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Selenium improves the content of vitamin C in the fruit of strawberry by regulating the enzymes responsible for vitamin C metabolism

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Abstract: To investigate how sodium selenite (Na_2SeO_3) regulated the content of vitamin C (Vc) in strawberry fruit, we explored the effects of Na_2SeO_3 on the enzymes responsible for Vc metabolism. The findings showed that 10 mg/L Na_2SeO_3 improved the activities of ascorbate peroxidase (APX), monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR), glutathione reductase (GR), L-galactono-1,4-lactone dehydrogenase (GalLDH) at periods of young fruit (YFP), small fruit (SFP), middle fruit (MFP), large fruit (LFP), white fruit (WFP), colour-changed fruit (CFP) and ripen fruit (RFP). 30 mg/L Na_2SeO_3 improved the activities of APX, MDHAR, GR and GaILDH at YFP, LFP, WFP, CFP and RFP. 60 mg/L Na_2SeO_3 improved the activities of MDHAR, GR and GaILDH at all periods studied. In addition, 10 mg/L Na_2SeO_3 decreased the activity of ascorbate oxidase (AAO) at WFP and CFP. 30 mg/L Na_2SeO_3 decreased AAO activity at MFP, LFP, WFP and CFP. 60 mg/L Na_2SeO_3 decreased AAO activity at YFP, SFP, MFP, LFP, WFP and CFP. Meanwhile, all concentrations of Na_2SeO_3 significantly increased the contents of Vc and Se. Among different concentrations, 30 mg/L Na_2SeO_3 had better effects on the enzymes responsible for Vc metabolism, which further improved Vc content in strawberry fruit. Besides, all concentrations of Na_2SeO_3 increased fruit average weight, number of fruits per plant and fruit yield, compared with control. The above results indicated that Na_2SeO_3 could improve the content of Vc in fruit and fruit yield of strawberries, especially for 30 mg/L Na_2SeO_3.

Keywords: trace element; enzymatic activity; nutritional quality; *Fragaria* × *ananassa*; fruit growth and development

Due to the nectarean taste and high nutrition, strawberry fruit is deeply loved by people. As an antioxidant, vitamin C (Vc) is regarded as the main indicator to evaluate the fruit quality of strawberries (Giampieri et al. 2012). The content of Vc is controlled by the enzymes responsible for its biosynthesis, recycling and degradation, including ascorbate peroxidase (APX), monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR), glutathione reductase (GR), L-galactono-1,4-lactone dehydrogenase (GalLDH) and ascorbate oxidase (AAO). Thus, we can increase Vc content in strawberry fruit by regulating the above enzymes responsible for Vc metabolism.

In plants, much evidence showed that Vc accumulation can be regulated by many chemicals, such as mineral elements and phytohormones (Miret and Munné-Bosch 2016, Narváez-Ortiz et al. 2018). For trace element selenium (Se), studies indicated that appropriate concentrations of Se showed positive effects on the growth, yield and stress resistance of plants (Chu et al. 2013, Ojekunle and Sodipe 2020, Abedi et al. 2021). Ghasemian et al. (2021) reported that Se stimulated growth and the activities of antioxidant enzymes to alleviate salt stress in *Melissa officinalis* L. Xie et al. (2021) showed that Se improved the yield of *Lycopersicon esculentum* Miller under cadmium stress. The results of Ghasemian et

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al. (2021) and Xie et al. (2021) also indicated that Se could enhance the stress resistance of *M. officinalis* under salt stress and *L. esculentum* under cadmium stress, respectively. For fruit quality, Ren et al. (2021) showed that Se improved sugar content, sugar-acid ratio and yield of apples. Zhu et al. (2019) reported that Se improved the colour and nutrient content of grapefruit. Besides, Huang et al. (2018) confirmed that Se increased Vc content in strawberry fruit. In a previous study, we also found that Se increased Vc content in strawberry fruit (Zhang et al. 2020b). However, the physiological mechanism for the regulation of Vc content in strawberry fruit by Se is still unclear. Thus, it is interesting to investigate the effects of Se on the activities of enzymes in Vc metabolism, which will help people to understand the role of Se in improving Vc content in strawberry fruit.

In this study, we investigated the effects of Na_2SeO_3 on the activities of enzymes in Vc metabolism and the contents of Vc and Se in the young fruit period (YFP), small fruit period (SFP), middle fruit period (MFP), large fruit period (LFP), white fruit period (WFP), colour-changed fruit period (CFP) and ripen fruit period (RFP). Meanwhile, we investigated the effects of Na_2SeO_3 on fruit average weight, the number of fruits per plant and fruit yield per plant. Besides, we analysed the relationship between Vc content and the activities of enzymes in Vc metabolism. The aim of this study was to elucidate how Se regulated Vc content at the physiological level.

MATERIAL AND METHODS

Plant material and treatments. Strawberry cv. Sweet Charlie was used as the material. Plants with similar size and growth status were chosen and planted in pots containing 3.5 kg culture soil composed of 30% peat and 70% garden soil. In the culture soil, the contents of available nitrogen (N), phosphorus (P) and potassium (K) are 110.5, 100.0 and 120.7 mg/kg, respectively. In the soil, the content of total Se is 0.03 mg/kg. Then above pots were placed in the artificial chamber under 60% relative humidity, 25/15 °C (day/night), 600 μmol/m^2/s photosynthetic active radiation and 12-h photoperiod. From the budding stage, three groups of plants were treated with 10 (T1), 30 (T2) and 60 mg/L (T3) Na_2SeO_3 through foliar spraying, respectively. Plants were treated with Na_2SeO_3 every 7 days. The dosage of Na_2SeO_3 solution was 20 mL per pot. The control plants were only treated with the equivalent water. In total, the foliar spraying was done 3 times. Each treatment had five replicates. The fruits with similar size and growth status were sampled at different periods and used to analyse corresponding indicators. In order to investigate the effects of Na_2SeO_3 on fruit average weight, the number of fruits per plant and fruit yield per plant, each treatment had another five replicates.

Analysis of enzymes in the AsA-GSH cycle. The activities of APX, GR, MDHAR and DHAR were measured according to Shan et al. (2018). One unit of APX and DHAR was defined as the decrease of absorbance by 0.01 per min at 290 nm and 265 nm, respectively. One unit of GR and MDHAR was all defined as the decrease of absorbance by 0.001 per min at 340 nm.

Analysis of GalLDH and AAO. GalLDH activity was measured according to Shan and Liang (2010). One unit of GalLDH activity was defined as the amount of enzyme required to oxidise 1 nmol of Gal per min. AAO activity was measured at 265 nm (Shan et al. 2018). One unit of AAO activity was defined as the amount of enzyme required to oxidise 1 μmol of ascorbate (AsA) to dehydroascorbic acid (DHA) per min.

Measurement of Vc and Se contents. Vc content was measured according to Farajzadeh and Nagizadeh (2003). Se content was measured according to Zheng et al. (2020) through flame atomic absorbance spectrometry (Shimadzu AA-7000, Kyoto, Japan).

Analysis of fruit average weight, number of fruits per plant and fruit yield per plant. At RFP, all the mature fruits of different treatments were sampled, numbered and weighted. Then fruit average weight, number of fruits per plant and fruit yield per plant were calculated.

Statistical analysis. The results were presented as the mean value of 5 replications. Means were analysed by one-way analysis of variance and Duncan's multiple range test at $P < 0.05$.

RESULTS AND DISCUSSION

Effects of Na_2SeO_3 on the activities of enzymes in the AsA-GSH cycle. Different concentrations of Na_2SeO_3 had different effects on the activities of APX, DHAR, MDHAR and GR in fruit at each period, compared with control (Figure 1). At YFP, T1, T2 and T3 enhanced the activities of APX, DHAR, MDHAR and GR. At SFP, T1, T2 and T3 improved the activities of MDHAR and GR. Besides, T1 also improved the activities of APX and DHAR, but T2 reduced DHAR activity. At MFP, T1, T2 and T3 improved the activi-

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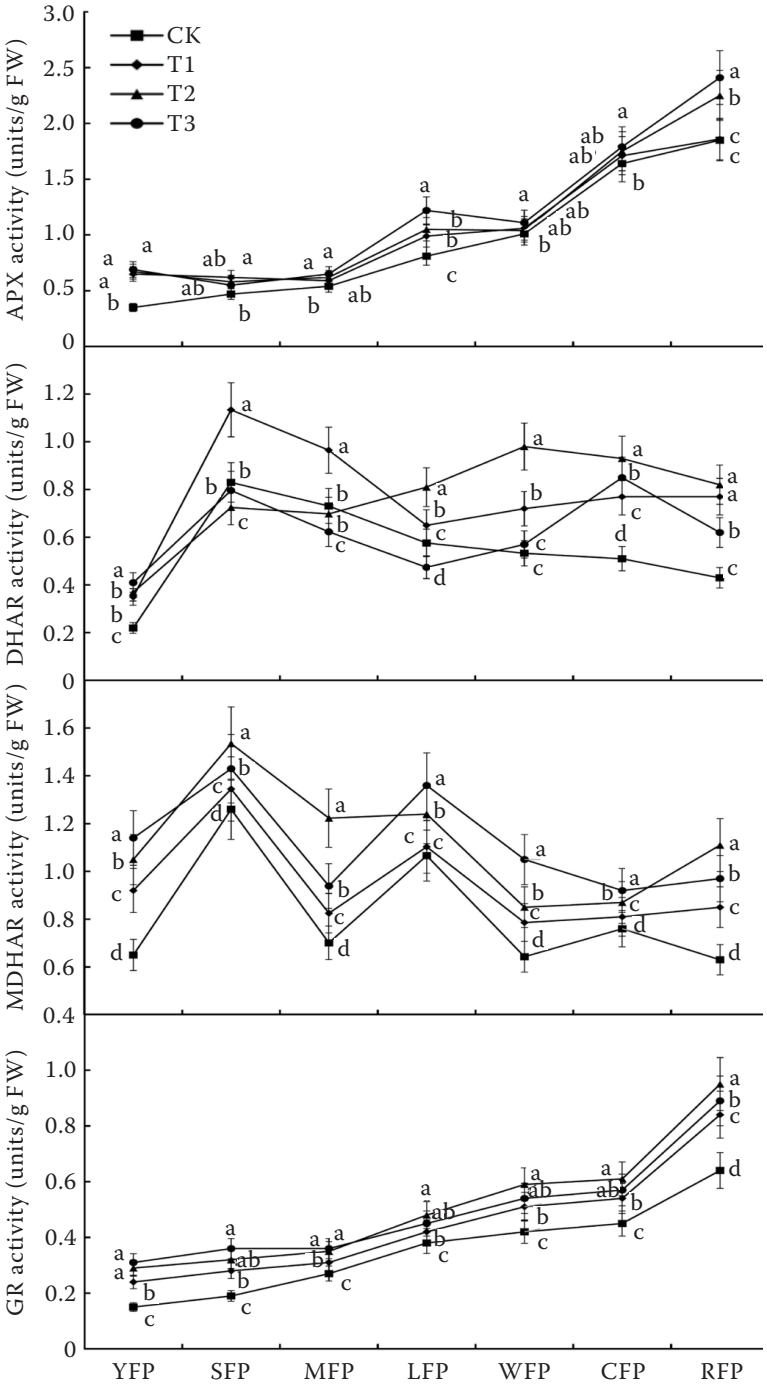

Figure 1. Effects of sodium selenite (Na_2SeO_3) on the activities of ascorbate peroxidase (APX), dehydroascorbate reductase (DHAR), monodehydroascorbate reductase (MDHAR) and glutathione reductase (GR) in strawberry fruit at different growth periods. The plants were treated as follows: CK – distilled water; T1 – 10 mg/L Na_2SeO_3; T2 – 30 mg/L Na_2SeO_3; T3 – 60 mg/L Na_2SeO_3. Different letters represent significant differences between treatments at each period ($P < 0.05$); FW – fresh weight; YFP – young fruit period; SFP – small fruit period; MFP – middle fruit period; LFP – large fruit period; WFP – white fruit period; CFP – colour-changed fruit period; RFP – ripen fruit period

ties of MDHAR and GR. In addition, T1 improved DHAR activity, and T2 and T3 improved APX activity. However, T3 reduced DHAR activity. At LFP, T1, T2 and T3 improved the activities of APX and GR. Besides, T1 and T2 increased DHAR activity, T2 and T3 increased MDHAR activity, but T3 reduced DHAR activity. At WFP, T1, T2 and T3 improved MDHAR activity. T1 and T2 improved the activities of DHAR and GR. T3 improved APX activity. At CFP, T1, T2 and T3 improved the activities of DHAR, MDHAR and GR. T3 increased APX activity. At RFP, T1, T2 and T3 improved the activities of DHAR, MDHAR and GR. T2 and T3 improved APX activity. Among different concentrations, T2 had better effects on the activities of the above enzymes at different periods.

Wu et al. (2017) reported that Se enhanced APX activity in cabbage. In this study, we found that Na_2SeO_3 improved APX activity in strawberry fruit

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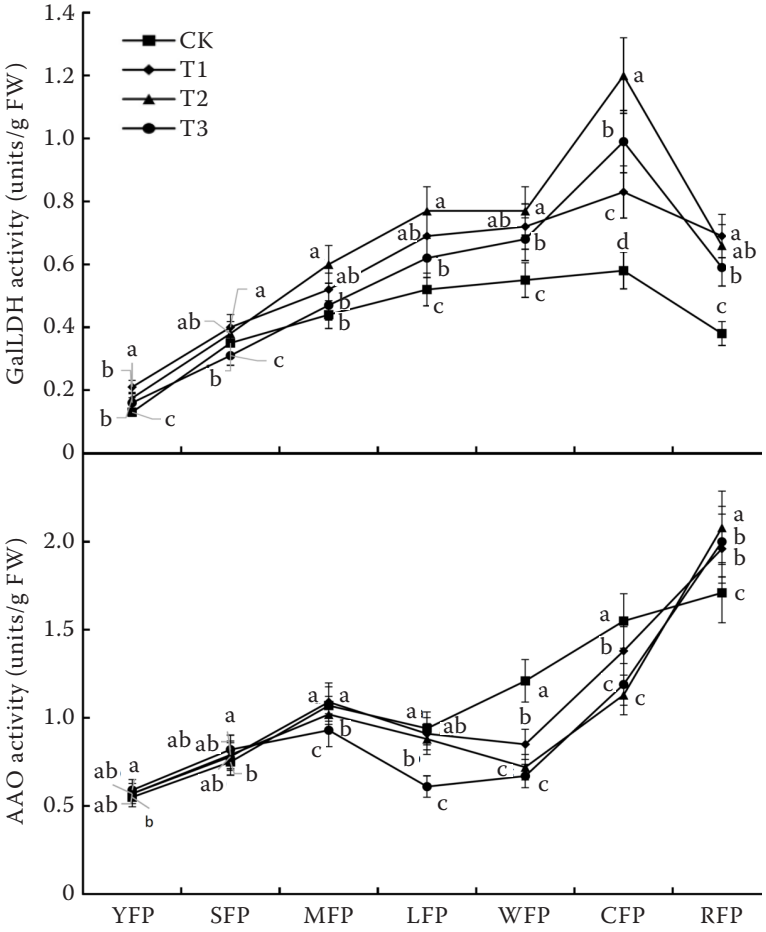

Figure 2. Effects of sodium selenite (Na_2SeO_3) on the activities of L-galactono-1,4-lactone dehydrogenase (GalLDH) and ascorbate oxidase (AAO) in strawberry fruit at different growth periods. The plants were treated as follows: CK – distilled water; T1 – 10 mg/L Na_2SeO_3; T2 – 30 mg/L Na_2SeO_3; T3 – 60 mg/L Na_2SeO_3. Different letters represent significant differences between treatments at each period ($P < 0.05$); FW – fresh weight; YFP – young fruit period; SFP – small fruit period; MFP – middle fruit period; LFP – large fruit period; WFP – white fruit period; CFP – colour-changed fruit period; RFP – ripen fruit period

during each period, which was consistent with Wu et al. (2017). We showed that Vc content in strawberry fruit treated by Se was a positive correlation with APX activity, which was not consistent with the previous study (Shan et al. 2017). This phenomenon may be due to the promotion of APX activity induced by Se, which was a trigger for the increase in Vc content by enhancing Vc biosynthesis and recycling in fruit. Moreover, Silva et al. (2020) reported that Se enhanced GR activity in plants. We found that Se increased GR activity in strawberry fruit, which is consistent with the previous study (Silva et al. 2020). As reported, Se exists in plants in the form of selenocysteine, which is the active centre component of glutathione peroxidase (GSH-PX). GSH-PX can catalyse the transformation from GSH into GSSG (Zhang et al. 2020a). This expla-

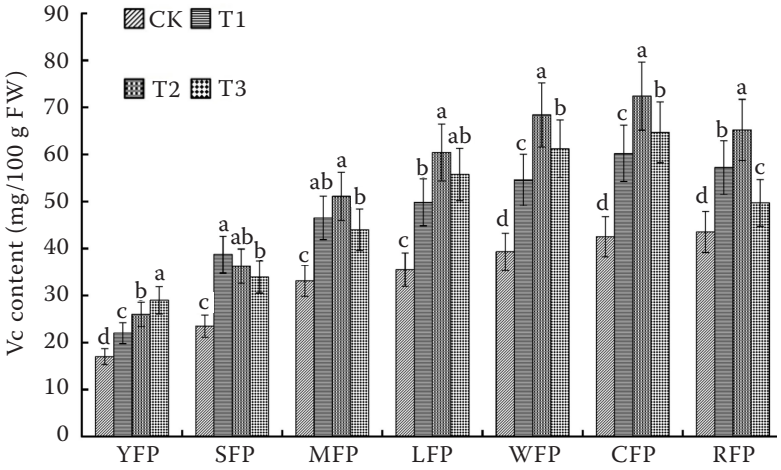

Figure 3. Effects of sodium selenite (Na_2SeO_3) on the vitamin C (Vc) content of strawberry fruit at different growth periods. The plants were treated as follows: CK – distilled water; T1 – 10 mg/L Na_2SeO_3; T2 – 30 mg/L Na_2SeO_3; T3 – 60 mg/L Na_2SeO_3. Different letters represent significant differences between treatments at each period ($P < 0.05$); FW – fresh weight; YFP – young fruit period; SFP – small fruit period; MFP – middle fruit period; LFP – large fruit period; WFP – white fruit period; CFP – colour-changed fruit period; RFP – ripen fruit period

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nation also provides a basis for the promotion of GR activity in strawberry fruit under Se treatment. Huang et al. (2018) found that Se increased MDHAR activity in strawberry fruit under low temperature, which further improved Vc content. Lu et al. (2020) showed that Na_2SeO_3 enhanced DHAR activity in lily cut flowers. In this study, we found that Na_2SeO_3 enhanced the activities of MDHAR and DHAR in strawberry fruit during each period, which was consistent with previous studies (Huang et al. 2018, Lu et al. 2020). Besides, we showed that Vc content was positively correlated with the activities of MDHAR and DHAR at each period. High activities of MDHAR and DHAR, respectively, accelerated the reduction process from monodehydroascorbic acid (MDHA) to Vc and dehydroascorbic acid to Vc, which was responsible for the increase in Vc content under Se treatment.

Effects of Na_2SeO_3 on enzymatic activities of GalLDH and AAO. Different concentrations of Na_2SeO_3 had also different effects on the activities of GalLDH and AAO in fruits at each period, compared with control (Figure 2). At YFP, T1, T2 and T3 enhanced the activities of GalLDH and AAO. At SFP, T1 and T2 improved the activities of GalLDH and AAO, but T3 only improved AAO activity. At MFP, T1, T2 and T3 improved GalLDH activity. However, T1 increased AAO activity, and T2 and T3 reduced AAO activity. At LFP, WFP and CFP, T1, T2 and T3 improved GaILDH activity and reduced AAO activity. At RFP, T1, T2 and T3 improved the activities of GalLDH and AAO. Compared with other concentrations, T2 had better effects on the activities of the above enzymes at different periods.

GalLDH is a key enzyme responsible for the biosynthesis of Vc. Zhang et al. (2020b) showed that Na_2SeO_3 enhanced GalLDH activity in strawberry fruit under cadmium stress. Our study indicated that Se significantly increased GalLDH activity in strawberry fruit after MFP, which is consistent with previous results (Zhang et al. 2020b). Besides, we found that GalLDH activity was positively correlated with Vc content at each period, which suggested that Se increased Vc content through GalLDH. Up to now, there is no report on the effect of Se on AAO activity in plants. We found that Se improved AAO activity in the early and late growth stages of strawberry fruit, but reduced AAO activity during the middle growth stage of strawberry fruit. However, the mechanism for this phenomenon is still unexplored.

Effects of Na_2SeO_3 on Vc content in fruits. All concentrations of Na_2SeO_3 significantly increased Vc content in fruit at each period, compared with control (Figure 3). Compared with other concentrations, T2 had a better positive effect on Vc content. Compared with control, from YFP to RFP, T1 respectively increased Vc content by 29.41, 64.77, 40.40, 40.28, 38.93, 41.65 and 31.49%. Through Pearson correlation analysis, we found that the activities of APX, DHAR, MDHAR, GalLDH and GR were positively correlated with Vc content at each period (Table 1). At YFP, Vc content had significant correlations with the activities of DHAR (r = 0.956), MDHAR (r = 0.989) and GR (r = 0.984). At SFP, Vc content showed significant correlation with APX activity (r = 0.985). At LFP and WFP, Vc content had a significant correlation with GR activity (r = 0.980 and 0.998). At CFP, Vc content showed significant correlations with the activities of GaILDH (r = 0.978), DHAR (r = 0.998) and GR (r = 0.999). At RFP, Vc content only had a significant correlation with DHAR activity (r = 0.958). Besides, Vc content showed a positive correlation with AAO activity at YFP, SFP and RFP, but showed a nega-

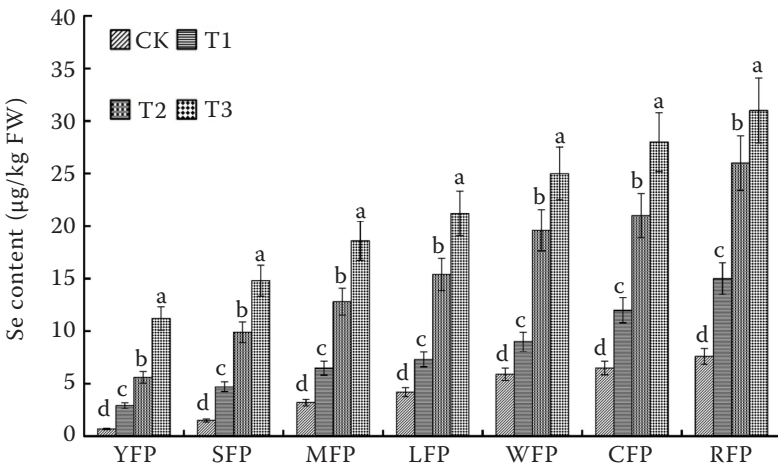

Figure 4. Effects of sodium selenite (Na_2SeO_3) on the selenium (Se) content of strawberry fruit at different growth periods. The plants were treated as follows: CK – distilled water; T1 – 10 mg/L Na_2SeO_3; T2 – 30 mg/L Na_2SeO_3; T3 – 60 mg/L Na_2SeO_3. Different letters represent significant differences between treatments at each period (P < 0.05); FW – fresh weight; YFP – young fruit period; SFP – small fruit period; MFP – middle fruit period; LFP – large fruit period; WFP – white fruit period; CFP – colour-changed fruit period; RFP – ripen fruit period

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Table 1. Correlation analysis between vitamin C (Vc) content and related enzyme activities

	Vc content						
	YFP	SFP	MFP	LFP	WFP	CFP	RFP
GalLDH	0.304	0.436	0.889	0.858	0.922	0.978*	0.84
APX	0.885	0.985*	0.716	0.822	0.54	0.863	0.277
DHAR	0.956*	0.36	0.095	0.393	0.739	0.998**	0.958*
MDHAR	0.989*	0.617	0.838	0.764	0.73	0.807	0.825
AAO	0.943	0.608	–0.219	–0.478	–0.943	–0.962*	0.842
GR	0.984*	0.753	0.78	0.980*	0.998**	0.999**	0.822

*at the level of 0.05 (double-tailed), the correlation was significant; **at the level of 0.01 (double-tailed), the correlation was significant; YFP – young fruit period; SFP – small fruit period; MFP – middle fruit period; LFP – large fruit period; WFP – white fruit period; CFP – colour-changed fruit period; RFP – ripen fruit period; GalLDH – L-galactono-1,4-lactone dehydrogenase; APX – ascorbate peroxidase; DHAR – dehydroascorbate reductase; MDHAR – monodehydroascorbate reductase; AAO – ascorbate oxidase; GR – glutathione reductase

tive correlation with AAO activity at other periods. Especially for CFP, Vc content showed a significant negative correlation with AAO activity (r = –0.962).

Effects of Na_2SeO_3 on Se content in fruits. All concentrations of Na_2SeO_3 significantly increased Se content in fruit during every period, compared with control (Figure 4). Compared with control, from YFP to RFP, T1 respectively increased Se content by 314.29, 213.33, 103.125, 73.81, 52.54, 84.62 and 97.37%, T2 respectively increased Se content by 700.0, 560.00, 300.0, 266.67, 232.20, 223.07 and 242.11%, T3 respectively increased Se content by 1 500.0, 886.67, 481.25, 404.76, 323.73, 330.769 and 307.90%. The above results indicated that Se content in fruits increased with the increase in Na_2SeO_3 concentration at each period. In consumer fruits, higher doses of Se can cause health risks to a human. Thus, the Se content in strawberry fruit can not harm human health after its application in production. According to the standard of the National Health Authority of China, Se content in fruits should be lower than 100 μg/kg (GB13105-1991 Health Standard for Selenium in Food) (Ministry of Health of the People's Republic of China 2010). In this study, we showed that Se content in strawberry fruits treated with different concentrations of Na_2SeO_3 was all lower than 100 μg/kg. Therefore, the amount of Se used in this study was in agreement with the requirements of food safety.

Effects of Na_2SeO_3 on fruit average weight, number of fruits per plant and fruit yield per plant. All concentrations of Na_2SeO_3 increased fruit average weight, compared with control (Figure 5). However, there is no significant difference among all treatments. For the number of fruits per plant and fruit yield per plant, all concentrations of Na_2SeO_3 significantly increased

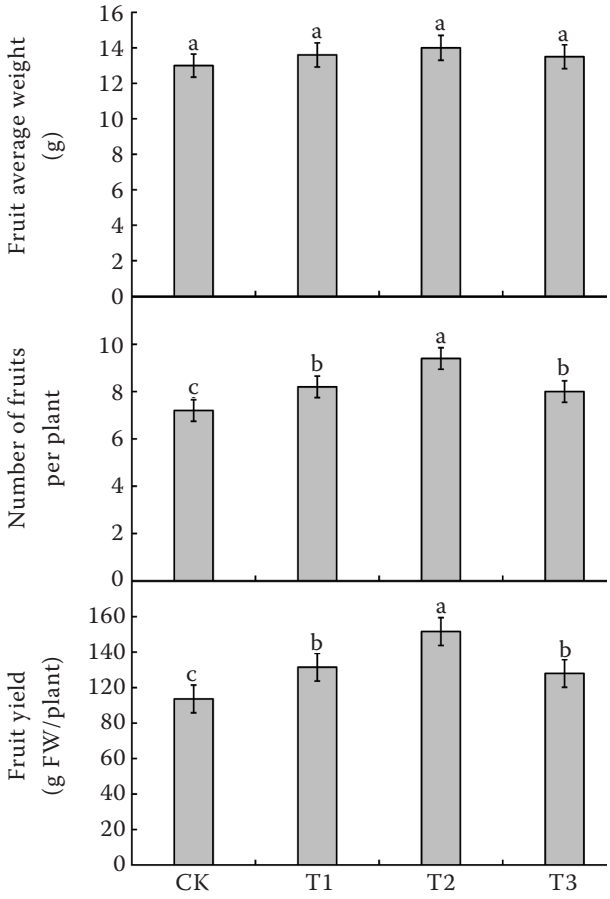

Figure 5. Effects of sodium selenite (Na_2SeO_3) on fruit average weight, number of fruits per plant and fruit yield of strawberry at different growth periods. The plants were treated as follows: CK – distilled water; T1 – 10 mg/L Na_2SeO_3; T2 – 30 mg/L Na_2SeO_3; T3 – 60 mg/L Na_2SeO_3. Different letters represent significant differences between treatments at each period (P < 0.05); FW – fresh weight

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these two indexes, compared with control. The above results indicated that Na_2SeO_3 could improve the fruit yield of strawberries by increasing the number of fruits per plant. Compared with other concentrations, T2 had a better positive effect on fruit average weight, number of fruits per plant and fruit yield per plant.

In conclusion, our study showed that Se enhanced the activities of enzymes responsible for Vc metabolism, which further increased the Vc content of strawberry fruit. Among different concentrations, 30 mg/L Na_2SeO_3 had the best positive effect on the improvement of Vc content in strawberry fruit by regulating enzymes responsible for Vc metabolism.

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