-1} and 26% greater panicle number plant^{-1} for $NP_{100} + K_{25} + Si_{75}$ and $NP_{100} + Si_{100}$, respectively, up to 52% higher spikelet number panicle^{-1} and 13% higher filled grain percentage (for $NP_{100} + K_{100}$) compared with NP_{100} (Table 4). The detrimental effect of decreasing soil water potential was observed on all these yield components with 13%, 15%, 23%, and 11% reduction in tiller number plant^{-1}, panicle number plant^{-1}, spikelet number panicle^{-1}, and filled grain percentage, respectively, at –30 kPa compared with 0 kPa. Wet direct-seeded plants had 6%, 8%, 9%, and 5% higher tiller number plant^{-1}, panicle number plant^{-1}, spikelet number panicle^{-1}, and filled grain percentage, respectively, compared with transplanted plants. The significant interaction between fertilizer dose and soil water potential (Table 1) indicated that NP_{100} had lower 1000-grain weight across soil water potential levels, while there was largely no difference in other fertilizer doses irrespective of soil water potential levels (Table 5). A maximum increase up to 17%, 16%, and 17% at 0, –15, and –30 kPa, respectively, in 1000-grain weight was recorded for different fertilizer doses compared with NP_{100}. Decreasing soil water potential caused a significant reduction in 1000-grain weight, which was common for all fertilizer doses, except for $NP_{100} + Si_{100}$, with different proportions ranging from 7% (NP_{100}) to 14% ($NP_{100} + K_{100}$) at –30 kPa compared with 0 kPa.

The three-way interaction among fertilizer dose, cultivation method, and soil water potential was significant for grain yield (Table 1). Wet direct-seeded plants had similar grain yield at 0 kPa regardless of fertilizer doses and the same was true for transplanted plants at –15 and –30 kPa (Table 6). Fertilizing wet direct-seeded plants with $NP_{100} + K_{100}$ resulted in 51% and 40% higher grain yield than NP_{100} at –15 and –30 kPa, respectively. The corresponding difference for transplanted plants at 0 kPa was 32%. The two cultivation methods had no difference in grain yield across fertilizer doses and soil water potential

Table 3 Effect of fertilizer dose, soil water potential, and cultivation method on stomatal conductance and free proline content of rice

Fertilizer dose	Cultivation method	Stomatal conductance (mmol H_2O m^{-2} s^{-1})			Free proline content (µg g^{-1} fresh weight)		
		0 kPa	– 15 kPa	– 30 kPa	0 kPa	– 15 kPa	– 30 kPa
NP_{100}	Wet direct seeding	0.22 ± 0.02abA	0.18 ± 0.01abAB	0.16 ± 0.04abB	84.6 ± 2.6bcB	91.3 ± 2.33bcA	106.1 ± 2.3dA
	Transplanting	0.26 ± 0.03aA	0.23 ± 0.02aAB	0.20 ± 0.02aB	70.6 ± 7.6cdB	78.0 ± 6.1cA	85.3 ± 3.4eA
$NP_{100}+K_{100}$	Wet direct seeding	0.18 ± 0.03bA	0.16 ± 0.02bA	0.09 ± 0.05cB	94.3 ± 2.0abC	112.6 ± 4.3abB	148.6 ± 10.7aA
	Transplanting	0.19 ± 0.01bA	0.18 ± 0.02abA	0.12 ± 0.04abcB	76 ± 8.9cdC	93 ± 4.5bcB	110.3 ± 6.1cdA
$NP_{100}+Si_{100}$	Wet direct seeding	0.19 ± 0.02bA	0.16 ± 0.03bAB	0.11 ± 0.01bcB	96 ± 2.3abC	114.6 ± 12.8aB	147.3 ± 4.1aA
	Transplanting	0.21 ± 0.05abA	0.17 ± 0.01bAB	0.13 ± 0.02abB	85 ± 7.5bcB	97 ± 8.1bcB	123.6 ± 4.6bcA
$NP_{100}+K_{75}+Si_{25}$	Wet direct seeding	0.23 ± 0.03abA	0.18 ± 0.02abAB	0.15 ± 0.03abB	103.3 ± 8.8aB	113.0 ± 5.4ab B	132.1 ± 6.1abA
	Transplanting	0.19 ± 0.02bA	0.19 ± 0.04abA	0.13 ± 0.02abcB	86.1 ± 5.1bcB	92.6 ± 3.7bcB	121.3 ± 5.2bcdA
$NP_{100}+K_{50}+Si_{50}$	Wet direct seeding	0.22 ± 0.03abA	0.15 ± 0.02bB	0.12 ± 0.01abcB	95.6 ± 2.3abB	116 ± 3.8aA	124.1 ± 3.1bcA
	Transplanting	0.21 ± 0.02abA	0.20 ± 0.01abA	0.14 ± 0.02abcB	74.6 ± 4.1cdB	87.0 ± 5.6cA	92.8 ± 3.7deA
$NP_{100}+K_{25}+Si_{75}$	Wet direct seeding	0.22 ± 0.01abA	0.14 ± 0.03bB	0.13 ± 0.04abcB	92 ± 6.6abB	105.3 ± 2.9abA	113.6 ± 3.8cdA
	Transplanting	0.19 ± 0.03bA	0.15 ± 0.02bAB	0.12 ± 0.01abcB	64 ± 3.4kB	77.6 ± 6.2cA	83.3 ± 7.2eA

Means followed by the same lowercase letters within a column and means followed by the same uppercase letters within a row are statistically similar based on Tukey's honest significant difference test at $P \leq 0.05$; data are means of three replications ± standard errors

Table 4 Individual effect of fertilizer dose, soil water potential, and cultivation method on yield components of rice

Factor	Tiller number $plant^{-1}$	Panicle number $plant^{-1}$	Spikelet number $panicle^{-1}$	Filled grain percentage
Fertilizer dose				
NP_{100}	18.6 ± 0.48b	14.1 ± 0.61b	70.1 ± 3.9e	69 ± 1.3b
$NP_{100}+K_{100}$	21.9 ± 0.59a	17.2 ± 0.66a	106.3 ± 4.1a	78 ± 0.9a
$NP_{100}+Si_{100}$	19.5 ± 0.43ab	17.8 ± 0.59a	102.1 ± 4.9ab	75 ± 3.3ab
$NP_{100}+K_{75}+Si_{25}$	20.3 ± 0.61ab	16.8 ± 0.41a	94.1 ± 4.1bc	77 ± 1.2a
$NP_{100}+K_{50}+Si_{50}$	21.6 ± 0.46ab	16.1 ± 0.58ab	86.7 ± 3.7 cd	73 ± 1.4ab
$NP_{100}+K_{25}+Si_{75}$	22.2 ± 0.53a	15.2 ± 0.55ab	77.6 ± 3.2d	72 ± 1.6ab
Soil water potential				
0 kPa	22.1 ± 0.46a	16.9 ± 0.51a	101.2 ± 3.3a	80 ± 1.7a
– 15 kPa	20.6 ± 0.42b	16.1 ± 0.45a	90.4 ± 3.1b	74 ± 0.9a
– 30 kPa	19.3 ± 0.29b	14.3 ± 0.42b	77.8 ± 2.8c	71 ± 1.1b
Cultivation method				
Wet direct seeding	21.6 ± 0.48a	16.9 ± 0.61a	93.4 ± 2.6a	76 ± 0.7a
Transplanting	20.4 ± 0.41b	15.7 ± 0.53b	85.6 ± 2.9b	73 ± 1.3b

Means followed by the same letters within a column are statistically similar based on Tukey's honest significant difference test at $P \leq 0.05$; data are means of three replications ± standard errors

levels. Harvest index was significantly affected by the three-way interaction among fertilizer dose, cultivation method, and soil water potential (Table 1). Harvest index ranged between 36.2% ($NP_{100}+K_{50}+Si_{50}$ for wet direct-seeded plants) and 53.5% ($NP_{100}+K_{100}$ for transplanted plants) at 0 kPa (Table 6). The corresponding respective range at –15 and –30 kPa was 26.1% (NP_{100} for wet direct-seeded plants) to 45.1% ($NP_{100}+K_{75}+Si_{25}$ for wet direct-seeded plants) and 20.2% (NP_{100} for transplanted plants) to 31.6% ($NP_{100}+K_{100}$ for wet direct-seeded plants). The two cultivation methods had largely similar harvest index across fertilizer doses and soil water potential levels. Harvest index showed a significant reduction with decreasing soil water potential and the maximum decrease (52%) was noted for transplanted plants fertilized with $NP_{100}+Si_{100}$ at –30 kPa compared with 0 kPa.

Table 5 Interaction effect between fertilizer dose and soil water potential on 1000-grain weight and water productivity of rice

Fertilizer dose	1000-grain weight (g)			Water productivity (kg m^{-3})		
	0 kPa	− 15 kPa	− 30 kPa	0 kPa	− 15 kPa	− 30 kPa
NP_{100}	24.1 ± 1.4bA	23.2 ± 1.7bA	22.4 ± 0.8bA	0.30 ± 0.01aB	0.41 ± 0.03bB	0.53 ± 0.02bA
$NP_{100}+K_{100}$	28.3 ± 0.8aA	26.1 ± 1.1abAB	24.2 ± 1.1abB	0.40 ± 0.04aC	0.52 ± 0.02aB	0.75 ± 0.03aA
$NP_{100}+Si_{100}$	26.2 ± 1.4abA	26.8 ± 0.7aAB	26.1 ± 0.5aA	0.36 ± 0.04aC	0.48 ± 0.01abB	0.64 ± 0.02abA
$NP_{100}+K_{75}+Si_{25}$	27.5 ± 0.5aA	26.8 ± 0.8aAB	24.1 ± 0.8abB	0.39 ± 0.01aC	0.51 ± 0.02abB	0.69 ± 0.02abA
$NP_{100}+K_{50}+Si_{50}$	25.8 ± 0.9abA	25.3 ± 1.4abAB	22.6 ± 0.6bB	0.38 ± 0.02aC	0.50 ± 0.02abB	0.69 ± 0.04abA
$NP_{100}+K_{25}+Si_{75}$	26.6 ± 1.4abA	26.6 ± 0.9aA	23.4 ± 0.7abB	0.35 ± 0.01aC	0.48 ± 0.01abB	0.62 ± 0.01abA

Means followed by the same lowercase letters within a column and means followed by the same uppercase letters within a row are statistically similar based on Tukey's honest significant difference test at $P \leq 0.05$; data are means of three replications ± standard errors

Table 6 Effect of fertilizer dose, soil water potential, and cultivation method on grain yield and harvest index of rice

Fertilizer dose	Cultivation method	Grain yield (g $plant^{-1}$)			Harvest index (%)		
		0 kPa	− 15 kPa	− 30 kPa	0 kPa	− 15 kPa	− 30 kPa
NP_{100}	Wet direct seeding	22.5 ± 3.3bA	15.8 ± 1.7bB	14.2 ± 1.7bB	38 ± 1.8cA	26 ± 1.5cAB	21 ± 2.6bB
	Transplanting	23.1 ± 0.9bA	18.3 ± 1.3abAB	13.6 ± 1.1bB	37 ± 2.7cA	26 ± 1.8cAB	20 ± 1.1bB
$NP_{100}+K_{100}$	Wet direct seeding	27.4 ± 0.79abA	23.8 ± 0.4aAB	19.9 ± 0.61aB	50 ± 1.3abcA	41 ± 2.9abAB	32 ± 3.8aB
	Transplanting	30.4 ± 3.4aA	20.2 ± 1.1abB	17.3 ± 0.76abB	54 ± 2.1aA	38 ± 1.8abB	28 ± 2.6abB
$NP_{100}+Si_{100}$	Wet direct seeding	25.6 ± 2.8abA	20.6 ± 0.9abAB	15.6 ± 1.1abB	41 ± 2.3bcA	38 ± 1.8abA	31 ± 0.67aB
	Transplanting	28.6 ± 0.92abA	20.5 ± 0.76abB	16.4 ± 1.3abB	51 ± 1.1abA	30 ± 1.9bcB	25 ± 1.4abB
$NP_{100}+K_{75}+Si_{25}$	Wet direct seeding	28.7 ± 1.7abA	20.4 ± 2.3abB	14.8 ± 2.1abB	47 ± 1.1abcA	45 ± 3.7aA	26 ± 2.3abB
	Transplanting	25.4 ± 0.99abA	16.6 ± 1.4bB	16.7 ± 0.75abB	46 ± 2.8abcA	32 ± 3.7bcB	29 ± 1.9abB
$NP_{100}+K_{50}+Si_{50}$	Wet direct seeding	24.2 ± 1.3abA	19.4 ± 1.5abAB	16.1 ± 1.2abB	36 ± 1.6cA	30 ± 2.6bcA	21 ± 3.8bB
	Transplanting	27.6 ± 0.86abA	22.1 ± 0.76abAB	18.7 ± 0.53abB	40 ± 0.71cA	27 ± 2.2bcB	25 ± 2.1abB
$NP_{100}+K_{25}+Si_{75}$	Wet direct seeding	24.6 ± 0.4abA	18.3 ± 1.6abAB	15.8 ± 0.4abB	40 ± 2.0cA	31 ± 1.5bcA	23 ± 1.6abB
	Transplanting	23.2 ± 1.4bA	17.6 ± 1.3abB	15.1 ± 1.8abB	38 ± 1.8cA	29 ± 2.4bcB	25 ± 1.2abB

Means followed by the same lowercase letters within a column and means followed by the same uppercase letters within a row are statistically similar based on Tukey's honest significant difference test at $P \leq 0.05$; data are means of three replications ± standard errors

The two-way interaction between fertilizer dose and soil water potential had a significant effect on water productivity (Table 1). There was no difference in water productivity of different fertilizer doses at 0 kPa; however, $NP_{100}+K_{100}$ had 27% and 42% higher water productivity than NP_{100} at –15 and –30 kPa, respectively (Table 5). There was a progressive increase in water productivity with decreasing soil water potential across fertilizer doses ranging from 77% (NP_{100}, $NP_{100}+K_{75}+Si_{25}$, $NP_{100}+K_{25}+Si_{75}$) to 88% ($NP_{100}+K_{100}$).

4 Discussion

Crop yield is the final output resulted from cumulative action of all metabolic reactions of plants including photosynthesis, respiration, and transpiration, which are adversely affected by water-deficit stress (Vaghar and Ehsanzadeh 2018). It reduces nutrient acquisition from soil, leaf water potential, tissue water content, and cell turgidity resulting in a decrease in E due to a partial stomatal closure that restricts CO_2 entry into the leaf for photosynthesis (Yin et al. 2010). Overproduction of ROS in plants is the consequence of water-deficit stress due to disequilibrium between electron excitation and utilization, which is detrimental to cell membranes, photosynthetic pigments, nucleic acids, and proteins in maintaining optimum cellular function (Lubitz et al. 2019). Reactive oxygen species are small molecule metabolites of oxygen that play dual function in plants: (i) as toxic compounds at high concentrations produced under environmental stress conditions causing oxidative cell injuries and (ii) as important signaling molecules for normal biologic processes regulating plant growth and development, and responses to biotic and abiotic stresses (Rejeb et al. 2014; Del Rio 2015; Huang et al. 2019). Chlorophyll degradation is one of the most significant indicators of plant susceptibility and it has been reported that chlorophyll integrity in the photosystems is damaged by drought stress resulting in an altered chlorophyll ultrastructure, inhibition of Rubisco activity with lower light-harvesting capacity, and lower photosynthetic efficiency (Yin et al. 2010; Zhang et al. 2015; Vaghar and Ehsanzadeh 2018). Drought also trims down photoassimilation and inhibits the translocation of photosynthates through stomatal and mesophyll limitation (Zivcak et al. 2014; Najafabadi and Ehsanzadeh 2017). The promotion of root growth by mineral nutrient application under drought conditions has been reported to facilitate the extraction of water and nutrients from deeper soil layers to improve plant tolerance (Hu and Schmidhalter 2005). Potassium and Si both have significant roles in alleviating the negative impact of drought stress in which plants adopt several intrinsic coping mechanisms to mitigate oxidative damages through strong antioxidant defense systems and osmotic adjustment to optimize cellular processes (Vassileva et al. 2009; Abid et al. 2018).

Water-deficit stress during the panicle initiation stage causes a reduction in LRWC, which inhibits carbohydrate metabolism and cell division of floral organ limiting spikelet fertility with lower filled grain percentage (Boyer and Westgate 2004; Najafabadi and Ehsanzadeh 2017). Spikelet sterility of rice under drought stress is a very common phenomenon, which might be due to decreased pollen viability and receptivity of the stigmatic surface impairing pollination and fertilization of embryo to produce grain (Gonzalez et al. 2019). Grain filling is also affected by impaired photosynthesis with limited available photosynthates, which is not enough for sufficient sink formation (Fu et al. 2011). Remobilization of photoassimilate from leaf to the grain and translocation of photosynthates from source to sink are impaired due to water-deficit stress negatively affecting grain filling with lower filled grain percentage (Rang et al. 2011). In the present study, yield components, such as tiller number plant^{-1}, panicle number plant^{-1}, and 1000-grain weight, were decreased with an increasing severity of water-deficit stress resulting in an increase in the total number of sterile spikelet panicle^{-1}, which might be due to an assimilate shortage and inhibition of photoassimilate translocation to the developing grain during the grain filling stage. It has been reported that limited supply of assimilate to the developing grain (source limitation) is one of the primary causes of grain yield reduction of rice under limited soil water availability (Zhang et al. 2015; Ullah et al. 2020). In the present study, grain yield and yield components of rice were severely impacted by water-deficit stress. Similarly, Yang et al. (2019) also observed that drought stress at the flowering stage of rice had a strong influence on physiological traits, yield components, and yield. Higher water productivity at lower soil moisture regime was observed across all fertilizer combinations in comparison to 0 kPa (Table 5). This is primarily due to lower total water input rather than higher grain yield.

Potassium has a substantial role on enzyme activation, protein synthesis, photosynthesis, stomatal regulation, and plant-water relations (Sharma et al. 2012; Zain et al. 2014). The present study revealed that most of the physiological parameters, such as leaf greenness, LRWC, P_n, E, and g_s, were highly influenced by K fertilization ($NP_{100}+K_{100}$) under reduced soil water potential (−30 kPa). Maximum leaf greenness and LRWC were observed in plants treated with $NP_{100}+K_{100}$ indicating that K enhances water and nutrient uptake of rice most likely by penetrating roots deeper in soil profile, thereby enhancing plant's ability to cope with drought stress (Römheld and Kirkby 2010). This might be due to the K-mediated promotion of root growth resulting in an increase in root surface area, which ultimately enhances uptake of water and mineral nutrients, thereby regulating stomatal functions by maintaining osmotic and turgor potential of cell under water-deficit stress (Zain and Ismail 2016). These enhanced water uptake and mineral acquisition confer greater chlorophyll integrity (stay green) in rice leaf as was also evident during the present study. It is well known that K is a key osmotic driver of plant cell under osmotic stress, while N and Mg are structural and functional components of chlorophyll (*a* and *b*) present in photosynthetic apparatus (chloroplast ultrastructure), consisted of grana and stroma. In addition, K and Mg both expedite well-structured organization of grana and stroma lamellae for chlorophyll integrity that improves efficiency of light absorption and Rubisco diffusion to facilitate carbon assimilation (Tränkner et al. 2018). Our results are also in line with Kanai et al. (2011) who observed that K fertilization significantly controlled E and also had a protective role in chlorophyll content of leaf under water-deficit stress. Similarly, a drastic reduction in g_s and E was observed under K fertilization ($NP_{100}+K_{100}$) indicating that K^+ significantly reduces E by decreasing osmotic potential of mesophyll cells (Li et al. 2017). Pumping K^+ from guard cell causes a reduction in turgor pressure inducing stomatal closure, which is the initial response of plants exposed to drought stress (Taiz and Zeiger 2010). Stomatal closure reduces transpirational water loss with a simultaneous decrease in stomatal CO_2 influx resulting in a decline in P_n (Chaves et al. 2009). Under water-deficit stress, K plays an essential role in activating the ATP synthase enzyme and regulating the stomatal aperture through balancing CO_2 entry and water vapor removal from intercellular spaces to optimize CO_2 fixation and the utilization of photoassimilate (Waraich et al. 2012; Wang et al. 2017; Li et al. 2018). The present findings are in close agreement with these researchers where plants fertilized with $NP_{100}+K_{100}$ exhibited better P_n over other fertilizer doses, especially at the lowest soil water potential of –30 kPa. Osmotic adjustment is the key adaptation of plants at cellular level to minimize the harmful effects of drought stress through maintaining leaf turgor for improved g_s and efficient intake of CO_2 (Farooq et al. 2009, 2010). Likewise, free proline is the most important compatible solute accumulating in plants exposed to drought stress, which allows plants to maintain a low osmotic potential with improved gas exchange and strong antioxidant systems nullifying the lethal effect of oxidative stress on cells against dehydration (Teixeira and Pereira 2007; Ellouzi et al. 2017). Higher accumulation of free proline in rice leaf in response to K fertilization at the lowest soil water potential (–30 kPa) was evident in the present study, which might be due to K-induced stimulation of biosynthesis of various osmolytes (e.g., free proline, soluble sugar, and glycine betaine) crucial for cellular function under water-deficit stress (Zain et al. 2014; Raza et al. 2014). An improvement in physiological and biochemical performance of rice is closely associated with K-mediated detoxification of ROS, rapid plant signaling systems, activation of antioxidant defense systems, and biosynthesis of osmolytes, which enable plants to cope with drought stress (Demidchik 2014; Jatav et al. 2014).

The highest spikelet number panicle^{-1} and filled grain percentage were observed in plants fertilized with K along with N and P ($NP_{100}+K_{100}$) indicating that K has a significant role in grain formation and in determining the final grain yield of rice (Table 4). An improved water and nutrient supply in plants raised from K fertilization might have resulted in better mobilization and translocation of nutrients towards panicle improving carbohydrate metabolism, which is critical for enhanced grain filling. It was observed that different combinations of K- and Si-fertilized rice plants had a steady increase in yield components, grain yield, harvest index, and water productivity compared with the control (NP_{100}), which were maximized at $NP_{100}+K_{100}$ in terms of grain yield and harvest index when soil water potential was the lowest (–30 kPa). Higher grain yield with K fertilization even at severe soil moisture availability could be attributed to more chlorophyll biosynthesis, improved stomata regulation, greater enzyme activity, and enhanced photosynthetic efficiency resulting in more carbohydrate accumulation and translocation for grain formation (Divito and Sadras 2014; Islam and Muttaleb 2016). It has been reported that K fertilization enhances N and P uptake leading to luxurious vegetative growth with delaying physiological maturity, which prolongs grain filling period resulting in more grain yield (Ye et al. 2019). Luxurious vegetative growth inevitably enhances leaf area, which is among the major determinants of biomass accumulation, especially in cereal crops. More assimilate formation and its partitioning to the developing grains helps in maximizing the percentage of filled grains and ultimately grain yield, which is facilitated by longer vegetative growth. Potassium regulates the partitioning of carbohydrates, which is crucial for improving grain filling through remobilization of assimilates from source to sink under suboptimal environments (Zahoor et al. 2017); otherwise, traffic load in phloem due to accumulated carbohydrates might decrease the rate of photosynthesis (Pan et al. 2017; Liang et al. 2017; Zhang et al. 2019). It can be concluded that exogenous soil application of K improves grain yield, harvest index, and water productivity of rice through physiological and biochemical amelioration under water-deficit stress.

Moreover, Si is considered a multi-talented element and it benefits rice under water-deficit stress because of its enhanced water retention capacity (Zargar et al. 2019), increased chlorophyll content (Yin et al. 2010), and improved leaf orientation for maximum light interception (Yoshida et al. 1969). Root growth is another vital indicator of plant tolerance against water-deficit stress, and it was observed that different combinations of Si with K fertilization on rice had better root proliferation over the control (NP_{100}). Similarly, SDM was maximized at $NP_{100}+K_{50}+Si_{50}$ indicating that shoot growth is influenced equally by both K and Si fertilization. This luxurious vegetative growth under combination of K and Si fertilization suggests that Si could have potential role on SDM and RDM accumulation through increased cell division and enlargement of apical meristem. The results of the present study are in close agreement with Ullah et al. (2019a) who observed that root system of rice was positively impacted by K fertilization at 120 kg ha^{-1}, while application of monosilicic acid at 300 kg ha^{-1} (60 kg ha^{-1} soluble Si) enhanced rice SDM with improved grain yield by 34–45% (Ullah et al. 2018b). This result might be due to Si-mediated improvement of root hydraulic conductance and root activity resulting in an efficient absorption of water and mineral, especially P, from soil to maintain a higher photosynthetic rate with more dry matter production under water-deficit stress (Chen et al. 2011; Luyckx et al. 2017; Schaller et al. 2021). Similarly, Schaller et al. (2020) reported enhanced soil hydraulic conductivity and improved water holding capacity of Si-fertilized soil, which are the major reasons of Si-mediated improvement in growth and productivity of most crops. The authors argued that it is the increased water retention in soil rather than Si accumulation in plants, which helps plants sustain under stressful conditions (Kuhla et al. 2021). The better growth and yield attributes at lower soil water potential of –30 kPa in Si-fed plants observed in the present study could be attributed to better soil moisture retention and a concomitant increased plant available water in soils compared with plants without Si supplementation. Moreover, Si can enhance root water uptake under drought stress through active accumulation of soluble sugars and amino acids (Zhu and Gong 2014). Silicon-mediated improvement in growth and yield of rice under water-deficit stress has been largely credited to an enhanced water use efficiency, which is an important determinant of crop productivity (Gomaa et al. 2021).

In the present study, a reduction in soil water potential caused a significant decrease in P_n across all fertilizer combinations, and plants fertilized with $NP_{100}+Si_{100}$ had 42% higher P_n over the control (NP_{100}) at severe drought stress

(− 30 kPa), which was also statistically at par with almost all other combination of fertilizers, indicating that both K and Si had a positive role in maintaining P_n under limiter water availability (Fig. 3A). This improved P_n of Si-fertilized plants ($NP_{100}+Si_{100}$) under water-deficit stress might be due to a Si-mediated increase of intercellular CO_2 concentration of leaf with moderate g_s ensuring an ample supply of CO_2 for optimum photosynthesis, which is a pre-requisite for grain formation (Li et al. 2020). This claim has been also supported by Chaves et al. (2009) and Kang et al. (2016) who mentioned that photosynthesis is the physiological basis of plant growth and development and Si improves drought tolerance by reducing oxidative damage of lipid and protein with a significant rise in P_n. Stomatal conductance and E are important parameters influencing plant-water relations (Farooq et al. 2009) and the formation of a silica-cuticle double layer on leaf epidermal tissue might be responsible for a reduction in leaf transpiration (Yoshida et al. 1969). A reduction of cuticular and stomatal transpiration along with an improved photosynthetic C fixation is one of the Si-mediated drought tolerance mechanisms in plants (Zhu and Gong 2014). Despite an overall reduction in growth and yield at lower soil moisture regimes, the beneficial effect of Si was evident on panicle number plant^{-1} and 1000-grain weight, which were significantly improved with $NP_{100}+Si_{100}$. Silicon-mediated water and mineral nutrient supply in plants might have resulted in an enhanced mobilization and translocation of nutrients towards panicle improving carbohydrate metabolism, a pre-requisite for grain filling (Schaller et al. 2021). This better performance in growth and yield of Si-fertilized rice at lower soil moisture regime could be credited to more accumulation of carbohydrate as also reported by Crooks and Prentice (2017) and Das et al. (2021a). Ullah et al. (2018a) also reported a significant improvement in panicle number plant^{-1}, 1000-grain weight, and grain yield of rice with Si application as monosilicic acid. Our results are also consistent with Cuong et al. (2017) who reported that Si application in combination with the recommended dose of NPK fertilizer enhanced grain yield and nutrient uptake of rice. High shoot Si content under Si supplementation in rice was observed in the present study, which might be resulted from the deposition of Si on cell wall strengthening cell membrane and altering membrane permeability (Wang et al. 2020). We observed no notable difference in yield and physiological performance of rice under the two studied cultivation methods. Therefore, Si fertilization holds promise irrespective of cultivation methods for enhancing grain yield of rice under water-deficit condition.

5 Conclusion

Growth, physiological traits, and yield of rice were adversely affected by reduced soil water potential level maintained through AWD irrigation. Exogenous soil application of different combinations of K and Si fertilizers were beneficial even at the lowest soil water potential (− 30 kPa). Growth, yield, and physiological response of rice were poor when no K or Si was applied in combination with N and P (NP_{100}). There was no considerable difference among different K and Si fertilizers combination for most of the evaluated parameters; nevertheless, reducing K share below 50% was not effective for some parameters, such as LRWC, spikelet number panicle^{-1}, and P_n. The two cultivation methods (wet direct seeding and transplanting) had largely similar response. Although the negative effect caused by water-deficit stress cannot be fully compensated by K and Si fertilization in rice, it could be minimized for better growth, yield components, and yield through physiological and biochemical regulation under limited water supply. Thus, combining K and Si with major nutrients (N and P) in a fertilizer management program where the share of K is at least 50% could be a promising approach to minimize the harmful impact of water-deficit stress in rice established through either wet direct seeding or transplanting method.

Funding This work was supported by the Bangabandhu Science and Technology Fellowship Trust, Bangladesh and the Asian Institute of Technology, Thailand.

Data Availability Not applicable.

Code Availability Not applicable.

Declarations

Conflict of Interest The authors declare no competing interests.

References

Abid M, Ali S, Qi LK, Zahoor R, Tian Z, Jiang D, Snider JL, Dai T (2018) Physiological and biochemical changes during drought and recovery periods at tillering and jointing stages in wheat (*Triticum aestivum* L.). Sci Rep 8:4615. https://doi.org/10.1038/s41598-018-21441-7

Ahmed M, Hassen FU, Khurshid Y (2011) Does silicon and irrigation have impact on drought tolerance mechanism of sorghum? Agric Water Manag 98:1808–1812. https://doi.org/10.1016/j.agwat.2011.07.003

Alam A, Hariyanto B, Ullah H, Salin KR, Datta A (2021) Effects of silicon on growth, yield and fruit quality of cantaloupe under drought stress. Silicon 13:3153–3162. https://doi.org/10.1007/s12633-020-00673-1

Bates LS, Waldren RP, Teare ID (1973) Rapid determination of free proline for water-stress studies. Plant Soil 39:205–207. https://doi.org/10.1007/BF00018060

Boyer JS, Westgate ME (2004) Grain yields with limited water. J Exp Bot 55:2385–2394. https://doi.org/10.1093/jxb/erh219

Chakma R, Saekong P, Biswas A, Ullah H, Datta A (2021) Growth, fruit yield, quality, and water productivity of grape tomato as affected by seed priming and soil application of silicon under drought stress. Agric Water Manag 256:107055. https://doi.org/10.1016/j.agwat.2021.107055

Carrijo DR, Lundy ME, Linquist BA (2017) Rice yields and water use under alternate wetting and drying irrigation: a meta-analysis. Field Crops Res 203:173–180. https://doi.org/10.1016/j.fcr.2016.12.002

Chareesri A, De Deyn GB, Sergeeva L, Polthanee A, Kuyper TW (2020) Increased arbuscular mycorrhizal fungal colonization reduces yield loss of rice (*Oryza sativa* L.) under drought. Mycorrhiza 30:315–328. https://doi.org/10.1007/s00572-020-00953-z

Cha-um S, Supaibulwatana K, Kirdmanee C (2006) Water relation, photosynthetic ability and growth of Thai jasmine rice (*Oryza sativa* L. ssp. *indica* cv. KDML 105) to salt stress by application of exogenous glycinebetaine and choline. J Agron Crop Sci 192:25–36. https://doi.org/10.1111/j.1439-037X.2006.00186.x

Cha-um S, Yooyongwech S, Supaibulwatana K (2010) Water deficit stress in the reproductive stage of four indica rice (*Oryza sativa* L.) genotypes. Pak J Bot 42:3387–3398

Chaves MM, Flexas J, Pinheiro C (2009) Photosynthesis under drought and salt stress: regulation mechanisms from whole plant to cell. Ann Bot 103:551–560. https://doi.org/10.1093/aob/mcn125

Chaves MM, Pereira JS, Maroco J, Rodrigues ML, Ricardo CPP, Osorio ML, Carvalho I, Faria T, Pinheiro C (2002) How plants cope with water stress in the field? Photosynthesis and growth. Ann Bot 89:907–916. https://doi.org/10.1093/aob/mcf105

Chen D, Wang S, Yin L, Deng X (2018) How does silicon mediate plant water uptake and loss under water deficiency? Front Plant Sci 9:281. https://doi.org/10.3389/fpls.2018.00281

Chen W, Yao X, Cai K, Chen J (2011) Silicon alleviates drought stress of rice plants by improving plant water status, photosynthesis and mineral nutrient absorption. Biol Trace Elem Res 142:67–76. https://doi.org/10.1007/s12011-010-8742-x

Crooks R, Prentice P (2017) Extensive investigation into field-based responses to a silica fertiliser. SILICON 9:301–304. https://doi.org/10.1007/s12633-015-9379-3

Cuong TX, Ullah H, Datta A, Hanh TC (2017) Effects of silicon-based fertilizer on growth, yield and nutrient uptake of rice in tropical zone of Vietnam. Rice Sci 24:283–290. https://doi.org/10.1016/j.rsci.2017.06.002

Das D, Basar NU, Ullah H, Salin KR, Datta A (2021a) Interactive effect of silicon and mycorrhizal inoculation on growth, yield and water productivity of rice under water-deficit stress. J Plant Nutr 44:2756–2769. https://doi.org/10.1080/01904167.2021.1927087

Das D, Basar NU, Ullah H, Attia A, Salin KR (2021b) Datta A (2021b) Growth, yield and water productivity of rice as influenced by seed priming under alternate wetting and drying irrigation. Arch Agron Soil Sci 10(1080/03650340):1912320

Dasgupta P, Das BS, Sen SK (2015) Soil water potential and recoverable water stress in drought tolerant and susceptible rice varieties. Agric Water Manag 152:110–118. https://doi.org/10.1016/j.agwat.2014.12.013

Datta A, Sindel BM, Kristiansen P, Jessop RS, Felton WL (2009) The effects of temperature and soil moisture on chickpea (*Cicer arietinum* L.) genotype sensitivity to isoxaflutole. J Agron Crop Sci 195:178–185. https://doi.org/10.1111/j.1439-037X.2009.00362.x

Del Rio LA (2015) ROS and RNS in plant physiology: an overview. J Exp Bot 66:2827–2837. https://doi.org/10.1093/jxb/erv099

Demidchik V (2014) Mechanism and physiological roles of K^+ efflux from root cells. J Plant Physiol 171:696–707. https://doi.org/10.1016/j.jplph.2014.01.015

Divito GA, Sadras VO (2014) How do phosphorus, potassium and sulphur affect plant growth and biological nitrogen fixation in crop and pasture legumes? A meta-analysis. Field Crops Res 156:161–171. https://doi.org/10.1016/j.fcr.2013.11.004

Ellouzi H, Sghayar S, Abdelly C (2017) H_2O_2 seed priming improves tolerance to salinity; drought and their combined effect more than mannitol in *Cakile maritima* when compared to *Eutrema salsugineum*. J Plant Physiol 210:38–50. https://doi.org/10.1016/j.jplph.2016.11.014

Etesami H (2018) Can interaction between silicon and plant growth promoting rhizobacteria benefit in alleviating abiotic and biotic stresses in crop plants? Agric Ecosyst Environ 253:98–112. https://doi.org/10.1016/j.agee.2017.11.007

Farooq M, Basra SMA, Wahid A, Ahmad N (2010) Changes in nutrient-homeostasis and reserves metabolism during rice seed priming: consequences for seedling, emergence and growth. Agric Sci China 9:191–198. https://doi.org/10.1016/S1671-2927(09)60083-3

Farooq M, Wahid A, Kobayashi N, Fujita D, Basra SMA (2009) Plant drought stress: effects, mechanisms and management. Agron Sustain Dev 29:185–212. https://doi.org/10.1051/agro:2008021

Fu J, Huang Z, Wang Z, Yang J, Zhang J (2011) Pre-anthesis non-structural carbohydrate reserve in the stem enhances the sink strength of inferior spikelets during grain filling of rice. Field Crops Res 123:170–182. https://doi.org/10.1016/j.fcr.2011.05.015

Gonzalez VH, Lee EA, Lukens LL, Swanton CJ (2019) The relationship between floret number and plant dry matter accumulation varies with early season stress in maize (*Zea mays* L.). Field Crops Res 238:129–138. https://doi.org/10.1016/j.fcr.2019.05.003

Gomaa MA, Kandil EE, El-Dein AAMZ, Abou-Donia MEM, Ali HM, Abdelsalam NR (2021) Increase maize productivity and water use efficiency through application of potassium silicate under water stress. Sci Rep 11:224. https://doi.org/10.1038/s41598-020-80656-9

Guntzer F, Keller C, Meunier JD (2012) Benefits of plant silicon for crops: a review. Agron Sustain Dev 32:201–213. https://doi.org/10.1007/s13593-011-0039-8

Hoseinian Y, Bahmanyar MA, Sadegh-zade F, Emadi M, Biparva P (2020) Effects of different sources of silicon and irrigation regime on rice yield components and silicon dynamics in the plant and soil. J Plant Nutr 43:2322–2335. https://doi.org/10.1080/01904167.2020.1771577

Hu Y, Schmidhalter U (2005) Drought and salinity: a comparison of their effects on mineral nutrition of plants. J Plant Nutr Soil Sci 168:541–549. https://doi.org/10.1002/jpln.200420516

Huang H, Ullah F, Zhou D-X, Yi M, Zhao Y (2019) Mechanisms of ROS regulation of plant development and stress responses. Front Plant Sci 10:800. https://doi.org/10.3389/fpls.2019.00800

Hussain F, Bronson KF, Yadvinder S, Singh B, Peng S (2000) Use of chlorophyll meter sufficiency indices for nitrogen management of irrigated rice in Asia. Agron J 92:875–879. https://doi.org/10.2134/agronj2000.925875x

Ilyas M, Nisar M, Khan N, Hazrat A, Khan AH, Hayat K, Fahad S, Khan A, Ullah A (2021) Drought tolerance strategies in plants: a mechanistic approach. Plant Growth Regul 40:926–994. https://doi.org/10.1007/s00344-020-10174-5

Islam A, Muttaleb A (2016) Effect of potassium fertilization on yield and potassium nutrition of Boro rice in a wetland ecosystem of Bangladesh. Arch Agron Soil Sci 62:1530–1540. https://doi.org/10.1080/03650340.2016.1157259

Jatav KS, Agarwal RM, Tomar NS, Tyagi SR (2014) Nitrogen metabolism, growth and yield responses of wheat (*Triticum* *aestivum* L.) to restricted water supply and varying potassium treatments. J Indian Bot Soc 93:177–189

Kanai S, Moghaieb RE, El Shemy H, Panigrahi R, Mohapatra PK, Ito J, Nguyen NT, Saneoka H, Fujita K (2011) Potassium deficiency affects water status and photosynthetic rate of the vegetative sink in green house tomato prior to its effects on source activity. Plant Sci 180:368–374. https://doi.org/10.1016/j.plantsci.2010.10.011

Kang J, Zhao W, Zhu X (2016) Silicon improves photosynthesis and strengthens enzyme activities in the C_3 succulent xerophyte *Zygophyllum xanthoxylum* under drought stress. J Plant Physiol 199:76–86. https://doi.org/10.1016/j.jplph.2016.05.009

Kuhla J, Pausch J, Schaller J (2021) Effect on soil water availability, rather than silicon uptake by plants, explains the beneficial effect of silicon on rice during drought. Plant Cell Environ 44:3336–3346. https://doi.org/10.1111/pce.14155

Li X, Zhang X, Liu G, Tang Y, Zhou C, Zhang L, Lv J (2020) The spike plays important roles in the drought tolerance as compared to the flag leaf through the phenylpropanoid pathway in wheat. Plant Physiol Biochem 152:100–111. https://doi.org/10.1016/j.plaphy.2020.05.002

Li Y, Li H, Li Y, Zhang S (2017) Improving water-use efficiency by decreasing stomatal conductance and transpiration rate to maintain higher ear photosynthetic rate in drought-resistant wheat. Crop J 5:231–239. https://doi.org/10.1016/j.cj.2017.01.001

Li Z, Li Z, Letuma P, Zhao H, Zhang Z, Lin W, Chen H, Lin W (2018) A positive response of rice rhizosphere to alternate moderate wetting and drying irrigation at grain filling stage. Agric Water Manag 207:26–36. https://doi.org/10.1016/j.agwat.2018.05.022

Liang W, Zhang Z, Wen X, Liao Y, Liu Y (2017) Effect of non-structural carbohydrate accumulation in the stem pre-anthesis on grain filling of wheat inferior grain. Field Crops Res 211:66–76. https://doi.org/10.1016/j.fcr.2017.06.016

Liu P, Yin L, Deng X, Wang S, Tanaka K, Zhang S (2014) Aquaporin-mediated increase in root hydraulic conductance is involved in silicon-induced improved root water uptake under osmotic stress in *Sorghum bicolor* L. J Exp Bot 65:4747–4756. https://doi.org/10.1093/jxb/eru220

Lubitz W, Chrysina M, Cox N (2019) Water oxidation in photosystem II. Photosynth Res 142:105–125. https://doi.org/10.1007/s11120-019-00648-3

Luyckx M, Hausman JF, Lutts S, Guerriero G (2017) Silicon and plants: current knowledge and technological perspectives. Front Plant Sci 8:411. https://doi.org/10.3389/fpls.2017.00411

Maneepitak S, Ullah H, Datta A, Shrestha RP, Shrestha S, Kachenchart B (2019a) Effects of water and rice straw management practices on water savings and greenhouse gas emissions from a double-rice paddy field in the Central Plain of Thailand. Eur J Agron 107:18–29. https://doi.org/10.1016/j.eja.2019.04.002

Maneepitak S, Ullah H, Paothong K, Kachenchart B, Datta A, Shrestha RP (2019b) Effect of water and rice straw management practices on yield and water productivity of irrigated lowland rice in the Central Plain of Thailand. Agric Water Manag 211:89–97. https://doi.org/10.1016/j.agwat.2018.09.041

Miao BH, Han XG, Zhang WH (2010) The ameliorative effect of silicon on soybean seedlings grown in potassium-deficient medium. Ann Bot 105:967–973. https://doi.org/10.1093/aob/mcq063

Ming DF, Pei ZF, Naeem MS, Gong HJ, Zhou WJ (2012) Silicon alleviates PEG-induced water-deficit stress in upland rice seedlings by enhancing osmotic adjustment. J Agron Crop Sci 198:14–26. https://doi.org/10.1111/j.1439-037X.2011.00486.x

Najafabadi MY, Ehsanzadeh PP (2017) Salicylic acid effects on osmoregulation and seed yield in drought-stressed sesame. Agron J 109:1414–1422. https://doi.org/10.2134/agronj2016.11.0655

Pan Y, Lu Z, Lu J, Li X, Cong R, Ren T (2017) Effects of low sink demand on leaf photosynthesis under potassium deficiency. Plant Physiol Biochem 113:110–121. https://doi.org/10.1016/j.plaphy.2017.01.027

Panda D, Mishra SS, Behera PK (2021) Drought tolerance in rice: focus on recent mechanisms and approaches. Rice Sci 28:119–132. https://doi.org/10.1016/j.rsci.2021.01.002

Phukunkamkaew S, Tisarum R, Pipatsitee P, Samphumphuang T, Maksup S, Cha-um S (2021) Morpho-physiological response of indica rice (*Oryza sativa* sub. *indica*) to aluminium toxicity at seedling stage. Environ Sci Pollut Res 28:29321–29331. https://doi.org/10.1007/s11356-021-12804-1

Rang ZW, Jagadish SVK, Zhou QM, Craufurd PQ, Heuer S (2011) Effect of high temperature and water stress on pollen germination and spikelet fertility in rice. Environ Exp Bot 70:58–65. https://doi.org/10.1016/j.envexpbot.2010.08.009

Raza MAS, Saleem MF, Shah GM, Khan IH, Raza A (2014) Exogenous application of glycinebetaine and potassium for improving water relations and grain yield of wheat under drought. J Soil Sci Plant Nutr 14:348–364. https://doi.org/10.4067/S0718-95162014005000028

Rejeb KB, Abdelly C, Savouré A (2014) How reactive oxygen species and proline face stress together. Plant Physiol Biochem 80:278–284. https://doi.org/10.1016/j.plaphy.2014.04.007

Rizwan M, Ali S, Ibrahim M, Farid M, Adrees M, Bharwana SA, Rehman ZU, Qayyum MF, Abbas F (2015) Mechanisms of silicon-mediated alleviation of drought and salt stress in plants: a review. Environ Sci Pollut Res 22:15416–15431. https://doi.org/10.1007/s11356-015-5305-x

Ruensuk N, Rossopa B, Channu C, Paothong K, Prayoonsuk N, Rakchum P, Malumpong C (2021) Improving water use efficiency and productivity in rice crops by applying alternate wetting and drying with pregerminated broadcasting in farmers' fields. Agric Nat Resour 55:119–130. https://doi.org/10.34044/j.anres.2021.55.1.16

Römheld V, Kirkby EA (2010) Research on potassium in agriculture: needs and prospects. Plant Soil 335:155–180. https://doi.org/10.1007/s11104-010-0520-1

Ruiz-Sánchez M, Armada E, Muñoz Y, de Salamone IEG, Aroca R, Ruíz-Lozano JM, Azcón R (2011) *Azospirillum* and arbuscular mycorrhizal colonization enhance rice growth and physiological traits under well-watered and drought conditions. J Plant Physiol 168:1031–1037. https://doi.org/10.1016/j.jplph.2010.12.019

Santiago-Arenas R, Dhakal S, Ullah H, Agrawal A, Datta A (2021) Seeding, nitrogen and irrigation management optimize rice water and nitrogen use efficiency. Nutr Cycl Agroecosyst 120:325–341. https://doi.org/10.1007/s10705-021-10153-6

Santiago-Arenas R, Fanshuri BA, Hadi SN, Ullah H, Datta A (2020) Nitrogen fertiliser and establishment method affect growth, yield and nitrogen use efficiency of rice under alternate wetting and drying irrigation. Ann Appl Biol 176:314–327. https://doi.org/10.1111/aab.12585

Santiago-Arenas R, Hadi SN, Fanshuri BA, Ullah H, Datta A (2019) Effect of nitrogen fertiliser and cultivation method on root systems of rice subjected to alternate wetting and drying irrigation. Ann Appl Biol 175:388–399. https://doi.org/10.1111/aab.12540

Sardans J, Peñuelas J (2021) Potassium control of plant functions: ecological and agricultural implications. Plants 10:419. https://doi.org/10.3390/plants10020419

Sathe AP, Kumar A, Mandlik R, Raturi G, Yadav H, Kumar N, Shivaraj SM, Jaswal R, Kapoor R, Gupta SK, Sharma TR, Sonah H (2021) Role of silicon in elevating resistance against sheath blight and blast diseases in rice (*Oryza sativa* L.). Plant Physiol Biochem 166:128–139. https://doi.org/10.1016/j.plaphy.2021.05.045

Schaller J, Scherwietes E, Gerber L, Vaidya S, Kaczorek D, Pausch J, Barkusky D, Sommer M, Hoffmann M (2021) Silica fertilization improved wheat performance and increased phosphorus concentrations during drought at the field scale. Sci Rep 11:20852. https://doi.org/10.1038/s41598-021-00464-7

Schaller J, Cramer A, Carminati A, Zarebanadkouki M (2020) Biogenic amorphous silica as main driver for plant available water in soils. Sci Rep 10:2424. https://doi.org/10.1038/s41598-020-59437-x

Sharma P, Jha AB, Dubey RS, Pessarkali M (2012) Reactive oxygen species, oxidative damage, and antioxidative defense mechanism in plants under stressful conditions. J Bot 2012:217037. https://doi.org/10.1155/2012/217037

Sirisuntornlak N, Ghafoori S, Datta A, Arirob W (2019) Seed priming and soil incorporation with silicon influence growth and yield of maize under water-deficit stress. Arch Agron Soil Sci 65:197–207. https://doi.org/10.1080/03650340.2018.1492713

Taiz L, Zeiger E (2010) Plant Physiology, 5th edn. Sinauer Associates Inc., Publishers, Sunderland, Massachusetts, USA

Tarantino TB, Barbosa IS, Lima DDC, Pereira MDG, Teixeira LSG, Korn MGA (2017) Microwave-assisted digestion using diluted nitric acid for multi-element determination in rice by ICP OES and ICP-MS. Food Anal Method 10:1007–1015. https://doi.org/10.1007/s12161-016-0658-4

Teixeira J, Pereira S (2007) High salinity and drought act on an organ-dependent manner on potato glutamine synthetase expression and accumulation. Environ Exp Bot 60:121–126. https://doi.org/10.1016/j.envexpbot.2006.09.003

Tränkner M, Tavakol E, Jákli B (2018) Functioning of potassium and magnesium in photosynthesis, photosynthate translocation and photoprotection. Physiol Plant 163:414–431. https://doi.org/10.1111/ppl.12747

Tripathi DK, Singh VP, Prasad SM, Chauhan DK, Dubey NK, Rai AK (2015) Silicon-mediated alleviation of Cr(VI) toxicity in wheat seedlings as evidenced by chlorophyll florescence, laser induced breakdown spectroscopy and anatomical changes. Ecotoxicol Environ Safe 113:133–144. https://doi.org/10.1016/j.ecoenv.2014.09.029

Ullah H, Giri S, Attia A, Datta A (2020) Effects of establishment method and water management on yield and water productivity of tropical lowland rice. Exp Agric 56:331–346. https://doi.org/10.1017/S0014479719000395

Ullah H, Rahimi AZ, Datta A (2019a) Growth and yield of lowland rice as influenced by potassium application and cultivation method under alternate wetting and drying water regime. J Plant Nutr 42:1529–1542. https://doi.org/10.1080/01904167.2019.1628973

Ullah H, Santiago-Arenas R, Ferdous Z, Attia A, Datta A (2019b) Improving water use efficiency, nitrogen use efficiency, and radiation use efficiency in field crops under drought stress: a review. Adv Agron 156:109–157. https://doi.org/10.1016/bs.agron.2019.02.002

Ullah H, Mohammadi A, Datta A (2018a) Growth, yield and water productivity of selected lowland Thai rice varieties under different cultivation methods and alternate wetting and drying irrigation. Ann Appl Biol 173:302–312. https://doi.org/10.1111/aab.12463

Ullah H, Luc PD, Gautam A, Datta A (2018b) Growth, yield and silicon uptake of rice (*Oryza sativa*) as influenced by dose and timing of silicon application under water-deficit stress. Arch Agron Soil Sci 64:318–330. https://doi.org/10.1080/03650340.2017.1350782

Ullah H, Datta A, Shrestha S, Ud Din S (2017) The effects of cultivation methods and water regimes on root systems of drought-tolerant (RD6) and drought-sensitive (RD10) rice varieties of Thailand. Arch Agron Soil Sci 63:1198–1209. https://doi.org/10.1080/03650340.2016.1266077

Vaghar M, Ehsanzadeh P (2018) Comparative photosynthetic attributes of emmer and modern wheats in response to water and nitrogen supply. Photosynthetica 56:1224–1234. https://doi.org/10.1007/s11099-018-0825-5

Vandegeer RK, Zhao C, Cibils-Stewart X, Wuhrer R, Hall CR, Hartley SE, Tissue DT, Johnson SN (2021) Silicon deposition on guard cells increases stomatal sensitivity as mediated by K^+ efflux and consequently reduces stomatal conductance. Physiol Plant 171:358–370. https://doi.org/10.1111/ppl.13202

Vassileva V, Simova-Stoilova L, Demirevska K, Feller U (2009) Variety-specific response of wheat (*Triticum aestivum* L.) leaf mitochondria to drought stress. Plant Res 122:445–454. https://doi.org/10.1007/s10265-009-0225-9

Wang C, Yamamoto H, Narumiya F, Munekage YN, Finazzi G, Szabo I, Shikanai T (2017) Fine-tuned regulation of the K^+/H^+ antiporter KEA3 is required to optimize photosynthesis during induction. Plant J 89:540–553. https://doi.org/10.1111/tpj.13405

Wang L, Ashraf U, Chang C, Abrar M, Cheng X (2020) Effects of silicon and phosphatic fertilization on rice yield and soil fertility. Soil Sci Plant Nutr 20:557–565. https://doi.org/10.1007/s42729-019-00145-5

Waraich EA, Ahmad R, Halim A, Aziz T (2012) Alleviation of temperature stress by nutrient management in crop plants: a review. J Soil Sci Plant Nutr 12:221–244. https://doi.org/10.4067/S0718-95162012000200003

Yan GC, Nikolic M, Ye MJ, Xiao ZX, Liang YC (2018) Silicon acquisition and accumulation in plant and its significance for agriculture. J Integr Agric 17:2138–2150. https://doi.org/10.1016/S2095-3119(18)62037-4

Yang X, Wang B, Chen L, Li P, Cao C (2019) The different influences of drought stress at the flowering stage on rice physiological traits, grain yield and quality. Sci Rep 9:3742. https://doi.org/10.1038/s41598-019-40161-0

Ye T, Li Y, Zhang J, Hou W, Zhou W, Lu J, Xing Y, Li X (2019) Nitrogen, phosphorous and potassium fertilization affects the flowering time of rice (*Oryza sativa* L.). Glob Ecol Conserv 20:e00753. https://doi.org/10.1016/j.gecco.2019.e00753

Yin Y, Li S, Liao W, Lu Q, Wen X, Lu C (2010) Photosystem II photochemistry, photoinhibition and the xanthophyll cycle in heat stressed rice leaves. J Plant Physiol 167:959–966. https://doi.org/10.1016/j.jplph.2009.12.021

Yoshida S, Navasero SA, Ramirez EA (1969) Effects of silica and nitrogen supply on some leaf characters of the rice plant. Plant Soil 31:48–56. https://doi.org/10.1007/BF01373025

Zahoor R, Dong H, Abid M, Zhao W, Wang Y, Zhou Z (2017) Potassium fertilizer improves drought stress alleviation potential in cotton by enhancing photosynthesis and carbohydrate metabolism. Environ Exp Bot 137:73–83. https://doi.org/10.1016/j.envexpbot.2017.02.002

Zain NAM, Ismail MR, Puteh A, Mahmood M, Islam MR (2014) Drought tolerance and ion accumulation of rice following application of additional potassium fertilizer. Commun Soil Sci Plant Anal 45:2502–2514. https://doi.org/10.1080/00103624.2014.932374

Zain NAM, Ismail MR (2016) Effects of potassium rates and types on growth, leaf gas exchange and biochemical changes in rice (*Oryza sativa*) planted under cyclic water stress. Agric Water Manag 164:83–90. https://doi.org/10.1016/j.agwat.2015.09.022

Zargar SM, Mahajan R, Bhat JA, Nazir M, Deshmukh R (2019) Role of silicon in plant stress tolerance: opportunities to achieve a sustainable cropping system. 3 Biotech 9:73. https://doi.org/10.1007/s13205-019-1613-z

Zhang J, Lin Y, Zhu L, Yu S, Kundu SK, Jin Q (2015) Effects of 1-methylcyclopropene on function of flag leaf and development of superior and inferior spikelets in rice cultivars differing in panicle types. Field Crops Res 177:64–74. https://doi.org/10.1016/j.fcr.2015.03.003

Zhang J, Lu Z, Pan Y, Ren T, Cong R, Lu J, Li X (2019) Potassium deficiency aggravates yield loss in rice by restricting the translocation of non-structural carbohydrates under *Sarocladium oryzae* infection condition. Physiol Plant 167:352–364. https://doi.org/10.1111/ppl.12896

Zhu Y, Gong H (2014) Beneficial effects of silicon on salt and drought tolerance in plant. Agron Sustain Dev 34:455–472. https://doi.org/10.1007/s13593-013-0194-1

Zivcak M, Kalaji HM, Shao HB, Olsovska K, Brestic M (2014) Photosynthetic proton and electron transport in wheat leaves under prolonged moderate drought stress. J Photochem Photobiol B Biol 137:107–115. https://doi.org/10.1007/s11120-013-9885-3