Ecological Processes

RESEARCH

Open Access

Application of jasmonic acid boosts accelerative effects of silicon addition on rice defense against invasion of apple snails (Ampullariidae)

Wei Li[1], Hua Yu[1], Wen-Hong Dai[1], Yao-Bin Song[1*] and Ming Dong[1,2*]

Abstract

Background The invasion of apple snails (*Pomacea* spp.) has a serious negative impact on the yield of aquatic crops, including rice, which is a vital food source for more than half of the global population and irreplaceable in maintaining the global food security of human society. So far, it has been unclear whether jasmonic acid (JA) application can enhance the effects of silicon addition on the defense of crops like rice against the invasion of apple snails. Rice plants were grown in a greenhouse and subjected to treatments involving the addition of silicon (sodium silicate) and JA (methyl jasmonate). Then, in an indoor experiment, apple snails were fed with the leaves of the rice plants that had undergone the treatments. Growth and growth-related traits for rice plants and apple snails and defense-related mechanic characters for rice plants were measured.

Results Silicon addition significantly increased rice growth, leading to improved biomass and relative chlorophyll content. JA application did not affect the growth of rice plants but increased their foliar nitrogen and carbon content disproportionally, leading to a reduced C/N ratio. JA application increased the levels of tannins, total phenolics, and flavonoids in rice leaves. Silicon addition increased the tannin, total phenolic, and flavonoid content in rice leaves, particularly when supplied with JA. Silicon addition could also enhance the force of fracture in rice leaves. In addition, the foliar sulfur and silicon content increased with the addition of silicon, and the combination of silicon addition and JA application resulted in the highest foliar silicon content. Both silicon addition and JA application significantly decreased weight gain, leaf consumption, relative growth rate, and cellulase activity of apple snails, indicating a strong interaction.

Conclusions Overall, these findings indicated that both silicon addition and JA application enhanced the defense of rice against apple snails and impeded the growth of these snails. JA application amplified the impact of silicon addition on rice's defense mechanism. This study provides new insights into controlling biological invasions and their impact on crop yield.

Keywords Apple snail, Invasive animal, Jasmonic acid, Plant defense, Plant–herbivore interaction, Silicon

*Correspondence:
Yao-Bin Song
ybsong@hznu.edu.cn
Ming Dong
dongming@hznu.edu.cn
Full list of author information is available at the end of the article

Background

Rice is one of the most important food crops in the world, providing sustenance for half of the global population (Li et al. 2014). The presence of insect pests poses a significant risk to the productivity of agricultural crops (Oerke 2006), thereby further endangering global food security (Bradshaw et al. 2016). The alien apple snail (*Pomacea* spp.) is a freshwater and amphibious snail native to South America (Hayes et al. 2015). It has been widely spread throughout Asia due to multiple introduction events, as well as its remarkable reproductive and dispersal capabilities (Byers et al. 2013; Wang et al. 2023). As one of the world's most invasive aquatic species, apple snail has been found to cause a decrease in macrophyte biomass, water quality, and algal production in the invasive range (Carlsson et al. 2004; Carlsson and Lacoursière 2005; Fang et al. 2010), and more seriously, it has adversely impacted rice yield (Horgan et al. 2014; Constantine et al. 2023). The apple snail enjoys consuming rice seedlings as its primary food source. In rice fields with seedlings, the density of apple snails can reach up to 55 per square meter (Zhou et al. 2015). In the rice field ecosystem, the apple snails are voracious eaters, capable of feeding continuously for 24 h (Pan et al. 2014). Furthermore, apple snails often feed on the base of rice plants, leading to the destruction of the entire crop (Schnorbach 1995). The production of rice in agriculture is significantly decreased by the apple snails.

Jasmonic acid (JA) is an indispensable hormone in plants' defense against herbivores (Bruinsma et al. 2007; Chen et al. 2011). Plants evolve in different ways to defend against herbivores (Zhang et al. 2010). The JA signaling pathway in plants is a crucial defense mechanism activated by wounds or chewing from herbivores (Farmer and Ryan 2017). A field experiment showed that the common evening primrose (*Oenothera biennis*) increased leaf JA levels after an invasion by Japanese beetle (*Popillia japonica*) (McArt et al. 2013). Plants treated with exogenous JA exhibit the same defensive response when damaged by herbivores, resulting in an increase in various defensive substances (Wasternack and Parthier 1997). Feeding herbivores with leaves treated with JA led to reduced leaf consumption, decreased relative growth rates, and lowered herbivore oviposition-site selection (van Dam et al. 2000; Bruinsma et al. 2007). However, whether JA can serve as a potential natural agent to resist invasive herbivores such as apple snails remains unclear.

Wetland ecosystems significantly influence the global biogeochemical silicon cycle (Struyf and Conley 2009). Wetland plant tissues often contain more than 1% dry weight of silicon, which may greatly impact plant nutrition and nutrient cycling (Schoelynck et al. 2010; Schaller et al. 2016). Silicon is abundant in the Earth's crust and is believed to enhance plant growth and resistance to biotic and abiotic stresses, especially in grasses (Sommer et al. 2006; Reynolds et al. 2016; Song et al. 2020). It has been widely reported that silicon plays a significant role in plant defense against herbivores. For instance, Johnson et al. (2020) reported a negative relationship between the absorption of silicon in soybean leaves and the relative growth rate (RGR) of its herbivores. Acevedo et al. (2021) found that the deposition of silicon in non-glandular trichomes can enhance maize plant defense against chewing herbivores. Islam et al. (2022a) initially discovered that silicon can aid plants, including those with low silicon accumulation, in defending against pests using biocontrol methods. Usually, silicon increases plant physical defense, making it harder digestible and abraded (Massey and Hartley 2009; Hartley et al. 2015). Silicon is also capable of activating the plant metabolic defense pathways as well as the defense-related genes (Shi et al. 2010; Ryalls et al. 2023). Silicon also stimulates the release of volatile organic compounds (VOCs), which can attract herbivore predators (Kvedaras et al. 2010). JA can enhance silicon assimilation in plants, and silicon can activate the JA signaling pathway, improving plant defense against insects (Ye et al. 2013). However, whether the interaction between the two can protect plants from invasive herbivores is still unknown.

A greenhouse experiment was conducted to investigate the roles of silicon and JA, as well as their interactions, in plant defense against invasive herbivores. Individuals of apple snails were fed with leaves of different treated plants in the laboratory. The plant defense performance and growth of snails were measured. We aimed to examine the potential interaction between silicon and JA in enhancing plant defense mechanisms. Specifically, we propose the following scientific questions: (1) Can silicon help reduce the damage caused by apple snails on rice crops? (2) Can JA reduce stress in apple snails feeding on rice and interact with silicon?

Materials and methods

Experimental materials

We obtained rice seeds (Jiahe 212A × Zhonghui 7245) from the Chinese Academy of Agricultural Sciences for our rice cultivation experiments. There are two species of apple snail (*Pomacea canaliculata* and *Pomacea maculata*) that are extensively invading in China (Qin et al. 2023). However, we did not identify the species of the apple snail collected from the river. Apple snails of similar sizes were collected from a rural river in Hangzhou, China (30°32′N, 120°1′E). To acclimatize, we fed the apple snails with lettuce (*Lactuca sativa*) in the laboratory for two weeks. We measured the snail feeding metrics including weight gain, leaf consumption, RGR and

cellulase activity of apple snails. Plant defense primarily encompasses physical defense and secondary metabolic defense. Physical defense involves the relevant physical structures and mechanical properties of plants. Secondary metabolite defense entails the release of diverse secondary metabolites. Consequently, the leaf defense characteristics of rice in this experiment encompassed the force of fracture as well as secondary metabolic defenses, such as the concentrations of tannin, flavonoid, and total phenolic.

Experimental design

Plant growth

The rice seeds from the Chinese Academy of Agricultural Sciences were sterilized with alcohol and then placed in a well-lit incubator at a temperature of up to 25 °C. Once the seeds had taken root in the tenth inner layer, we transplanted them into 2-L pots containing field mud. We conducted the experiment with four treatments (Si×JA, Si, JA and Control), each having 12 replicates, resulting in a total of 48 rice basins. All the pots are situated in a greenhouse at the Xiasha Campus (30°32′N, 120°40′E) of Hangzhou Normal University, Hangzhou, Zhejiang, China. Two weeks later, we added silicon to the plants, half of the pots were filled with a solution containing 1.5 mM Na_2SiO_3 and the other half with a solution containing 3 mM NaCl to ensure that the osmolarity was consistent between treatments (Johnson et al. 2021). The solution was added every two weeks for the following three months. At the end of the experiment, half of the plants with Si addition or NaCl addition were further supplied with methyl jasmonate (MeJA). The MeJA can transform into JA within plants (Browse 2009). The JA treatment involved the addition of 1 mM MeJA, which had been pre-treated with 0.1% Tween 20 (Ye et al. 2013). This solution was then applied to the plant surface above the plant roots. The other half of the plants with Si addition or NaCl addition received a solution containing only Tween 20 (Fig. 1). Three days later, we harvested all the rice plants and brought them back to the laboratory. Then, half of the plants from each treatment group were just used to conduct a snail-feeding experiment. The remaining materials were utilized to assess biomass and other traits.

Feeding experiment

The apple snails were starved for 48 h before the feeding experiment. Then, we weighed them as the initial body mass. A total of 24 snails with similar physiological conditions were used for experiments, with each corresponding to one rice plant used for feeding trials. Each snail was placed in a 1.5 L plastic container along with the corresponding rice leaves and observed for a week afterward. The rice leaves consumed by snails were supplemented at

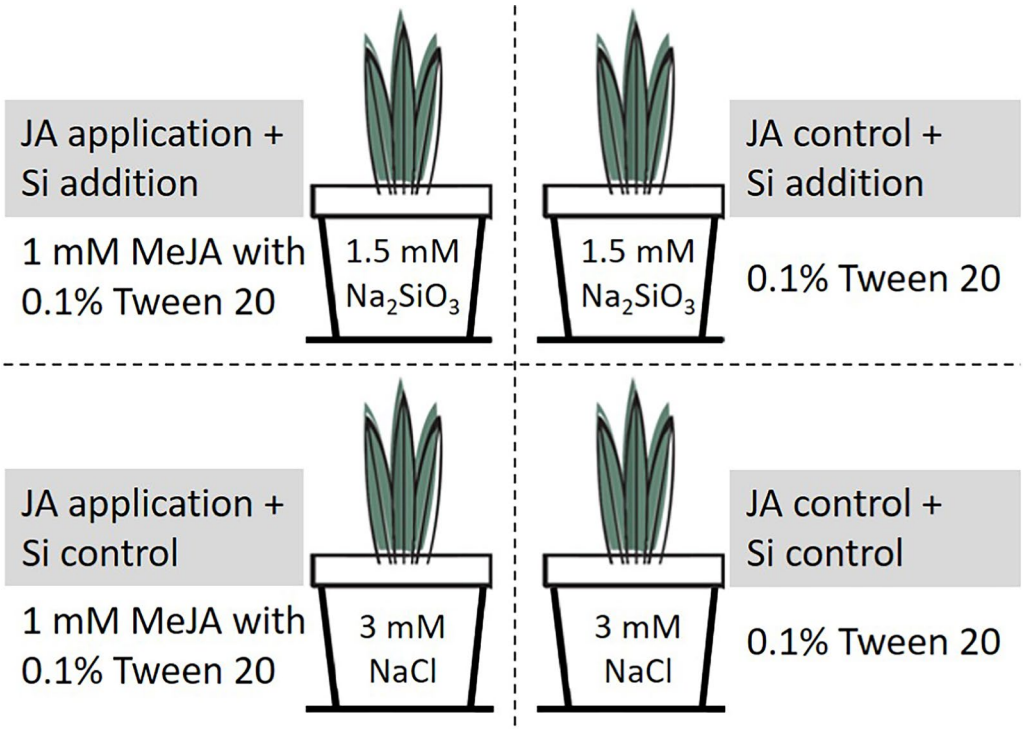

Fig. 1 Schematic diagram of rice treatments in the greenhouse experiment

Table 1 Two-way ANOVA analysis for snail feeding metrics, rice foliar elements contents, rice plant growth traits and rice leaf defense characteristics in response to Si addition and jasmonic acid (JA) application

Response variable	*df*	Si		Jasmonic acid (JA)		Si × JA	
		F	*p*	*F*	*p*	*F*	*p*
Rice plant growth traits							
Shoot mass	20	58.167	**<0.001**	0.285	0.599	0.752	0.396
Root mass	20	66.947	**<0.001**	2.136	0.159	1.912	0.182
Total mass	20	67.976	**<0.001**	0.717	0.407	1.155	0.295
Relative chlorophyll content	20	28.116	**<0.001**	1.594	0.221	2.760	0.112
C/N ratio	20	2.110	0.162	15.301	**0.001**	3.850	0.064
Rice foliar element contents							
Foliar nitrogen content	20	3.551	0.074	31.961	**<0.001**	4.815	**0.040**
Foliar carbon content	20	2.455	0.133	33.298	**<0.001**	2.250	0.149
Foliar sulfur content	20	91.610	**<0.001**	0.411	0.529	0.044	0.836
Foliar silicon content	20	142.756	**<0.001**	1.440	0.244	15.016	**0.001**
Rice leaf defense characteristics							
Total phenolic content	20	362.118	**<0.001**	280.887	**<0.001**	47.888	**<0.001**
Force of fracture	20	94.283	**<0.001**	0.618	0.441	0.007	0.933
Tannin content	20	19.101	**<0.001**	40.622	**<0.001**	1.413	0.248
Flavonoid content	20	5.784	**0.026**	13.382	**0.002**	1.789	0.196
Snail feeding metrics	20						
Relative growth rate	20	20.172	**<0.001**	19.371	**<0.001**	5.179	**0.034**
Cellulase activity	20	91.537	**<0.001**	103.458	**<0.001**	12.840	**0.002**
Weight gain	20	13.755	**0.001**	0.191	0.666	7.561	**0.012**
Leaf consumption	20	9.586	**0.006**	3.744	0.067	6.351	**0.020**

The *p*-values that are less than 0.05 are presented in bold

any time every day, and the consumption was recorded. At the end of the week, we measured the final snail mass and the amount of rice leaves they consumed.

Measurements

Plant sample analysis

We measured the relative chlorophyll content of the rice plants selected for the index determination. Before harvesting the rice plants, the relative chlorophyll content (SPAD) was determined by a portable chlorophyll fluorometer (SPAD-502Plus, Konica Minolta, Japan). Three well-growing leaves from each plant were chosen to determine the relative chlorophyll content. The average value represented the relative chlorophyll content of the rice plant. The Instron 3343, an electronic universal material testing machine, was used to measure the force of fracture of rice leaves. For the determination of the force of fracture, three leaves of every plant with similar growth status were selected. The blade width, thickness, and length were measured, along with the force required to tear them from the ends. This data was then used to calculate the elastic modulus as measured by Johnson et al. (2019). The force of fracture of the rice plant was determined by averaging the values of the three leaves. The harvested rice plants were then washed and dried. Rice was divided into two parts, root and shoot. Next, all the samples were dried in an oven at 60 °C until they reached a constant weight. The shoot mass and root mass of the rice were then weighed using an electronic balance. The samples were ground into a powder and then passed through a 40-mesh sieve. Total phenol content was determined using the method from Cheng et al. (2013). The flavonoid content was then determined using the method of Lin et al. (2014). The tannin content was then determined using the method from Makkar (2003). The silicon content was measured again using the method from Kraska and Breitenbeck (2010). Elemental Analyzer (vario PYRO cube; Elemental, Germany) was utilized to determine leaf carbon, nitrogen, and sulfur content (Hu et al. 2022). The foliar C/N ratio was calculated by the ratio of leaf C to leaf N. Six plants per treatment were determined in triplicates.

Snail feeding metrics

We anatomized the snail and separated the stomach and intestines from other tissue. Then, we used the DNS (3,5-dinitrosalicylic acid) method, as Kim et al. (2014a) described, to measure the cellulase activity of stomach and intestine tissues. The relative growth rate (RGR) of apple

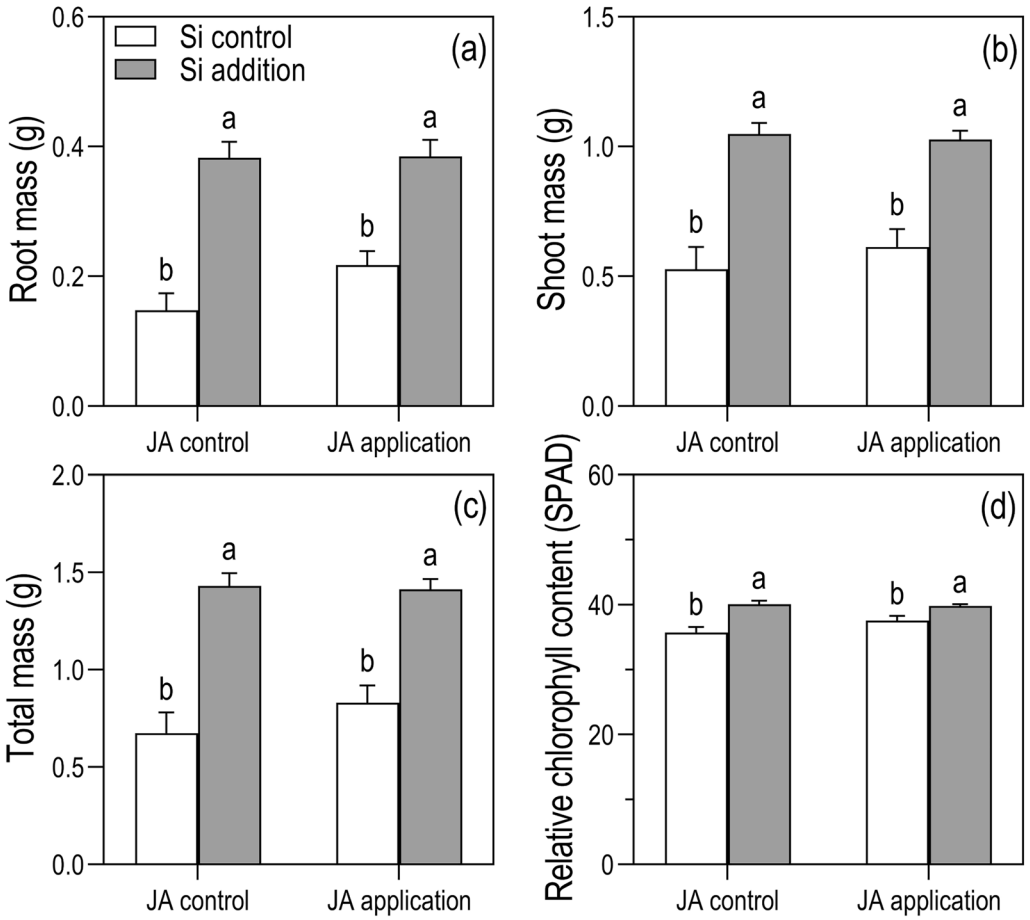

Fig. 2 Effects of Si addition and jasmonic acid (JA) application on root mass (**a**), shoot mass (**b**), total mass (**c**) and chlorophyll (**d**) of rice. Values are presented as means ± SE. Bars with *different letters* indicate significant differences ($p < 0.05$). The legends Si control refers to no silicon addition while Si addition indicates silicon addition

snails was calculated using the method developed by Johnson et al. (2021).

$$\text{RGR (mg mg}^{-1}\text{ day}^{-1}) = \left(\frac{\text{Final mass after feeding} - \text{Initial mass before feeding}}{\text{Initial mass before feeding} \bullet \text{days}}\right)$$

Statistical analyses

Plant growth, foliar element content, leaf defense, and snail feeding metrics were analyzed with two-way ANOVA for silicon addition and JA application. We conducted Duncan's Multiple Range Test to elucidate the significant differences between various treatment groups in terms of snail feeding metrics, rice plant growth traits, rice leaf defense characteristics, and rice foliar element contents. We conducted Spearman correlations to examine the relationship between snail feeding metrics, rice plant growth traits, rice leaf defense characteristics, and rice foliar element contents. All analyses were performed in SPSS 20.0 (International Business Machines Corporation).

In order to explore the effects of silicon addition and JA application on rice leaf defense characteristics and the growth of snails, we constructed a structural equation model. However, the high collinearity excluded some indicators from the model. At the same time, in order to simplify the equation, we deleted the path whose path coefficient is too low. We used the *piecewiseSEM* package (Lefcheck 2016) in R version 4.3.3 (R Core Team 2024) to conduct the structural equation model.

Results

Rice growth response to silicon addition and JA application

Silicon addition significantly affected the shoot mass, root mass, and total mass of rice; silicon addition tended to produce a higher mass in rice, JA application did not affect rice mass, and there was no interaction between silicon and JA (Table 1; Fig. 2a–c). Silicon addition significantly affected rice's relative chlorophyll content while JA had no impact

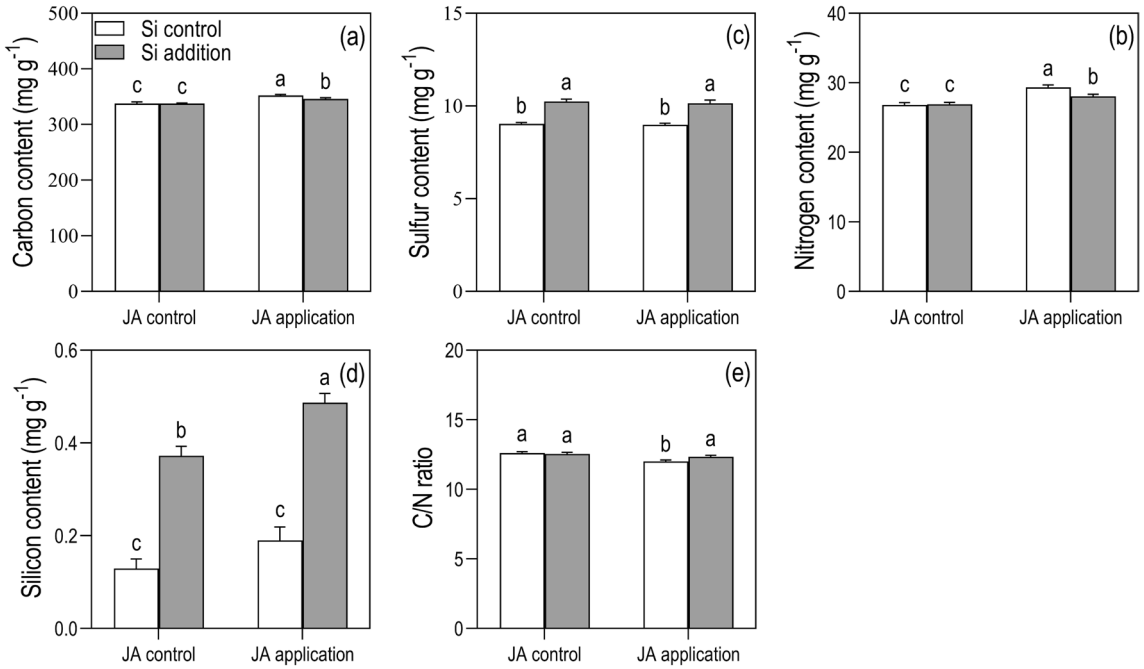

Fig. 3 Effects of Si addition and jasmonic acid (JA) application on carbon content (**a**), nitrogen content (**b**), sulfur content (**c**), silicon content (**d**) and C/N radio (**e**) of rice leaves. Values are presented as means ± SE. Bars with *different letters* indicate significant differences ($p < 0.05$)

on it and showed no interaction with silicon (Table 1; Fig. 2d).

Rice foliar elements response to silicon addition and JA application

JA application significantly increased the content of foliar carbon and nitrogen (Table 1; Fig. 3a, b). Silicon addition significantly affected foliar sulfur and silicon (Table 1). Silicon addition significantly increased the foliar sulfur content (Fig. 3c). Silicon content was significantly increased by silicon addition and especially supplied with JA (Fig. 3d). An interaction effect between silicon addition and JA application was observed on foliar nitrogen and silicon content (Table 1). The foliar C/N ratio was significantly affected by JA application but not silicon addition (Table 1; Fig. 3e).

Effects of silicon addition and JA application on rice defense

Tannin content was significantly affected by silicon addition and JA application, but there were no interactions between silicon addition and JA application (Table 1; Fig. 4a). Silicon addition significantly increased the content of total phenolic, and JA application also significantly affected the total phenolic content (Table 1; Fig. 4b). The tannin and total phenolic content were increased by silicon addition, especially supplied with JA (Fig. 4a, b). Silicon addition and JA application significantly increased flavonoid content (Table 1; Fig. 4c). The force of fracture was only significantly affected by silicon addition (Table 1; Fig. 4d). Silicon addition and JA application interactively affected the total phenolic content (Table 1).

Effects of silicon addition and JA application on snail growth

The weight gain and leaf consumption were significantly affected by silicon addition, and silicon addition and JA application tended to decrease the weight gain and leaf consumption (Fig. 5a, b). RGR and cellulase activity of apple snails were significantly decreased by silicon addition and JA application (Fig. 5c, d). Silicon addition and JA application interactively affected weight gain, leaf consumption, RGR and cellulase activity of snail growth (Table 1).

Correlations between snail herbivory and rice response

RGR was significantly correlated with weight gain ($r = 0.72$, $p < 0.001$), leaf consumption ($r = 0.68$, $p < 0.001$), cellulase activity ($r = 0.86$, $p < 0.001$), force of fracture ($r = -0.49$, $p = 0.015$), tannin content ($r = -0.60$, $p = 0.002$), flavonoid content ($r = -0.78$, $p < 0.001$), total phenolic content ($r = -0.69$, $p < 0.001$) and foliar silicon content ($r = -0.57$, $p = 0.004$) (Fig. 6). The cellulase activity was significantly correlated with force of fracture ($r = -0.59$, $p = 0.003$), tannin content ($r = -0.80$,

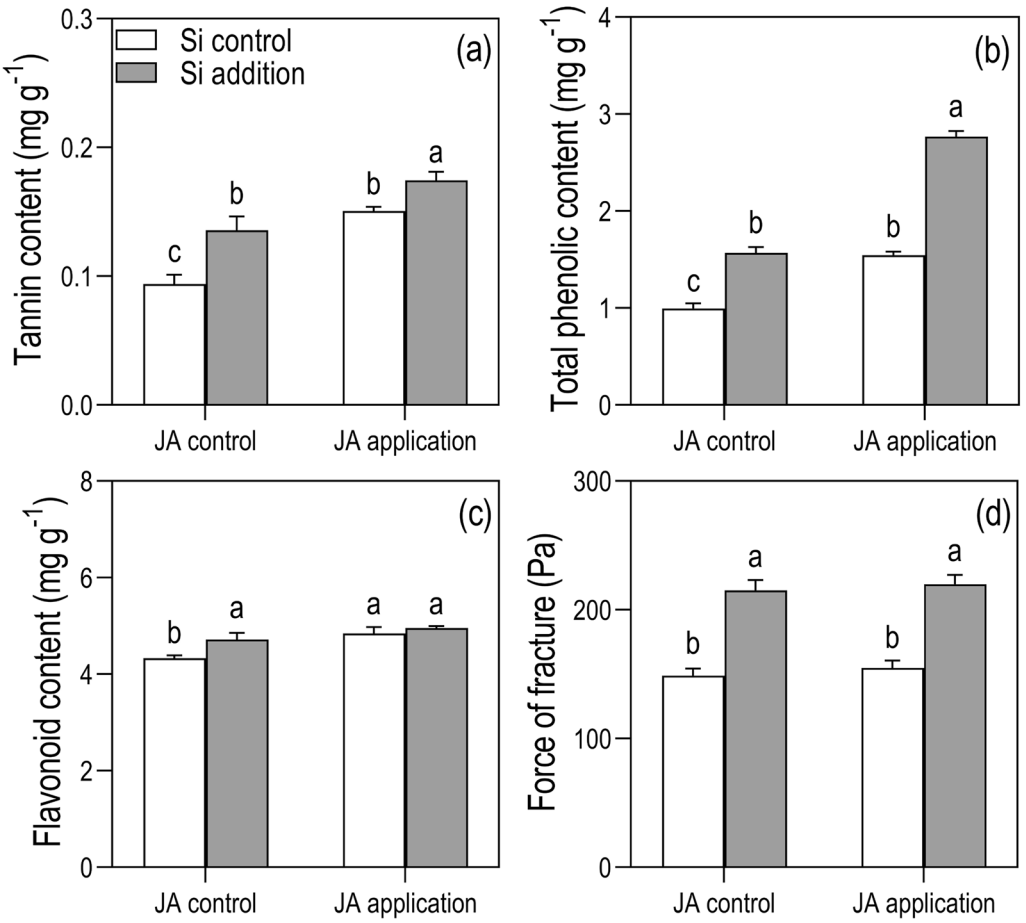

Fig. 4 Effects of Si addition and jasmonic acid (JA) application on tannin content (**a**), total phenolic content (**b**), flavonoid content (**c**) and force of fracture (**d**) of rice leaves. Values are presented as means ± SE. Bars with *different letters* indicate significant differences ($p < 0.05$)

$p < 0.001$), flavonoid content ($r = -0.74$, $p < 0.001$), total phenolic content ($r = -0.81$, $p < 0.001$), and foliar silicon content ($r = -0.73$, $p < 0.001$) (Fig. 6). The foliar silicon was significantly correlated with tannin content ($r = 0.62$, $p = 0.001$), flavonoid content ($r = 0.55$, $p = 0.005$), total phenolic content ($r = 0.79$, $p < 0.001$), force of fracture ($r = 0.74$, $p < 0.001$), total mass ($r = 0.81$, $p < 0.001$), relative chlorophyll content ($r = 0.74$, $p < 0.001$), and foliar sulfur content ($r = 0.73$, $p < 0.001$) (Fig. 6).

Effects of silicon addition and JA application on rice and apple snails

The combined effects of silicon addition and JA application jointly explained 80% of the variation in foliar silicon content. Silicon addition (standardized path coefficient $\beta = 0.893$, $p < 0.001$) showed a positive effect on the foliar silicon content (Fig. 7). Silicon addition ($\beta = 0.957$, $p < 0.001$) showed a positive effect on the force of fracture. The application of JA ($\beta = 0.217$, $p = 0.223$) and foliar silicon content ($\beta = 0.949$, $p = 0.022$) showed a positive effect on tannin content (Fig. 7). Foliar silicon content ($\beta = -0.363$, $p = 0.153$), tannin content ($\beta = -0.445$, $p = 0.002$), flavonoid content ($\beta = -0.278$, $p = 0.022$), and force of fracture ($\beta = -0.281$, $p = 0.193$) had a negative effect on the cellulase activity of apple snails (Fig. 7). Both JA application ($\beta = -0.457$, $p = 0.023$) and foliar silicon content ($\beta = -0.518$, $p = 0.151$) had a negative effect on the weight gain of apple snails (Fig. 7).

Discussion

Rice is a common model plant used to study the interaction between plants and silicon (Cooke and Leishman 2016). There is no doubt that silicon plays a crucial role in the growth of rice and significantly increases its biomass (Tavakkoli et al. 2011). Previous studies have demonstrated that the addition of silicon significantly impacts plants' ability to defend against insects (Hou and Han 2010; Acevedo et al. 2021). We observed significant effects of silicon addition on leaf defense

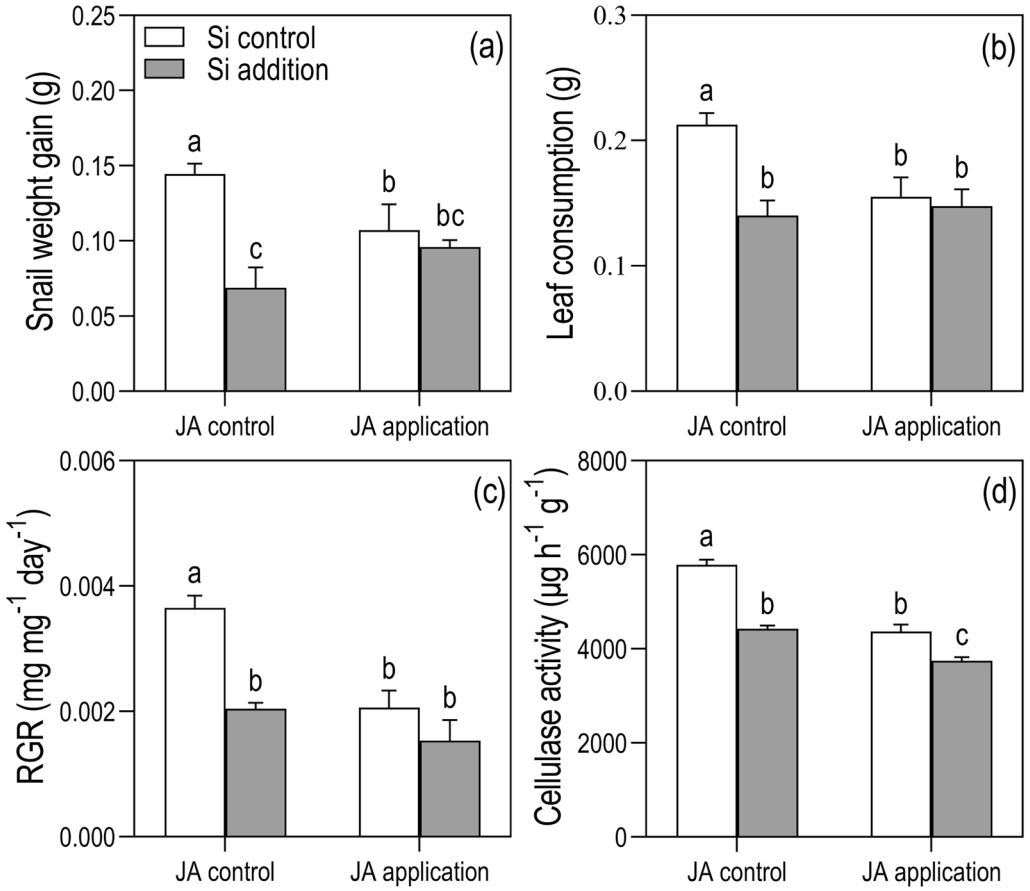

Fig. 5 Effects of Si addition and jasmonic acid (JA) application on weight gain (**a**), leaf consumption (**b**), relative growth rate (RGR) (**c**) and cellulase activity (**d**) of apple snails. Values are means ± SE. Bars with *different letters* indicate significant differences ($p < 0.05$)

characteristics and JA application on the secondary metabolites of rice leaves. In addition, the addition of silicon and JA has a negative effect on snail feeding metrics, and there is a strong interaction between them. Silicon addition and JA application show excellent results in rice defense against apple snails.

Effects of silicon addition and JA application on rice growth

Many studies focused on the effects of silicon addition on plant growth, but there is no consistent conclusion. Different species have different sensitivities to silicon, and the impact of silicon addition on plant growth varies significantly among different plant species (Soininen et al. 2013). Our results are in line with the findings of Meharg and Meharg (2015) that silicon addition significantly promotes the growth of rice. In our experiment, silicon addition enhances the relative chlorophyll content of rice, directly promoting plant growth performance. Moreover, silicon addition can increase the utilization of nitrogen, which plays a crucial role in plant growth (Cuong et al. 2017). The sulfur and silicon content in rice leaves significantly increased with silicon supply, as sulfur is essential for plant growth (Bloem et al. 2007). In addition, enhancing the force of fracture in plants by using silicon can increase the rigidity of plant stems, enabling them to support more biomass mechanically (Liang et al. 2013). Although JA application has no effect on rice biomass, it increases rice leaves' nitrogen and carbon content. JA application caused a decrease in the C/N ratio of rice leaves, indicating increased vegetative growth (Lin and Chang 2017). The addition of silicon enhances rice growth, leading to increased biomass. JA application also boosts rice growth, but short application durations do not correspond to increased biomass in our study. This may be caused by the fact that the JA application time is too short, and the effect of JA is not evident.

JA application can increase the silicon content of rice with silicon addition

The role of silicon enhances plants' resistance to herbivores in three ways: through physical defense, secondary

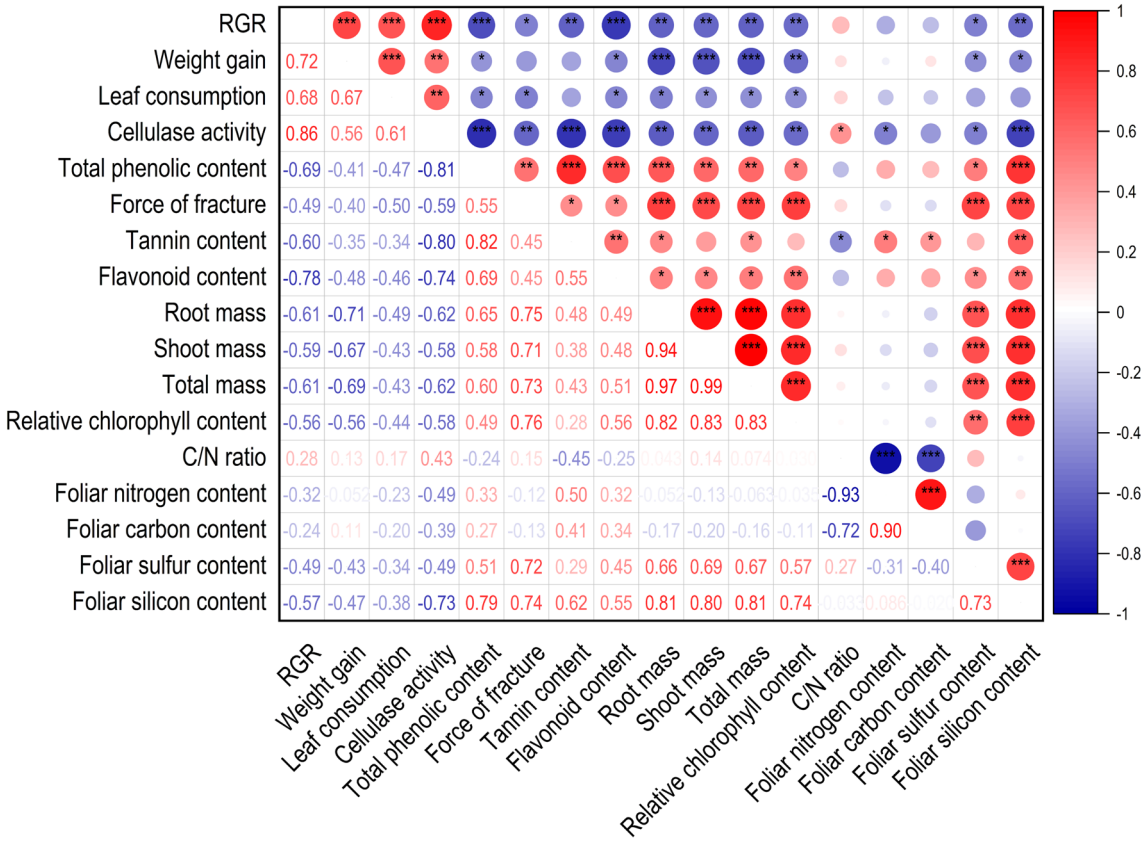

Fig. 6 Spearman analysis of the correlations between the snail feeding metrics (i.e., relative growth rate (RGR), weight gain, leaf consumption, and cellulase activity), rice plant growth traits (i.e., root mass, shoot mass, total mass, relative chlorophyll content, and C/N ratio), rice leaf defense characteristics (i.e., tannin content, total phenolic content, flavonoid content, and force of fracture), and rice foliar element contents (i.e., foliar nitrogen content, foliar carbon content, foliar sulfur content and foliar silicon content). The color *red* indicates a positive correlation, while the color *blue* indicates a negative correlation. The intensity of the color shading represents the magnitude of the correlation coefficient. The size of the circular color block represents the strength and significance of the correlation coefficient. Numbers indicate the correlation coefficient. $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$

metabolite defense, and the release of VOCs (Ma 2004; Ye et al. 2013; Liu et al. 2017). Our results indicated that adding silicon significantly improved the force of fracture, whereas JA application had no effect. This may lead to herbivores taking longer to feed, thereby decreasing the risk of predators grazing the leaves. Previous research has indicated that the deposition of silicon in plant cell walls and its covalent crosslinking with hemicelluloses result in improved cell mechanical properties, and this process also leads to an increase in lignin and phytoalexin production (Sun et al. 2010; He et al. 2015; Kido et al. 2015). Feeding herbivores with high-silicon plant can cause their mouthparts to wear off, which limits their nutrient uptake (Massey et al. 2006; Massey and Hartley 2009).

Silicon is recognized for its ability to boost plants' ability to defend themselves against insect attacks. Our results suggest that silicon addition leads to increased levels of tannin, total phenolic, and flavonoid in rice leaves, especially when combined with JA application. It has been confirmed that silicon can trigger the JA signaling pathways associated with herbivore infestation and plant damage (Kim et al. 2014b). Moreover, the addition of silicon in our study enhanced sulfur uptake in rice. Sulfur is an essential element necessary for the growth and development of higher plants (Aziz et al. 2016). Sulfur-containing compounds are commonly found in plants and play a crucial role in plant defense against herbivores (Broekaert et al. 1995; Falk et al. 2007). Plants supplied with JA exhibit similar effect when infested by herbivores. Additionally, silicon interacts with JA and is closely related to JA signaling pathways, promoting the accumulation of JA, and JA application enhances the plant uptake of silicon (Ye et al. 2013). JA application has no effect on

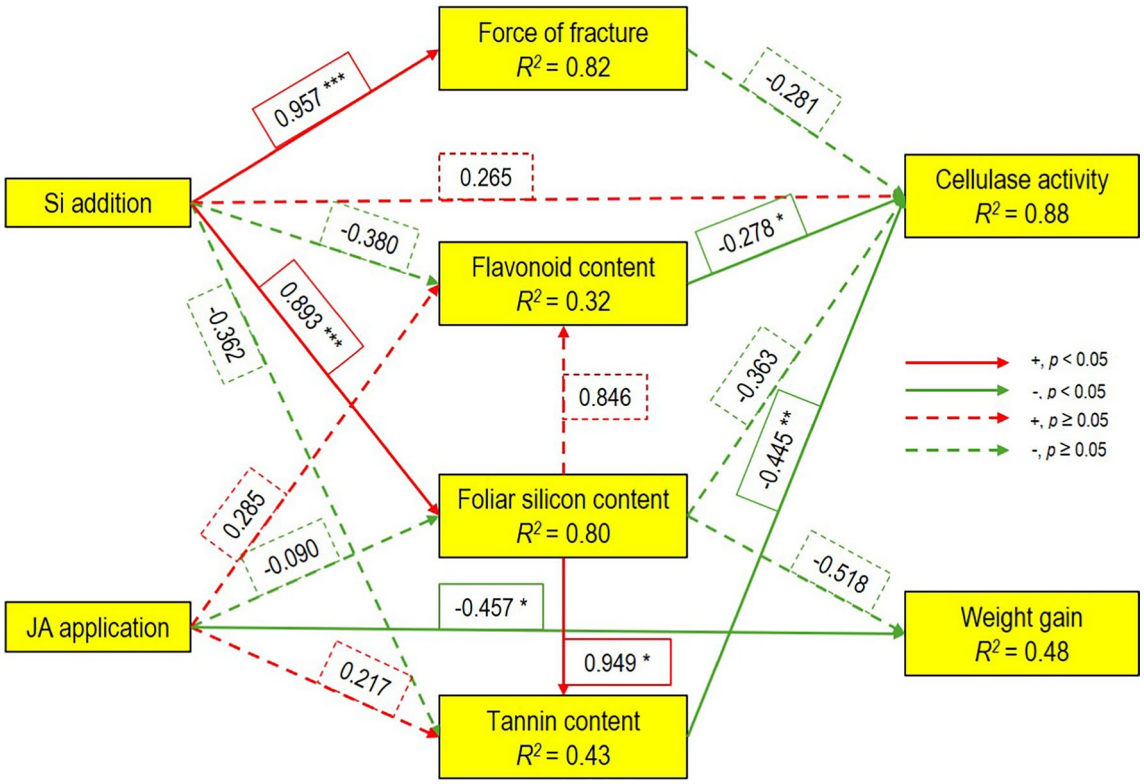

Fig. 7 The effects of Si addition and jasmonic acid (JA) application on rice's leaf resistance characteristics, leaf element content, and the weight gain and cellulase activity of apple snails were analyzed using a structural equation model. *Red* and *green arrows* represent significant positive and negative pathways, respectively, and ***$p < 0.001$; **$p < 0.01$; *$p < 0.05$, while *red* and *green dash lines* represent positive and negative pathways but non-significant, respectively. R^2 represents the proportion of variance that is explained by each dependent variable in the model. The model's Fisher's *C* is 16.205, with a *p*-value of 0.094. The AIC value is 335.543

fracture force, while silicon addition and JA application significantly increase rice leaves' tannin, total phenolic, and flavonoid content. These metabolites exhibit the highest level in rice leaves with silicon addition and JA application. Supplementing rice with silicon and JA can enhance its defense against herbivores and improve the efficacy of each other.

Silicon addition and JA application interactively affected snail-feeding metrics

Previous research findings have indicated that the application of silicon and JA can remarkably inhibit the growth of herbivores (Ryalls et al. 2023). Silicon and JA increased the release of VOCs, disrupting the ability of herbivores to recognize host plants (Kvedaras et al. 2010). Silicon addition and JA application led to an increase in superoxide dismutase (SOD), peroxidase (POD) and catalase (CAT), which can protect plants from reactive oxygen species while reactive oxygen species directly cause damage to herbivores (Shi et al. 2010; He et al. 2011). Silicon addition and JA application significantly increased the production of a variety of secondary metabolisms (Hall et al. 2019). Some of the secondary metabolisms produced by plants can be harmful to herbivores (Rani and Pratyusha 2014). The content of phenols in food decreased the growth of the apple snail (Qiu et al. 2011). In our results, there is a negative correlation between the total phenolic content in rice leaves and the RGR, cellulase activity, and weight gain of apple snails. Silicon addition significantly increased the silicon content in plants, resulting in improved physical defense mechanisms (Schurt et al. 2012). Herbivores show an aversion to high-silicon plants (Islam et al. 2022b). In addition, silicon addition increases the production of protease inhibitors in plants, which can inhibit the protease activity of herbivores (Ye et al. 2013). We consistently observed that feeding on rice leaves supplemented with silicon significantly reduces the cellulase activity of apple snails, especially when combined with JA application. Silicon deposits in plant cell walls serve as physical barriers to block the destruction caused by herbivores (Hartley et al. 2015). Biological silicon present in the diet of herbivores can lead to increased wear of their mouthparts (Massey and Hartley 2009). Feeding on high-silicon plants hinders

herbivore digestion, limiting their acquisition of essential carbon and nitrogen for growth (Massey and Hartley 2009). Silicon addition and JA application significantly decreased the growth of apple snails and leaf consumption. The application of JA enhanced the plants' absorption of silicon, which improved their defense against apple snails. According to the structural equation model, the addition of silicon enhanced the mechanical strength of rice leaves and affected the growth of the snail. At the same time, silicon addition also increased the silicon content of rice leaves. The increased silicon content in the leaves led to higher levels of secondary metabolites in rice leaves, which, in turn, negatively affected snail cellulase activity and weight gain. On the other hand, JA treatment directly increased the levels of secondary metabolites in rice leaves, which in turn affected the growth of the apple snail.

Conclusions

Although JA application did not impact rice growth directly, it significantly enhanced the defense of rice against apple snails. Furthermore, JA application enhanced the positive effects of silicon addition on rice defense against apple snails. Silicon addition and JA application significantly reduced leaf consumption of apple snails, leading to a decrease in their RGR. This means that silicon addition and JA application simultaneously could reduce the biomass loss of rice due to the herbivory of invasive snails. Therefore, combined application of silicon and JA could be a way to increase the yield of rice and decline the performance of the invasive apple snails at least in rice ecosystems.

Acknowledgements
We thank Yuyu Shen, Yue Chen, Juan Yang, Fangmin Fei, Kai Shi and Jiajie Shi for their kind help with the experiment. We are especially grateful to Zhenqiu Cao for his help with statistical analyses.

Author contributions
Conceptualization: WL, YBS and MD; methodology: WL and YBS; experiments conducted & data collection: WL and HY; data analysis: WL, HY and WHD; writing-original draft preparation: WL; writing-review & editing: WL, HY, WHD, YBS and MD; supervision: YBS and MD.

Funding
This work was supported by "Pioneer" and "Leading Goose" R&D Program of Zhejiang (2024C03226) and NSFC (grant no. 32371580).

Availability of data and materials
The datasets used and/or analyzed during the current study are available from the corresponding author upon reasonable request.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare that they have no competing interests.

Author details
[1]Key Laboratory of Hangzhou City for Ecosystem Protection and Restoration, College of Life and Environmental Sciences, Hangzhou Normal University, Hangzhou 311121, China. [2]Ecological Security and Protection Key Laboratory of Sichuan Province, Mianyang Normal University, Mianyang 621000, China.

Received: 30 October 2024 Accepted: 19 February 2025
Published online: 06 March 2025

References

Acevedo FE, Peiffer M, Ray S et al (2021) Silicon-mediated enhancement of herbivore resistance in agricultural crops. Front Plant Sci 12:631824. https://doi.org/10.3389/fpls.2021.631824
Aziz M, Nadipalli R, Xie XT et al (2016) Augmenting sulfur metabolism and herbivore defense in *Arabidopsis* by bacterial volatile signaling. Front Plant Sci 7:458. https://doi.org/10.3389/fpls.2016.00458
Bloem E, Haneklaus S, Salac I et al (2007) Facts and fiction about sulfur metabolism in relation to plant-pathogen interactions. Plant Biol 9:596–607. https://doi.org/10.1055/s-2007-965420
Bradshaw CJA, Leroy B, Bellard C et al (2016) Massive yet grossly underestimated global costs of invasive insects. Nat Comm 7:12986. https://doi.org/10.1038/ncomms12986
Broekaert WF, Terras FRG, Osborn CRW (1995) Plant defensins: novel antimicrobial peptides as components of the host defense system. Plant Physiol 108:1353–1358. https://doi.org/10.1104/pp.108.4.1353
Browse J (2009) Jasmonate passes muster: a receptor and targets for the defense hormone. Ann Rev Plant Biol 60:183–205. https://doi.org/10.1146/annurev.arplant.043008.092007
Bruinsma M, Van Dam NM, Van Loon JJA et al (2007) Jasmonic acid-induced changes in (*Brassica oleracea*) affect oviposition preference of two specialist herbivores. J Chem Ecol 33:655–668. https://doi.org/10.1007/s10886-006-9245-2
Byers JE, McDowell WG, Dodd SR et al (2013) Climate and pH predict the potential range of the invasive apple snail (*Pomacea insularum*) in the southeastern United States. PLoS ONE 8:56812. https://doi.org/10.1371/journal.pone.0056812
Carlsson NOL, Lacoursière JO (2005) Herbivory on aquatic vascular plants by the introduced golden apple snail (*Pomacea canaliculata*) in Lao PDR. Biol Invasions 7:233–241. https://doi.org/10.1007/s10530-004-0741-4
Carlsson NOL, Brönmark C, Hansson LA (2004) Invading herbivory: the golden apple snail alters ecosystem functioning in Asian wetlands. Ecology 85:1575–1580. https://doi.org/10.1890/03-3146
Chen JS, Lei NF, Liu Q (2011) Defense signaling among interconnected ramets of a rhizomatous clonal plant, induced by jasmonic-acid application. Acta Oecol 37:355–360. https://doi.org/10.1016/j.actao.2011.04.002
Cheng KC, Wu JY, Lin JT et al (2013) Enhancements of isoflavone aglycones, total phenolic content, and antioxidant activity of black soybean by solid-statefermentation with *Rhizopus* spp. Europ Food Res Tech 236:1107–1113. https://doi.org/10.1007/s00217-013-1936-7
Constantine KL, Makale F, Mugambi I et al (2023) Assessment of the socio-economic impacts associated with the arrival of apple snail (*Pomacea canaliculata*) in Mwea irrigation scheme, Kenya. Pest Manage Sci 79:4343–4356. https://doi.org/10.1002/ps.7638
Cooke J, Leishman MR (2016) Consistent alleviation of abiotic stress with silicon addition: a meta-analysis. Funct Ecol 30:1340–1357. https://doi.org/10.1111/1365-2435.12713
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
Falk KL, Tokuhisa JG, Gershenzon J (2007) The effect of sulfur nutrition on plant glucosinolate content: physiology and molecular mechanisms. Plant Biol 9:573–581. https://doi.org/10.1055/s-2007-965431
Fang L, Wong PK, Lin L et al (2010) Impact of invasive apple snails in Hong Kong on wetland macrophytes, nutrients, phytoplankton and

filamentous algae. Freshwater Biol 55:1191–1204. https://doi.org/10.1111/j.1365-2427.2009.02343.x
Farmer EE, Ryan CA (2017) Octadecanoid precursors of jasmonic acid activate the synthesis of wound-inducible proteinase. Plant Cell 4:129–134. https://doi.org/10.1105/tpc.4.2.129
Hall CR, Waterman JM, Vandegeer RK et al (2019) The role of silicon in antiherbivore phytohormonal signalling. Front Plant Sci 10:1132. https://doi.org/10.3389/fpls.2019.01132
Hartley SE, Fitt RN, McLamon EL et al (2015) Defending the leaf surface: intra- and inter-specific differences in silicon deposition in grasses in response to damage and silicon supply. Front Plant Sci 6:35. https://doi.org/10.3389/fpls.2015.00035
Hayes KA, Burks RL, Castro-Vazquez A et al (2015) Insights from an integrated view of the biology of apple snails (Caenogastropoda: Ampullapiidae). Malacologia 58:245–302. https://doi.org/10.4002/040.058.0209
He JP, Chen FD, Chen SM et al (2011) Chrysanthemum leaf epidermal surface morphology and antioxidant and defense enzyme activity in response to aphid infestation. J Plant Physiol 168:687–693. https://doi.org/10.1016/j.jplph.2010.10.009
He CW, Ma J, Wang LJ (2015) A hemicellulose-bound form of silicon with potential to improve the mechanical properties and regeneration of the cell wall of rice. New Phytol 206:1051–1062. https://doi.org/10.1111/nph.13282
Horgan FG, Figueroa JY, Almazan MLP (2014) Seedling broadcasting as a potential method to reduce apple snail damage to rice. Crop Prot 64:168–176. https://doi.org/10.1016/j.cropro.2014.06.022
Hou ML, Han YQ (2010) Silicon-mediated rice plant resistance to the Asiatic rice borer (Lepidoptera: Crambidae): effects of silicon amendment and rice varietal resistance. J Econ Entomol 103:1412–1419. https://doi.org/10.1603/ec09341
Hu YK, Liu GF, Pan X et al (2022) Contrasting nitrogen cycling between herbaceous wetland and terrestrial ecosystems inferred from plant and soil nitrogen isotopes across China. J Ecol 110:1259–1270. https://doi.org/10.1111/1365-2745.13866
Islam T, Moore BD, Johnson SN (2022a) Plant silicon defences reduce the performance of a chewing insect herbivore which benefits a contemporaneous sap-feeding insect. Ecol Entomol 47:951–958. https://doi.org/10.1111/een.13183
Islam T, Moore BD, Johnson SN (2022b) Silicon suppresses a ubiquitous mite herbivore and promotes natural enemy attraction by altering plant volatile blends. J Pest Sci 95:423–434. https://doi.org/10.1007/s10340-021-01384-1
Johnson SN, Ryalls JMW, Barton CVM et al (2019) Climate warming and plant biomechanical defences: silicon addition contributes to herbivore suppression in a pasture grass. Funct Ecol 33:587–596. https://doi.org/10.1111/1365-2435.13295
Johnson SN, Rowe RC, Hall CR (2020) Silicon is an inducible and effective herbivore defence against *Helicoverpa punctigera* (Lepidoptera: Noctuidae) in soybean. Bull Entomol Res 110:417–422. https://doi.org/10.1017/s0007485319000798
Johnson SN, Waterman JM, Wuhrer R et al (2021) Siliceous and non-nutritious: nitrogen limitation increases anti-herbivore silicon defences in a model grass. J Ecol 109:3767–3778. https://doi.org/10.1111/1365-2745.13755
Kido N, Yokoyama R, Yamamoto T et al (2015) The matrix polysaccharide (1;3,1;4)-β-d-glucan is involved in silicon-dependent strengthening of rice cell wall. Plant Cell Physiol 56:268–276. https://doi.org/10.1093/pcp/pcu162
Kim JJ, Kwon YK, Kim JH et al (2014a) Effective microwell plate-based screening method for microbes producing cellulase and xylanase and its application. J Microbiol Biotech 24:1559–1565. https://doi.org/10.4014/jmb.1405.05052
Kim YH, Khan AL, Waqas M et al (2014b) Regulation of jasmonic acid biosynthesis by silicon application during physical injury to *Oryza sativa* L. J Plant Res 127:525–532. https://doi.org/10.1007/s10265-014-0641-3
Kraska JE, Breitenbeck GA (2010) Simple, robust method for quantifying silicon in plant tissue. Comm Soil Sci Plant Anal 41:2075–2085. https://doi.org/10.1080/00103624.2010.498537
Kvedaras OL, An M, Choi YS et al (2010) Silicon enhances natural enemy attraction and biological control through induced plant defences. Bull Entomol Res 100:367–371. https://doi.org/10.1017/s0007485309990265
Lefcheck JS (2016) piecewiseSEM: Piecewise structural equation modelling in R for ecology, evolution, and systematics. Methods Ecol Evol 7:573–579. https://doi.org/10.1111/2041-210X.12512
Li JY, Wang J, Zeigler RS (2014) The 3,000 rice genomes project: new opportunities and challenges for future rice research. GigaScience 3:8. https://doi.org/10.1186/2047-217X-3-8
Liang SJ, Li ZQ, Li XJ et al (2013) Effects of stem structural characters and silicon content on lodging resistance in rice (*Oryza sativa* L.). Res Crops 14:621–636. https://doi.org/10.5555/20133370205
Lin JA, Chang YCA (2017) Partitioning of nitrogen and carbon in phalaenopsis and their progressive changes with plant growth and development. HortScience 52:1530–1536. https://doi.org/10.21273/HORTSCI12484-17
Lin Y, Lu MF, Liao HB et al (2014) Content determination of the flavonoids in the different parts and different species of *Abelmoschus esculentus* L. by reversed phase-high performance liquid chromatograph and colorimetric method. Pharmacogn Mag 10:278–284. https://doi.org/10.4103/0973-1296.137368
Liu J, Zhu JW, Zhang PJ et al (2017) Silicon supplementation alters the composition of herbivore induced plant volatiles and enhances attraction of parasitoids to infested rice plants. Front Plant Sci 8:1265. https://doi.org/10.3389/fpls.2017.01265
Ma JF (2004) Role of silicon in enhancing the resistance of plants to biotic and abiotic stresses. Soil Sci Plant Nutr 50:11–18. https://doi.org/10.1080/00380768.2004.10408447
Makkar HPS (ed) (2003) Quantification of tannins in tree and shrub foliage: a laboratory manual. Springer, Dordrecht. https://doi.org/10.1007/978-94-017-0273-7
Massey FP, Hartley SE (2009) Physical defences wear you down: progressive and irreversible impacts of silica on insect herbivores. J Animal Ecol 78:281–291. https://doi.org/10.1111/j.1365-2656.2008.01472.x
Massey FP, Ennos AR, Hartley SE (2006) Silica in grasses as a defence against insect herbivores: contrasting effects on folivores and a phloem feeder. J Animal Ecol 75:595–603. https://doi.org/10.1111/j.1365-2656.2006.01082.x
McArt SH, Halitschke R, Salminen JP et al (2013) Leaf herbivory increases plant fitness via induced resistance to seed predators. Ecology 94:966–975. https://doi.org/10.1890/12-1664.1
Meharg C, Meharg AA (2015) Silicon, the silver bullet for mitigating biotic and abiotic stress, and improving grain quality, in rice? Environ Exp Bot 120:8–17. https://doi.org/10.1016/j.envexpbot.2015.07.001
Oerke EC (2006) Crop losses to pests. J Agric Sci 144:31–43. https://doi.org/10.1017/S0021859605005708
Pan DL, Zhang JH, Long J et al (2014) Impacts of golden apple snail (*Pomacea canaliculata*) on water quality and microbes. Chin J Eco-Agric 22:58–62. https://doi.org/10.3724/SP.J.1011.2014.30482
Qin Z, Zhang JE, Yang JH et al (2023) Niche conservatism and geographical range expansion of *Pomacea canaliculata* and *Pomacea maculata* in non-native United States and China. Biol Invasions 25:3391–3405. https://doi.org/10.1007/s10530-023-03100-9
Qiu JW, Chan MT, Kwong KL et al (2011) Consumption, survival and growth in the invasive freshwater snail *Pomacea canaliculata*: does food freshness matter? J Mollus Stud 77:189–195. https://doi.org/10.1093/mollus/eyr005
R Core Team (2024) R: a language and environment for statistical computing. R Foundation for Statistical Computing
Rani PU, Pratyusha S (2014) Role of castor plant phenolics on performance of its two herbivores and their impact on egg parasitoid behaviour. BioControl 59:513–524. https://doi.org/10.1007/s10526-014-9590-y
Reynolds OL, Padula MP, Zeng RS et al (2016) Silicon: potential to promote direct and indirect effects on plant defense against arthropod pests in agriculture. Front Plant Sci 7:744. https://doi.org/10.3389/fpls.2016.00744
Ryalls JMW, Gherlenda AN, Rowe RC et al (2023) Silicon supplementation and jasmonate activation synergistically increase phenolic defences against a legume herbivore. J Ecol 111:2208–2217. https://doi.org/10.1111/1365-2745.14170
Schaller J, Schoelynck J, Struyf E et al (2016) Silicon affects nutrient content and ratios of wetland plants. Silicon 8:479–485. https://doi.org/10.1007/s12633-015-9302-y
Schnorbach HJ (1995) The golden apple snail (*Pomacea canaliculata* Lamarck), an increasingly important pest in rice, and methods of control with Bayluscid. Pflanzenschutz-Nachrichten Bayer 48:313–346

Schoelynck J, Bal K, Backx H et al (2010) Silica uptake in aquatic and wetland macrophytes: a strategic choice between silica, lignin and cellulose? New Phytol 186:385–391. https://doi.org/10.1111/j.1469-8137.2009.03176.x
Schurt DA, Rodrigues FA, Reis RD et al (2012) Physical resistance of leaf sheaths of rice plants supplied with silicon and infected by *Rhizoctonia solani*. Tropic Plant Pathol 37:281–285. https://doi.org/10.1590/s1982-56762012000400008
Shi GR, Cai QS, Liu CF et al (2010) Silicon alleviates cadmium toxicity in peanut plants in relation to cadmium distribution and stimulation of antioxidative enzymes. Plant Growth Regul 61:45–52. https://doi.org/10.1007/s10725-010-9447-z
Soininen EM, Bråthen KA, Jusdado JGH et al (2013) More than herbivory: levels of silica-based defences in grasses vary with plant species, genotype and location. Oikos 122:30–41. https://doi.org/10.1111/j.1600-0706.2012.20689.x
Sommer M, Kaczorek D, Kuzyakov Y et al (2006) Silicon pools and fluxes in soils and landscapes: a review. J Plant Nutrit Soil Sci 169:310–329. https://doi.org/10.1002/jpln.200690016
Song YB, Hu YK, Pan X et al (2020) Association of leaf silicon content with chronic wind exposure across and within herbaceous plant species. Global Ecol Biogeogr 29:711–721. https://doi.org/10.1111/geb.13062
Struyf E, Conley DJ (2009) Silica: an essential nutrient in wetland biogeochemistry. Front Ecol Environ 7:88–94. https://doi.org/10.1890/070126
Sun WC, Zhang J, Fan QH et al (2010) Silicon-enhanced resistance to rice blast is attributed to silicon-mediated defence resistance and its role as physical barrier. Europ J Plant Pathol 128:39–49. https://doi.org/10.1007/s10658-010-9625-x
Tavakkoli E, Lyons G, English P et al (2011) Silicon nutrition of rice is affected by soil pH, weathering and silicon fertilisation. J Plant Nutrit Soil Sci 174:437–446. https://doi.org/10.1002/jpln.201000023
van Dam NM, Hadwich K, Baldwin IT (2000) Induced responses in *Nicotiana attenuata* affect behavior and growth of the specialist herbivore *Manduca sexta*. Oecologia 122:371–379. https://doi.org/10.1007/s004420050043
Wang YY, Zhang YX, Lv H et al (2023) Efficacy of giant river prawn *Macrobrachium rosenbergii* in controlling the invasive snail *Pomacea canaliculata*: implications for ecological farming. Diversity 15:1001. https://doi.org/10.3390/d15091001
Wasternack C, Parthier B (1997) Jasmonate-signalled plant gene expression. Trends Plant Sci 2:302–307. https://doi.org/10.1016/S1360-1385(97)89952-9
Ye M, Song YY, Long J et al (2013) Priming of jasmonate-mediated antiherbivore defense responses in rice by silicon. Proc Natl Acad Sci USA 110:E3631–E3639. https://doi.org/10.1073/pnas.1305848110
Zhang PJ, Shu JP, Dicke M et al (2010) Different headspace profiles in wild crucifer species in response to *Plutella xylostella* herbivory and exogenous jasmonic acid application. Insect Sci 17:29–37. https://doi.org/10.1111/j.1744-7917.2009.01283.x
Zhou B, Xie CYD, Yan XH et al (2015) Invasion and hazard of *Pomacea canaliculata* in Jiangxi Province and regularity of its outbreak in rice field. J Ecol Rural Environ 31:902–909. https://doi.org/10.11934/j.issn.1673-4831.2015.06.016

Publisher's Note