Effects of exogenous sucrose and selenium on plant growth, quality, and sugar metabolism of pea sprouts

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Abstract

BACKGROUND: Pea sprouts are considered a healthy food. Sucrose is a key nutritional factor affecting taste and flavor. Meanwhile, selenium (Se) is an essential micronutrient that plays multiple roles in wide variety of physiological processes and improves crop quality and nutritional value. Nonetheless, the effects of the combination of sucrose and Se treatment on growth, quality, and sugar metabolism of pea sprouts have not been explored.

RESULTS: The results revealed that sucrose at 10 mg L\(^{-1}\) obviously increased fresh weight, vitamin C, soluble protein, soluble sugar, fructose, glucose, and sucrose contents. Se treatments also improved nutritional quality, but higher Se (2.5 mg L\(^{-1}\)) significantly inhibited the growth of seedlings. Interestingly, the combined application of sucrose (10 mg L\(^{-1}\)) and Se (1.25 mg L\(^{-1}\)) could effectively promote vitamin C, sucrose, and fructose contents, especially the Se content, compared with Se application alone. Additionally, there were significant differences in the regulation of sugar metabolism between Se alone and combined application of sucrose and Se. Acid invertase and neutral invertase play a pivotal role in the accumulation of soluble sugar under Se treatments alone, and acid invertase might be the key enzyme to limit sugar accumulation under combined application of sucrose and Se.

CONCLUSION: The moderate combined application of sucrose (10 mg L\(^{-1}\)) and Se (1.25 mg L\(^{-1}\)) more effectively regulated sugar metabolism and improved nutritional quality than Se application alone did.

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Keywords: pea sprouts; sucrose; selenium; nutritional quality; sugar metabolism

INTRODUCTION

Sucrose is one of the final products of plant photosynthesis, providing not only energy for life activities of animals and plants, but also acting as an important signal molecule for regulating growth and development.\(^1\) It can enhance plant growth and increase yield of crops.\(^2-5\) Using 0.05% exogenous sucrose significantly increased the content of total phenol and vitamin C in mung bean sprouts without affecting the sprout growth and moisture content.\(^6\) Sucrose also promoted the transport of polyphenols and changed the aroma components of tea trees.\(^7\) Moreover, Inna et al. examined the effects of sucrose on mesocarp pigment and concluded that sucrose may regulate the synthesis of anthocyanin and phenolic compounds in peach fruit.\(^8\) Exogenous sucrose treatment has been shown to promote nutritional quality\(^9\) and to significantly increase the content of ascorbic acid, anthocyanins, and polyphenols in broccoli sprouts.\(^10\) In addition, exogenous sucrose had a great influence on the growth and quality of flowering Chinese cabbage. Appropriate sucrose concentration treatment significantly increased the total soluble sugar content and the content of reducing sugar.\(^11\) Morkunas et al. showed that exogenous sucrose caused a marked increase in endogenous soluble sugars content (sucrose, glucose, and fructose), isoflavone glycosides, and free aglycones in the embryo axes.\(^12\) Thus, treatment with a suitable concentration of sucrose can increase plant yield and improve its quality.
Selenium (Se) is an important trace element for optimal health and development of humans and other mammals, and a low level of Se in humans can lead to a risk of cardiovascular diseases, cancer,\textsuperscript{15-17} and other problems caused by free radicals.\textsuperscript{18} Avery and Hoffmann noted that the immune system relies on an adequate dietary Se intake.\textsuperscript{19} Therefore, Se enrichment has become one of the concerns of food nutrition quality. Meanwhile, Se is a beneficial mineral for plants with regard to growth, quality, and higher tolerance under adverse climatic conditions.\textsuperscript{20,21} The application of Se in plants could significantly increase endogenous Se content\textsuperscript{22,23} and other nutritive ingredients, such as vitamin C.\textsuperscript{23,24} Soluble sugar and soluble protein,\textsuperscript{25,26} as well as regulate sugar metabolism.\textsuperscript{27}

Pea (\textit{Pisum sativum} L.) sprouts – being nutritious and providing health benefits – are one of the most common vegetables consumed in China and many other countries. Sucrose is a key nutritional factor affecting the taste and flavor of food, and Se is an essential micronutrient that plays multiple roles in a wide variety of physiological processes and improves crop quality and nutritional value. Hence, it is possible that the combination of sucrose and Se enrichment may be beneficial to the production of flavor and the nutritional value of pea sprouts. Thus, this study investigates the effects of individual and combined applications of sucrose and Se on plant growth, nutritional quality, and sugar metabolism in pea sprouts.

**MATERIALS AND METHODS**

**Materials and reagents**

Pea seeds (Sijilv, Huizhou, China), sodium selenate (XiYa, Shandong, China), and sucrose (GCRF, Guangzhou, China) were used. The experiments were conducted at the vegetable culture laboratory of South China Agricultural University. This study was carried out in two phases. The first stage was to screen the most suitable sucrose concentration by exploring the effects of different exogenous sucrose concentrations on growth and quality of pea sprouts. On the basis of the optimal exogenous sucrose concentration selected in the first stage, the second-stage experiment examined the effects of different concentrations of Se alone and in combination with sucrose on fresh weight, quality, and sugar metabolism of pea sprouts.

The first stage consisted of five different concentrations of sucrose treatments: a control (pure water, CK), 5 mg L\textsuperscript{-1} sucrose (T5), 10 mg L\textsuperscript{-1} sucrose (T10), 20 mg L\textsuperscript{-1} sucrose (T20), and 40 mg L\textsuperscript{-1} sucrose (T40). The second stage consisted of individual and combined applications of Se and sucrose as follows: 0.625 mg L\textsuperscript{-1} Se (S1), 1.25 mg L\textsuperscript{-1} Se (S2), 2.5 mg L\textsuperscript{-1} Se (S3), 10 mg L\textsuperscript{-1} sucrose + 0.625 mg L\textsuperscript{-1} Se (TS1), 10 mg L\textsuperscript{-1} sucrose + 1.25 mg L\textsuperscript{-1} Se (TS2), and 10 mg L\textsuperscript{-1} sucrose + 2.5 mg L\textsuperscript{-1} Se (TS3). Each treatment contained four replicates.

We used 50 g of pea seeds (about 260 seeds) in each replicate. First, the pea seeds were soaked with 1000 mL distilled water for 8 h; then, the pea seeds were taken out and spread on a plastic tray (30 cm × 50 cm). After sowing, to each plastic tray was added 1600 mL of the solutions of the different treatments, and then the pea seeds were covered with a layer of wet gauze and cultured in a room at 25 °C for 15 h in darkness; the gauze was subsequently removed and the trays subjected to conditions of 25 °C, 150 lx light intensity, and 75% relative humidity. When the pea sprouts had grown to about 12 cm (7 days after sowing), the plants were harvested to determine the various indexes.

**Biometric measurements**

The edible parts of pea sprouts were collected 7 days (about 12 cm height) after sowing. The fresh weight was measured using an electronic balance. Thirty plants were used as a sample group for each treatment. The plant samples were frozen in liquid nitrogen and stored at −80 °C until biochemical analyses. Four replicates were performed for each biochemical measurement.

**Quality index determination**

The vitamin C content was measured using molybdenum blue colorimetry.\textsuperscript{28} Fresh pea sprouts samples (2 g) were ground into a homogenate with 25 mL oxalic acid-ethylenediaminetetraacetic acid solution (w/v). After centrifugation for 10 min, supernatant (1 mL) was used to determine the content of vitamin C using an ultraviolet (UV) spectrophotometer at 760 nm.

The soluble sugar content was measured according to the Coomassie brilliant blue G-250 dye method.\textsuperscript{28} Fresh pea sprouts samples (1 g) were heated in a boiling water bath with 10 mL distilled water twice for 30 min each time. The combined extract was mixed with 1 mL zinc acetate and 1 mL potassium ferrocyanide. The absorbance was measured at 630 nm using a UV spectrophotometer after standing for 15 min.

The cellulose content was determined using anthrone colorimetry.\textsuperscript{28} Dry pea sprouts samples (0.2 g) were ground using a high-speed centrifuge and digested with sulfuric acid for 30 min, and then the volume was fixed with sulfuric acid to 100 mL. The filtrate (5 mL) was diluted to 100 mL with distilled water. Then, 2 mL extract, 0.5 mL 2% anthrone, and 5 mL concentrated sulfuric acid were mixed and shaken. The absorbance was measured at 620 nm using a UV spectrophotometer after standing for 12 min.

The fructose, glucose, and sucrose contents were determined using a Waters high-performance liquid chromatograph (Massachusetts, America). Fresh pea sprouts samples (0.5 g) were ground using a refrigerated grinder and swirled with 4 mL 90% ethanol for 30 s, and then placed in a water bath at 80 °C for 20 min. After centrifugation for 10 min, the supernatant was dried using a rotary evaporator and then vortexed with 2 mL ultrapure water for 1 min. After centrifugation at 12 000 × g for 10 min, the supernatant obtained was filtered through an extraction column (GracePure™ SPE C18-Max 100 mg/1 mL) and then a filter membrane (0.45 μm) and then transferred into a test bottle. The chromatographic separation was carried out on the Waters high-performance liquid chromatograph system with an Agilent NH2 column (4.6 mm × 250 mm), and the mobile phase comprised acetonitrile and water (volume ratio: 75:25). A flow rate of 1 mL min\textsuperscript{-1} was employed throughout the analysis. The column temperature was controlled at 35 °C, and the volume of solution injected into the column was 10 μL.

The Se content was determined using inductively coupled plasma mass spectrometry.\textsuperscript{29} Dry pea sprouts samples (0.5 g) were ground using a high-speed centrifuge and digested with 5 mL nitric acid for 1 h. After cooling, the digestion solution was transferred to a temperature-controlled electric heating plate and heated for 30 min; then the volume was made up to 50 mL with distilled water. After the blank experiment, the signal
response values of the elements needed to be detected and the signal response values of the internal standard elements were measured respectively.

**Enzyme activity determination**

Fresh pea sprouts samples (1 g) and 2 mL precooled extraction buffer (5 mmol L\(^{-1}\) magnesium chloride, 1 mmol L\(^{-1}\) ethylenediaminetetraacetic acid, 0.1% mercaptoethanol, 0.1% TritonX-100, 0.1 mol L\(^{-1}\) phosphate buffer, pH 7.5) were ground to homogenate in an ice-water bath, washed with 1 mL extraction buffer three times, and centrifuged for 15 min. To the precipitates was added 3 mL extraction solution again and extracted once. The supernatants were combined twice, and the volume was constant to 10 mL, which were the enzyme extract for the determination of the activity of acid invertase (AI), neutral invertase (NI), and sucrose synthase (SS). The activities of AI, NI, and SS were determined using the reducing sugar content differential method, following the method of Wang et al.\(^{30}\)

**Data processing and analysis**

Data are expressed as mean plus/minus standard error (\(n = 4\) replicates) and were analyzed by one-way analysis of variance using SPSS Statistics 19.0 software (IBM Corp., Armonk, NY, USA). Means were compared using Duncan’s test, and differences were considered significant at \(P < 0.05\). The figures were generated using Origin 2018c (OriginLab Corp., Northampton, MA, USA).

**RESULTS**

**Effects of exogenous sucrose on fresh weight and nutritional quality of pea sprouts**

With the increase of sucrose concentrations, the fresh weight first increased and then decreased. Compared with CK, the fresh weight of T5, T10, and T20 treatments significantly increased by 5.53%, 11.93%, and 3.76% respectively, but it significantly reduced 3.44% under T40 treatment (Fig. 1(a)).

Compared with CK, the vitamin C content of T5, T10, and T20 treatments significantly increased by 11.96%, 19.57%, and 11.96% respectively, whereas there was no significant difference between T40 treatment and CK. The soluble protein content of T5, T10, T20, and T40 treatments significantly increased by 11.65%, 14.42%, 11.83% and 8.88% respectively (Fig. 1(b) and (c)).

Compared with CK, the fructose content of T5, T10, T20, and T40 treatments significantly increased by 5.02%, 10.33%, 10.51%, and 3.98%, and the glucose content increased by 0.51%, 9.96%, 12.75%, and 3.27% respectively (Fig. 2(b) and (c)).

The content of soluble sugar and endogenous sucrose obviously increased with the increase of sucrose concentrations. Compared with CK, the soluble sugar content of T10, T20, and T40 treatments significantly increased by 4.04%, 5.80%, and 10.45%

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**Figure 1.** The effects of exogenous sucrose – control (CK, pure water), T5 (5 mg L\(^{-1}\) sucrose), T10 (10 mg L\(^{-1}\) sucrose), T20 (20 mg L\(^{-1}\) sucrose), T40 (40 mg L\(^{-1}\) sucrose) – on (a) plant fresh weight, (b) vitamin C content, (c) soluble protein content, and (d) cellulose content in pea sprouts. Data are the mean plus/minus standard error (\(n = 4\)). Different letters above columns show significant differences (\(P < 0.05\)) between treatments. FW, fresh weight.
respectively, and the sucrose content significantly increased by 10.70%, 14.64%, 14.99%, and 20.14% respectively (Fig. 2(a) and (d)). Sucrose treatments had no significant influences on cellulose content (Fig. 1(d)).

The aforementioned results demonstrated that the 10 mg L\(^{-1}\) sucrose treatment not only significantly increased the fresh weight but also significantly improved the nutritional quality of pea sprouts. Therefore, the combined application of sucrose and different Se concentrations was carried out based on a concentration of 10 mg L\(^{-1}\) exogenous sucrose in the second-phase experiments.

**Effects of exogenous Se and combined application of sucrose and Se on fresh weight and nutritional quality of pea sprouts**

The fresh weight of S3 treatment significantly decreased by 15.59% compared with CK, but there was no significant difference among CK, S1, and S2 treatments. The combined applications of sucrose and Se significantly reduced fresh weight, and the fresh weight of TS1, TS2, and TS3 treatments significantly reduced by 4.49%, 5.34%, and 13.74% respectively compared with CK. These results indicated that the higher the Se concentration, the worse the fresh weight (Fig. 3(a)).

The vitamin C content of S2 treatment significantly increased by 8.79% compared with CK, but there was no significant difference among CK, S1, and S3 treatments. The combined applications of sucrose and Se significantly increased vitamin C content compared with Se treatment alone. Compared with CK, the vitamin C content of TS1, TS2, and TS3 treatments significantly increased by 16.60%, 17.58%, and 16.60% respectively, but there was no significant difference among them (Fig. 3(b)).

Compared with CK, the soluble protein content under S1, S2, and S3 treatments significantly increased by 26.32%, 29.56%, and 37.96% respectively. Similarly, the soluble protein content gradually increased with increasing Se concentration on the basis of 10 mg L\(^{-1}\) sucrose (Fig. 3(c)).

The cellulose content of S2 and S3 treatments significantly decreased by 6.19% and 8.25% respectively compared with CK, but S1 treatment had no obvious effect on cellulose content. Similarly, the variation trend of cellulose content under combined application treatments was consistent with that of Se treatments alone (Fig. 3(d)).

Compared with CK, the soluble sugar content of S1, S2, and S3 treatments significantly increased by 4.77%, 13.29%, and 10.91% respectively, and that of TS2 and TS3 treatments significantly increased by 6.14% and 3.75% respectively, but there was no significant difference between CK and TS1 treatment, as well as TS2 and TS3 treatments (Fig. 4(a)).

Compared with CK, the soluble sugar content of S1, S2, and S3 treatments significantly increased by 26.32%, 29.56%, and 37.96% respectively, compared with CK, the fructose content of the S1, S2, and S3 treatments significantly increased by 29.54%, 77.57%, and 121.90% respectively, and that of TS1, TS2, and TS3 treatments.

The fructose content significantly increased with an increase in Se concentrations. Compared with CK, the fructose content of the S1, S2, and S3 treatments significantly increased by 29.54%, 77.57%, and 121.90% respectively, and that of TS1, TS2, and TS3 treatments.

**Figure 2.** The effects of exogenous sucrose – control (CK, pure water), T5 (5 mg L\(^{-1}\) sucrose), T10 (10 mg L\(^{-1}\) sucrose), T20 (20 mg L\(^{-1}\) sucrose), T40 (40 mg L\(^{-1}\) sucrose) – on contents of (a) soluble sugar, (b) fructose, (c) glucose, and (d) endogenous sucrose in pea sprouts. Data are the mean plus/minus standard error (\(n = 4\)). Different letters above columns show significant differences (\(P < 0.05\)) between treatments. FW, fresh weight.
treatments significantly increased by 64.83%, 123.57%, and 56.87% respectively, but there was no statistically significant difference between the TS1 and TS3 treatments. (Fig. 4(b)). Compared with the CK, the glucose content of the S1, S2, and S3 treatments significantly increased by 51.80%, 52.46%, and 47.75% respectively, but there was no significant difference among the three Se treatments. The glucose content significantly increased by 14.04%, 54.25%, and 4.33% respectively under TS1, TS2, and TS3 treatments, but there was no significant difference between TS1 and TS3 treatments or between TS3 treatment and CK (Fig. 4(c)).

The endogenous sucrose content of S1, S2, and S3 treatments significantly decreased by 8.71%, 13.38%, and 19.73% respectively compared with CK. The combined treatments of Se and sucrose significantly increased the endogenous sucrose content compared with that of Se treatments alone, but there was no significant difference among the three combined application treatments (Fig. 4(d)).

With the increase of Se concentrations, endogenous Se content obviously increased. Compared with CK, the endogenous Se content of S1, S2, and S3 treatments significantly increased by 37.16%, 47.54%, and 65.85% respectively. Similarly, the combined treatments of sucrose and Se also significantly increased endogenous Se content, and the highest endogenous Se content was found in the TS2 treatment (Fig. 5(a)).

Effects of exogenous Se and combined application of sucrose and Se on sugar metabolism in pea sprouts

Different concentrations of Se significantly increased SS activity, but there was no significant difference among the three Se treatments. On the basis of 10 mg L\(^{-1}\) sucrose, SS activity showed an increasing trend with increase in Se concentration; but except for the SS activity of the TS3 treatment demonstrating a significant increase, there was no significant difference among the CK, TS1, and TS2 treatments. The results revealed that Se treatments alone could significantly increase the SS activity compared with the combined application treatments (Fig. 5(b)).

NI activity could be induced by different Se concentrations (Fig. 5(c)). Compared with CK, the NI activity of the S1, S2, and S3 treatments increased by 3.80%, 30.37%, and 17.72% respectively. With an increase in Se concentration, the NI activity of the TS1, TS2, and TS3 treatments demonstrated a decreasing trend. The varying trend of NI activity was the same as the soluble sugar of Se treatment alone, but we did not find that the change rule of any kind of sugar was consistent with that of NI activity in combined applications of Se and sucrose.

Different concentrations of Se demonstrated a significant influence on AI activity (Fig. 5(d)). Compared with CK, the AI activity of the S1, S2, and S3 treatments increased by 40.52%, 74.21%, and 47.37% respectively, and that of the TS1, TS2, and TS3 treatments increased by 2.63%, 44.99%, and 17.37% respectively. These data

Figure 3. The effects of exogenous Se alone – control (CK, pure water), S1 (0.625 mg L\(^{-1}\) Se), S2 (1.25 mg L\(^{-1}\) Se), S3 (2.5 mg L\(^{-1}\) Se) – and combined application of sucrose and Se – control (CK, pure water), TS1 (10 mg L\(^{-1}\) sucrose + 0.625 mg L\(^{-1}\) Se), TS2 (10 mg L\(^{-1}\) sucrose + 1.25 mg L\(^{-1}\) Se), TS3 (10 mg L\(^{-1}\) sucrose + 2.5 mg L\(^{-1}\) Se) – on (a) plant fresh weight, (b) vitamin C content, (c) soluble protein content, and (d) cellulose content in pea sprouts. Data are the mean plus/minus standard error (\(n = 4\)). Different letters above columns show significant differences (\(P < 0.05\)) between treatments. FW, fresh weight.
showed that, with or without sucrose, the highest AI activities were observed under 1.25 mg L\(^{-1}\) Se treatment. Furthermore, the varying trend of AI activity was the same as the soluble sugar of Se treatments alone, and it was basically consistent with that of soluble sugar, fructose, and glucose contents of combined application of sucrose and Se.

**DISCUSSION**

**Effects of exogenous sucrose and Se on fresh weight**

Sucrose has an important role in regulating many processes, such as carbohydrate metabolism, sucrose transport, and anthocyanin accumulation.\(^1\) Exogenous sucrose – the optimum concentration of which is different for various plants – promoted plant growth of maize,\(^2\) nut,\(^3\) peach,\(^4\) and lily.\(^5\) Therefore, it is necessary to screen the suitable exogenous sucrose concentration for promoting plant growth of pea sprouts. In this study, our results revealed that different concentrations of sucrose have different effects on the growth of sprouts. Interestingly, we found that the largest fresh weight was induced by a sucrose concentration of 10 mg L\(^{-1}\), but an excessive high concentration of sucrose (40 mg L\(^{-1}\)) could significantly inhibit the growth of pea sprouts.

Spraying Se nutrition was an effective method for Se-enriched vegetable production.\(^6\) Se can protect plants from abiotic stress and promote plant growth.\(^7\) Many studies reported that different Se concentrations have different effects on plant growth, with low Se being beneficial to plant growth but high Se inhibiting plant growth.\(^8,9\) This is consistent with our results that lower Se (0–1.25 mg L\(^{-1}\)) had no obvious effects on fresh weight, but high Se (2.5 mg L\(^{-1}\)) significantly decreased fresh weight in pea sprouts. In addition, the combined application of sucrose and Se decreased fresh weight to some extent compared with CK, but there was no significant difference when compared with Se application alone. The aforementioned results indicated that Se and sucrose in a certain range of concentrations can promote plant growth but that there is a concentration effect.

**Effects of exogenous sucrose and Se on nutritional quality**

Exogenous sucrose enhanced vitamin C\(^10,11\) and soluble protein\(^12,13\) in plants. It has been reported that exogenous sucrose did not change the endogenous sucrose content in leaf and stalk tissues, but it was decreased in sheath tissues. Glucose and fructose contents decreased in leaves and sheaths, but it did not change in stalk due to the sucrose supply.\(^14\) Foliar application of 50 mg L\(^{-1}\) sucrose remarkably increased the contents of total soluble sugar, reducing sugar, sucrose, fructose, and glucose, but high concentration obviously decreased soluble sugar content in flowering Chinese cabbage.\(^15\) Our results showed that, with
an increase in sucrose, the contents of vitamin C, soluble protein, fructose, and glucose were increased obviously in the range 0–10 mg L\(^{-1}\) and then decreased gradually at a level of 20–40 mg L\(^{-1}\). With the increase of exogenous sucrose in the range 0–40 mg L\(^{-1}\), the contents of endogenous sucrose were increased gradually. It can be seen that a suitable sucrose treatment could effectively improve the nutritional quality of pea sprouts.

It has been reported that Se treatments increased vitamin C, soluble sugar and soluble protein, and Se contents of crops. Liang et al.\(^{38}\) showed that Se treatments could significantly increase the content of vitamin C of leaf and stem and decrease the contents of soluble protein in stem and soluble sugar in leaf in flowering Chinese cabbage. Though the content of total soluble sugar in lettuce was enhanced by spraying Se on the leaf, the content of crude fiber and vitamin C was increased by low Se but decreased by high Se.\(^{34}\) These findings showed that the effects of different concentrations of Se on the nutritional quality of different crops and organs were different. Our results showed that Se treatments significantly increased the content of soluble protein, soluble sugar, fructose, glucose, and Se but decreased the sucrose content in pea sprouts. The combined application of sucrose and Se increased the content of vitamin C, soluble protein, soluble sugar, fructose, glucose, sucrose, and Se in pea sprouts but decreased cellulose content. Moreover, we found that the suitable combined application of sucrose and Se (1.25 mg L\(^{-1}\) Se + 10 mg L\(^{-1}\) sucrose) could effectively promote the contents of vitamin C, endogenous fructose and sucrose, and Se compared with Se application alone, and to increase the contents of soluble protein, fructose, and glucose compared with sucrose (10 mg L\(^{-1}\)) application alone. Thus, Se or sucrose could improve the nutritional quality of pea sprouts, and the suitable combined application could significantly improve some nutritional quality than sucrose or Se treatment alone, especially play an important role in sugar synthesis.

**Effects of exogenous sucrose and Se on sugar metabolism**

AI, NI, and SS are important enzymes that regulate the sugar metabolism of plants.\(^{27,37,39}\) The accumulations of sucrose and fructose were related to increases in the activities of AI, NI, and SS, whereas the glucose content displayed opposite effects under exogenous sucrose treatment in sugarcane.\(^{37}\) Se could increase the AI activity but had no obvious effect on the activities of NI and SS in berries, and AI activity showed a significant positive correlation with glucose and fructose.\(^{27}\) However, Ren et al.\(^{39}\) reported that AI activity was not significantly correlated with sucrose content during fruit development. It can be seen that the roles of enzymes related to sugar metabolism were different
in different crops. Our present research showed that the order of enzyme activities in pea sprouts is AI > NI > SS (Fig. 5). Se treatments significantly increased the activities of AI, NI, and SS, and the highest AI activity and NI activity were observed under the medium Se (1.25 mg L\(^{-1}\)), but the SS activity did not change with the change of Se concentrations. The change of SS activity was consistent with that of glucose content, and it can be seen that Se increased the SS activity and was accompanied by an acceleration in the degradation of sucrose and led to a significant increase of glucose content in pea sprouts. The content of fructose and sucrose has no obvious correlation with AI and NI or SS under Se treatments. The change of soluble sugar content was basically consistent with that of the activities of AI and NI, and it could be speculated that AI and NI play a pivotal role in the accumulation of soluble sugar.

On the basis of 10 mg L\(^{-1}\) sucrose, different Se concentrations obviously affected the activities of AI and NI as well as SS. High Se (2.5 mg L\(^{-1}\)) promoted SS activity, low Se (0.625 mg L\(^{-1}\)) increased NI activity, and medium Se (1.25 mg L\(^{-1}\)) improved AI activity. Our results also showed that the changes of soluble sugar, fructose, and glucose were basically consistent with that of AI activity, but there was no obvious correlation for either NI or SS activity. It can be inferred that AI might be the major enzyme involved in the accumulations of these three sugars under combined application of sucrose and Se. This finding is in agreement with other reports showing that AI was the main sucrose-hydrolyzing enzyme and was substantially higher than SS activity,\(^{27,40}\) In summary, Se, sucrose, or their combined applications could regulate sugar metabolism by affecting the activities of AI, NI, and SS, but there were differences in their roles in sugar metabolism. AI could be regarded as the key restriction enzyme to the accumulation of sugar, with an increase of AI activity being an important reason for sugar increase in pea sprouts.

**CONCLUSION**

This study demonstrated that the individual and combined application of sucrose and Se had remarkable effects on plant growth and nutritional quality of pea sprouts. Sucrose at 10 mg L\(^{-1}\) significantly increased plant growth and improved nutritional quality, which resulted in the highest plant fresh weight, content of vitamin C, soluble protein, fructose and glucose, and higher content soluble sugar and sucrose, but had no significant influences on cellulose content. Lower Se (0–1.25 mg L\(^{-1}\)) had no obvious effect on plant growth, whereas high Se (2.5 mg L\(^{-1}\)) significantly inhibited plant growth and led to a decrease of plant fresh weight. The highest contents of vitamin C, soluble sugar, and glucose were observed under 1.25 mg L\(^{-1}\) Se, whereas the highest contents of soluble protein, fructose, and endogenous Se were recorded under 2.5 mg L\(^{-1}\) Se. Se treatments had no obvious effect on sucrose content, but higher Se (1.25–2.5 mg L\(^{-1}\)) significantly decreased cellulose content. Compared with Se application alone, the suitable combined application of exogenous sucrose and Se (1.25 mg L\(^{-1}\) Se + 10 mg L\(^{-1}\) sucrose) was more beneficial in improving nutritional quality, which resulted in significant increases in the vitamin C, sucrose, fructose, and Se contents. Both Se alone and the combined application of exogenous sucrose and Se could affect the activities of AI, NI, and SS. AI and NI play a pivotal role in the accumulation of soluble sugar under Se treatments alone, whereas AI might be the key enzyme to limit sugar accumulation under the combined application of sucrose and Se, and an increase of AI activity was an important reason for sugar increase in pea sprouts.

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**CONFLICTS OF INTEREST**

The authors have no conflict of interest.

**AUTHOR CONTRIBUTIONS**

X. Yang and Y. Kang designed the research; C. Tan and L. Zhang performed the experiments and wrote the paper; R. Huang and X. Chai analyzed the data; X. Duan reviewed the manuscript.

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