Antagonistic Relationship between Selenate and Sulfate Uptake in Onion (*Allium cepa*): Implications for the Production of Organosulfur and Organoselenium Compounds in Plants

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The relationship between S and Se uptake in onion plants was investigated in solution culture. In the absence of Se, plant S concentrations ranged from 0.6 to 1.45% at S solution culture levels of 0.8 mol m^{-3} (standard nutrient solution) and 14.8 mol m^{-3} SO_4 (gypsum saturated), respectively. Increasing levels from 1 to 8 g m^{-3} SeO_4^{2-}-Se did not increase Se content beyond 158 ± 19 μg/plant, although plant concentrations ranged from 200 to over 1000 μg of Se/g of dry matter. At a constant Se level, increasing S in solution culture reduced plant dry matter Se concentration by 80%. When the antagonistic relationship between these two elements is expressed as a molar ratio, S/Se in plant dry matter is nearly identical to S/Se in solution culture. These data suggest that S must be supplied at relatively low levels to produce high concentrations of plant Se.

Keywords: *Selenium; sulfur; organoselenium; organosulfur; onion; Allium cepa*

INTRODUCTION

Selenium (Se) is an essential micronutrient for animals because of the role of selenocysteine as the twenty-first essential amino acid (Stadtman, 1996) and is obtained via a food web that ultimately rests on the inadvertent uptake of Se by higher plants, for which no essential nor beneficial role has been firmly established except for Se-hyperaccumulator plants (Lauchli, 1993; Stadtman, 1996). The chemistry and biochemistry of selenium is more easily expressed in terms of the better-known sulfur chemistry because of the great similarities in chemical properties that selenium and sulfur share by virtue of being adjacent group VIA elements, leading to significant interactions from both a chemical and biological standpoint. The sulfur equivalents of selenide (Se^{2-}), elemental Se, thioselenate ($Se_2O_3^{2-}$), selenite (SeO_3^{2-}), and selenate (SeO_4^{2-}) are sulfide, elemental S, thiosulfate, sulfite, and sulfate, respectively. When Se is assimilated into amino acids by bacteria, plants, and animals, the Se analogs of S amino acids, selenocysteine and selenomethionine, are synthesized. The function of the Se analogs is not equivalent to that of the S amino acids, and excessive Se assimilation by plants results in toxicity, growth limitation, and death. The selenium chemistry of plants has been reviewed several times (Brown and Shrift, 1982; Anderson and Scarf, 1983), most recently by Lauchli (1993).

Interaction between S and Se uptake and assimilation by plants is expected, particularly when S and Se are present as sulfate (SO_4^{2-}) and selenate (SeO_4^{2-}), their most chemically stable forms in aerated, neutral and near-neutral natural waters. Antagonistic sulfate/

selenate interactions in uptake have been reported in single cells, excised roots, and whole plants (Lauchli, 1993).

A suite of unique organosulfur compounds present in the various vegetable *Allium* species, including onion (*A. cepa*) and garlic (*A. sativum*), possess medicinal properties, among them chemopreventative (Belman et al., 1987; Block, 1992), cardiopreventative (Block, 1992; Goldman et al., 1995; Goldman et al., 1996), and other health-related effects. In general, organosulfur compounds based on garlic sulfoxides have been shown to inhibit carcinogenesis by acting as blocking agents and effectively preventing carcinogen activation (Wattenberg, 1992; Fenwick and Hanley, 1985a−c). These organosulfur compounds have been shown to increase glutathione *S*-transferase activity (Sparnins et al., 1986) and inhibit *N*-nitrosodiethylamine-induced carcinogenesis of the lungs and forestomach of mice (Wattenberg et al., 1989). Glutathione *S*-transferase aids in the detoxification of carcinogens, and thus its promotion may be valuable in chemoprevention. Diallyl sulfide (DAS) has been shown to inhibit *N*-nitrosomethylbenzylamine-induced cancer in rats (Wargovich et al., 1988). Brady et al. (1988) showed that DAS inhibits metabolism of nitrosamines in rats. Similar inhibition of tumor growth by DAS has been detected in mice (Sumiyoshi and Wargovich, 1990). Although alk(en)-yl-based sulfoxides, such as those from onion, have received little attention as chemopreventative agents, the similarity in relationship between these compounds and the allyl sulfoxides from garlic suggests parallel investigations with onion, one of the world's most widely consumed vegetable crops.

Dietary intake of crops grown in Se-poor soils has been associated with increased rates of certain cancers in humans (Jackson, 1988), and Se is thought to play a role in reducing the growth of cancerous tumors in animal systems (Axley et al., 1991) and lung, colorectal, and prostate cancers in humans (Clark et al., 1996). In studies using Se-enriched garlic, Ip and Ganther (1992) demonstrated that organoselenium compounds are more

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active than S analogs in chemoprevention. Further investigation revealed that Se-enriched garlic was superior to unenriched garlic in suppression of mammary tumors in cancer-treated mice (Ip et al., 1992; Ip and Lisk, 1995). Feeding Se-enriched garlic and onion to cancer-induced rats reduced total tumor yield but did not cause excessive Se accumulation in animal tissues (Ip and Lisk, 1994a,b), suggesting that Se-enriched vegetables may be a better delivery source for organoselenium analogs than the commonly used selenite or selenomethionine. At present, the active organoselenium chemopreventative agents in preparations from Se-enriched medium plant tissues have not yet been fully identified. Cai et al. (1995b) proposed that enhanced levels of selenocysteine were responsible for a reduction in mammary tumor growth in carcinogen-treated mice fed a diet that included Se-enriched garlic, although clinical evidence has yet to be produced. Furthermore, there are potentially scores of Se analogs of specific organosulfur compounds in alliaceous species that may require investigation for phytopharmaceutical activity.

Despite clinical findings demonstrating the chemopreventative attributes of organoselenium and organosulfur compounds, little research has been conducted to investigate the efficiency of S and Se uptake, assimilation, and possible competitive inhibition in alliaceous plants. Characterization of this relationship should be critical for the production of Se-enriched *Allium* tissues for pharmacological investigation. For most of the world's cultures, onion consumption exceeds garlic consumption. Onion also produces greater edible bulb biomass than garlic, making it an additional and perhaps important target for Se-enriched vegetables for human consumption. The objective of this experiment was to evaluate the relationship between S and Se accumulation by onion plants grown in solution culture.

EXPERIMENTAL PROCEDURES

Onion sets of the pungent, long-day cultivar "Stuttgarter" were grown in a hydroponic system using half-strength modified Hoagland solution containing 0.8 mol m^{-3} SO$_4^{2-}$-S (Hoagland and Arnon, 1950) to which S and Se were added as CaSO$_4$ and Na$_2$SeO$_4$, respectively. A partial factorial arrangement of S and Se treatments was established. The response to increasing SO$_4^{2-}$-S on plant S uptake was tested with nutrient solutions containing 0.8, 4.8, 10.8, and 14.8 mol m^{-3} SO$_4^{2-}$-S. The response to increasing Se concentration in solution on plant Se uptake was tested by Se treatments of 1, 2, 4, and 8 g m^{-3} SeO$_4^{2-}$-Se at a constant level of 0.8 mol m^{-3} SO$_4^{2-}$-S. The interaction response was tested at 4 g m^{-3} SeO$_4^{2-}$-Se and SO$_4^{2-}$-S levels of 0.8, 4.8, 10.8, and 14.8 mol m^{-3}.

Onion sets were placed in slit foam plugs inserted in fitted lids of plastic 2-L containers. Each lid was equipped with four receptacles and an opening for an aeration tube. Containers were placed in a completely randomized design on a greenhouse bench. The experimental unit was a single plant, four of which were placed in each container. Duplicate containers were established for certain treatments (0.8, 4.8, 10.8, and 14.8 mol m^{-3} SO$_4^{2-}$-S at 0 Se and 0.8 mol m^{-3} SO$_4^{2-}$-S at 4 g m^{-3} SeO$_4^{2-}$-Se). Plants were grown under natural light in a greenhouse during the normal bulbing photoperiod for long-day onion plants in Wisconsin. Solutions were replaced at weekly intervals. At 60 days, plants were separated into leaf, root, and bulb portions, weighed, and lyophilized. Bulb tissue was assessed for S and Se by ICP-AES and ICP-MS, respectively. Regression analyses were performed using mean plant S and Se concentrations and contents on a per container basis.
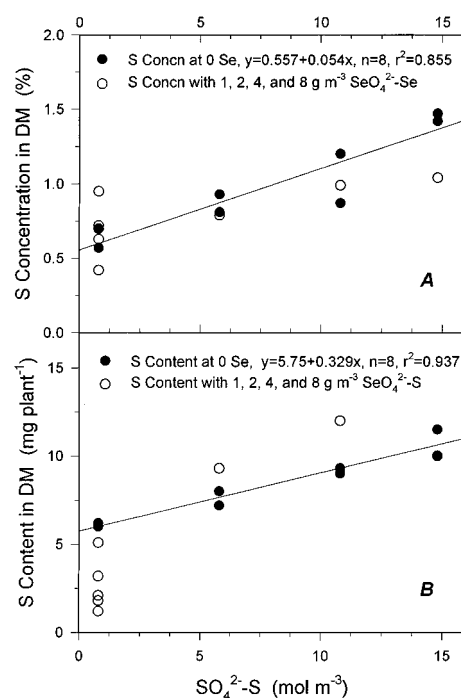

Figure 1. Relationship between SO$_4^{2-}$-S in nutrient culture and S concentration in dry matter (A) and S content of plants (B). Each point is the mean of four plants in a container.

RESULTS AND DISCUSSION

Effect of Increasing Sulfate on S Accumulation. Increased levels of SO$_4^{2-}$-S in nutrient solutions raised S levels in onion plant dry matter (Figure 1A,B). This response was linear for both S concentration in dry matter and S content per plant (expressed as percent dry matter and milligrams S/plant, respectively). Concentrations of S in dry matter were 0.6% at the lowest level of solution culture S tested, 0.8 mol m^{-3} SO$_4^{2-}$-S, the level present in the modified Hoagland's solution. Sulfur concentrations reached 1.45% when S solution culture levels were at their highest, 14.8 mol m^{-3} SO$_4^{2-}$, at which level the hydroponic solutions were saturated with respect to CaSO$_4$·2H$_2$O.

Sulfur levels in onion bulb dry matter have been previously shown to respond to increases in sulfate levels in nutrient solutions ranging from S-stress to S-sufficient. Unlike the work of Randle et al. (1993, 1995) and Freeman and Mossadeghi (1973), the low S levels in our experiment were not intended to induce S deficiency but were instead intended to obtain near-optimal growth at concentrations typical of standard solution culture. Maximum reported S concentrations in onions grown in nutrient culture are ~0.36% S at 2 mol m^{-3} SO$_4^{2-}$ (Randle et al., 1993), 0.50% S at 1.5 mol m^{-3} SO$_4^{2-}$-S (Freeman and Mossadeghi, 1973), and 0.43% S at 1.55 mol m^{-3} SO$_4^{2-}$-S (Randle et al., 1995). At our lowest sulfate level (0.8 mol m^{-3} SO$_4^{2-}$-S), the bulb S concentration for the cultivar used in this study was slightly higher (0.6% S) than those previously reported at comparable S levels. Levels of SO$_4^{2-}$-S reported here are the highest reported for onions grown in solution culture, and S concentrations in bulb dry matter were more than doubled (1.45% S). Our highest S level, 14.8 mol m^{-3} SO$_4^{2-}$-S, was equal to that set by gypsum solubility, although higher levels could have been tested by adding Na$_2$SO$_4$ at the risk of reducing dry matter accumulation due to salinity damage.
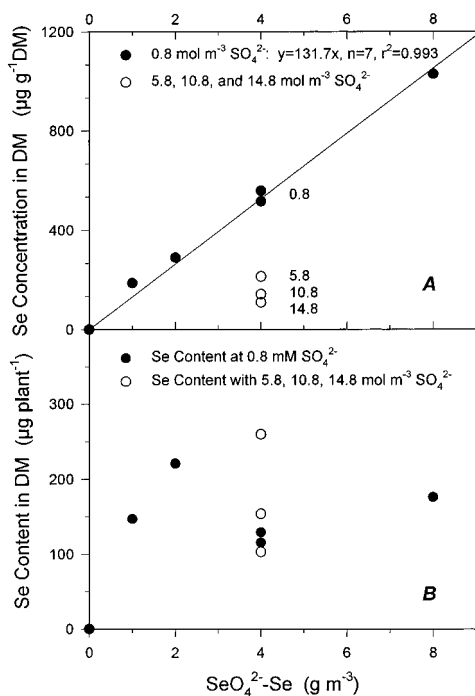
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Figure 2. Relationship between SeO_4^{2-}-Se in nutrient culture and Se concentration in dry matter (A) and S content of plants (B). Each point is the mean of four plants in a container.

Sulfur fertility can affect both concentration and ratios of organosulfur compounds in onion and thereby affect both the unique health and culinary characteristics of onion plants. Sulfur fertilizers have been shown to increase both total S content and flavor components in onion bulbs (Platenius, 1944; Freeman and Mossadeghi, 1973; Paterson, 1979), including those responsible for pungency (Randle et al., 1993). Onion possesses three S-containing flavor precursors, known collectively as *S*-alk(en)yl-L-cysteine sulfoxides (ACSO), which, when cleaved by the enzyme alliinase, hydrolyze to form the unique flavors associated with onion. Ratios of the ACSO compounds can be altered substantially by modification of S fertility (Randle et al., 1995). At low S fertility, methylcysteine sulfoxide (MCSO) is the most prevalent of the three ACSOs, and 95% of bulb S is tied up in S flavor compounds. However, at higher S fertility, propylcysteine sulfoxide (PCSO) is the most abundant ACSO, and only 40% of total bulb S is tied up in S flavor compounds. The ACSOs are direct precursors of thiosulfinates, which influence some of the unique medicinal qualities of onion (Block, 1992). Because ACSO quality and quantity are directly related to thiosulfinate content, enhanced S uptake presents an opportunity to modify the medicinal qualities of the onion plant.

Effect of Increasing Selenate on Se Accumulation. Increasing levels of solution culture Se increased Se concentration in dry matter (Figure 2A) but did not significantly increase Se content per plant beyond 158 ± 19 μg/plant (Figure 2B). A range of concentrations from 200 μg of Se/g of dry matter to over 1000 μg of Se/g of dry matter were obtained in plants grown in 1 g m^{-3} and 8 g m^{-3} Se, respectively. Therefore, high Se levels in solution culture led to high Se concentrations in dry matter but low Se content due to Se-limited growth. The optimal production of organoselenium compounds in onion plants must therefore take into account Se toxicity levels. These data indicate that
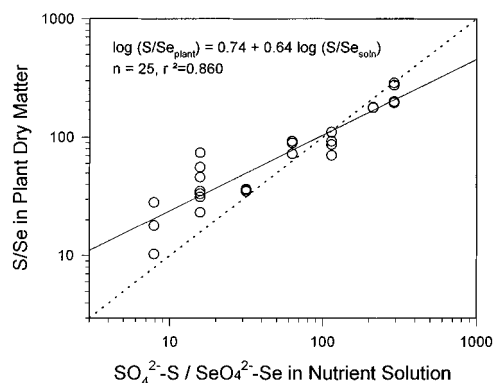

Figure 3. Relationship between the S/Se molar ratio in nutrient culture and in plant dry matter for onion plants grown at varying S and Se levels in a hydroponic system. Each point represents an individual plant in a container. Dotted line is 1/1, indicating no preference.

increasing Se concentrations in solution culture beyond ~2 g m^{-3} does not increase Se content in onion.

Work by Hamilton and Beath (1964) demonstrated that between 33 and 55% of total bulb Se accumulated by field-grown onion plants had been assimilated into organoselenium compounds. The seleno amino acids selenocysteine and Se-methylselenocysteine have been identified in selenium-enriched garlic, onion, and broccoli by Cai et al. (1995a,b). These workers suggested that the relative abundance of these two seleno amino acids is dependent upon Se concentration in plants. Furthermore, they proposed that enhanced levels of selenocysteine were responsible for a reduction in mammary tumor growth in carcinogen-treated mice fed a Se-enriched garlic diet. At present, however, little is known regarding the characterization and quantification of other organoselenium compounds in plant species grown in Se-enriched media. Furthermore, parallel investigations of plant response to increasing Se levels in solution culture, such as those reported above for increasing S levels, have yet to be reported.

Competitive Nature of S and Se. Addition of S to solution cultures at a constant level of Se reduced Se concentration but not Se content of onion tissue. Se concentrations of over 500 μg/g of dry matter (measured at 0.8 mol m^{-3} SO_4^{2-}-S and 4 g m^{-3} SeO_4^{2-}-Se) were reduced to slightly over 100 μg/g of dry matter (measured at 14.8 mol m^{-3} SO_4^{2-}-S and 4 g m^{-3} SeO_4^{2-}-Se). This 80% decrease in plant dry matter Se concentration indicates that S must be supplied at relatively low levels to produce high concentrations of plant Se and points toward a significant competitive relationship between the two elements. Each level of increase in solution culture S (0.8, 5.8, 10.8 mol m^{-3}) caused approximately 50% reductions in plant Se concentration except for the final level (14.8 mol m^{-3}), where the reduction was closer to 30%. These data demonstrate that S must be carefully managed if organoselenium compounds are to be efficiently produced in onion plants. Addition of Se to solution cultures at a constant level of S reduced S uptake but did not affect S concentration. Sulfur uptake dropped from 5.1 mg/plant at 1 g m^{-3} Se to 1.2 mg/plant at 8 g m^{-3} Se. These findings indicate that high Se availability caused a reduction in S content per plant, underscoring the importance of Se toxicity.

When the antagonistic relationship between these two elements is expressed as a molar ratio, S/Se in plant dry matter is nearly identical to S/Se in solution culture (Figure 3). A slight preference for S is observed when

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S/Se in solution culture is low. Thus, sulfate and selenate uptake must be considered jointly in attempts to produce a reliable source of organosulfur and/or organoselenium compounds in plants. Such sulfate/selenate antagonistic uptake interactions have been noted in single cells (Smith, 1976; Breton and Surdin-Kerjan, 1977), excised roots (Legett and Epstein, 1956; Ferrari and Renosto, 1972), and whole plants (Shennan et al., 1990; Mikkelsen et al., 1988; Bell et al., 1992; Wu and Huang, 1991), even at the field level (Severson and Gough, 1992). The basis for this interaction in S/Se uptake has been attributed to competitive inhibition for binding sites at the high-affinity permease responsible for sulfate uptake (Lauchli, 1993). However, our finding runs contrary to the concept of a "natural" S/Se ratio (Cai et al., 1995b) for garlic (*A. sativum*) and demonstrates that this ratio is in fact dependent upon the bioavailability of both elements.

Our results suggest that production of organoselenium compounds in plants on seleniferous soils may be compromised by levels of S. Those sources of Se in soil, weathering of shale and mine tailings, and those processes that form seleniferous soils, evaporation of shallow water table and accumulation of mining leachate (Boon, 1989), are the same sources and processes that often cause sulfate accumulation in soils. Therefore, seleniferous soils may not necessarily lead to seleniferous vegetation if high sulfate levels are a mitigating factor in Se accumulation in plants. Interestingly, many of the sites of seleniferous vegetation denoted by Boon (1989) in the continental United States, principally in the Western Great Plains and Mountain States, are within regions delineated by Beaton et al. (1971) as S-deficient. On the other hand, the soils of the Central Valleys of California, including the San Joaquin Valley, are often both seleniferous and gypsic (Fujii et al., 1988), but not noted by Boon (1989) as having seleniferous vegetation.

Our data demonstrate that, in the absence of Se, addition of S increases S concentration and S content in onion tissues. Similarly, at a low level of S in solution culture, an increase of Se causes an increase in plant Se concentration; however, the Se content does not increase due to limitations on plant growth. At a relatively high rate of Se in solution culture, Se uptake was suppressed by increasing S concentration in solution culture, indicating a competitive relationship between these two elements. These findings suggest that careful management of both S and Se levels is necessary for the production of seleniferous onion tissues.

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