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Interaction between Atmospheric Hydrogen Sulfide Deposition and Pedospheric Sulfate Nutrition in *Brassica oleracea* L.

By

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Key words: APS reductase, *Brassica oleracea*, cysteine, glutathione, hydrogen sulfide, hydrogen sulfide deposition, sulfate reduction, sulfate uptake, sulfur deficiency, sulfur nutrition.

Summary

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Brassica oleracea L. is able to utilize H_2S as sulfur source for growth and it can replace pedospheric sulfate as sulfur source. The foliage forms an active sink for atmospheric H_2S, which is directly metabolized into cysteine and subsequently into other organic sulfur compounds. H_2S exposure results in an increased size and changed composition of the thiol pool. However, the overall foliar H_2S uptake by *B. oleracea* appears to be under strict metabolic control and the uptake and metabolism of H_2S by the shoot and that of sulfate by the roots appear to be in tune and adjusted to the actual sulfur requirement for growth. H_2S exposure results in a decrease in sulfate reduction in the shoots at the site of adenosine 5'-phosphosulfate reductase and in a down-regulation of the sulfate uptake by the roots. H_2S impact studies show to be a useful tool for studying the signals involved in the regulation of sulfur metabolism and its interaction with nitrogen metabolism.

A modulation of sulfur nutrition by changing the levels of atmospheric and pedospheric sulfur also shows promise in the studies on i) the potential and usefulness of the channeling of extra sulfur into specific sulfur pools, ii) the role of sulfur compounds (e.g. glutathione) in the protection of plants against oxidative and environmental stress, iii) sulfur-induced resistance of plants against

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pests and iv) the function of secondary sulfur compounds in plants and the mutual regulation of sulfur and nitrogen metabolism in plants.

Introduction

Sulfur is an essential element for crop plants, however, its content strongly varies between species, from 0.03 to 2 mmol g^{-1} dry weight (0.1 to 6 % of dry weight; Duke & Reisenauer 1986, Schnug 1998, Pedersen & al. 1998). Plants absorb sulfur in the form of sulfate by the roots, which needs to be reduced prior to its metabolism into organic compounds, viz. amino acids, proteins and various other cellular components, including thiol compounds and so-called secondary sulfur compounds. The major proportion of the reduced sulfur in plants (up to 90 %) is present as cysteine and methionine residues in proteins (Giovanelli 1990, Stulen & De Kok 1993). There is a strong mutual interaction between sulfur and nitrogen uptake and metabolism by plants and the organic nitrogen/organic sulfur ratio in plants is generally around 20 (Stulen & De Kok 1993).

The crops' sulfur requirement can be defined as the "the minimum rate of the sulfur uptake and utilization, which is sufficient to obtain the maximum yield, quality and fitness of a crop". This is equivalent to "the minimum content of sulfur in the crop associated with maximum yield" and this is regularly expressed as kg sulfur in the harvested crop ha^{-1}. In physiological terms the plants' sulfur requirement can be expressed as the sulfur flux (the rate of sulfur uptake, reduction and metabolism) needed per gram plant biomass produced at various stages of the plants' life cycle (De Kok & al. 2000). When a plant is in the vegetative growth period, the sulfur flux (S_{flux}) can be estimated by calculating $S_{flux} = S_{content} \cdot RGR$, where S_{flux} is expressed as µmol g^{-1} plant day^{-1}, S content represents the total plants' sulfur content (µmol g^{-1} plant) and RGR the relative growth rate of the plant during the growth period (g g^{-1} plant day^{-1}). Values on total sulfur flux of various plant species grown at optimal growth conditions and nutrient supply may range from 0.02 to 0.1 mmol sulfur g^{-1} plant dry weight day^{-1} (De Kok & al. 2000).

Sulfur fertilization is not always optimal to meet the crops' sulfur requirement, since the amount of sulfur in most modern fertilizers is too low for optimal crop production (Schnug 1993, 1998, Schnug & Haneklaus 1998). Presently, sulfur deficiency appears to be the most abundant nutrient stress and it occurs frequently throughout the world (Ceccotti & Messick 1997, Ceccotti & al. 1998). It has been established that the ongoing reduction of atmospheric sulfur deposits as the consequence of strict regulations on industrial sulfur emissions in modern industrialized countries is one of the main causes of the occurrence of sulfur deficiency in crops, which needs to be compensated by altered sulfur fertilizer practice (Schnug 1993, 1998, Ceccotti & Messick 1997, Schnug & Haneklaus 1998). Sulfur deficiency results in a loss of crop production, crop resistance to pests and food quality (Schnug 1993, 1998, Stuiver & al. 1997, Schnug & Haneklaus 1998, Pedersen & al. 1998). In addition, sulfur deficiency will decrease nitrogen efficiency, resulting in increased nitrogen leaching from the soil (SCHNUG 1998).

Sulfur is relatively inexpensive and it can be applied to the soil using a variety of different sulfate- and elemental sulfur-based fertilizers, however, ammonium sulfate and single superphosphate still appear to be the most applied sulfur sources for plants (CECCOTTI & MESSICK 1997, CECCOTTI & al. 1998). In addition to pedospheric sulfur, plants are also able to utilize foliarly deposited atmospheric sulfur gases, viz. SO_2 and H_2S, as sulfur source for plants (DE KOK 1990, DE KOK & al. 1998, 2000). It has been estimated that only foliar sulfur deposits at chronic atmospheric SO_2 and H_2S levels of 0.05 $\mu l\ l^{-1}$ and higher substantially contribute to the plants' sulfur fertilization (DE KOK & al. 1998, 2000, STULEN & al. 1998). However, such high atmospheric levels are only likely to occur in heavily polluted areas.

Plants may have to deal with variation in sulfur supply, though to some extent they have the physiological plasticity to adapt to limited or excess sulfur supply. Adaptation may occur by changing the efficiency of the uptake and reduction of sulfur by alteration of the level and expression of sulfate transporter proteins and the enzymes involved in sulfate reduction (DAVIDIAN & al. 2000, HAWKESFORD & WRAY 2000). There is still a lack of knowledge on the regulation of uptake and assimilation of sulfur 'on a whole plant level' and on the mechanisms (e.g. signals, shoot/root interactions) involved.

Curly kale (*Brassica oleracea*) can be considered as a species with a relatively high sulfur requirement for growth, and the total sulfur content in seedlings is approximately 0.5 mmol g^{-1} dry weight (1.6 %; DE KOK & al. 2000). Half of the sulfate taken up by the seedlings is reduced and subsequently incorporated into organic compounds, predominantly in the protein fraction, resulting in an organic N/S ratio of 15 (DE KOK & al. 2000). H_2S is a phytotoxic gas (DE KOK & al. 1998), however, curly kale appears not to be very susceptible to the toxic effects of H_2S and growth is only significantly reduced at atmospheric H_2S levels higher than 0.4 $\mu l\ l^{-1}$ (DE KOK & al. 2000, WESTERMAN & al. 2000c). Therefore curly kale appears to be an ideal species for studying the interaction between atmospheric and pedospheric sulfur nutrition (DE KOK & al. 2000, WESTERMAN & al. 2000a,b, 2001a,b).

The present paper briefly reviews the recent results on the impact of atmospheric H_2S on the regulation of uptake and assimilation of sulfate in *Brassica oleracea*, which are is to utilize atmospheric H_2S as sulfur source for growth.

Uptake and Metabolism of Atmospheric H_2S

The uptake of hydrogen sulfide (H_2S) by shoots of curly kale showed saturation kinetics with respect to the atmospheric concentration (DE KOK & al. 1997, STUIVER & DE KOK 2001, Fig. 1). The kinetics are largely determined by the rate of metabolism of the absorbed H_2S into cysteine, catalyzed by *O*-acetylserine(thiol)lyase, and can be described by the Michaelis-Menten equation.

The apparent maximal H_2S uptake by curly kale shoots ($J(H_2S_{max})$ and $K[H_2S]$, the concentration at which ½ $J(H_2S_{max})$ is reached are 1.4 µmol g^{-1} fresh weight h^{-1} and 0.5 µl l^{-1} H_2S, respectively (Fig.1.).

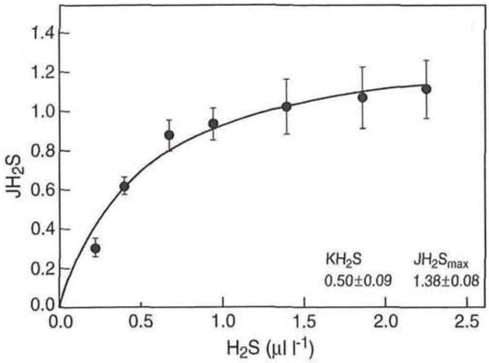

Fig. 1. Uptake kinetics of atmospheric H_2S by shoots of *Brassica oleracea* ($K[H_2S]$, µl l^{-1}; $J(H_2S)$, µmol g^{-1} fresh weight h^{-1}). Data derived from STUIVER & DE KOK 2001.

When curly kale was grown under sulfate-deprived conditions, plants developed sulfur deficiency symptoms (STUIVER & al. 1997) and H_2S uptake kinetics were substantially altered (STUIVER & DE KOK 2001). Shoots of SO_4^{2-}-deprived plants had a lower affinity to H_2S uptake, whereas the maximal H_2S uptake rate was higher. When SO_4^{2-}-deprived plants were simultaneously exposed to 0.2 µl l^{-1} H_2S all S deficiency symptoms disappeared and H_2S uptake kinetics returned rapidly to values observed for S-sufficient shoots (STUIVER & DE KOK 2001). The activity of the H_2S-fixating enzyme *O*-acetylserine (thiol)lyase was hardly affected upon either prolonged H_2S exposure or SO_4^{2-} deprivation (STUIVER & DE KOK 2001, WESTERMAN & al. 2001a). Evidently, the activity of *O*-acetylserine (thiol)lyase was not the rate-limiting step in the H_2S uptake by shoots (Fig. 2). The significance of the *in situ* availability and rate of synthesis of the substrate *O*-acetylserine for *O*-acetylserine(thiol)lyase as determining factor in the uptake kinetics of H_2S needs further evaluation.

Exposure of curly kale to H_2S resulted in a rapid accumulation of thiols (up to 3-fold) in the shoots (WESTERMAN & al. 2000a, Fig. 3). The increase in thiols in the shoots depended on the atmospheric H_2S level and it already reached maximal values after 6 hours of exposure, irrespective of the atmospheric level. In addition to glutathione, generally the most abundant thiol compound present in plant tissue, also substantial amounts of cysteine accumulated upon H_2S exposure (WESTERMAN & al. 2000a). Still, the total thiol content only accounted for a minor proportion of the organic sulfur fraction in the shoot (2 %) even after H_2S exposure (DE KOK &

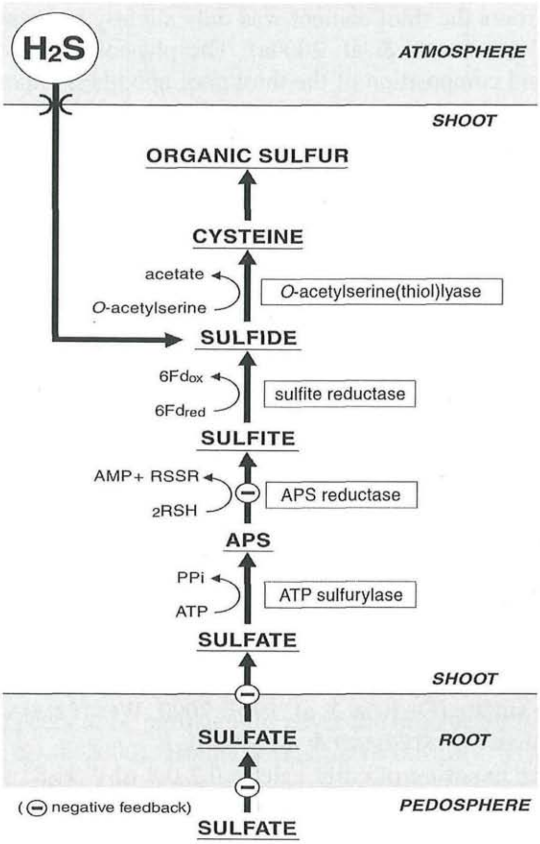

Fig. 2. Metabolism of sulfate and atmospheric H_2S and probable sites of feedback regulation.

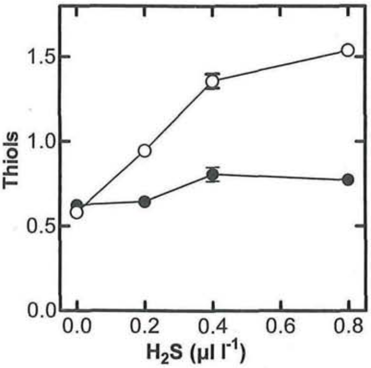

Fig. 3. Thiol levels (µmol g^{-1} fresh weight) in shoots (o) and roots (•) of *Brassica oleracea* upon H_2S exposure for 3 days. Data derived from WESTERMAN & al. 2000a.

al. 2000). In the roots the thiol content was only slightly increased after 2 days of H_2S exposure (WESTERMAN & al. 2000a). The physiological background of the changes in size and composition of the thiol pool upon H_2S exposure needs still to be resolved. The subcellular site of metabolism of the deposited H_2S is still unknown. *O*-Acetylserine(thiol)lyase, the enzyme responsible for the fixation of atmospheric H_2S into cysteine, is present in both chloroplasts and cytosol. The increase in the size and the change in composition of the thiol pool upon H_2S exposure could be due to an enhanced synthesis of cysteine in the cytosol, beyond the existing systems of feedback control of sulfate reduction and assimilation in the chloroplast (DE KOK & al. 2000).

Impact of H_2S Exposure on Metabolism of Pedospheric Sulfate

Curly kale is able to utilize H_2S as sulfur source for growth and at an atmospheric level of 0.2 $\mu l\ l^{-1}$ and higher it can replace pedospheric sulfate as sulfur source (DE KOK & al. 1997, 2000, Fig. 2). Moreover, the total sulfur content of both shoot and roots is also hardly affected by H_2S, even after prolonged exposure to levels up to 0.8 $\mu l\ l^{-1}$ H_2S (DE KOK & al. 2000, WESTERMAN & al. 2001b). The uptake and metabolism of both H_2S by the shoot and sulfate by the roots appear to be in tune and adjusted to the actual sulfur requirement for growth. H_2S exposure hardly affects the sulfate (DE KOK & al. 1997, 2000, WESTERMAN & al. 2000a) and glucosinolate content (WESTERMAN & al. 2001b).

Short-term exposure of curly kale to 0.2-0.8 $\mu l\ l^{-1}$ H_2S, atmospheric levels which have shown to be sufficient to meet the sulfur requirement of the plant, resulted in a down-regulation of the assimilatory sulfate reduction pathway in the shoots at the site of adenosine 5'-phosphosulfate reductase (WESTERMAN & al. 2001a, Fig. 4). This enzyme is believed to be a prime regulation point in the sulfate reduction pathway and its activity changed rapidly in response to an alteration in sulfur nutrition (LEUSTEK & SAITO 1999, HAWKESFORD & WRAY 2000). The adenosine 5'-phosphosulfate reductase activity in the shoots was maximally reduced by 80 % and the decrease in activity was already substantial after one day of exposure to 0.2 $\mu l\ l^{-1}$ H_2S. In the roots, its activity remained unaltered upon exposure to H_2S. The activities of ATP-sulfurylase, serine acetyltransferase and *O*-acetylserine (thiol)lyase in both shoot and roots were not affected upon exposure to H_2S (WESTERMAN & al. 2001a). Sulfide, *O*-acetylserine or cysteine are the most likely regulators of adenosine 5'-phosphosulfate reductase (HAWKESFORD & al. 1995, LEUSTEK & SAITO 1999) and the relation between the pattern of thiol accumulation and changes in activity of adenosine 5'-phosphosulfate reductase upon H_2S exposure needs further to be assessed.

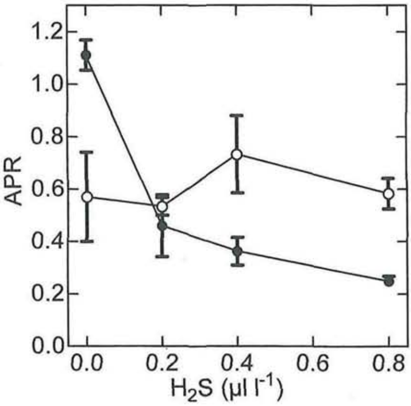

Fig. 4. Adenosine 5'-phosphosulfate reductase activity (µmol g^{-1} fresh weight h^{-1}) in shoots (●) and roots (o) of *Brassica oleracea* upon H_2S exposure for 3 days. Data derived from WESTERMAN & al. 2001a.

Exposure of curly kale to H_2S also resulted in a decrease in sulfate uptake by the roots (WESTERMAN & al. 2000a,b, Fig. 5). At 0.2 µl l^{-1} H_2S, a level sufficient to meet the sulfur requirement of plants for growth, the sulfate uptake was maximally decreased by 50 % after 3 or 4 days of exposure. A higher reduction in sulfate uptake appears not to be necessary, since the proportion of sulfur absorbed from the atmosphere appears to be sufficient to cover the organic sulfur requirement for growth (DE KOK & al. 2000). Higher levels up to 0.8 µl l^{-1} H_2S did not further affect the sulfate uptake. The nitrate uptake was not affected upon exposure to 0.2-0.8 µl l^{-1} H_2S (WESTERMAN & al. 2000a). When curly kale was exposed to 0.2 µl l^{-1} H_2S the sulfate uptake measured during a dark or light period was decreased to the same extent (WESTERMAN & al. 2000b). Both the xylem loading and the net sulfate uptake rate were decreased by 42 % after 6 days of exposure to 0.4 µl l^{-1} H_2S. This suggested that the xylem loading was not the limiting factor in the uptake of sulfate by the roots (WESTERMAN & al. 2000b). When curly kale was exposed to 0.4 µl l^{-1} H_2S and grown on a nutrient solution containing ^{35}S-sulfate, the specific radioactivity of the labeled S of the insoluble fraction (mainly proteins) of the shoot and root was decreased more than the specific radioactivity of the labeled S of the soluble fraction (mainly sulfate). This demonstrated that the major proportion of the metabolized atmospheric H_2S was incorporated into proteins (WESTERMAN & al. 2000b). The change in partitioning of the labeled sulfur upon H_2S exposure was similar in roots and shoot, which suggested that the roots were dependent on the shoot for their organic sulfur supply.

If curly kale was grown under sulfate-deprived conditions for one week it resulted in a so-called de-repression of the sulfate transporter activity, which resulted in a 2-fold higher sulfate uptake capacity after transfer to a sulfate-containing solution, while nitrate uptake was decreased by 50 % (WESTERMAN & al. 2000a). When sulfate-deprived plants were exposed to 0.25 µl l^{-1} H_2S, plant biomass production and nitrate uptake were restored but the sulfate uptake after transfer to a sulfate-containing solution remained high. Also here, H_2S exposure resulted in an increase in the thiol and cysteine content of both shoot and roots, whereas the content of sulfate remained low (WESTERMAN & al. 2000a).

In order to get more insight into the interaction between atmospheric and pedospheric sulfur nutrition, the impact of exposure to H_2S on sulfur metabolism was investigated in two cultivars of *Brassica oleracea* with a different sulfur requirement, viz. curly kale and Chinese cabbage. Measurements on the total sulfur content and growth of the two varieties showed that Chinese cabbage had a lower requirement for sulfur than curly kale (WESTERMAN & al. 2001b). Similarly the sulfate uptake rate of Chinese cabbage was lower than that of curly kale. The nitrate uptake rate of Chinese cabbage was higher compared to curly kale, which could be explained by its higher relative growth rate. Despite the lower requirement for sulfur of Chinese cabbage, the sulfate uptake rate was decreased to the same extent in both varieties, whereas the total sulfur content remained unaffected upon exposure to 0.25 $\mu l\ l^{-1}$ H_2S. Both in curly kale and Chinese cabbage a large proportion of total S was present as sulfate (WESTERMAN & al. 2001b).

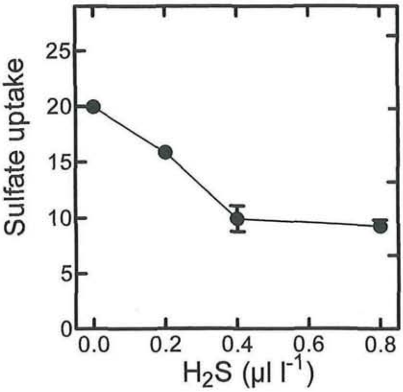

Fig. 5. Sulfate uptake ($\mu mol\ g^{-1}$ plant fresh weight $[72\ h]^{-1}$) by *Brassica oleracea* upon H_2S exposure for 3 days. Data derived from WESTERMAN & al. 2000a.

A modulation of sulfur nutrition by changing the levels of atmospheric and pedospheric sulfur nutrition also show promise in the studies on i) the potential and usefulness of the channeling of extra sulfur into specific sulfur pools (e.g. sulfur-rich proteins) by mastering of genes in order to facilitate improved crop quality, ii) the role of sulfur compounds (e.g. glutathione) in the protection of plants against oxidative and environmental stress, iii) sulfur-induced resistance of plants against pests, iv) the function of secondary sulfur compounds in plants and v) the mutual regulation of sulfur and nitrogen metabolism in plants.

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