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Promotion of Growth in Mungbean (*Phaseolus aureus* Roxb.) by Selenium is Associated with Stimulation of Carbohydrate Metabolism

Jahid Ali Malik · Sanjeev Kumar · Prince Thakur · Suchi Sharma · Navneet Kaur · RamanPreet Kaur · D. Pathania · Kalpna Bhandhari · Neeru Kaushal · Kamaljit Singh · Alok Srivastava · Harsh Nayyar

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Abstract The mungbean plants were grown hydroponically in the absence (control) or presence of 0.1, 0.25, 0.50 and 0.75 ppm selenium (as sodium selenate) for 10 days. The growth of shoots and roots increased with application of selenium with greater extent in shoots. With 0.5 and 0.75 ppm Se levels, the shoot growth was stimulated by 24% to 27% over control, respectively, while the roots showed a corresponding increase of 18–19%, respectively. The shoot-to-root ratio was enhanced significantly with Se application and maximum effects occurred at 0.75 ppm Se. A significant increase was observed in chlorophyll and cellular respiration ability with 0.5 and 0.75 ppm selenium. The increase in growth by selenium was accompanied by elevation of starch, sucrose and reducing sugars. The activity of starch hydrolysing enzymes—amylases and sucrose hydrolysing enzyme—invertase was stimulated significantly with selenium. This was associated with elevation of activities of sucrose synthesising enzymes—sucrose synthase and sucrose phosphate synthase. It was concluded that increase in growth of shoots and roots by application of Se was possibly the result of up-regulation of enzymes of carbohydrate metabolism thus providing energy substrates for enhanced growth.

Keywords Carbohydrates · Enzymes · Nutrition · *Phaseolus aureus* · Selenium

Introduction

Selenium (Se) is an essential trace element for animals, humans and micro-organisms [1], but its requirement for the plants remains controversial. In animals and humans, selenium is an essential component of several enzymes and proteins such as glutathione peroxidase that

J. A. Malik · S. Kumar · P. Thakur · S. Sharma · N. Kaur · R. Kaur · D. Pathania · K. Bhandhari · N. Kaushal · K. Singh · H. Nayyar (✉)
Department of Botany, Panjab University, Chandigarh 160 014, India
e-mail: harshnayyar@hotmail.com

A. Srivastava
Department of Chemistry, Panjab University, Chandigarh 160 014, India

reduces hydrogen peroxide and other hydroperoxides with glutathione as reducing agent), the thioredoxin reductases whose function is to convert the oxidised forms of thioredoxins back to their reduced forms, the iodothyronine deiodinase that converts tetraiodothyronine, T4, to the active triiodothyronone, T3. The functions of some of other selenoproteins are not yet fully understood but possibly have a role in Se transport and regulation of cellular redox balance [2]. In plants, Se may serve a role in antioxidative mechanisms and indicated to be a component of glutathione peroxidase [3]. Previous reports suggest that trace amounts of Se may enhance the growth of some plant species, though at higher concentrations, Se can be toxic to the plants [4, 5] due to its pro-oxidative effects and incorporation into amino acids in place of sulphur [6]. Se at very low levels (0.1 mg/kg) was reported to delay the senescence and promote the growth of ageing seedlings in lettuce [7]. Supplementation of fertilizers with Se stimulates the plant yields [8]. Moreover, Se treatment has been reported to improve growth in plants subjected to various abiotic stresses such as UV [9], salt [10] and drought [11]. The exact mechanism of stimulation of growth in plants by Se is not yet understood. Earlier, Pennanen et al. [12] reported that the plant growth promoted by Se was the result of starch accumulation in chloroplasts. In potato, Turakainen et al. [13] reported that increase in size of the tubers was associated with starch accumulation by Se application. Considering the involvement of Se in stimulation of growth at its low concentrations, its role in affecting the various components of carbohydrate metabolism was examined in the present study using mungbean (*Phaseolus aureus* Roxb.) seedlings, hitherto unknown to the best of our knowledge.

Materials and Methods

The mungbean seeds (cv SML 668) procured from Punjab Agricultural University, Ludhiana, India were sterilised for 2 min by 0.1% mercuric chloride, washed thoroughly with distilled water. These were subsequently grown hydroponically in the absence (control) and presence of 0.1, 0.25, 0.50 and 0.75 ppm concentrations of selenium (as sodium selenate) under controlled conditions (30/25°C/13 h light/11 h dark) of the growth chamber. The growth of seedlings was recorded on tenth day. The leaves of 10-day-old seedlings were subjected to analysis of the following parameters.

Growth, Chlorophyll and 2,3,5 Triphenyl Tetrazolium Chloride Reduction Ability The seedlings were measured for growth of roots and shoots on tenth day, and shoot-to-root ratio was calculated. The total chlorophyll [14] and 2,3,5 triphenyl tetrazolium chloride (TTC) reduction ability [15] were estimated from the leaves of the 10-day-old seedlings and have been elaborated earlier [16].

Carbohydrates

The sucrose content was assayed as per the enzymatic method of Jones et al. [17]. The leaf tissue was extracted with 80% ethanol at 80°C thrice for 1.5 h each extraction. The extracts were pooled, evaporated at 40°C in an air-circulating oven and subsequently used for assay of sucrose. Aliquots of 200 μl from standard sucrose and samples were added to 1 ml of reaction mixture composed of imidazole buffer 100 mm (pH 6.9; 40 mM imidazole base,

60 mM imidazole–HCl), 0.4 mM NADP+, 1 mM ATP, 5 mM $MgC1_2$, 0.5 mM dithiothreitol, 0.02% (*w*/*v*) BSA, 20 μg ml^{-1} yeast invertase (EC3.2.1.26), 2 μg ml^{-1} yeast hexokinase (EC 2.7.1.1), 1 μg ml^{-1} yeast P-glucoisomerase (EC 5.3.1.9) and incubated for 30 min at 25°C to allow conversion of glucose and fructose to glucose 6-P. The absorption was read at 340 nm. Eighty-five microlitres of glucose 6-P dehydrogenase (70 U ml^{-1}) added, mixed well and re-read after about 5 min when absorbance became constant. Blanks were run with 200 μl of extract and 1 ml of reaction mixture without invertase. The readings obtained from each sample were converted to sucrose concentration using a standard curve.

For measuring reducing sugars and starch, the plant material (oven-dried) was homogenised in hot ethanol (80%) and centrifuged at 2,000 rpm for 10 min. The supernatant was clearly decanted off. Subsequently, 3 ml of ethanol (80%) was added to the residue and re-centrifuged. The extraction was repeated twice to ensure the complete recovery of sugars. The residue was stored for starch analysis. The supernatant was pooled and evaporated to dryness in China dish on a boiling water bath. The residue was eluted with 5 ml of 20% ethanol and subjected to analysis for reducing sugars. For estimation of reducing sugars, 1 ml of dinitrosalicylic acid reagent was added to 1 ml of ethanol extract (prepared as above). The reaction mixture was boiled for 12 min, 2 ml of distilled water was added and absorbance was recorded at 560 nm against a blank containing 80% ethanol in place of ethanol extract. The concentration of reducing sugars was calculated from a standard curve plotted with known concentration of glucose [18]. The starch content was measured using acid hydrolysis method given by McCready et al. [19]. The residue of ethanol extract was washed with 80% ethanol to remove all the traces of soluble sugars. To the residue, 5 ml of distilled water and 6.5 ml of 52% perchloric acid were added to extract the starch by placing the samples at 0°C for 20 min. The mixture was centrifuged, and the extract was retained. The process was repeated thrice using fresh perchloric acid, and the extract was diluted to final volume 100 ml. To 0.5 ml of diluted extract, 4.5 ml of distilled water was added followed by addition of 10 ml of cold anthrone sulfuric acid reagent in ice bath. The sample mixture was heated at 100°C for 8 min and cooled rapidly to room temperature. The absorbance was measured at 630 nm. The final content of starch was calculated from a standard curve plotted with known concentration of glucose. For assay of amylases and invertase, the leaf tissue were homogenised with buffer (20 mmol/l sodium acetate, pH 5.4, containing 10 mmol/l $CaCl_2$) and the homogenate was centrifuged at 20,000 rpm for 10 min at 4°C.

Enzymes

For extraction of enzymes, the leaf tissue was homogenised in a chilled HEPES buffer–NaoH (50 mmol/l) pH 7, 2 mmol MgCl2, 1 mmol/l EDTA, 2 mmol/l DTT as per the method of Dejardin et al. [20]. The activity of sucrose synthase was assayed according to the method of Hawker [21]. The enzyme extract was added to the reaction mixture comprising of 0.015 M UDPG, 0.05 M fructose and 0.2 M Tris–HCl buffer pH 8.2 containing 0.025 M $MgSO_4$. The above-mentioned reaction mixture was incubated at 37°C for 30 min, and the reaction was stopped by heating the contents in boiling water for 10 min and then cooled. The residual fructose was destroyed by adding 0.5 ml of 6% KOH and heating the contents in boiling water bath for 20 min. After cooling the contents to room temperature, 1 ml of 1% resorcinol solution and 3 ml of 30% HCl were added to

it. The tubes were incubated at 80°C for 10 min, and the intensity of developed pink colour was read at 490 ηm. The concentration of sucrose was calculated from standard graph prepared by using sucrose as standard (40–280 mg/ml). The sucrose phosphate synthase activity was assayed using the anthrone test [22]. During the process, 70 μl of the reaction mixture including the extract was adjusted to a final concentration of 4 mM Fru 6-P, 20 mM Glc 6-P, 3 mM UDPG, 50 mM Hepes–KOH (pH), 5 mM $MgCl_2$ and 1 mM EDTA. The reaction mixture was incubated for 15 min at 37°C and subsequently 70 μl 30% (*w*/*v*) of KOH was added and followed by heating at 95°C for 10 min. To this, 1 m**l** 0.14% (*w*/*v*) anthrone in 95% H_2SO_4 was then added. The mixture was incubated 20 min at 37°C, and absorbance was recorded at 650 nm. The activity of amylases was measured using the method of Shuster and Gifford [23], while invertase was measured as per the method of Nygaard [24], described elsewhere [25]. The data was subjected to statistical analysis using AGRISTAT. Mean values ± SE were worked out. ANOVA was applied to replicated data, and LSD ($P<0.05$) was calculated.

Results

The seeds were grown in the presence of 0.1, 0.25, 0.50 and 0.75 ppm Se concentrations. The growth of the seedlings was observed on tenth day as length of roots and shoots (Table 1). The shoot length was enhanced to a greater extent than the root length. Thus, at lower concentrations (0.1 and 0.25 ppm), Se application resulted in 13–18% increase in shoot length over control that increased to about 24–27% with higher concentrations (0.5 and 0.75 ppm). The root growth was stimulated by 18–19% with 0.5 and 0.75 ppm Se concentrations. The shoot-to-root ratio was increased appreciably by all Se levels with highest effects observed at 0.75 ppm (Table 1). The chlorophyll content showed slight increase (12% over control) with 0.25 ppm Se but a significant increase was observed with higher Se concentrations (18–19% over control; Table 2). The TTC reduction ability reflects the respiration status of the tissues. It increased with Se in both the organs with greater effect on shoots (Table 2). An increase of 12% and 8% occurred in respiration with 0.25 ppm Se in shoots and roots, respectively. It enhanced further (20% in shoots and 11% in roots over control) with 0.5 ppm Se and remained higher with 0.75 ppm Se.

The starch content increased by 7% (0.1 ppm Se) to 20% (0.75 ppm) in shoots while the roots showed a corresponding increase of 8% and 15% with these concentrations over control (Fig. 1a). The activity of amylases increased with Se application. In case of α-amylase, the activity increased by 10% with 0.25 Se in both roots and shoots (Fig. 1b). At 0.5 ppm, the shoots showed slightly but significantly greater activity (19.5% over control)

Table 1 Effect of selenium (as sodium selenate) on growth of 10-day-old mungbean seedlings (Mean ± SE)

Concentration of selenium (ppm)	Root growth (cm)	Shoot growth (cm)	Shoot/root ratio
Control (no selenium)	5.3±0.12	3.6±0.11	0.60±0.03
0.1	6.0±0.10	4.0±0.11	0.66±0.02
0.25	6.25±0.12	4.2±0.14	0.67±0.02
0.50	6.26±0.10	4.5±0.11	0.71±0.03
0.75	6.3±0.09	4.7±0.12	0.74±0.02
LSD ($P<0.05$)	0.12	0.084	0.03

Table 2 Effect of selenium (as sodium selenate) on total chlorophyll content and TTC reduction ability in leaves of 10-day-old mungbean seedlings (Mean ± SE)

Concentration of selenium (ppm)	Total chlorophyll content (mg/g fresh weight)	TTC reduction ability (OD_{530}/g fw)
Control (no selenium)	1.36±0.07	0.41±0.03
0.1	1.36±0.06	0.45±0.04
0.25	1.52±0.07	0.46±0.027
0.50	1.60±0.05	0.49±0.025
0.75	1.63±0.06	0.52±0.02
LSD (P<0.05)	0.11	0.03

than roots (16.5% over control; Fig. 1c). The activity with 0.75 ppm was also higher in shoots than roots. Relatively, β-amylase showed larger increase with 0.1 ppm Se application in both the organs. At 0.25 and 0.50 ppm, the activity of β-amylase was 15% and 17% higher over control in shoots compared to 12% and 13% increase, respectively in roots. At 0.75 ppm Se, the activity was at par with 0.5 ppm in both the organs.

The sucrose content (Fig. 2a) in shoots increased by 28% and 23% with 0.5 and 0.75 ppm Se concentrations, respectively over control. In roots, a corresponding increase of 10% and 12% was observed with these concentrations. With Se application, the extent of increase in sucrose content was greater than for starch in shoots. At lower Se levels (0.1 and 0.25 ppm), the reducing sugars (glucose, fructose) increased slightly without any significant difference between the roots and shoots (Fig. 2b). The reducing sugars increased by 29% in roots and 35% in shoots over their respective controls with 0.5 ppm Se. At higher Se level, no further increase was observed in both the organs. The sucrose synthesising enzymes, namely sucrose synthase (Fig. 3a) and sucrose phosphate synthase (SPS; Fig. 3b), elevated with Se application. The sucrose synthase showed increase of 11% to 22% in shoots and 5–19% in roots over control with Se. The activity of sucrose phosphate synthase increased by 34% over control with 0.5 ppm Se compared to 23% increase in roots. The activity decreased with 0.75 ppm Se in both the organs. The activity of invertase (Fig. 3c) elevated by 31% in shoots and 10% in roots with 0.50 ppm Se application with slight increase at higher (0.75 ppm) Se concentration.

Discussion

The growth of shoots and roots was unaffected at lower Se concentrations (0.1 and 0.25 ppm) but showed increase with application of 0.5 and 0.75 ppm selenium. The shoot growth was improved to a larger extent than the root growth. Our studies regarding stimulation of growth by Se are similar to a previous study on potato where Se application led to formation of large sized tubers [13] as well as in improvement in growth of plants growing under stress conditions [10].

We evaluated the possible reasons associated with increase in growth by Se application. It was observed that the chlorophyll content increased significantly with Se application in our studies, which is in agreement with the positive effects of Se treatment in delaying the loss of chlorophyll in senescing *Vicia faba* plants [26] and drought-stressed wheat plants [11]. Similarly, Se application was reported to increase the chlorophyll content in an alga

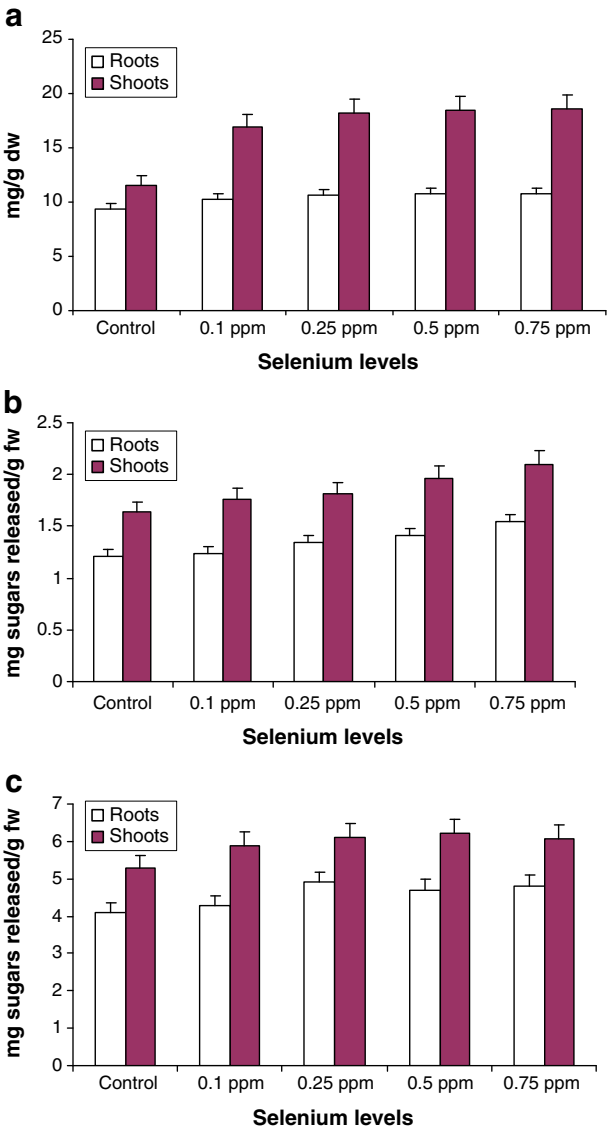

Fig. 1 Effect of selenium (as sodium selenate) on **a** starch content, **b** α-amylase and **c** β-amylase activity in leaves of 10-day-old mungbean seedlings (Mean ± SE). *Bars* represent standard error. LSD ($P<0.0.5$): starch (roots—0.15, shoots—0.11), α-amylase (roots—0.13, shoots—0.11) and β-amylase (roots—0.08, shoots—0.11)

Spirulina [27]. In contrast, Se treatment at its higher levels caused inhibition in chlorophyll content in mungbean seedlings [28]. The Se-treated plants showed significant increase in cellular respiration that is in agreement with the previous studies on *Eruca sativa* plants [29] and potato tubers [30].

With application of Se, the starch accumulation increased in both roots and shoots. The accumulation of starch in our studies is in accordance with comparable effects obtained in potato tubers with Se application [13]. The shoots of Se-treated plants showed greater starch content than the roots. Starch, a storage product, reflects the ability of plants to show photosynthesis. Its greater accumulation in shoots by Se application might be the (a) result

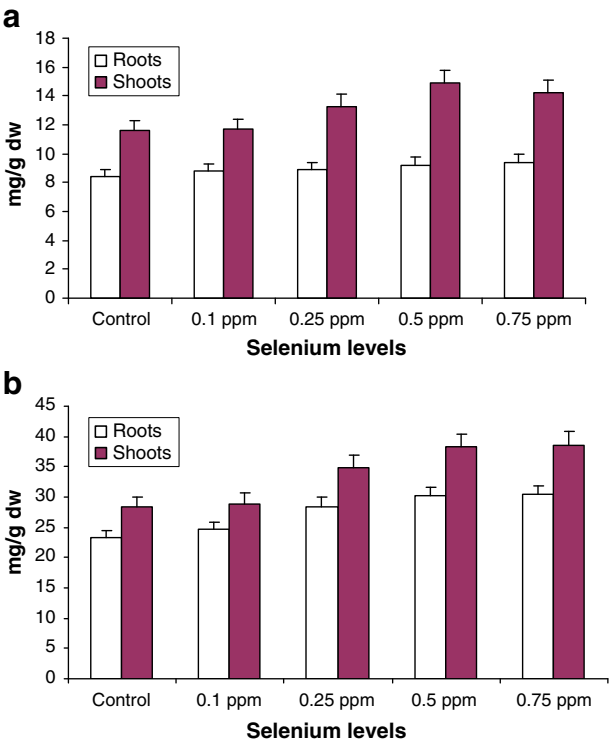

Fig. 2 Effect of selenium (as sodium selenate) on **a** sucrose content and **b** reducing sugars in leaves of 10-day-old mungbean seedlings (Mean ± SE). *Bars* represent standard error. LSD ($P<0.0.5$): sucrose (roots—0.11, shoots—0.13) and reducing sugars (roots—0.13, shoots—0.14)

of enhancement in photosynthesis, (b) decrease in transport of carbohydrates to roots [13] and/or (c) decrease in starch degradation. Earlier studies even suggested the association of selenium with accumulation of starch granules in the chloroplasts of young lettuce leaves [12]. In our studies, the starch hydrolysing enzymes—amylases (break down starch into simple sugars) had higher activity in shoots than in roots, hence, the greater starch content in shoots appear to be related to its increase in its biosynthesis rather than its degradation.

Sucrose content was increased to a greater level in shoots than in roots, which was related to higher activity of its biosynthetic enzymes—SPS and sucrose synthase in the shoots relative to roots. Additionally, sucrose transport might be reduced into the roots with Se treatment leading to elevation of sucrose levels in the shoots. With Se application, the degree of increase was greater for sucrose (up to 28% over control in shoots) than for starch (up to 20% than control) suggesting greater diversion of triose-phosphates towards sucrose generation. Simultaneously, we found invertase (converts sucrose into glucose and fructose) to increase significantly with Se application. The reducing sugars (glucose and fructose) that are used as respiratory substrates [31] were found to be elevated in Se-treated plants that were related to enhanced activities of amylases and invertase. It is pertinent to mention that the increase in activity of invertase was higher than amylases suggesting greater contribution of sucrose towards generation of reducing sugars.

The cellular respiration increased with Se application that coincided with the elevated levels of reducing sugars. The increase in respiration might assist to provide adequate energy needs for the growth stimulated by selenium. The cellular respiration and hexoses (reducing sugars) were greater in shoots than in roots that possibly resulted in higher

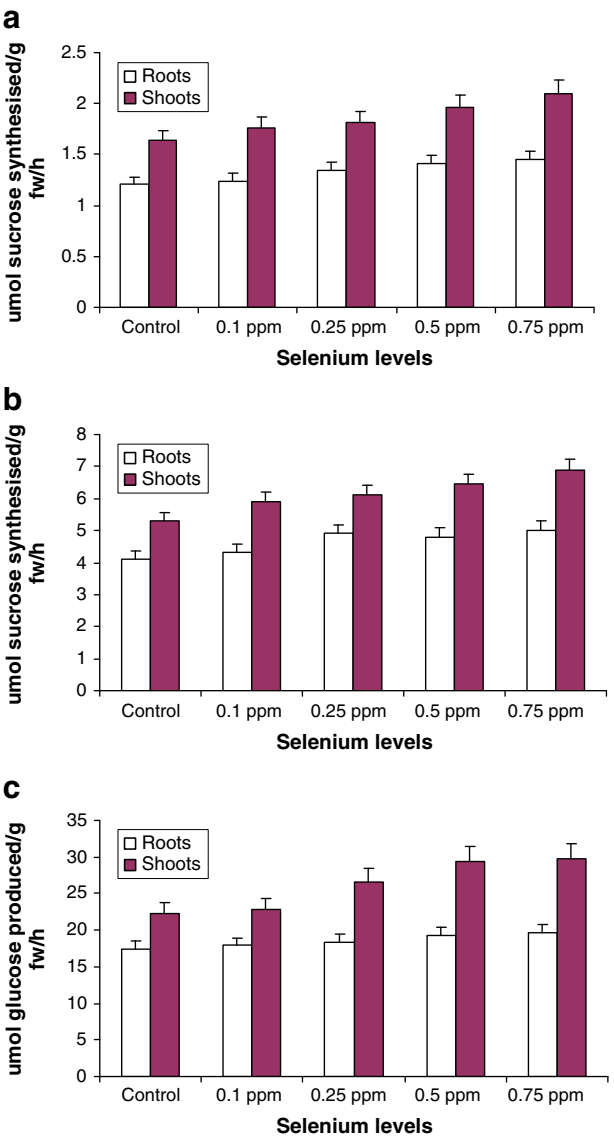

Fig. 3 Effect of selenium (as sodium selenate) on **a** sucrose synthase and **b** sucrose phosphate synthase and **c** invertase activity in leaves of 10-day-old mungbean seedlings (Mean ± SE). *Bars* represent standard error. LSD ($P<0.0.5$): sucrose synthase (roots—0.07, shoots—0.09), sucrose phosphate synthase (roots—0.11, shoots—0.13) and invertase (roots—0.12, shoots—0.14)

growth in the shoots. In a study on potato, larger tubers were produced with very low Se (0.075 mg Se kg^{-1} and 0/3 mg Se kg^{-1}) that was attributed to stimulation in the levels of starch and sugars [13]. Our studies, while corroborating these findings, have provided additional information about the stimulation of enzymes pertaining to carbohydrate metabolism.

Thus, the present study indicated that Se at lower levels can stimulate the plant growth, especially those of shoots by up-regulation of enzymes related to starch and sucrose catabolism leading to elevation of sugars that is accompanied by increase in cellular respiration to meet the energy needs required for faster growth.

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