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Distribution of Selenium in Different Biochemical Fractions and Raw Darkening Degree of Potato (*Solanum tuberosum* L.) Tubers Supplemented with Selenate

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Effects of Se fertilization on potato processing quality, possible changes in Se concentration and form in tubers during storage, and retransfer of Se from seed tubers were examined. Potato plants were grown at five selenate (SeO_4^{2-}) concentrations. Tubers were harvested 16 weeks after planting and were stored at 3−4 °C prior to analysis. The results showed that the Se concentration did not decrease during storage for 1−12 months. In tubers, 49−65% of total Se was allocated in protein fraction, which is less than found in plant leaves in a previous study. The next-generation tubers produced by the Se-enriched seed tubers had increased Se concentrations, which evidenced the relocation of Se from the seed tubers. At low levels, Se improved the processing quality of potato tubers by diminishing and retarding their raw darkening. The value of Se-enriched potato tubers as a Se source in the human diet was discussed.

KEYWORDS: Selenium; potato; *Solanum tuberosum* L.; biochemical fractions; enzymatic discoloration; storage

INTRODUCTION

In trace amounts, Se is an essential micronutrient for animals and humans, needed for the activity of antioxidative enzymes such as glutathione peroxidase (GSH-Px) and thioredoxin reductase (*1*, *2*) However, the range between its beneficial and toxic concentrations is quite narrow (*3*, *4*). Plant products are an important source of Se in human nutrition. The different chemical forms of Se vary in their biological efficiency, with the critical factor not being the total concentration but rather the amount of organic Se (*5*, *6*).

Although Se has not been demonstrated to be an essential element for plant growth, long-term studies have shown that trace amounts of Se do exert beneficial effects in plants. The positive responses have been attributed to its antioxidative effects that counteract oxidative stress, promote plant growth, and delay senescence (*7*−*12*). In general, the enhanced antioxidative capacity of Se-treated plants is associated with improved activity of glutathione peroxidase to inhibit oxidative damage to cells (*7*−*9*). Plants have an important role in converting Se into organic Se compounds, including selenoamino acids, and in providing it to animals and humans (*13*). A previous study on the allocation of added selenate in various fractions in ryegrass (*Lolium perenne* L.) and lettuce (*Lactuca sativa* L.) showed that plants utilize Se effectively in their amino acid and protein synthesis (*14*). In the cereal grains (*15*), and in the leaves of lupine (*Lupinus albus*), Indian mustard (*Brassica juncea*), and sunflower (*Helianthus annus*), inorganic Se was converted predominantly to selenomethionine (*16*). Most plants, including agricultural crops, are nonaccumulators, and their ability to accumulate large amounts of Se without toxic effects is low. Higher levels of Se in nonaccumulator plants result in toxicity because of nonspecific incorporation of Se instead of sulfur into methionine and cysteine (*17*).

Chemical components of potato, such as starch, reducing sugars, proteins, vitamins, and minerals, are very important for potato processing quality and nutritive value (*18*). Recently, selenate was demonstrated to enhance the growth of potatoes and the starch accumulation in tubers (*19*). Moreover, Se has been shown to decrease the total glycoalkaloid content in mature (*20*) and immature tubers (*21*). The Se fertilization is also found to increase the total and protein amino acid contents of tubers (*22*) while decreasing the nitrate content (*20*). The undesirable color due to raw darkening of potatoes after peeling or cutting is the most important factor decreasing their sensory quality. The rate of raw darkening is attributable to the activity of polyphenol oxidase (PPO) that catalyzes the oxidation of phenolic substrates such as tyrosine, chlorogenic acid, and caffeic acid to quinones. These quinones form a stable end product: a brown, black, and red pigment melanin (*23*, *24*). The enzymatic darkening is genetically controlled, but crop management, the growing and storage environments, and the length of storage

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influence the reaction rate and the degree of color formation (*23*, *24*). The reducing compounds, such as sulfites, citric acid, and ascorbic acid, are used to prevent enzymatic discoloration (*24*). Therefore, Se can be hypothesized to diminish the discoloration of tubers through its antioxidative function.

This study examined the effects of Se fertilization on potato processing quality, possible changes in Se concentration and form in tubers during storage, retransfer of Se from seed tubers to the next tuber generation, and the value of Se-enriched potato tubers as a source of dietary Se for humans.

MATERIALS AND METHODS

Plant Material and Experimental Designs. The potato tubers (cv. Satu) were planted and cultivated in a greenhouse and were supplemented with sodium selenate (Na_2SeO_4) at levels of 0, 0.0035, 0.01, 0.075, and 0.9 mg Se kg^{-1} quartz sand as described earlier by Turakainen et al. (*19*). In brief, the potato plants were grown under greenhouse conditions at 20−25/16 °C (day/night), at an intensity of ca. 220 μmol photons m^{-2} s^{-1} and a 16/8 day/night photoperiod at 50% relative humidity. The total amounts of nutrients added per pot were 3.0 g N, 1.0 g P, 4.8 g K, 1.8 g Ca, 0,18 g S, 0.02 g Fe, 0.136 g Mg, 8.3 mg Na, 2.7 mg B, 1.1 mg Mn, 0.8 mg Zn, 0.3 mg Cu, 0.3 mg Ni, and 0.5 mg Mo. The tubers were grown in individual plastic 10-L pots containing 10 kg of quartz sand. The plants were arranged in a completely randomized block design with three replicates. There were 15 plants for each Se treatment. The tubers were harvested 16 weeks after planting and were stored for 1, 3, 6, or 12 months at 3−4 °C and at 75% relative humidity until analysis.

Retransfer of Selenium from Seed Tubers. The tubers harvested were planted the following year and were cultivated in a greenhouse to study the retransfer of Se from the seed tubers to the next tuber generation. Six seed tubers from each Se treatment were sprouted at 14 °C, 30 μmol m^{-2} s^{-1}, and 70% relative humidity for 60 days. After sprouting, one tuber was planted in each 10-L plastic pot containing limed (pH 5.9) and fertilized peat (110 mg N L^{-1}, 40 mg P L^{-1}, 220 mg K L^{-1}) (Kekkilä B2, Finland). The temperature in the greenhouse was 22/16 °C (day/night). The light intensity was ca. 220 μmol photons m^{-2} s^{-1} supplemented with 400 W high-pressure sodium lamps (Lucalox, LU 400/HO/T/40 NG, Hungary) in a 16-hour photoperiod at a relative humidity of 50%. The plants were arranged in a completely randomized design with six replicates. They were fertilized four times during the growing period with a nutrient solution (no Se supplementation) (Puutarhan Täyslannos, Kemira GrowHow, Finland), the total amount of nutrients per pot being 200 mg N, 70 mg P, and 300 mg K. Tubers were harvested 16 weeks after planting. The Se concentration of tubers at each sampling time was determined with two potatoes from five replicates in each Se treatment.

Analytical Procedures. *Analysis of Selenium.* Possible changes in Se concentrations in tubers during storage ($n = 3-5$ tubers per Se treatment) were determined. The tubers were frozen in liquid nitrogen and were stored at −20 °C until lyophilization. The lyophilized samples were ground in a mill through a 0.5-mm mesh screen (Cyclotec Sample Mill 1093, Foss Tecator, Höganäs, Sweden). The Se concentrations were determined by electrothermal atomic absoption spectrometry (AAS) at the wavelength 196.1 nm using established methods described by Kumpulainen et al. (*25*) and Ekholm (*26*). The Se concentration was recorded as μg per g dry weight (DW). To test the accuracy of the Se analysis, four in-house reference samples were included for every analytical round.

Separation of Biochemical Selenium Fractions. The principle was to extract inorganic and organic Se in samples and to separate the organic Se further into different biochemical fractions: soluble proteins, free amino acids, and finally into insoluble residue that contains mainly organic compounds such as proteins and polysaccharides. Separation was performed by a modification of the methods of Lazarus (*27*) and Gissel-Nielsen (*28*) described in Hartikainen et al. (*13*). A lyophilized and ground tuber sample of 5 g was extracted twice with 50 mL of deionised water, and the mixture was shaken for 30 min and was centrifuged for 20 min at 16 270*g* in tared tubes. Then, 25 mL of deionized water was added, and the mixture was shaken for 30 min and was centrifuged for 30 min at 19 700*g*. The supernatants were collected into the same tube after each centrifugation. The residue that remained solid after extraction was dried for 2 days at 70 °C and was weighed. The proteins in the supernatant were precipitated with 30 mL of 30% trichloroacetic acid. The solution was centrifuged for 40 min at 19 700*g*. The solid precipitate was dried for 2 days at 70 °C and was weighed. The supernatant was passed through a moist cation-exchange resin (10 g of Dowex 50W-8, Sigma-Aldrich Chemies GmbH, Steinheim, Germany) in class tube (215-mm long with 8-mm i.d.). The resin had been activated by elution with 50 mL of 1 M HCl, 200 mL of 0.2 M NaOH, and 50 mL of 1 M HCl. The flux was adjusted to 1 mL/min. The inorganic fraction was eluted from the column with 200 mL of 1 M HCl, and the column was rinsed with 50 mL of deionized water. The free amino acid residue was eluted from the column with 275 mL of 0.2 M NaOH. The inorganic and free amino acid fractions were evaporated in a rotation vacuum in a water bath (Büchi RE111, Büchi Laboratoriums-Technik-AG, Flawil, Switzerland). The inorganic residue was redissolved in deionized water to a total volume of 25 mL. The free amino acid residue was redissolved in 0.01 M HCl to a total volume of 25 mL. Se extracted on different steps was determined by the method described in Kumpulainen et al. (*25*) and Ekholm (*26*).

Raw Darkening. The effect of Se supplementation on the raw darkening of tubers was determined twice during the storage period: after a 1-month storage and again after an 8-month storage. Sensory analyses were carried out using the standard method used in official potato variety trials by Potato Research Station in Finland. Ten tubers per Se treatment with three replicates were split longitudinally into two halves. Exactly 30 and 60 min after splitting, the degree of the total discolored area on the surface of each tuber was evaluated by three sensory panelists. The darkening was rated on a scale of 9−1, with 9 standing for no darkening (0%), 7 for less than 10%, 5 for less than 30%, 3 for less than 70%, and 1 for unacceptable discoloration (100%). One tuber was split immediately before the onset of both evaluation sessions and was used as a reference sample. The weighted index was calculated using the formula $(a_1 \times 0 + a_2 \times 1 + a_3 \times 5 + a_4 \times 10 + a_5 \times 10)/(\Sigma a_{1-5}) \times 20$, where the subscripts 1−5 refer to the number of tubers graded by the darkening values of 9, 7, 5, 3, and 1, respectively. The index emphasizes the proportion of discolored potato tubers. An acceptable upper limit for the raw darkening index is <20.

Data Analysis. Statistical analysis was performed using SAS version V8.2 for Windows (SAS Institute Inc., Cary, NC). Data were tested using analysis of variance in the GLM procedure. Significantly different mean values between Se treatments were separated with Duncan's multiple-range tests. Differences at $P \leq 0.05$ were considered significant. Differences between two storage times (1 month and 12 months) at various Se treatments were tested by the procedure of PROC NPAR1WAY using the Wilcoxon signed rank-test (SAS Institute, Cary, NC). Differences at $P \leq 0.05$ were considered significant.

RESULTS

Selenium Concentration of Stored Tubers. As expected, the Se concentration of tubers was higher with larger Se supplementation (**Table 1**). In general, the storage did not markedly affect the Se concentration of the tubers. Only slight increases were observed. At the Se supplementation level of 0.01 mg kg^{-1}, the Se concentration was significantly highest in the tubers stored for 12 months, whereas at the level of 0.075 mg kg^{-1}, increased concentrations were observed in the tubers already after storing for 3 months.

The Distribution of Selenium in Different Biochemical Fractions. The relative distribution of Se between different biochemical fractions in the tubers stored for 1, 6, and 12 months, expressed as a percentage (%) of the total Se, is depicted in **Figure 1**. In calculations, the weight of each fraction was taken into account. In the Se-supplied tubers, 22−36% of the total Se was found in the soluble protein fraction, 24−43% in

Table 1. Se Concentration in Potato Tubers Stored for 1, 3, 6, or 12 Months[a,b]

Se added mg kg^{-1} quartz sand	storage time months			
	1	3	6	12
0	0.01a	0.01a	0.01a	0.01a
0.0035	0.07a	0.12a	0.08a	0.10a
0.01	0.18b	0.21b	0.18b	0.22a
0.075	1.15b	1.38a	1.42a	1.37a
0.9	15.73a	16.33a	16.25a	15.52a

[a] Potato plants had been supplemented with selenate at various levels (0, 0.0035, 0.01, 0.075, and 0.9 mg Se kg^{-1} quartz sand). Means followed with different letters within a row are significantly different at $P \leq 0.05$, $n = 3$–5. [b] Se concentration (μg g^{-1} DW).

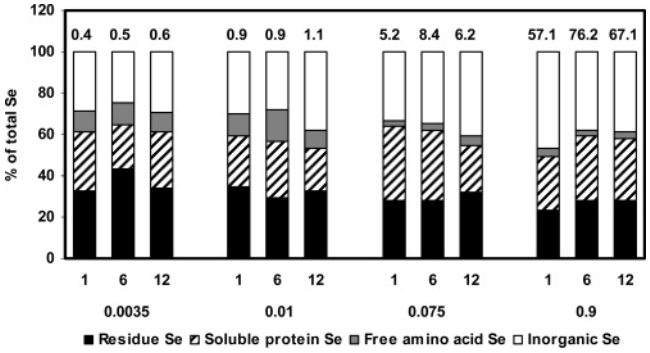

Figure 1. Relative distribution of total Se (% of total Se) in different biochemical fractions of potato tubers stored for 1, 6, or 12 months. Potato plants had been supplemented with selenate at various levels (0.0035, 0.01, 0.075, and 0.9 mg Se kg^{-1} quartz sand). The total Se (μg) in 5 g of (DW) plant material is shown above bars; $n = 2$–4.

Table 2. Se Concentrations in Different Biochemical Fractions of Tubers Cultivated with Increasing Se Levels (0.0035, 0.01, 0.075, and 0.9 mg kg^{-1} Quartz Sand) and Stored for 1, 6, or 12 Months

storage time month	Se added mg kg^{-1} quartz sand	residue (ng g^{-1} DW of the fraction)	soluble proteins (ng g^{-1} DW f the fraction)	inorganic[a] (ng mL^{-1})	free amino acid[a] (ng mL^{-1})
1	0.0035	29	758	4	1
	0.01	75	1516	11	4
	0.075	304	11 187	85	9
	0.9	3047	118 706	1432	150
6	0.0035	49	729	5	2
	0.01	64	1665	10	5
	0.075	529	13 807	112	11
	0.9	4637	129 387	1103	87
12	0.0035	53a	1146	7	3
	0.01	83a	2080	18	4
	0.075	467a	11 793	106	11
	0.9	4120a	131 086	939	114

[a] Total volume of the fraction was 25 mL. Differences between two storage times (1 month and 12 months) at various Se treatments are tested by the Wilcoxon signed rank-test; $n = 2$–4. No means differed significantly from each other ($P \leq 0.05$).

residue, 25−47% in inorganic, and 3−15% in the free amino acid fractions. The relative proportion of Se in free amino acids was lowest in the tubers cultivated at the two highest Se levels (0.075 and 0.9 mg kg^{-1}) (**Figure 1**). The Se concentrations (ng per g DW or per mL) measured during storage in different biochemical fractions at the different Se supplementation levels are shown in **Table 2**. In general, the concentrations diminished in the following order (**Table 2**): soluble proteins > insoluble residue > inorganic > free amino acids. When the storage time was increased from 1 month to 12 months, Se seemed to increase in the protein fraction in all Se treatments while it seemed to decline in inorganic and in free amino acid fractions at the Se treatment of 0.9 mg kg^{-1} (**Table 2**).

Processing Quality. In the fresh-cut tubers, the observed color scale varied from light pink to medium gray. After a 1-month storage, at Se addition level of 0.01 mg kg^{-1}, the lowest darkening degree of tubers was observed 30 min after splitting: no tubers with moderate discoloration were recorded (scale 5) (**Figure 2**a). However, the lowest darkening index (3.5) was observed in the tubers at the Se supplementation of 0.0035 mg kg^{-1} (**Figure 2a**) where the number of the tubers with moderate discoloration (scale 7) was lower than at the supplementation level of 0.01 mg Se kg^{-1} (**Figure 2a**). By contrast, the high Se dosages of 0.075 and 0.9 mg kg^{-1} seemed to promote discoloration; more tubers belonged in scales 5 and 3 and had higher a darkening index (12.3 and 9.0, respectively) than other Se treatments (**Figure 2a**). In all Se treatments, the darkening became more pronounced when the tubers were exposed to oxygen for 60 min, and the darkening index becoming unacceptably high (>20) (**Figure 2c**). When the time span after splitting became longer, the low (0.0035 mg kg^{-1}) to medium (0.075 mg kg^{-1}) Se supplementations diminished the number of tubers with a marked discoloration (scale 5−3) (**Figure 2c**, **d**).

Interestingly, in the tubers stored for 8 months, the raw darkening degree decreased in all Se treatments (**Figure 2b**, **d**). The Se supplementations of 0.0035 and 0.01 mg kg^{-1} delayed the darkening process; as compared with tubers stored for 1 month, more tubers with no discoloration (in scale 9) or with low discoloration (scale 7) were recorded 30 min after splitting (**Figure 2b**). Furthermore, 60 min after splitting, the tubers supplemented with 0.0035 mg Se kg^{-1} showed the lowest darkening degrees (scale 9−7) (**Figure 2d**). Compared with the control treatment, the Se-supplemented tubers were more resistant to darkening; more tubers with no discoloration (scale 9) and fewer tubers with high discoloration (scale 5) were observed. In the Se-supplemented tubers stored for 8 months, the darkening index was lower than in the control tubers at both 30 and 60 min after splitting, and the index was below the upper acceptable limit of 20 (**Figure 2b**, **d**).

Selenium Concentration in the Next Tuber Generation. The relative tuber yields produced by the seed tubers fertilized with increasing Se dosages and stored for 2, 3, or 8 months are given in **Table 3**. The most distinct outcome was that at each Se level the yield increased with increasing storage time. On the contrary, the next-generation tubers produced by the Se-enriched seed tubers were higher in Se than those produced by the control tubers cultivated without Se addition (**Table 4**). Certainly, the seed tubers produced at the lower Se levels of 0.0035 and 0.01 mg kg^{-1} increased the Se concentration in the next tuber generation only slightly (by 0.01 μg g^{-1} DW) (**Table 4**). The seed tubers enriched with Se at the highest addition level (0.9 mg Se kg^{-1}) produced the highest Se concentration in the next-generation tubers when stored for 2−3 months. When the storage time increased to 8 months, the concentration drastically dropped (**Table 4**).

DISCUSSION

In accordance with previous studies (*19*−*21*), the Se concentration in the tubers increased with increasing Se fertilization level (**Table 1**). The concentration did not decline during storage for 1−12 months at 3−4 °C, indicating that no volatile Se compounds were produced. Losses of Se from roots and shoot are shown to take place in many plants, when Se is converted

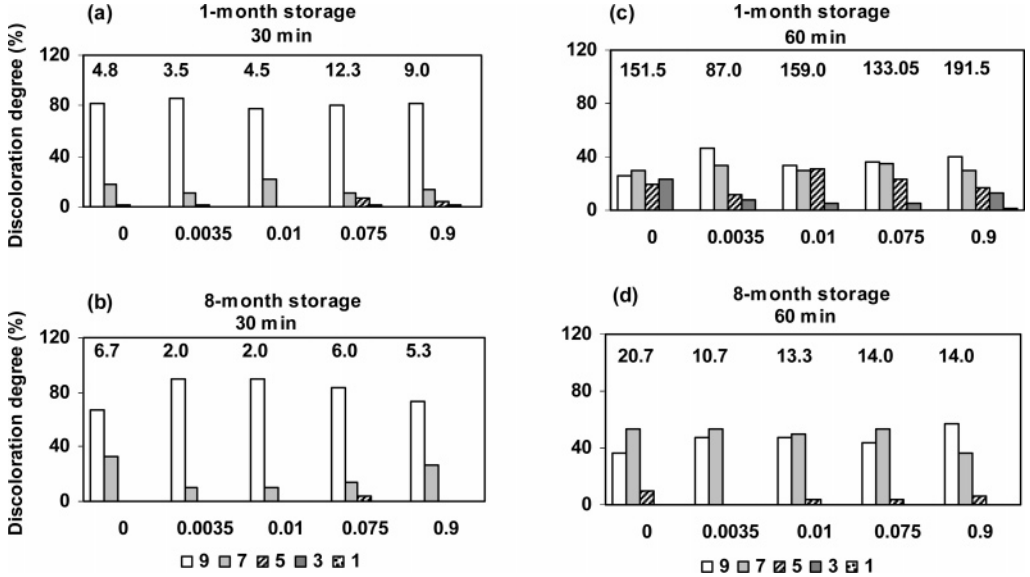

Figure 2. Raw darkening degree of potato tubers cultivated at various Se addition levels (0, 0.0035, 0.01, 0.075, and 0.9 mg kg^{-1}) and stored for 1 month (a, c) or 8 months (b, d) as determined after 30 min (a, b) and 60 min (c, d) after splitting. The darkening was rated on a scale of 9–1, with 9 representing no darkening (0%), 7 < 10% darkening, 5 < 30% darkening, 3 < 70% darkening, and 1 unacceptable discoloration (100%). The values of the raw darkening index are presented above the bars. The acceptable upper limit for the darkening index is <20.

Table 3. Tuber Yield (g $Plant^{-1}$) of Plants Produced by Se-Enriched Seed Tubers Cultivated at Different Se Addition Levels (0, 0.0035, 0.01, 0.075, and 0.9 mg kg^{-1}) and Stored for 2, 3, and 8 Months Before Planting[a]

storage time	Se added mg kg^{-1} quartz sand				
months	0	0.0035	0.01	0.075	0.9
2	651.2 ± 35	655.1 ± 31	665.1 ± 36	658.2 ± 16	658.7 ± 49
3	761.8 ± 42	739.5 ± 45	738.8 ± 22	732.9 ± 41	733.5 ± 25
8	1074.4 ± 44	1029.1 ± 48	1092.1 ± 53	1109.0 ± 58	1129.0 ± 49

[a] Results are presented as means ± SD; $n = 6$.

Table 4. Se Concentration of Next-Generation Tubers Produced by Seed Se-Enriched Tubers Cultivated at Increasing Se Addition Levels and Stored for 2, 3, or 8 Months Before Planting[a,b]

	storage time before planting		
Se added mg kg^{-1}	2 months	3 months	8 months
0	0.00a	0.00a	0.00a
0.0035	0.01a	0.01a	0.01a
0.01	0.01a	0.01a	0.01a
0.075	0.05a	0.03a	0.03a
0.9	0.76a	0.65a	0.25b

[a] Means with different letters (a, b) within a row are significantly different ($P \leq 0.05$) as tested by Duncan's Test; $n = 3$–4. [b] Se (μg g^{-1} DW).

into and released as volatile compounds (*17*). However, there are no previous studies on whether potato tubers are able to volatilize Se during growth or storage. They are living, active plant organs also during storage, but their biochemical activity is retarded by low temperature. Consequently, also the production of volatile Se can be minimized. This assumption is supported by results obtained with cabbage leaf homogenates showing that high temperature markedly increases the rate of Se volatilization (*29*). Our results revealed that Se-enriched potato tubers can be stored at low storage temperature up to 12 months without Se losses. This finding means that the improved nutritive value of potato tubers obtained by Se fertilization can be maintained during long-term storage. However, the highest Se supplementation level of 0.9 mg kg^{-1} raised the Se concentration of tubers to a level (~16 μg g^{-1} DW) too high for human dietary needs (**Table 1**).

In conformity with the increase in total Se, also the Se concentration in the different biochemical fractions of potato tubers increased in proportion to Se supplementation level (**Table 2**). In all Se-enriched tubers, the majority of Se was allocated to soluble and insoluble (the residual fraction) protein fractions (**Figure 1**). In the protein fractions, Se seemed to increase when storage time increased from 1 month to 12 months. On the contrary, at the Se treatment of 0.9 mg kg^{-1}, it declined in the inorganic and free amino acid fractions. These changes in different Se fractions indicate that some biochemical processes continued in the tubers during storage despite low temperature. Moreover, in the tubers produced at the highest Se addition levels (0.075 and 0.9 mg kg^{-1}), the prolonged storage resulted in transfer of Se from the inorganic and free amino acid fractions to soluble and insoluble (residue) protein fractions. The tubers stored for 1 month were still in a state of dormancy and, thus, their metabolic activity can be assumed to have been limited.

In terms of human nutrition, the amount of organic Se compounds in edible parts of plants such as in potato tubers is important, since they are considered to be more efficient than inorganic Se forms in increasing the Se content and the activity of GSH-Px in plasma and muscle tissue (*14*). According to a previous study of Hartikainen et al. (*13*), at the low Se supplementation levels (8, 16, and 33 g kg^{-1} soil) in lettuce leaves on average 82% and in ryegrass leaves on average 78% of total Se were bound in the protein fraction. These figures are higher than those obtained here where the protein bound fraction constituted on average 49−65% of total Se. This difference suggests that compared with plant leaves, in tubers Se is less efficiently bound in proteins. The lower protein-bound Se in tubers than in leaves may be related to tubers' lower protein content. On the other hand, de Souza et al. (*30*) have shown that the roots are unable to reduce selenate, indicating that the reduction of selenate to organic Se occurs in chloroplasts. If Se is assimilated in chloroplasts, it is possible that selenoamino acids may be exported from leaves into tubers. However,

Stadlober et al. (*15*) showed that the applied selenate was transformed to selenomethionine in cereal seeds and then was incorporated in proteins, indicating that there are some metabolic pathways for Se also in seeds. Accordingly, in tubers selenate may be assimilated into organic Se compounds in plastids.

The sensory analyses of the split tubers supported the hypothesis that the Se fertilization of potato diminishes the tuber discoloration. The beneficial effect of Se on the processing quality was more unambiguous in the tubers stored for 8 months than in those stored only for 1 month (**Figure 2**). Furthermore, the results showed that the number of darkening-resistant tubers increased especially at the low Se addition levels (0.0035 and 0.01 mg kg^{-1}) where the darkening degree diminished and the discoloration reaction was retarded. The delayed discoloration reaction can be attributed to the antioxidative function of Se in plant cells. Previous studies have shown that at proper levels Se acts in plants as an antioxidant, diminishing the oxidative reactions in cells caused by UV-B radiation, low temperature, senescing, and high salt concentration (*9*−*12*). The enzymatic discoloration is an oxidation reaction where Se may act as an oxygen scavenger, diminishing the availability of molecular oxygen for PPO reactions and, thus, retarding the darkening reaction. Alternatively, the effect of Se on darkening could be associated with the protein and amino acid content of tubers. Munshi et al. (*22*) showed that selenite application increased the protein content of tubers and decreased the content of free amino acids, such as tyrosine, in the cortex region of potato tubers. Free tyrosine is considered one of the key substrates for enzymatic darkening in potatoes (*23*), and therefore the lower tyrosine content of tubers may decrease the degree of discoloration. The increase in the proportion of protein-bound Se (**Figure 1**) during storage may also have an influence on the degree of discoloration.

The follow-up experiment demonstrated that Se can be at least partly relocated from the seed tuber to the next yield: the higher the Se concentration was in the seed tuber, the higher it was also in the next-generation tubers (**Table 4**). However, the seed tubers have to be relatively high in Se to have a marked effect on the Se concentration in the next generation. Moreover, at the highest supplementation level (0.9 mg Se kg^{-1}), the relocation of Se from the 8-month-stored seed tubers was less efficient than from the tubers stored for 1 month. This may be the result of the decrease in the easily mobilizable inorganic Se observed in the seed tubers where the storage was prolonged from 1 month to 12 months (**Figure 1**, **Table 2**). Another possible explanation is the dilution of Se because of higher tuber biomass of the progeny crop produced by the seeds of advanced age (**Table 3**). The seed tubers stored for 8 months produced 42% higher yield than those stored for 1 month because of the release of dormancy and the increased physiological age of seed tubers.

The results of the present study show that, in terms of human nutrition, the Se fertilization may improve the nutritive value of potato by increasing the amount of organic Se compounds in tubers. Organic Se forms, in turn, are considered to be more efficient than inorganic Se forms in increasing the Se content and the activity of GSH-Px in plasma and muscle tissue (*14*). However, the highest Se supplementation level of 0.9 mg kg^{-1} raised the Se concentration of tubers to a level ($\sim$16 μg g^{-1} DW) too high for human dietary needs (**Table 1**). The Se concentration remaining constant during storage of 1−12 months indicated that the improved nutritive value of potato tubers can be maintained in proper storage conditions. The Se-enrichment of the tubers also increased their resistance against enzymatic discoloration reactions thus improving their sensory quality of importance to consumers.

ABBREVIATIONS USED

GSH-Px, glutathione peroxidase; PPO, polyphenol oxidase; Se, selenium.

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