Foliar Spraying Suitable Dosage of Silicon Fertilizer on Wheat Suppressed Inoculated Aphid Reproduction by Activating Plant Induced Defense Response

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Abstract

Background: Although the ability of silicon to induce plant resistance against some insect is known, it is still unknown that the effect of the different concentrations of silicon on activates the secondary defense system in wheat, and then influence the life cycle table of wheat aphids. In this experiment, different levels of silicon (Si) fertilizer was applied to change the secondary defense system of wheat, to study the impact on the life table parameters of aphid (*Sitobion avenae* F.) (Hemiptera: *Aphididae*), and to explore the mechanism of Si application in enhancing wheat resistance to aphids. Wheat seedlings were cultured in a hydroponic experiment with the seven different levels of Si (0, 0.3, 1, 2, 3, 4, 5 and 9 mmol/L).

Results: Our findings indicated that the application of Si can suppress the net reproductive rate (R_0), intrinsic rate of increase (r_m), mean generation time (T), finite rate of increase (λ), and prolong the population doubling time (t) of aphid. Besides, aphid infection elicited immune responses in wheat, which was enhanced by Si: Between the treatments, a foliar application of Si improved the activity of four defense enzymes (PAL, PPO, CAT, LOX), and increased the content of signal transduction substances (JA, SA) and secondary metabolites (tannin, alkaloids, lignin, total phenolics and flavonoids). Moreover, the results of the correlation analysis showed that the concentration of Si in wheat was positively associated with the activities of defense enzymes and the concentrations of secondary metabolites and signal transduction substances. There was a significant positive correlation between the activities of four defense enzymes and the concentrations of secondary metabolites and signal transduction substances in wheat. Furthermore, the activities of defense enzymes, the concentrations of secondary metabolites and signal transduction substances and Si in wheat were negatively associated with the R_0 , T , r_m , λ and positively related to the t of the life table parameters from the aphid.

Conclusions: In conclusion, the current result suggested that the application of Si can increase the signal transduction pathway of wheat and regulate the secondary metabolism by influencing the concentration of Si in wheat. As a result, the application of Si affected the life table parameters of aphids and enhanced the resistance of wheat. Also that 3 mmol/L Si application was more beneficial to enhance the resistance of wheat than higher or lower concentrations. The application of Si in wheat might provide an important basis for pest management control.

Background

Aphids are piercing and sucking by feeding on the phloem of wheat (Dedryver *et al.*, 2010). Aphids can build extraordinary populations under the right conditions due to high reproductive potential (parthenogenesis), shorter generation times, higher population intrinsic growth rate, and a high proportion of viviparous females in the population (Chapman *et al.*, 2018; Kaitlin *et al.*, 2018). Therefore, the occurrence of aphids is extremely harmful to agricultural production. For a long time, aphids are primarily controlled by insecticides. But on the one hand, overdependence on insecticides can lead to the emergence of insecticide-resistant aphid populations (Foster *et al.*, 2014), reduce the control effect against aphids. On the other hand, the application of pesticides may also adversely affect the growth of

non-targeted insects, and result in unintended environmental or nontarget impacts. Therefore, the use of integrated pest control has always received great attention.

Plants are not always in a passive position when facing the occurrence of pests in nature. In the process of long-term co-evolution with pests, plants have developed complex resistance mechanisms to resist the invasion and damage of various pests. The mechanisms of defense against the aphids include constitutive resistance and induced resistance, the defense response of plants to aphids reveals the defense response of wheat to aphids (Wu and Baldwin, 2010; Zhou *et al.*, 2015). Among them, the former refers to the resistance of the plant itself when it is not invaded by aphids, and the latter is the resistance induced by aphids. Research shown that aphid infection increases in ROS levels, and induces the up expression of genes involved in signaling pathways and some defensive enzymes (Lu *et al.*, 2015; Batyrshina *et al.*, 2020; Zhang *et al.*, 2019; Leybourne *et al.*, 2019), activates the signal transduction pathway, induces the activity of defense enzymes and the accumulation of defensive metabolites in the plant (Karban, 2011; Han *et al.*, 2009; Teresa *et al.*, 2017; Kang, *et al.*, 2018), thereby increasing resistance to aphids. The PPOs are important enzymes in plants that regulate feeding, growth, and development of insects (He *et al.*, 2011). And PAL is one key and rate-limiting enzyme in both the shikimate and phenylpropanoid pathways. The intermediate products of this pathway are phenols, and the final products are non-volatile secondary metabolites such as lignins, flavonoids, and isoflavones (Fraser and Chapple, 2011; Wu and Baldwin, 2010; Vera *et al.*, 2015). In *R. padi*, a concentration of total phenol in resistant cultivars was thought to be positively correlated with the mortality of aphids (Leszczynski *et al.*, 2011). In Morkunas (2016), a very high accumulation of flavonoids was particularly observed in leaf cells of pea seedling by aphids feeding. Besides, in plant-aphid interactions, it has been observed that plants activate the jasmonic acid (JA)-and/or salicylic acid (SA)-dependent pathways, which should activate aphid defense through their antagonistic or synergistic cross-communication (Coppola *et al.*, 2013; Züst and Agrawal, 2016; Wang *et al.*, 2017). Such as Zhang *et al.* (2019) found that aphid feeding induces the expression of several genes involved in the SA, JA, and ET signaling defense pathways and various reactive oxygen species-scavenging genes in wheat triggers strong ROS-scavenging activity and increases the activity of antioxidant enzymes. Also, plants can produce non-volatile (such as alkaloids, Tannin, and quinones), volatile and semi-volatile secondary metabolites (such as mono-, cyanogenic glucosides and glucosinolates), which are toxic, repellents, or antidigestive (War *et al.*, 2011 a, b; Cascone *et al.*, 2015; Aljbory and Chen, 2018; Sarker and Mahmoud, 2015; Li *et al.*, 2019).

Studies have shown that the application of Si can reduce fecundity, reproductive period, longevity, r_m , and R_0 of aphid, and alter survival, reproduction, and host plant preferences of sucking insects—which were found in wheat (Dias *et al.*, 2014; Gomes *et al.*, 2008; Korndorfer *et al.*, 2011). Its internal mechanism is considered to involve the following aspects. First, as a beneficial element, Si is accumulated for subsequent deposition as amorphous hydrated silica, forming a cuticle-Si double layer in the leaf blade of the plant (Luyckx 2017; Debona 2017), or form a polysilicon acid complex with low solubility and strong stability, and increase the intensive cell silicification in the frequency of silicified cells per unit area of leaf epidermal cells, improve the abrasion resistance of plant tissues, and reduce the palatability and

digestibility of tissues (Hao *et al.*, 2008; Matoh, 1986; Law, 2011; Cai, 2008). Cell silicification can play a pivotal role in the quality of a wide variety of monocot and dicot plant species and help them, whether directly or indirectly, counteract abiotic and/or biotic stresses (Tripathi *et al.*, 2017; Luyckx *et al.*, 2017; Adil *et al.*, 2020). Secondly, the study found the application of Si can increase the activities of some defense enzymes, and the accumulation of lignins, phenolic compounds, phytoalexins in plants (Ma *et al.*, 2016; Han, 2016; Abbas *et al.*, 2015; Ye *et al.*, 2013; Cai, 2008; Rahman *et al.*, 2015; Tripathi *et al.*, 2017). And Si can also induce the release of insect-resistant chemicals from the epidermis or mesophyll of wheat, reduce the reproductive capacity of aphids, and improve the insect resistance of plants (Ye *et al.*, 2013; Van *et al.*, 2013; Sivanesan *et al.*, 2014). However, it is rarely reported about the systematic research on the effects of different concentrations of Si on the signal transduction, the activity of defense enzymes, and various secondary defense substances, and then affects the secondary defense system in wheat, and to explore the impact on the life cycle table of grain aphid.

The grain aphid (*Sitobion avenae* F.) is the dominant species among natural aphid populations (Xu *et al.*, 2017), especially in the Huanghuai wheat region of China, it is the main pest affecting wheat production. In the current study, a culture experiment was used to set different Si supply levels to study the parameters of the life cycle of inoculated aphids, and affect the level of Signal conducting substance (JA, SA), defensive enzyme (PAL, PPO, CAT, LOX) activity and secondary metabolites (tannin, alkaloids, lignin, total phenolics and flavonoids) in wheat under the conditions of aphid infecting. Systematically explore the effect of different concentrations of Si on the defense response of wheat induced by aphid feeding, to further clarify the influence of silicon on wheat aphid resistance and its internal mechanism.

Results

Effect of Si on life table parameters of aphid

Performance parameters in the growth and development of the wheat aphid varied among treatments but were generally better on T4 treatment compared to that for other treatments (Table 1). Compared with control, all treatments decreased the net reproductive rate (R_0), the mean generation time (T), the intrinsic rate (r_m), the finite rate of increase (λ) and prolonged the population doubling time (t) of the wheat aphid. Among them, the R_0 of the wheat aphid decreased by 14.50%-40.30%; the r_m and λ at T4 treatment significantly decreased by 9.90%, 2.62%, respectively; the T at T3, T4 treatments was significantly lower, but, from the whole view, $T4 < T3 < T5 < T7 < T2 < T6 < T1$. The t at T4 treatment was significantly prolonged by 8.61%.

Uptake of Si by wheat

The concentration of Si in the wheat varied among treatments (Fig.1). Compared with control, other treatments increased the concentration of Si in the wheat. In particular, a comparison of Si levels among

Si treatments revealed that it was significantly higher ($P<0.01$) in the T4 treatment as compared to that of the remaining Si treatments (Fig. 1).

Effect of Si on the activities of the enzyme activity of wheat

The PAL, PPO, CAT, and LOX are major defense enzymes of secondary metabolism. In Si-sprayed (+Si) wheat, 1, 2, 3, 4, 5mmol/L of Si improved the PAL activity in leaves of wheat, were significantly higher than those in control, 0.3, 9mmol/L of Si-sprayed (+Si) wheat, becoming highest at 3mmol/L (Fig. 2A).

Activities of PPO increased with Si foliar spray treatments. Maximum PPO activity was noted with the treatment at T4, and significantly higher than other treatments. However, in other treatments, the activities of PPO were not different between +Si and -Si plants (Fig. 2B).

In the CAT, the first increase in enzyme activity was found during T1, followed by the next increase starting from T2, becoming highest at T4 treatment, and then decreased, and the increased range was 10.51%-100.20% but was generally higher than control.

Analyses of LOX activity in leaves of wheat seedlings showed markedly higher activity of this enzyme at the different Si treatments than in the control (Fig. 2D). In particular, a comparison of the LOX activity in wheat among Si treatments revealed that it was remarkably higher ($P<0.01$) in the T4 treatment as compared to that of the remaining Si treatments.

Effect of Si on the concentrations of secondary metabolites of wheat

Analysis of variance indicated that the levels of secondary metabolites were increased by Si application. The levels of secondary metabolites in the wheat varied among Si treatments (Fig. 3). In general, as the concentration of Si application increases, the content of secondary biomass first increases and then decreases, the maximum values of these parameters are seen with the application of Si at T4 treatment, followed by T3 treatment, which was significantly higher than other Si treatments (Fig. 3A, B, C, E). However, the concentration of total phenolic (D) was observed that no dramatic difference among the T1, T2, T3, T5. Up-regulation of tannin (Fig. 3A), lignin (Fig. 3C) and alkaloids (Fig. 3 E) were higher by T5-T6-T7 treatments compared to T1, T2. However, the content of flavonoids (B) and total phenolic (Fig. 3D) were opposite. The concentration of lignin (Fig. 3C) and alkaloids (Fig. 3E) recorded in wheat were a slow increased, but, T2-T6 treatments were higher than control and T1. In these secondary metabolites, a comparison of Si levels among Si treatments revealed that it was increased range was 1.50%-74.96%, but were generally higher than control (Fig. 3).

Effect of Si on the concentrations of signal transduction substances of wheat

We analyzed endogenous SA and JA levels after Si application. JA levels were increased with Si application (Fig. 4). In particular, a comparison of JA levels among Si treatments revealed that it was significantly higher ($P<0.01$) in the T4 treatment as compared to that of the remaining Si treatments (Fig. 3). Endogenous hormone SA also exhibited a similar pattern as JA. Endogenous JA levels were significantly increased at all concentrations of Si application as compared to that of the control, and this tendency was consistently observed in all indicators (Fig. 4).

Correlation between the activities of the defense enzymes, secondary metabolites and signal transduction substances in wheat at the different concentrations of Si in aphid-infection wheat

PCA analysis was conducted to report the impact of the levels of Si on the dispersion of the defense enzymes activity, secondary metabolites and signal transduction substances of wheat. PCA score plot was given in Fig. 5A showed that PC1 and PC2 contributing 36.3% and 19.2 % respectively to the total variance. The loading plot explained that PAL, PPO, Si, phenolic, lignin, JA contributes to PC1, whereas tannin, alkaloid, SA contribute to PC2. However, flavonoids, CAT contributed to both PC1 and PC2 (Fig. 5B). The elements such as the defense enzymes activity, secondary metabolites and signal transduction substances of wheat were analyzed by plotting the correlation matrix (Fig. 6A). The concentration of the activities of defense enzymes (include PAL, PPO, LOX, and CAT) was significantly positively associated with the concentrations of secondary metabolites (include tannin, phenolic, flavonoids, lignin, and alkaloid) and JA and Si in wheat. Moreover, the activities of PAL and PPO presented a positive correlation with SA. There was a significant positive correlation between the levels of secondary metabolites and signal transduction substances and Si in wheat. Additionally, Fig. 6A found a positive correlation between the concentration of Si from wheat and signal transduction substances in wheat at the different concentrations of Si after aphid infection. Our data was further confirmed by the analysis of the heat-map (Fig. 6B).

Correlation between the life table parameters of aphid and biochemical indexes in wheat at the different concentrations of Si in aphid-infection wheat

As shown in (Fig. 7), R_0 and T were dramatically negatively associated with the levels of secondary metabolites and signal transduction substances and Si in wheat. The r_m and $\bar{x}$ of the life table

parameters from aphid were dramatically negatively associated with the activities of PPO, the concentrations of secondary metabolites (include phenolic, flavonoids, lignin, and alkaloid) and signal transduction substances and Si in wheat. Additionally, the Fig. 7 found a significant positive correlation between the t of the life table parameters from aphid and the activities of the enzymes (include PPO, LOX), the concentrations of secondary metabolites (include tannin, phenolic, flavonoids and alkaloid), signal transduction substances and Si in wheat.

Discussion

Life table parameters have been used to measure aphid performance on different host plants (Laamari *et al.*, 2008; Obopile and Ositile, 2018). Among them, the net reproductive rate (R_0), Intrinsic rate of increase (r_m), finite rate of increase (λ), mean generation time (T) and population doubling time (t) values reflect the common effects of development durations, survival rates and reproductive values of aphids (Polat *et al.*, 2015; Güncan and Gümüş, 2017). These values are the best markers, which determine the effect of host plants on aphids (Polat, 2018). Research has shown that Si enhances the resistance of plants to herbivores through reducing the feeding and R_0 and r_m of insects (Yang *et al.*, 2017; Teixeira *et al.*, 2020). This study showed that the application of Si increased the accumulation of Si in wheat and decreased the R_0 , T , r_m and λ , prolonged the t of aphid, so that the resistance of wheat to aphid was improved. The resistance level of the genotype to the pest attack was thought to be involved in the T and t , and the higher the resistance of the genotype to the pest attack, the higher were the values for T and t (Kennedy and Abou 1979; Machacha *et al.*, 2012). This study has shown that Si shortness T , maybe the insect's lifecycle was slowed down in Si-treated plants (James, 2003; Connick, 2011), and shortened the time (T) from birth to the first reproduction of aphids and accelerated the death of aphids. It shows that the application of silicon may increase the resistance of wheat to aphids. Besides, Han *et al.* (2015) have shown that the r_m , λ and R_0 of the rice leaf folder population were all reduced at both the low and high Si addition rates. But we found that the Si was 3 mmol/L, the aphid resistance was the best. Because when the Si concentration is too high, it may be produced Si poison, changed the permeability of the cell membrane, and affected the normal defense of the leaves. This correlation study has shown that the accumulation of Si was significantly negatively correlated with the R_0 , T , r_m , λ of aphid, and was dramatically positively correlated with the t of aphid. The results of Dias *et al.* shown that Si fertilization induced antibiosis resistance in wheat plants to apterous morphs as shown by reduced fecundity, reproductive period, longevity, r_m , and R_0 (Dias *et al.*, 2014), but the underlying mechanisms were unclear.

When wheat is attacked by aphids, the exception of chemical control that harms the environment, it can enhance the wheat's resistance by increasing the thickness of the phloem of wheat leaves (Hao *et al.*, 2008; Matoh, 1986; Law, 2011; Cai, 2008), strengthening the signal transduction pathway, improving the activity of defense enzymes and the accumulation of defensive metabolites in wheat (Karban, 2011; Han *et al.*, 2009; Kang *et al.*, 2018). Predecessors used N, K, P, Si and other elements on crops to induce crops to produce more defense substances (Comadira *et al.*, 2015; Yang *et al.*, 2017; Muhammad *et al.*, 2015). Studies have shown that the application of Si can improve antioxidant enzyme activities, and the

accumulation of lignin, phenolic compounds, phytoalexins and signal transduction chemicals in plants (Ma *et al.*, 2016; Han, 2016; Abbas *et al.*, 2015; Ye *et al.*, 2013; Debona *et al.*, 2017). In this study, different levels of Si were applied to influence the Si content in wheat, which in turn affected the secondary defense mechanism in wheat. The results of this study showed that Si increases in the activities of defense enzymes, the accumulation of signal transduction substances and secondary metabolites. Moreover, the content of JA was higher than that of SA under the different Si levels, which may be SA and JA act antagonistically, where SA inhibits the activity of JA and vice versa (Maffei *et al.*, 2007). This study showed that a positive correlation has been observed among the accumulation of Si in wheat and the activities of defense enzymes, and the accumulation of signal transduction substances and secondary metabolites. Si may be increased the phloem defense, participated in the secondary metabolism and other physiological processes of wheat, increased the biochemical mechanisms of defense against the aphids, as a result of this the fecundity of aphids are decreased.

Most of the previous studies have separately analyzed some antioxidant enzymes and certain secondary metabolites in plants, to explore the internal mechanism of the decrease in density of piercing insects or the change of some indicators of the lifetable parameters. For example, Yang and Teixeira *et al.* (2020) shown that the application of Si hindered the feeding of brown planthopper (*Nilaparvata lugens*, BPH) by changing the enzyme activity and the content of some substances in the antioxidant system in plants, and improving silicification of leaf sheaths that BPH feed on, as well as reduced the R_0 and r_m of the sap-sucking cabbage aphid, *Brevicoryne brassica* L. (Hemiptera: *Aphididae*) by changing the Si content of collard leaves, total glucosinolates, and leaf cell wall thickness. This test systematically linked the defensive signal substances, defensive enzyme activities, and defensive secondary substances under the feeding condition of aphids with the aphid life cycle table, and explored the internal mechanism of different silicon levels affecting its internal mechanism. This correlation study has shown that the activities of defense enzymes and the accumulation of signal transduction substances and secondary metabolites were remarkably negatively correlated with the R_0 , T , r_m , λ of aphid, and was significantly positively correlated with the t of aphid. PAL and PPO, as key enzymes of most phenols, can also catalyze the formation of lignin (Liu and Rahe, 1997), promote lignification in cell wall thickness and tissues, and increase the hardness of plants, and reduce the digestibility of insects (He *et al.*, 2011; Abdul *et al.*, 2012). Additionally, PAL is also involved in the synthesis of phytoalexin, SA, and flavonoids. The flavonoids can be used as a growth regulator and signaling molecules (Peer and Murphy, 2006; Vera *et al.*, 2015). Flavonoids are cytotoxic and interact with different enzymes through complexation, and have been investigated as feeding deterrents against many insect pests. Both flavonoids and isoflavonoids protect the plant against insect pests by influencing the behavior, and growth and development of insects (Simmonds, 2003; War *et al.*, 2012). Besides, flavonoids can scavenge the free radicals including ROS, and reduce their formation by chelating the metals (Vera *et al.*, 2015; Alinian *et al.*, 2016; Hamada *et al.*, 2016). Tannin has a strong deleterious effect on phytophagous insects and can affect insect growth and development by binding to the proteins, reduce nutrient absorption efficiency, and cause midgut lesions (Sharma *et al.*, 2009; Barbehenn and Peter, 2011). The presence of secondary compounds such as alkaloids, limonoids, and cucurbitacins tends to reduce palatability, thereby making plants a less

preferred host food source for insects (Aoyama and Labinas, 2012), thus reducing its survival rate and reproduction rate (Zhang *et al.*, 2017). Furthermore, SA signals the release of plant volatiles that attract the natural enemies of insect pests (de Boer *et al.*, 2004), and enhances wheat defense mechanisms against the aphid. However, the Si application method used in most studies is rhizosphere Si application (Teixeira *et al.*, 2020; Ma *et al.*, 2015), but this experiment was foliar spraying, and the Si content of leaf was higher than rhizosphere Si application. Since Si is easily deposited in plants, and once deposited, Si is not remobilized (Raven, 1983).

Conclusions

In conclusion, in the present study, we revealed that the perception of aphid infestation by wheat seedlings and the application of Si induces a whole sequence of potential defensive reactions. It is proposed that the application of Si can enhance secondary metabolism, and reduce the R_0 , T , r_m , λ , prolong the t , thus enhances wheat defense mechanisms against the aphid. Additionally, the content of TEOS was 3 mmol/L, the aphid resistance was the best.

Methods

Materials and methods

Test design

Four germinated seeds were sown in each polyethylene plastic pot that was filled with 700 ml of Hoagland's nutrient solution. In the hydroponic culture experiments, the nutrient solutions were renewed every 3 days. Wheat seedlings were grown in a growth chamber at 70% relative humidity, a photoperiod of 14:10 (L: D), a light intensity of 3000lx. The whole wheat plants were sprayed with the different concentration of Si that was 0 (CK), 0.3 (T1), 1 (T2), 2 (T3), 3 (T4), 4 (T5), 5 (T6), 9 (T7) mmol/L on wheat with the second expanded leaves and trifoliate heart respectively. When the 4 leaf of wheat seedlings started to unfold, the nymphs were transferred onto the plants. In this experiment, each seedling grew a nymph on the entire plant, and 4 wheat plants were planted in each pot, each treatment consisted of 15 individuals. Per plant were checked and nymphs born were removed daily. Adult longevity, nymphal production, and mortality were recorded daily until the aphids died, and missing adult aphids resulting from escape or predation were counted as censored observations on the day of their disappearance. To prevent the aphids from escaping, each plant was covered with a cellophane cover with an opening at the upper end, and a cover made of 80 mesh (0.178 mm. nylon net is covered at the opening). After the aphid died, the wheat was sampled and stored at -80°C.

Plant culture

The wheat seed used in the experiment was Zhengmai 9023, which were provided by Qiule Seed Co., Ltd., Zhengzhou China. Wheat seeds surface were sterilized with 10% H₂O₂ for 30 min and rinsed thoroughly with distilled water four times, then soaked 24 h with distilled water and germinated on moist filter paper for 2 days in petri dishes, and germinated at 25°C. The germinating seeds were sown on moistened gauze fixed to the plastic tray containing distilled water at 25°C. When the seedlings grow to two leaves, wheat seeds with consistent germination was selected and transplanted into a plastic pot to be cultured in a light culture room for later use. The nutrient solution was Hoagland's nutrient solution (Arditti and Dunn 1969): Ca(NO₃)₂·4H₂O 0.945g/L, KNO₃ 0.607g/L, MgSO₄·7H₂O 0.493g/L, NaH₂PO₄·2H₂O 0.156g/L, H₃BO₃ 2.86mg/L, MnCl₂·4H₂O 1.81mg/L, ZnSO₄·7H₂O 0.22mg/L, CuSO₄·5H₂O 0.08mg/L, Na₂MoO₄·H₂O 0.02mg/L, EDTA-NaFe 10.525g/L.

Aphid culture

Aphids were the dominant species of *Sitobion avenae* in Huanghuai region, China. *Sitobion avenae* F used in our study were provided by Henan Academy of Agricultural Sciences. The aphid was then reared on wheat in a greenhouse at 20°C, 70% relative humidity, and a photoperiod of 14:10 (L: D), and the light intensity of 3000lx for being used in experiments.

Si preparation

TEOS: First, 4 ml of absolute ethyl alcohol and 190 ml of distilled water are fully stirred for 0.5h, then the mixed solution of 0, 0.0134, 0.0448, 0.0896, 0.1344, 0.1792, 0.224, 0.4032 ml distilled water and TEOS, respectively, 4 ml of absolute ethyl alcohol and 2 ml of Tween 80 is slowly dropped and fully stirred for 2h.

Measurement indexes and methods

Determination of the life table parameters of aphid

The parameters are calculated as follows (Birch, 1948; Hsin and Hsi, 1985; Chi, 1988):

1) The net reproductive rate (R_0) is recorded as the number of offspring that females produce in a period equivalent to the time from birth to adult death, is calculated as: $R_0 = \sum l_x m_x$

2) The mean generation time (T) is the time of each aphid from birth to the first reproduction, is calculated as: $T = \sum x l_x m_x / R_0$

3) The intrinsic rate (r_m): The maximum instantaneous growth rate of a population in an ideal state, and it reflects the population's expansion ability in an ideal state, which can be used to measure the

population's fitness, is calculated as: $r_m = \ln R_0 / T$

4) The finite rate of increase (λ) refers to the total growth rate of the population in a certain period time, and refers to the population growth trend in a long period time, is calculated as: $\lambda = e^{r_m}$

5) The population doubling time (t): Population doubling time in a certain period time, is calculated as: $t = \ln 2 / R_0$

Where x is the age interval (days), lx is the age-specific survival, mx is the total number of nymphs produced by each aphid for a period equal to their corresponding x .

Enzyme activity assays

The activities of PAL, CAT, LOX, and PPO were determined using commercial assay kits (Suzhou Keming Biotechnology Co., Ltd, Jiangsu, China) according to the manufacturer's instructions.

Secondary metabolites assays

Measurement of lignin content (Lin and Kao, 2001)

Wheat leaves were homogenized with a pestle in a mortar in 95% ethanol. The homogenate was centrifuged at 13860 g for 5 min. The pellet was washed three times with 95% ethanol and twice with a mixture of ethanol and hexane (1:2, v/v). The dried sample was washed once with 2 ml acetyl bromide in acetic acid (1:3, v/v). Then 1 ml acetyl bromide in acetic acid (1:3, v/v) was added to the pellet and incubated at 70°C for 30 min. After cool down, 0.9 ml of 2 mol/L NaOH and 0.1 ml 7.5 mol/L hydroxylamine hydrochloride were added, and the volume was made up to 10 ml with acetic acid. After centrifugation at 13860g for 5 min, the absorbance of the supernatant was measured at 280 nm (A_{280}).

Total Phenolic Content (Tawaha *et al.*, 2007)

100 mg dried leaves were weighed into a PE and extracted with 5 ml of distilled water at 100°C for 30 min in a shaking water bath. After cooling, the extract was centrifuged at 3500 g for 10 min, and the supernatant was recovered and stored at 4°C until used for the total phenolic content assay. The total phenolic content was estimated by using the Folin–Ciocalteu colorimetric method (Folin and Ciocalteu, 1927), using gallic acid as a standard phenolic compound.

Determination of total flavonoid content (Uarrotta *et al.*, 2014)

For extraction, the wheat dried in a hot oven (60°C) for 1 h. Next, 100 mg dried leaves were weighed into a PE and extracted with 95% ethanol (1:60, v/v) at ultrasound in shaking for 12 h. For that, 1 ml of extract solution was mixed with 0.3 ml 5% sodium nitrite (v/v). After 6 min, 0.3 ml 10% aluminum nitrate. After 6 min, 4 ml 4% sodium hydroxide, and 50% ethanol to a total volume of 10 ml. The mixture was well mixed

and incubated at room temperature for 15 min versus reagent blank containing water instead of the sample. The absorbance of the resulting solution was measured at 700 nm by using a microplate reader. Rutin was used as the standard for the quantification of the total amount of flavonoids. Results were expressed as milligrams of rutin equivalent per gram of dry weight (mg/g).

Determination of tannin (Hagerman and Butler, 1978)

Tannin was extracted from 100 mg dried leaves with 10 ml of distilled water at 60°C for 12 h. After centrifugation at 5000 g for 5 min, the supernatant was collected and used for tannin measurements. The tannin content was estimated by using the F–D reagent colorimetric method, and then absorbance was read at 680 nm. Tannic acid was used as a standard tannin compound.

Determination of alkaloids (Ehmann, 1977)

The dried leaves powders (100 mg) were extracted with 80% aqueous methanol (MeOH) (0.2 L×2) at room temperature for 1.5 hours through sonication and were then filtered. The filtrate was evaporated to 1/4 volume in vacuo. The MeOH extract was suspended in 0.1 mol/L HCl (20 ml), vacuum filtration and adjust pH = 9 with concentrated MeOH, and then After 30 minutes, the filtrate was extracted three times with an equal volume of chloroform, and the organic phase was evaporated to dryness, and 70% constant volume of 25 ml. A sample of the extract was added with Ehmann reagent, and then absorbance was read at 555 nm. Quantitative measurements were performed, based on a standard calibration curve of gramine in distilled water.

Signal transduction substances and Si assays

Endogenous JA was measured by GC-MS-SIM (McCloud, 1997; Jang, 2018)

A total of 0.5 g dried sample was extracted with a solution of acetone and 50 mM citric acid (70:30 v/v), and [9, 10-²H₂] 9, 10 dihydro-JA (20 ng) was added as an internal standard. The aqueous solution was then filtered and extracted with 10 ml of diethyl ether three times. Both JAs (endogenous JA and the internal standard) were eluted with 10 ml of diethyl ether and acetic acid (98:2 v/v). The sample was adjusted to 50 µL with dichloromethane after the evaporation of solvents and etherification of the residue with excess diazomethane. Then, the extracts were analyzed by GC-MS-SIM.

Endogenous free SA was measured by high-performance liquid chromatography (HPLC) (Jang, 2018).

A 0.2 g freeze-dried sample was sequentially extracted with 90% and 100% methanol in a centrifuge (10,000×g). Both extracts were dried in a vacuum. The dry pellets were resuspended in 2.5 ml of 5% trichloroacetic acid and the supernatant was partitioned with ethyl acetate/cyclopentane/isopropanol (49.5:49.5:1, v/v). The top layer was transferred to a 4 ml vial and dried with purified N gas. The SA was again suspended in 1 ml of 70% methanol and analyzed by HPLC.

The Si content of rice leaves was determined by the colorimetric molybdenum blue method described by van der Vorm (1987).

Statistical Analysis

The mean life table parameters of aphids and the content of nutritional reserves of wheat in treatments were analyzed using SPSS and EXCEL and were drawing using Origin 2016. PCA and heat-map were analyzed using meta analyst. Differences were compared using a t-test at significance levels of $P < 0.05$ or $P < 0.01$.

Abbreviations

TEOS: Tetraethyl orthosilicate; R_0 : The net reproductive rate; T: The mean generation time; r_m : The intrinsic rate; λ : The finite rate of increase; t: The population doubling time; PAL: Phenylalanine ammonia-lyase; CAT: Catalase; LOX: Lipoxygenase; PPO: Polyphenol oxidase; POD: Peroxidase; ROS: Reactive oxygen species; SOD: Superoxide dismutase; H_2O_2 : Hydrogen peroxide; JA: Jasmonic acid; PAL: Phenylalanine ammonia-lyase; SA: Salicylic acid; ET: Ethylene

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Availability of data and materials

The authors declare that all the experiments performed in this study comply with the institutional, national, or international guidelines. The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Competing interests

The authors declare that they have no competing interests.

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Authors' contributions

Conceived and designed the experiments: YJ, YLH, FMY. Performed the experiments: XXQ, CW, ZLZ. Analyzed the data: XXQ, YJ. Contributed reagents/materials/analysis tools: YLH, FMY. Wrote the paper: XXQ. All authors have read and approved the manuscript.

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Tables

Table 1 Effect of Si on life table parameters of aphid

Treatment (mmol/L)	R_0	T	r_m	λ	t
CK	67.77±1.075a	15.95±0.000a	0.27±0.007a	1.31±0.009a	2.62±0.005e
T1	57.94±0.001b	15.93±0.001ab	0.26±0.003bc	1.29±0.001bc	2.72±0.002cd
T2	50.94±0.432d	15.81±0.169ab	0.26±0.014ab	1.30±0.018ab	2.81±0.070ab
T3	43.35±0.727e	15.61±0.126b	0.26±0.000ab	1.30±0.000ab	2.70±0.087de
T4	40.46±0.216f	15.33±0.060b	0.24±0.010d	1.27±0.001d	2.87±0.006a
T5	52.03±0.786d	15.88±0.128ab	0.25±0.000cd	1.28±0.000cd	2.81±0.003abc
T6	54.38±0.962c	15.95±0.705a	0.26±0.030ab	1.30±0.004ab	2.67±0.029de
T7	55.82±1.042c	15.80±0.003ab	0.25±0.001bc	1.29±0.001bc	2.73±0.002bcd

Note: Silicon is represented by "Si". Life table parameters include net reproduction rate (R_0), intrinsic growth rate (r_m), finite growth rate (λ), average childbearing time (T) and population doubling time (t). CK, T1-T7 represent different treatments, which are spraying different levels of Si that was 0 (CK), 0.3 (T1), 1 (T2), 2 (T3), 3 (T4), 4 (T5), 5 (T6), 9 (T7) mmol/L on wheat. Numbers followed by different letters within a row are significantly different according to the t-test ($P < 0.05$).

Figures

Figure 1

Individual Si mean levels present in wheat at the different concentrations of Si. Note: Silicon is represented by "Si". Different lowercase letters indicate significant differences between treatments. Error bars represent mean $\pm$ SD. CK, T1-T7 represent different treatments, which are spraying different concentrations of Si that was 0 (CK), 0.3 (T1), 1 (T2), 2 (T3), 3 (T4), 4 (T5), 5 (T6), 9 (T7) mmol/L on wheat.

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Figure 2

The effect of the activity of defense enzymes in aphid-infection wheat at the different concentrations of Si, i.e., PAL activity (A), PPO activity (B), CAT activity (C), LOX activity (D). Note: Silicon is represented by "Si". Different lowercase letters indicate significant differences between treatments. Error bars represent mean $\pm$ SD. CK, T1-T7 represent different treatments, which are spraying different concentrations of Si that was 0 (CK), 0.3 (T1), 1 (T2), 2 (T3), 3 (T4), 4 (T5), 5 (T6), 9 (T7) mmol/L on wheat.

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Figure 3

The effect of the levels of secondary metabolites in aphid-infection wheat at the different concentrations of Si. (A) Tannin; (B) flavone; (C) lignin; (D) total phenolic; and (E) alkaloids. Note: Silicon is represented by "Si". Different lowercase letters indicate significant differences between treatments. Error bars represent mean $\pm$ SD. CK, T1-T7 represent different treatments, which are spraying different concentrations of Si that was 0 (CK), 0.3 (T1), 1 (T2), 2 (T3), 3 (T4), 4 (T5), 5 (T6), 9 (T7) mmol/L on wheat.

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Figure 4

The effect of the levels of signal transduction substances in aphid-infection wheat at the different concentrations of Si. Note: Silicon is represented by "Si". Different lowercase letters indicate significant differences between treatments. Error bars represent mean $\pm$ SD. CK, T1-T7 represent different treatments, which are spraying different concentrations of Si that was 0 (CK), 0.3 (T1), 1 (T2), 2 (T3), 3 (T4), 4 (T5), 5 (T6), 9 (T7) mmol/L on wheat.

Figure 4

The effect of the levels of signal transduction substances in aphid-infection wheat at the different concentrations of Si. Note: Silicon is represented by "Si". Different lowercase letters indicate significant differences between treatments. Error bars represent mean $\pm$ SD. CK, T1-T7 represent different treatments, which are spraying different concentrations of Si that was 0 (CK), 0.3 (T1), 1 (T2), 2 (T3), 3 (T4), 4 (T5), 5 (T6), 9 (T7) mmol/L on wheat.

Figure 5

Principal component analysis (PCA) of Si induced variation in the defense enzymes activity, secondary metabolites and signal transduction substances of wheat. (A) variation in the defense enzymes activity, secondary metabolites and signal transduction substances indicators of wheat among the treatments analyzed by PCA; (B) loading of the defense enzymes activity, secondary metabolites and signal transduction substances indicators of wheat to PC1 and PC2. PC1, first principal component; PC2, second principal component.

Figure 5

Principal component analysis (PCA) of Si induced variation in the defense enzymes activity, secondary metabolites and signal transduction substances of wheat. (A) variation in the defense enzymes activity, secondary metabolites and signal transduction substances indicators of wheat among the treatments analyzed by PCA; (B) loading of the defense enzymes activity, secondary metabolites and signal transduction substances indicators of wheat to PC1 and PC2. PC1, first principal component; PC2, second principal component.

Figure 6

Analysis of Si induced variation in the defense enzymes activity, secondary metabolites and signal transduction substances of wheat by cluster analysis. (A) correlation matrix showing correlation among the various indicators; (B) heatmap analysis of various indicators.

Figure 6

Analysis of Si induced variation in the defense enzymes activity, secondary metabolites and signal transduction substances of wheat by cluster analysis. (A) correlation matrix showing correlation among the various indicators; (B) heatmap analysis of various indicators.

Figure 7

Correlation between the life table parameters of aphid and biochemical indexes in wheat at the different concentrations of Si in aphid-infection wheat. Note: Silicon is represented by "Si". Life table parameters include net reproduction rate (R0), intrinsic growth rate (rm), finite growth rate (λ), average childbearing time (T) and population doubling time (t). The number indicates the degree of correlation between indicators. The significant difference among treatments was determined by ANOVA and is represented by * ($P < 0.05$). * and ** showed a significant correlation at 0.05 and 0.01 levels, respectively.

Figure 7

Correlation between the life table parameters of aphid and biochemical indexes in wheat at the different concentrations of Si in aphid-infection wheat. Note: Silicon is represented by "Si". Life table parameters include net reproduction rate (R₀), intrinsic growth rate (r_m), finite growth rate (λ), average childbearing time (T) and population doubling time (t). The number indicates the degree of correlation between indicators. The significant difference among treatments was determined by ANOVA and is represented by * (P<0.05). * and ** showed a significant correlation at 0.05 and 0.01 levels, respectively.