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Effects of Selenium Treatments on Potato (*Solanum tuberosum* L.) Growth and Concentrations of Soluble Sugars and Starch

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The effect of selenium (Se) treatments on potato growth and Se, soluble sugar, and starch accumulation was investigated. Potato plants were cultivated in quartz sand without or with sodium selenate (0, 0.075, 0.3 mg Se kg^{-1} sand). In young potato plants, Se treatment resulted in higher starch concentrations in upper leaves. The tuber yield of Se-treated potato plants was higher and composed of relatively few but large tubers. At harvest, the starch concentration in tubers did not differ significantly between treatments. The higher Se addition (0.3 mg Se kg^{-1}) may have delayed the aging of stolons and roots, which was observed as high concentrations of soluble sugar and starch. Together with the earlier results showing elevated starch concentration in Se-treated lettuce, the findings of this research justify the conclusion that Se has positive effects also on potato carbohydrate accumulation and possibly on yield formation.

KEYWORDS: Potato tuber; roots; selenium; soluble sugars; starch; stolons; upper leaves

INTRODUCTION

Selenium is an essential micronutrient for human and livestock (*1*−*3*). The Recommended Dietary Allowance (RDA) of Se for both women and men is 55 μg/d (*4*). In Finland, soils are very low in bioavailable Se, which was reflected in the quality of domestic agricultural products. Consequently, the intake of Se by humans was below the recommended level (*5*−*7*). For this reason, in Finland since 1984, NPK fertilizers have been supplemented with sodium selenate (*8*).

Although Se has not been classified as an essential nutrient for plant growth, its beneficial effects on plant carbohydrate metabolism and growth, including its stress-resisting function, have been shown recently by many authors (*9*−*13*). However, it has also been established that its effects on plants are concentration-dependent, and in general, plants have low tolerance to it (*10*, *15*−*17*). Selenite (SeO_3^{2-}) application is reported to increase the glucose concentration in the leaves of bean plants (*Phaseolus vulgaris*) (*9*), to enhance the growth of coffee plants (*Coffea arabica*), and to increase the concentration of soluble sugars and caffeine in their leaves (*10*). The foliar applications of Se enhanged the quality and yield of green tea leaves (*14*). Furthermore, application of Se as selenite to potato plants has been found to increase both total and protein amino acid contents (*18*) and to decrease the glycoalkaloids and nitrate accumulation in tubers (*19*). Studies on lettuce (*Lactuca sativa* L.), and ryegrass (*Lolium perenne* L.) have indicated that low concentrations of Se strengthens antioxidative capacity and promotes plant growth, especially at the senescing stage, or under UV-stress conditions (*11*−*13*). A similar Se-induced increase in antioxidative activity has also been found in tea leaves (*20*).

Moreover, Se is able to alleviate photooxidative stress and to activate defense mechanisms in potato chloroplasts (*21*). Electromicroscopic studies have shown an enhanced accumulation of starch grains in Se-treated lettuce plants, coincidentally with improved plant growth (*22*). Whether the increased accumulation of starch was due to improved starch synthesis, reduced assimilate export, or changes in sink strength were not investigated. The aims of this study were to investigate the effect of selenium on potato growth, carbohydrate accumulation, and yield.

MATERIALS AND METHODS

Growth Conditions and Plant Material. Potato tubers (*Solanum tuberosum* L. cv. Satu) were presprouted at 15 °C under natural light in a greenhouse for three weeks before planting. Potato plants were grown in a greenhouse at 15−25 °C under a 16 h day and 30−50% relative humidity. The light intensity was controlled by shading curtains to maintain the photon flux density within the range of 200−500 μmol m^{-2} s^{-1}. Natural daylight was supplemented with 400 W high-pressure sodium lamps (Lucalox, LU 400/HO/T/40 NG, Hungary). The tubers were grown in individual 10-l plastic pots containing 10 kg quartz sand (grain size 0.1−0.6 cm, SP-Minerals Oy Ab, Nilsiän kvartsi, Finland). Before planting, a modified Hoagland nutrient solution (*23*) and 7 g of dolomite pot^{-1} (Saxo Mineral Oy, Loukolampi, Finland) were mixed into quartz sand. After liming, the pH of the sand culture was about 6.4 (in 0.01 M $CaCl_2$). The plants were fertilized a second time 10 weeks after planting by adding the same modified Hoagland solution

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in amounts corresponding to one-half that given at the first fertilization. The total amounts of nutrients added per pot were 3.0 g of N, 1.0 g of P, 4.8 g of K, 1.8 of Ca, 0.18 g of S, 0.02 g of Fe, 0.136 g of Mg, 8.3 mg of Na, 2.7 mg of B, 1.1 mg of Mn, 0.8 mg of Zn, 0.3 mg of Cu, 0.3 mg of Ni, and 0.5 mg of Mo. Selenium was dissolved in deionized water and applied after shoot tips emergency three times at one-week intervals to the surface of the quartz sand in quantities corresponding to a total addition of 0.075 mg (lower addition) or 0.3 mg (higher addition) Se kg^{-1} quartz sand (supplied as sodium selenate, H_2SeO_4, Sigma). Control plants were treated with deionized water. During the experiment the pots were placed at random in the greenhouse.

Five plants (4 weeks after planting), 10 plants (8 and 13 weeks after planting) and eight plants (15 weeks after planting) per treatment were randomly sampled. The youngest leaves were collected 4 and 8 weeks after planting. Sampling was done between 9 a.m. and 3 p.m. Roots and stolons were collected 4, 8, 13, and 15 weeks after planting. Tubers were harvested 15 weeks after planting, and the tuber yield, the mean tuber weight, and the mean number of tubers per pot were determined. Soluble sugars and starch concentration of tubers were determined 15 weeks after planting. To study the effect of Se application on potato quality during storing, the soluble sugar concentration of tubers was determined 5 months after harvest. Prior to sugar and starch analysis, roots, stolons, and tubers were rinsed under running water. Roots and stolons were weighed and frozen immediately in liquid nitrogen and then stored at −20 °C until analyzed. The tubers were stored at 4 °C in 80% relative humidity before analysis. Samples for sugar, starch, and Se analysis were freeze-dried (Heto Dry Winner FD 8−85, Heto-Holten A/S, Allerød, Denmark), weighed (dry matter g/plant) and ground into fine powder with an electrical mill (1093 Cyclotec Sample Mill, Foss Tecator, Höganäs, Sweden, or with IKA A10, Janke & Kunkel GmbH & Co, Staufen, Germany).

Analysis of Soluble Sugars and Starch. Total soluble sugars were determined using an anthrone method (*24*). Soluble sugars were extracted from 10 mg of freeze-dried plant material with 500 μL of 80% ethanol. Extraction was done three times, followed by centrifugation at 1600*g* for 10 min. Supernatant was incubated at 70 °C for 30 min to inactivate invertase. A 0.25-mL aliquot of supernatant was mixed with 1.25 mL of ice-cold Anthron reagent (2 g Anthron in 1 L 72% sulfuric acid), and the mixture was heated in a boiling water bath for 11 min and cooled in ice. Absorbance was measured at 630 nm (Shimadzu UV-160A, Shimadzu Co., Kyoto, Japan). Starch concentration was determined spectrophotometrically as previously described (*25*). Soluble sugars and starch concentrations were presented as mg g^{-1} dry weight (DW). Tuber morphology was monitored 8, 13, and 15 weeks after planting.

Selenium Analysis. Selenium was analyzed according to the electrothermal atomic absorption spectrometric method (*26*) from the same plant material used for analysis of soluble sugars and starch. An in-house reference sample was included for every analytical round.

Leaf Photosynthesis. Leaf CO_2 exchange was measured with an open infrared gas analysis system using a temperature-controlled chamber equipped with two fans (LI-6400, LI−COR, Lincoln, NE). Measurements were taken at a chamber temperature of 24 °C, and a photosynthetic photon flux density (PPFD) of 500 μmol quanta m^{-2} s^{-1} was provided by a 6400−02B red light source. In measurement, a 6400−01 CO_2 mixer was used to set the control, and the reference concentrations with a target of 400 μmol mol^{-1}. Flow rate in the chamber was set at 500 μmol s^{-1}. In control and lower Se treatment (0.075 mg Se kg^{-1}), 4−5 leaflets from 9 to 10 plants were measured between 10 a.m. and 2 p.m., 4 and 8 weeks after planting.

Data Analysis. The data were tested using analysis of variance (ANOVA) in the GLM procedure of SAS version 6.12 (SAS Institute Inc., Cary, NC). Significantly different means between treatments were separated with Duncan's Multiple-range tests.

RESULTS

Selenium Concentrations and Plant Development. Selenium fertilization increased Se concentrations significantly in upper leaves, roots, and stolons (**Figure 1**, parts **a**−**c**). The peak concentration was obtained 4 weeks after planting, after which the concentrations diminished. However, 15 weeks after planting, the concentration in roots and stolons increased slightly at the higher Se level (0.3 mg kg^{-1}) (**Figure 1**, parts **a**−**c**). In upper leaves, the concentration was much higher than that in below ground plant parts (**Figure 1a**). With increasing Se application, the Se concentration of mature tubers was elevated from 2.1 to 7.4 μg g^{-1} dry weight (**Table 2**), and increased linearly with Se application levels ($y = 24.41x + 0.1254$, R^2=0.9987) (data not shown).

Growth of Leaves, Roots, and Stolons. The Se applications did not affect the biomass accumulation in upper leaves either 4 weeks after planting or 8 weeks after planting (**Figure 1d**). No differences were observed in fresh weight of roots between treatments 8 weeks after planting; the fresh weights of roots in Se treatments of 0, 0.075, and 0.3 mg Se kg^{-1} were 54.25 ± 2.9 g, 53.11 ± 1.9 g, and 55.76 ± 3.4 g, respectively. However, the applied Se reduced the dry weight of roots significantly, but later the negative effect disappeared (**Figure 1e**). Stolons of the control and the Se-treated plants reached their maximum size 8 weeks after planting (**Figure 1f**). The Se additions decreased the dry weight of stolons 4 weeks after planting but exerted only a slight positive effect on their growth 15 weeks after planting (**Figure 1f**).

The stolons of control plants were significantly shorter than those of Se-supplied plants 8 weeks after planting; in the control treatment, the mean stolon length per plant was 6.78 ± 0.5 cm; at the lower Se addition, it was 7.70 ± 0.6 cm; and at the higher Se addition level, it was 7.81 ± 0.7 cm. At the later growing stages, the differences between the treatments leveled off. The mean number of stolons did not differ between treatments during the growing period (data not shown).

Tuber Yield. The addition of Se did not change the morphology of tubers (data not shown), but it affected potato yield and average tuber size. Significantly higher yields were harvested from the Se-treated plants 15 weeks after planting (**Table 1**). Mean tuber weight correlated with total yield, the highest yield in Se-treated plants, was composed of relatively few but large tubers (**Table 1**).

Selenium Content. The Se content (Se concentration × dry biomass) in the upper leaves remained the same in all treatments 4 and 8 weeks after planting (**Figure 1g**), but in roots and stolons, Se content decreased with increasing Se additions (**Figure 1**, parts **h** and **i**). In all treatments, flowering initiated 4 weeks after planting, between the first (4 weeks after planting) and the second (8 weeks after planting) harvest. Selenium did not affect the development of foliage, monitored by leaf area, number of leaves and stems, or height of plants (data not shown).

Photosynthesis, Total Soluble Sugars and Starch Content. Measurements of CO_2 assimilation rate 4 and 8 weeks after planting showed no differences between treatments. In the first measurement, 4 weeks after planting, CO_2 assimilation rate (μmol m^{-2} s^{-1}) in Se treatments of 0 and 0.075 mg Se kg^{-1} were 16.73 ± 0.2 and 17.23 ± 0.1, respectively, while 8 weeks after planting the corresponding figures were 16.61 ± 0.1 and 16.17 ± 0.1. In roots, the peak concentration of soluble sugars was reached 8 weeks after planting, and it declined toward maturity (**Figure 1k**). In stolons, the peak concentration of soluble sugar was reached later, 15 weeks after planting (Figure 1l). However, the effect of Se on the concentrations of soluble sugars in roots and stolons was not systematic. At the highest Se addition (0.3 mg Se kg^{-1}), the highest soluble sugar concentration was observed in the upper leaves 4 weeks after planting (**Figure 1j**) and in the roots and stolons at maturity (**Figure 1**, parts **k** and **l**).

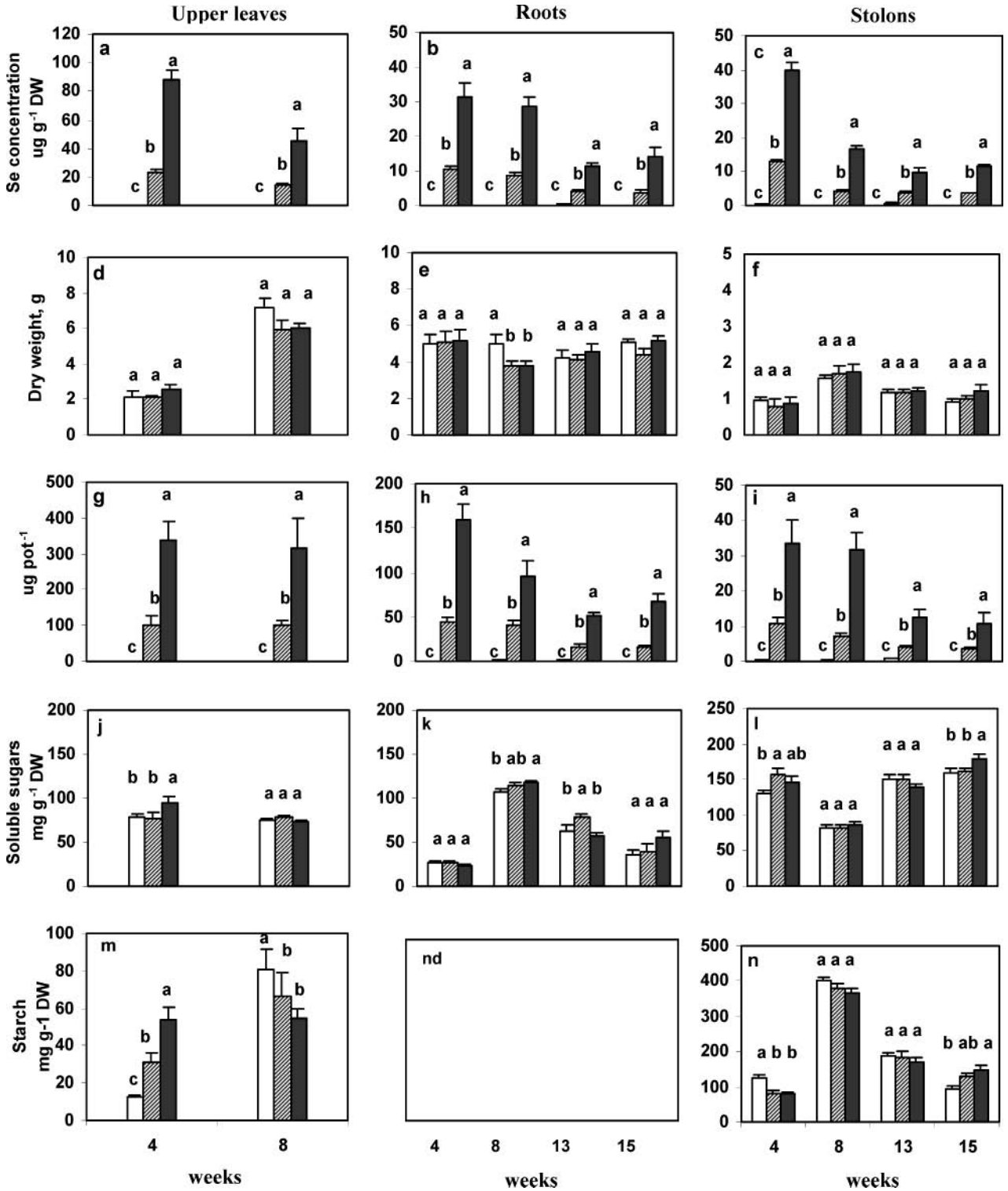

Figure 1. The effect of selenium application (0, white bar; 0.075, lined bar; 0.3, , shaded bar mg Se kg^{-1}) on Se concentration (**a**–**c**), dry weight (**d**–**f**), Se content (Se concentration × dry weight) (**g**–**i**), soluble sugar concentration (**j**–**l**), and starch concentration (**m**–**n**) in uppear leaves, roots, and stolons. Data are means ± SE; $n = 5$–10. nd = not determined. Columns marked with different letters are significantly different at $P \leq 0.05$.

Starch concentration of upper leaves was significantly higher 4 weeks after planting in Se-treated plants than that in control plants (**Figure 1m**). Later, 8 weeks after planting, this beneficial effect of Se was not found (**Figure 1m**). During early stolon development, the starch concentration was lowest in Se-treated plants (4 and 8 weeks after planting) (**Figure 1n**), whereas later in the growing period (15 weeks after planting) the starch concentration in stolons was almost 1.5 times higher in the Se-treated plants (**Figure 1n**). In Se-treated plants (0.075 mg Se kg^{-1}), about 10% higher starch concentrations were measured in the tubers 15 weeks after planting (**Table 1**). However, these differences in starch concentration were not statistically significant.

DISCUSSION

The fact that Se fertilization increased the Se concentration in potato plants in proportion to the addition level demonstrates

Table 1. Effect of Selenium Treatments on Tuber Yield, Number of Tubers, and Mean Tuber Weight of Plant Harvested 15 Weeks after Planting[a]

Se added (mg kg^{-1})	tuber yield (g) per plant	no. of tubers per plant	mean tuber wt (g) per plant
0	739.9 ± 12.4b	24.1 ± 2.4a	33.2 ± 3.8b
0.075	803.0 ± 14.0a	24.9 ± 1.2a	33.0 ± 2.3b
0.3	810.8 ± 13.1a	18.0 ± 1.3b	46.4 ± 2.9a

[a] Results are presented as means ± SE; $n = 8$. The values within a column with the same letter do not differ at $P \leq 0.05$ by Duncan test.

Table 2. Selenium Concentration of Tubers 15 Weeks after Planting, Soluble Sugars of Tubers 15 Weeks after Planting, and 5 Months after Harvest, and Starch Concentration in Tubers 15 Weeks after Planting at Various Selenium Addition Levels[a]

Se added mg kg^{-1}	Se concn μg g^{-1} DW	soluble sugars mg g^{-1} DW		starch mg g^{-1} DW
	15 weeks	15 weeks	5 months	15 weeks
0	0.0 ± 0.0c	56.0 ± 2.1a	47.7 ± 2.1a	508.7 ± 6.0a
0.075	2.1 ± 0.1b	56.0 ± 1.8a	49.4 ± 2.4a	563.1 ± 3.5a
0.3	7.4 ± 0.4a	44.0 ± 2.1a	44.7 ± 3.1a	512.1 ± 2.5a

[a] Results are presented as means ± SE; $n = 8$. The values within a column with the same letter do not differ at $P \leq 0.05$ by Duncan test.

that the added sodium selenate was efficiently utilized. The Se concentration of mature tubers was significantly lower than that in leaves, roots, or stolons, indicating that Se accumulation in tubers is not as efficient as it is in other plant parts. The Se content (Se concentration × dry weight) in upper leaves remained unchanged, while the Se concentration significantly diminished at the same time. This decline can be explained by dry matter dilution, owing to the simultaneous increase of the biomass of the upper leaves. Earlier findings show a similar dry matter dilution of Se in lettuce seedlings during the growing period (*11*). Selenium decline in the roots and stolons toward maturation cannot be explained by dry matter dilution, because the biomass of the stolons diminished at the same time. The result may indicate either that the rate of Se uptake was reduced in senescing plants or that volatilization or other losses of Se increased (*27*, *28*).

The higher accumulation of starch in the upper leaves in Se-treated plants indicates enhanced starch synthesis, reduced carbohydrate transport from the chloroplast, or increased efficiency of photosynthesis. Here, higher starch accumulation could not be explained by photosynthesis, which was not affected by any Se treatment. Carbohydrate transport was probably not affected, because photoassimilates were efficiently transported from leaves to below-ground plant parts. Previous research has shown an association between Se and accumulation of starch granules in the chloroplasts of young lettuce plants (*22*). The authors concluded that this growth-promoting effect was related to the role of Se as a protective element in plant chloroplast enzymes and carbohydrate metabolism. In the present study, the higher Se application (0.3 mg Se kg^{-1}) enhanced the accumulation of soluble sugars in the roots and stolons of mature aging plants, which suggests that Se may alter the partitioning of carbon into sinks other than tubers. Contrary to roots, stolons accumulated soluble sugars toward maturity. This finding indicates either that metabolic activity was not reduced or that carbohydrate reserves were converted to soluble sugars. The decrease in the final number of tubers at the higher Se application level (0.3 mg kg^{-1}) may also indicate an altered allocation pattern of assimilates. However, potato tuber formation and growth are flexible processes that are regulated by many interacting mechanisms. In addition, the growth of individual tubers varies considerably, allowing changes in growth pattern (*29*, *30*). Due to this complexity, the reasons for the variations of tuber size distribution in Se-treated plants (0.3 mg kg^{-1}) remain unclear.

It is noteworthy that in aging plants, the higher Se application (0.3 mg kg^{-1}) increased the carbohydrate accumulation in roots and stolons, suggesting that Se may have delayed accumulation of carbohydrates or the processes associated with senescence in potato roots and stolons. The elevated carbohydrate concentration in stolons may indicate that stolons are still active, or that they are used for carbohydrate storage. Some authors have suggested that stolons play a role in the storage of starch and in contributing to tuber growth (*31*, *32*). Previous studies have shown that the beneficial effect of Se is dependent on application level and plant age (*10*−*14*). At low concentrations, Se was able to resist senescence by counteracting oxidative stress in aging leaves and roots (*11*, *33*). We know of no studies concerning the senescence processes of stolons. Our findings for potato plants support previous studies of starch and carbohydrate accumulation in plants supplied with Se (*9*, *10*, *22*). Whether Se application has an effect on starch synthesis itself needs to be studied further. We conclude that Se may have a positive effect on yield formation via enhanced carbohydrate metabolism, and to some extent via the antioxidative effects of Se.

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