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Sulfate Uptake and Utilization by Two Varieties of *Brassica oleracea* with Different Sulfur Need as Affected by Atmospheric H₂S

By

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With 3 figures

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Summary

WESTERMAN S., BLAKE-KALFF M. M. A., DE KOK L. J. & STULEN I. 2001. Sulfate uptake and utilization by two varieties of *Brassica oleracea* with different sulfur need as affected by atmospheric H₂S. – *Phyton* (Horn, Austria) 41 (1): 49–62, with 3 figures. – English with German summary.

In order to get more insight into the interaction between atmospheric and pedospheric sulfur nutrition, the impact of H₂S on sulfur metabolism was investigated in two varieties of *Brassica oleracea* L., viz. curly kale and Chinese cabbage. Measurements on the total sulfur content and relative growth rate of the two varieties showed that Chinese cabbage had a lower need for sulfur and correspondingly a lower sulfate uptake rate than curly kale. Both in curly kale and Chinese cabbage a large proportion of total sulfur was present as sulfate. However, the sulfate content of the roots and shoot was hardly affected at pedospheric sulfate

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concentration levels ranging from 0.25 up to 10 mM, reflecting a carefully regulated sulfate uptake by the roots. Upon exposure to $0.25 \mu\text{l l}^{-1}$ H_2S , an atmospheric level sufficient to meet the sulfur need of the plants, the sulfate uptake by the roots was reduced in curly kale and Chinese cabbage by 54 and 30 %, respectively. H_2S exposure resulted in an increase in thiol level in the shoots, whereas that in the roots was hardly affected, demonstrating that thiols have limited significance in the shoot to root signaling of the regulation of the sulfate uptake. The contents of total sulfur, sulfate and glucosinolates remained unaffected upon H_2S exposure. Evidently there is a good coordination between the metabolism of atmospheric H_2S and pedospheric sulfate in both varieties of *Brassica oleracea*.

Zusammenfassung

WESTERMAN S., BLAKE-KALFF M. M. A., DE KOK L. J. & STULEN I. 2001. Wirkung von atmosphärischem H_2S auf die Sulfataufnahme und -verwertung bei zwei Varietäten von *Brassica oleracea* mit unterschiedlichem Schwefelbedarf. – Phytion (Horn, Austria) 41 (1): 49–62, mit 3 Abbildungen. – Englisch mit deutscher Zusammenfassung.

Um zur Klärung der Wechselwirkungen von atmosphärischem und pedosphärischem Schwefel beizutragen, wurde der Einfluß von H_2S auf den S-Stoffwechsel bei Krauskohl und Chinakohl, zwei Kulturformen von *Brassica oleracea* L., untersucht. Die Messungen des Gesamtschwefelgehaltes und die relative Wachstumsrate der beiden Varietäten ergaben, dass der Chinakohl einen geringeren Schwefelbedarf besitzt und in Übereinstimmung dazu auch eine geringere Aufnahme hat als der Krauskohl. Sowohl im Krauskohl als auch im Chinakohl liegt ein großer Anteil vom Gesamtschwefel als Sulfat vor. Die Sulfatgehalte der Wurzeln und Sprosse wurden jedoch kaum durch Sulfatkonzentrationen von 0,25 bis 10 mMol, wie sie im Boden vorliegen, beeinflusst; dies bedeutet eine wirksame Regulation der Sulfataufnahme durch die Wurzeln. Bei einer Einwirkung von $0,25 \mu\text{l l}^{-1}$ H_2S , der Gehalt ist ausreichend um den Schwefelbedarf der Pflanzen zu decken, wurde die Sulfataufnahme beim Krauskohl und Chinakohl um 54 % bzw. 30 % vermindert. H_2S Begasung hatte einen Anstieg im Thiolgehalt der Sprosse zur Folge, wogegen jener in den Wurzeln kaum beeinflusst war. Dies deutet darauf hin, dass die Thiole nur eine begrenzte Wirkung als Signal vom Spross zur Wurzel besitzen, um die Sulfataufnahme zu regulieren. Die Gehalte an Gesamtschwefel, Sulfat und Glukosinolate blieben bei H_2S -Einwirkung unbeeinflusst. Offensichtlich besteht eine gute Koordination zwischen dem Stoffwechsel von H_2S aus der Umgebungsluft und jenem vom bodenbürdigen Sulfat bei beiden Kulturformen von *Brassica oleracea*.

Introduction

Plant shoots form an active sink for atmospheric H_2S . This is taken up via the stomates and metabolized with high affinity into cysteine and subsequently incorporated into other organic sulfur compounds (DE KOK 1989, 1990, DE KOK & al. 1989, 1991, 1998, 2000). Atmospheric H_2S can serve as the sole sulfur source for growth in plants (DE KOK & al. 1997, 1998, 2000). Exposure to H_2S generally results in an increased size and

changes in the composition of the thiol pool (DE KOK 1989, 1990, STULEN & DE KOK 1993, BUWALDA & al. 1993, 1994, POORTINGA & DE KOK 1995).

Several studies have shown an interaction between atmospheric and pedospheric sulfur nutrition. The sulfate uptake by the roots and its loading into the xylem may be decreased by H_2S exposure (BRUNOLD & ERISMANN 1974, HERSCHBACH & al. 1995a,b, DE KOK & al. 1997, 1998). When curly kale (*Brassica oleracea* L.) was exposed to a H_2S level sufficient to meet its sulfur need for growth, it resulted in a partial (maximal 50%) repression of sulfate uptake by the roots (DE KOK & al. 1997, 1998, WESTERMAN & al. 2000). The uptake of sulfate into roots is mainly a transporter protein-mediated metabolic process (CRAM 1990, CLARKSON & al. 1993, HAWKESFORD & SMITH 1997). The sulfate uptake appears to be strongly related to the sulfur nutritional status of the plant. The signals that are involved in the regulation of sulfate transporter protein activity may be either the intracellular sulfate content, or a reduced sulfur compound such as glutathione (CRAM 1990, CLARKSON & al. 1993, SMITH & al. 1995, HAWKESFORD & SMITH 1997).

Members of the *Brassicaceae* are characterized by their high sulfur need for growth, however, a large proportion of the sulfur is present as sulfate in both roots and shoots (VAN DER KOOIJ & al. 1997, DE KOK & al. 2000). Since *Brassicaceae* originate from saline, sulfur-enriched environments, the surplus of sulfate taken up may not solely be utilized for growth, but also for the synthesis of organic secondary sulfur compounds, like glucosinolates or as an osmotic compound (ERNST 1990, BLAKE-KALFF & al. 1998, VAN DER KOOIJ & al. 1997, DE KOK & al. 2000). In the present study it was investigated to what extent the partial repression of the sulfate uptake in curly kale was related to a strategy of the *Brassicaceae* to take up a surplus amount of sulfate. The sulfate content of shoot and roots of curly kale was measured after transfer of the plants to various sulfate levels of the root environment. In order to increase insight into the interaction between atmospheric and pedospheric sulfur nutrition, the impact of exposure to H_2S on sulfur metabolism was investigated in two varieties of *Brassica oleracea* L., viz. curly kale and Chinese cabbage.

Materials and Methods

Plant material

Seeds of curly kale (*Brassica oleracea* L., cv. Bornick F1 (Nickerson-Zwaan, The Netherlands)) or Chinese cabbage (*Brassica oleracea* L., cv. Kasumi F1 (Nickerson-Zwaan, The Netherlands)) were germinated in vermiculite in a climate controlled room. 12-day-old seedlings were transferred into a 25% Hoagland nutrient solution: 1.25 mM $\text{Ca}(\text{NO}_3)_2 \cdot 4\text{H}_2\text{O}$, 0.23 mM KH_2PO_4 , 1.25 mM KNO_3 , 0.5 mM $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$, 11.6 μM H_3BO_3 , 2.3 μM $\text{MnCl}_2 \cdot 4\text{H}_2\text{O}$, 0.24 μM $\text{ZnSO}_4 \cdot 7\text{H}_2\text{O}$, 0.080 μM $\text{CuSO}_4 \cdot 5\text{H}_2\text{O}$, 0.13 μM $\text{Na}_2\text{MoO}_4 \cdot 2\text{H}_2\text{O}$; adjusted to pH 6 with KOH (30 l tanks, 60 plants per tank). Day and night temperatures were 22 and 18 °C, respectively, the relative humidity

was $65 \pm 5\%$ and the photoperiod was 12 h at a photon flux density of $250 \mu\text{mol m}^{-2} \text{s}^{-1}$ (PAR 400–700 nm), supplied by Osram TL 31 and 21 in a ratio of 2:1. For H_2S exposure experiments plants were transferred to 12 l stainless steel containers ($19.5 \times 15.0 \times 45.0 \text{ cm}$) filled with 25% Hoagland nutrient solution at 0.5 mM sulfate (30 plants per container).

Exposure to H_2S

Plants were exposed to H_2S in 150 l cylindrical stainless steel cabinets (diameter 0.6 m) with a polycarbonate top, as described by STUIVER & al. 1992. Day and night temperatures were 20 and 16 °C (± 1 °C), respectively, relative humidity was $55 \pm 5\%$ and the photoperiod was 14 h at a photon flux density of $250 - 300 \mu\text{mol m}^{-2} \text{s}^{-1}$ (PAR 400–700 nm range), with a Philips HPL(R)N (400W) light source. The air temperature was controlled by adjusting the cabinet wall temperature, the air exchange was 40 l min^{-1} and the air inside the cabinets was stirred continuously by a ventilator. Pressurized H_2S diluted with N_2 (1 ml l^{-1}) was injected into the incoming air stream and adjusted to the desired level by ASM electronic mass flow controllers (Bilthoven, The Netherlands). H_2S level in the cabinets was controlled with an SO_2 analyzer (model 9850) equipped with a H_2S converter (model 8770, Monitor Labs, Measurement Controls Corporation, Englewood, CO 80112, USA).

Thiol content

Water-soluble non-protein thiols were extracted according to STUIVER & al. 1992 and the content of the 5,5'-dithiobis(2-nitrobenzoic acid) reactive compounds of the 30,000 g supernatant was measured as described by DE KOK & al. 1988.

Anion content

Sulfate and nitrate were extracted and estimated by refractometric determination after HPLC separation, as described by STUIVER & al. 1992. The anions were separated on a IonoSpher A anion exchange column ($250 \times 4.6 \text{ mm}$; Chrompack, Middelburg, The Netherlands) and 25 mM potassium biphthalate (pH 4.3), containing 0.02 % NaN_3 , was used as a mobile phase. The flow rate was 1 ml min^{-1} ; detector temperature was kept at 25 °C by a waterbath (MAAS & al. 1986).

Glucosinolate content

Glucosinolates were extracted from 40 mg of lyophilized plant material, and the concentrations of individual compounds were measured by HPLC, using sinigrin as an internal standard, according to the protocols of HEANY & al. 1986.

Total sulfur content

Analysis of total sulfur of the samples was performed using a modification of the method as described by JONES 1995. Samples were dried at 80 °C for 24 h and powdered in a mortar. 50 mg of the samples were weighed into pyrex glass tubes. 50% $\text{Mg}(\text{NO}_3)_2 \cdot 6\text{H}_2\text{O}$ was added to saturate the material and thereafter it was dried in an oven at 100 °C overnight. The samples were ashed in an oven at 700 °C overnight. The residue was dissolved in 10 ml 20 % aqua regia (50 HNO_3 and 150 ml HCl in 1 l distilled water) and the volume was adjusted to 100 ml with distilled water. One Sulfa[®]Ver4Reagent Powder Pillow (HACH, Permachem[®]

reagents, Loveland, USA) containing BaCl_2 was added to 25 ml of the mixture and the turbidity was measured on a spectrophotometer (HACH DR/400V, Loveland, USA) at 450 nm.

Sulfate and nitrate uptake

For measurements on the sulfate and nitrate uptake, 3 plants were placed on vessels containing exactly 1 l of freshly prepared 25% Hoagland nutrient solution with 0.5 mM sulfate. At the start of the uptake measurements and after 24 h, after adjusting the nutrient solution to the original volume, an aliquot was taken from the nutrient solution. The sulfate and nitrate concentrations in the nutrient solution were determined by HPLC (see above). The anion uptake was calculated as the difference in ion content (μmol) between samples taken at the start and after 24 h of exposure, divided by the total root or plant fresh weight (g) after 24 h, and expressed as $\mu\text{mol g}^{-1} \text{FW } 24 \text{ h}^{-1}$.

The sulfur need (S_{need}) was calculated on basis of measurements on relative growth rate (RGR) and the total sulfur content (S_{content}) according to DE KOK & al. 2000:

$$S_{\text{need}} (\mu\text{mol g}^{-1} \text{ plant day}^{-1}) = \text{RGR} (\text{g g}^{-1} \text{ day}^{-1}) \times S_{\text{content}} (\mu\text{mol g}^{-1} \text{ plant})$$

The net sulfate uptake by the roots needed to meet plant sulfur need was calculated according to DE KOK & al. 2000:

$$\text{SO}_4^{2-} \text{ uptake } (\mu\text{mol g}^{-1} \text{ root day}^{-1}) = S_{\text{need}} (\mu\text{mol g}^{-1} \text{ plant day}^{-1}) \times P_{\text{weight}} (\text{g plant}) / R_{\text{weight}} (\text{g roots})$$

where P_{weight} and R_{weight} represent the weight of the plant and roots, respectively.

Results and Discussion

There were considerable differences in growth and in patterns of anion uptake and utilization by two varieties of *B. oleracea* L., curly kale and Chinese cabbage. The RGR and the nitrate uptake of Chinese cabbage were substantially higher than those of curly kale (Table 1). However, the uptake of sulfate by curly kale was approximately 2-fold higher than that of Chinese cabbage. There was also a difference in the utilization of the sulfate taken up between both varieties. The total S content of the shoot and roots of curly kale was respectively 4.2- and 2-fold higher than that of Chinese cabbage (Table 2). Similarly the content of sulfate and thiol compounds of the shoot and roots was higher in curly kale than that in Chinese cabbage (Fig. 1a,b,d,e), whereas that of nitrate was quite similar in both varieties (Fig. 1c,f).

In general, in higher plants the net nitrate uptake appears to be closely linked to the relative growth rate (RODGERS & BARNEIX 1988, TER STEEGE & al. 1999). The RGR of Chinese cabbage was 1.34 times higher and the nitrate uptake was 1.16 times higher than that of curly kale (Table 1). Apparently, the higher nitrate uptake by Chinese cabbage compared to that of curly kale was mainly the result of its higher relative growth rate.

Table 1.

The impact of H₂S exposure on the sulfate and nitrate uptake and growth of curly kale and Chinese cabbage. 12-day-old seedlings were grown on a 25% Hoagland nutrient solution with 0.5 mM sulfate for 1 week and were subsequently exposed to 0 and 0.25 µl l⁻¹ H₂S for another week. The uptake of sulfate and nitrate (µmol g⁻¹ FW [24 h]⁻¹), calculated on a root and plant fresh weight basis was measured over a 24-h period after transfer of the plants to a fresh 25% Hoagland nutrient solution at 0.5 mM sulfate (3 plants per 1 l) on day 7 after start of the exposure. The fresh weight (g) was measured on day 8 after start of the exposure and the RGR (% day⁻¹) was calculated on a fresh weight basis and was determined over the time interval of 8 days during the exposure period using the ln-transformed shoot fresh weight as described by HUNT 1982. Data represent the mean of 6 measurements with 3 plants in each (± SD). Significance of differences upon H₂S exposure: ***P < 0.001; *P < 0.05.

	Curly kale		Chinese cabbage	
	0 µl l ⁻¹ H ₂ S	0.25 µl l ⁻¹ H ₂ S	0 µl l ⁻¹ H ₂ S	0.25 µl l ⁻¹ H ₂ S
Fresh weight:				
Shoot	4.6 ± 0.3	5.1 ± 0.4	4.3 ± 1.1	4.0 ± 0.4
Roots	0.8 ± 0.1	0.8 ± 0.1	0.7 ± 0.2	0.6 ± 0.1
S/R ratio	6.0 ± 0.6	6.1 ± 0.4	6.4 ± 0.5	7.0 ± 0.6
RGR:				
Plant	17.7	17.4	23.8	22.8
Roots	16.4	15.7	23.1	21.3
Anion uptake:				
<i>On a plant FW basis</i>				
Sulfate	6.3 ± 0.9	3.0 ± 1.3***	3.3 ± 0.7	2.2 ± 0.7*
Nitrate	61.7 ± 3.3	55.9 ± 9.5	71.7 ± 6.7	66.1 ± 6.4
<i>On a root FW basis</i>				
Sulfate	40.8 ± 7.8	18.9 ± 7.6***	25.1 ± 5.4	17.6 ± 6.1*
Nitrate	349 ± 60	366 ± 76	532 ± 60	525 ± 59

Table 2.

The impact of H₂S exposure on the total sulfur content of curly kale and Chinese cabbage. Seedlings were transferred to a 25% Hoagland nutrient solution and were exposed to 0 and 0.25 µl l⁻¹ H₂S. The total sulfur content (µmol g⁻¹ FW) of the shoot and roots was determined after an exposure period of 13 days. Data represent the mean of 3 measurements with 3 plants in each (± SD). There were no significant differences upon H₂S exposure.

	Curly kale		Chinese cabbage	
	0 µl l ⁻¹ H ₂ S	0.25 µl l ⁻¹ H ₂ S	0 µl l ⁻¹ H ₂ S	0.25 µl l ⁻¹ H ₂ S
Total sulfur:				
Shoot	49.9 ± 1.8	50.8 ± 1.3	11.9 ± 2.6	12.9 ± 2.2
Roots	26.6 ± 2.9	26.1 ± 3.6	17.3 ± 5.8	11.8 ± 3.8

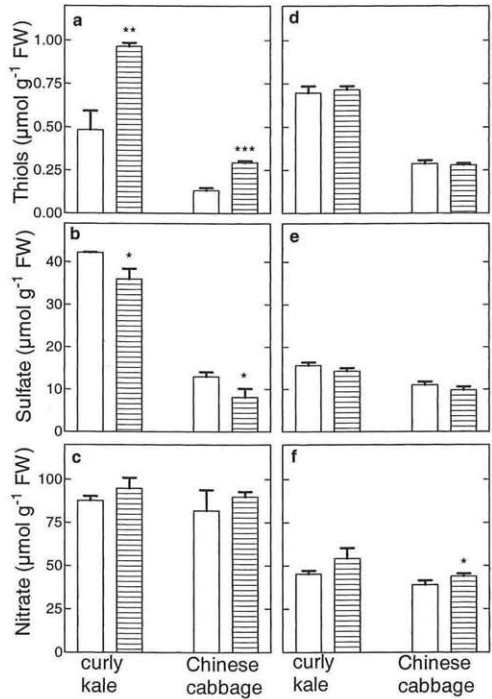


Fig. 1. The impact of H_2S exposure on the thiol, sulfate and nitrate content of curly kale and Chinese cabbage. Plants were exposed to 0 (open bars) and 0.25 $\mu\text{l l}^{-1}$ H_2S (striped bars) for 1 week. The thiol content (a,d), the sulfate content (b,e) and the nitrate content (c,f) of the shoot (a,b,c) and the roots (d,e,f) is shown. Data represent the mean of 6 measurements with 3 plants in each ($\pm$ SD). Significance of differences upon H_2S exposure: *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$.

The sulfur need for growth can be estimated from the RGR and the total sulfur content of the plant and can be expressed as the rate of sulfate uptake and its assimilation needed per gram plant biomass produced with time (DE KOK & al. 2000). By using the data on growth and total sulfur content of the plants shown in Table 1 and 2, curly kale and Chinese cabbage had an estimated sulfur need of 8.3 and 3.0 $\mu\text{mol g}^{-1} \text{ day}^{-1}$, respectively. The calculated net sulfate uptake to meet the sulfur need of curly kale and Chinese cabbage was 56 and 25 $\mu\text{mol g}^{-1} \text{ root day}^{-1}$, respectively. These calculated sulfate uptake values matched well with the actual measurements on the sulfate uptake of the plants shown in Table 1. From the present data it was evident that Chinese cabbage had a lower need for S than curly kale.

Chinese cabbage and curly kale showed a similar response to exposure to 0.25 $\mu\text{l l}^{-1}$ H_2S . The RGR of the plant and the roots was unaffected upon exposure (Table 1). The thiol content of the shoot increased approximately

two-fold, but was unaffected in the roots of both varieties (Fig. 1a,d). The sulfate content was slightly decreased in the shoot and the roots of both curly kale and Chinese cabbage upon H₂S exposure (Fig. 1b,e). In both varieties the nitrate content remained unaffected upon H₂S exposure (Fig. 1c,f). Upon exposure to 0.25 µl l⁻¹ H₂S, in Chinese cabbage the uptake of sulfate was decreased by 30% and in curly kale by 50%, whereas that of nitrate remained unaffected (Table 1). From previous studies it was obvious that this level of H₂S is sufficient to cover the organic sulfur need for growth (DE KOK & al. 1997, 2000, WESTERMAN & al. 2000). Still both varieties took up a substantial amount of sulfate, despite the lower sulfur need for growth of Chinese cabbage. This indicated that the reduction of the sulfate uptake by H₂S fumigation appeared not to be related to the sulfur need of the plant. The proportion of the sulfate taken up by the roots that ended up in the organic sulfur pool appeared to be replaced by the proportion of H₂S taken up from the atmosphere, since the total sulfur pool was hardly affected upon H₂S exposure in both varieties (Table 2). Apparently, there is a good coordination between the metabolism of atmospheric H₂S and pedospheric sulfate in both varieties of *Brassica oleracea*.

The role of glucosinolates as storage of S after the exposure to H₂S was determined in curly kale. Four different indolyl glucosinolates were present in both shoots and roots, although their contents differed with the type of plant tissue (Table 3). In addition, the roots also contained an aromatic glucosinolate which was absent in the shoots. No aliphatic

Table 3.

The impact of H₂S exposure on the glucosinolate content of curly kale. 12-day-old seedlings were grown on a 25% Hoagland nutrient solution with 0.5 mM sulfate for 1 week and were subsequently exposed to 0 and 0.2 µl l⁻¹ H₂S for another week. The glucosinolate content (µmol g⁻¹ DW) was determined of the shoot and roots (n.d., not detectable). Data represent the mean of 3 measurements with 3 shoots or 6 roots in each (± SD). There were no significant differences upon H₂S exposure.

	Shoot		Roots	
	0 µl l ⁻¹ H ₂ S	0.2 µl l ⁻¹ H ₂ S	0 µl l ⁻¹ H ₂ S	0.2 µl l ⁻¹ H ₂ S
Indolyl:				
3-Indolylmethyl	7.8 ± 1.6	11.0 ± 2.4	7.1 ± 0.6	7.1 ± 1.8
1-Methoxy-3-indolylmethyl	2.4 ± 0.6	2.9 ± 0.8	7.7 ± 0.7	1.2 ± 1.6
4-Methoxy-3-indolylmethyl	0.7 ± 0.2	0.6 ± 0.2	10.4 ± 0.7	10.8 ± 2.8
4-Hydroxy-3-indolylmethyl	1.2 ± 0.3	1.4 ± 0.5	11.7 ± 1.2	10.8 ± 2.8
Aromatic:				
2-Phenylethyl	n.d.	n.d.	10.6 ± 1.5	10.8 ± 3.6
Total:	12.1 ± 2.2	15.8 ± 3.6	37.0 ± 3.0	35.8 ± 8.8

glucosinolates were detected. The fraction of total sulfur that was present as glucosinolates ranged from approximately 3% in the shoot to 20% in the roots (Table 3; based on a dry matter content of 10% in the shoot and of 7% in the roots) (DE KOK & al. 1997). Glucosinolates are thought to play a role as sink for a surplus of sulfur (SCHNUG 1990). However, the influence of sulfur supply on the glucosinolate content was strongly dependent on the nitrogen supply (BLAKE-KALFF & al. 1998, ZHAO & al. 1994). When curly kale was grown with sufficient nitrate and sulfate in the nutrient solution and simultaneously exposed to $0.2 \mu\text{l l}^{-1}$ H_2S for 1 week, the glucosinolate content remained unaffected in both shoot and roots (Table 3).

Apparently, in the presence of an atmospheric H_2S level sufficient to cover the organic sulfur need for growth, the glucosinolates appeared to play a limited role as a sink for a surplus of sulfur in curly kale. This observation was in agreement with that found for *Arabidopsis thaliana* exposed to SO_2 (VAN DER KOOIJ & al. 1997). The partitioning of sulfur in the organic and inorganic fraction of the shoot and roots upon exposure to a H_2S level that was sufficient to meet the organic sulfur need of the plant needs to be further investigated.

Both in curly kale and in Chinese cabbage the fraction of the total sulfur content that was present in the inorganic form as sulfate was substantial and remained unaffected upon H_2S exposure in both varieties (Fig. 1). In sulfate-accumulating species the sulfate content of the vacuole can increase from 2–14% to 90% of total sulfur content. In the gypsophilous plant *Moricandia arvensis* (*Brassicaceae*) even 93% of total plant sulfur was present as sulfate (ERNST 1990). Whether the partial down-regulation of the sulfate uptake was related to a strategy of members of the *Brassicaceae* to take up a surplus of sulfate to retain a high inorganic sulfur pool, was investigated by transferring curly kale to various sulfate levels in the root environment.

A transfer of the plants to a nutrient solution containing 10 mM instead of 0.5 mM (the sulfate concentration in a 25% Hoagland nutrient solution) hardly affected the sulfate content of the shoot and roots, reflecting a carefully regulated sulfate uptake (Fig. 2). At 24 h after transfer of the plants to a nutrient solution containing 10 mM sulfate the sulfate content was even slightly lower in the shoots than that at 0.5 mM, but its content remained unaffected in the roots. After transfer of sulfur-deprived plants (grown at 0 mM sulfate for 1 week) to various levels of sulfate in the nutrient solution, the sulfate content of the shoot was approximately 1.5-fold higher than that of the plants which were grown before transfer at an ample supply of sulfate (0.5 mM, Fig. 3). This might be related to the derepression of the sulfate uptake system occurring in plants grown under sulfur-deprived conditions. The rate of sulfate uptake by the roots normally responds to changes in the sulfur nutritional status and is dere-

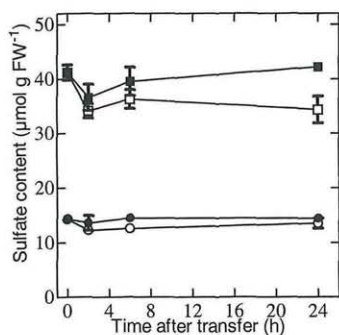


Fig. 2. The sulfate content of curly kale as affected by the sulfate concentration in the nutrient solution. 12 day old seedlings of curly kale were transferred into a 25% Hoagland nutrient solution at 0.5 mM sulfate for 2 weeks. The sulfate content was measured after 0, 2, 6 and 24 h in the shoot (squares) and roots (circles) after transfer of the plants to 0.5 (closed symbols) and 10 mM sulfate (open symbols). Data represent the mean of 3 measurements with 3 plants in each ($\pm$ SD).

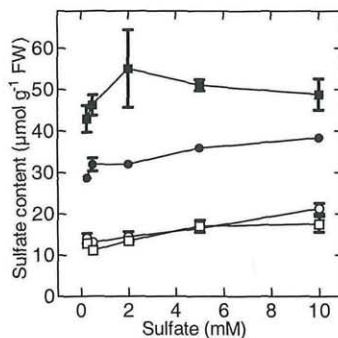


Fig. 3. The sulfate content of curly kale plants with a different sulfur nutritional status as affected by the sulfate concentration in the nutrient solution. 12-old-seedlings were grown on 0 (squares) or 0.5 mM sulfate (circles) in the root environment, and after 1 week plants were transferred to a 25% Hoagland nutrient solution containing 0.25, 0.5, 2, 5 and 10 mM sulfate. The sulfate content of the plants was measured in both shoot (closed symbols) and roots (open symbols) after one week of exposure. Data represent the mean of 3 measurements with 3 plants in each ($\pm$ SD).

pressed under sulfur-deprived conditions (HAWKESFORD & SMITH 1997, HAWKESFORD 2000). The sulfate content of the shoot of the plants that were sulfur-deprived before transfer to a nutrient solution containing sulfate levels up to 10 mM, remained high since sulfate stored in the mesophyll vacuoles is considered to be relatively immobile (CLARKSON & al. 1993). After transfer of sulfur-deprived plants and plants supplied with an ample amount of 0.5 mM of sulfate to a nutrient solution with levels up to 10 mM sulfate, the internal sulfate pool of curly kale was increased by a maximum of 30% in the shoot and roots after growth on a nutrient solution with 5 and 10 mM of sulfate for 1 week (Fig. 3). This indicated that the sulfate content in both the roots and shoots was kept within certain limits and was well regulated in curly kale. The partial repression of the sulfate uptake occurring upon H_2S exposure appears not to be related to a strategy of *Brassicaceae* to take up a surplus amount of sulfate.

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Recensio

[BACHLER J.] Bayerischer Forstverein [Ed.] 1998. *Sträucher in Wald und Flur*. Bedeutung für Ökologie und Forstwirtschaft. Natürliche Vorkommen in Wald- und Feldgehölzen. Einzeldarstellungen der Straucharten. – Gr. 8°, 569 Seiten, zahlr. Abb., größtenteils Farbfotos; geb. – ecomed Verlagsges., D-86899 Landsberg. – DM 128,–. – ISBN 3-609-69880-2.

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