SO2
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Chapter 5

Impact of sulfate nutrition on the utilization of atmospheric SO$_2$ as sulfur source for Chinese cabbage

Abstract

The ability of Chinese cabbage (*Brassica pekinensis*) to utilize SO$_2$ as sulfur source in relation to the sulfur status of the plant was investigated by subjecting seedlings to various treatments of sulfate deprivation and (re)-supply. If seedlings of Chinese cabbage were transferred to a sulfate-deprived nutrient solution directly after germination, plants became rapidly sulfur deficient, and plant development was impaired. Plant biomass production was decreased, dry matter content of the shoot increased and the shoot to root biomass ratio decreased. Sulfate deprivation resulted in a substantial decrease in the total S, sulfate, organic S and water-soluble non-protein thiol contents and in an increase in amino acid content of both shoot and root. The sulfate uptake capacity of the root was strongly increased whereas the nitrate uptake was decreased. Upon re-supply of sulfate the onset of sulfur deficiency symptoms was prevented and growth was restored, whereas the uptake of both sulfate and nitrate were quite similar to those of the sulfate-sufficient plants. A 6-day exposure to 0.12 $\mu$ l l$^{-1}$ SO$_2$ of sulfate-sufficient plants did not affect plant biomass production, dry matter content, shoot to root ratio, leaf development, the sulfur and nitrogen metabolite contents of shoot and root, or sulfate and nitrate uptake by the root. Exposure of sulfate-deprived plants to SO$_2$ resulted in enhanced total S, organic S and water-soluble non-protein thiol contents of the shoot. The contribution of SO$_2$ as sulfur source for these plants was rather limited. Apparently only the leaves, which were already present at the start of the exposure, benefited from the utilization of atmospheric SO$_2$ as sulfur source; exposure to SO$_2$ did not enhance leaf formation and sulfate uptake capacity was increased even more. If seedlings were first grown on a sulfate-containing nutrient solution for 7 days and subsequently transferred to a sulfate-deprived nutrient solution for 6 days and simultaneously exposed to SO$_2$, the plants benefited optimally from the foliarly absorbed sulfur. The development of sulfur deficiency symptoms was prevented and the number of formed leaves and plant biomass production was quite similar to that of sulfate-sufficient plants, whereas the root biomass production upon SO$_2$ exposure was even higher than that of sulfate-sufficient plants. However, the sulfate uptake capacity was still enhanced. This demonstrated that there is a poor interaction between the metabolism of SO$_2$ by the shoot and uptake and metabolism of sulfate taken up by the root. Evidently there was no strict and direct shoot to root signaling in tuning the sulfate uptake by the root and its transport to the shoot to the need for growth, via down-regulation of the sulfate uptake capacity and normalizing shoot to root biomass partitioning.

Introduction

Throughout the world sulfur deficiency of soils has become a major problem in agricultural crops due to an imbalance of sulfur in relation to N, P and K in most
commonly used fertilizers (Ceccotti and Messick, 1997; Schnug and Haneklaus, 1998). For instance, a recent survey in China revealed that one-fourth of a total of more than 18,000 soil samples from all over China appeared to be S deficient (Yang et al., 2005). Chinese cabbage (Brassica pekinensis) is a common and widely grown vegetable crop in China, with a high yield, a relatively short growing period and a high sulfur requirement for growth. In recent years around 26,000 ha y^−1 was used for cultivation of Chinese cabbage in the Beijing and Tianjin areas. It appeared that 30% of these soils were S deficient (Yang et al., 2005; Zhou et al., 2005). Pot experiments in the Beijing area showed that shoot biomass production of Chinese cabbage was increased by 50% when sulfur fertilization was optimized by applying 30 kg S ha^−1 (Yang et al., 2005).

In addition to sulfur deficiency, crops in China are at risk from air pollution, since vegetable producing areas are located around densely populated areas. High SO2 pollutant levels are the consequence of the rapid increase in energy use for economic growth and industrialization and an insufficient emission control (Emberson et al., 2001; Yang et al., 2002; Wang et al., 2004). For instance, in 2002, 22.4% of the cities in China had a higher annual average SO2 level than 0.024 µl l^−1. In these areas the level of sulfur fertilization might have to be adjusted to the level of local atmospheric sulfur deposition (Yang et al., 2005), since foliarly absorbed sulfur gases, viz. SO2 and H2S, contribute to the plants’ sulfur nutrition, despite their potential phytotoxicity. They may even replace sulfate taken up by the root as sulfur source for growth (De Kok, 1990; De Kok et al., 1997, 1998, 2002a; Stuiver et al., 1997; De Kok and Tausz, 2001; Durenkamp and De Kok, 2002, 2004; Haneklaus et al., 2003; Yang et al., 2003). Exposure of plants to atmospheric sulfur gases may reduce the uptake and transport of sulfate taken up by the root and its reduction and assimilation in the shoot (Herschbach et al., 1995a,b; Tausz et al., 1996, 2003; De Kok et al., 1998; Westerman et al., 2000a,b, 2001a,b).

The shoot of seedlings of a Dutch Chinese cabbage (Brassica pekinensis, cv Kasumi F1) formed a sink for atmospheric SO2. The foliarly absorbed SO2 was used as S source for growth, and exposure to levels of SO2 up to 0.18 µl l^−1 resulted in an increase in SO4^2− and total S contents in the shoot (Yang et al., 2003). SO2 was even beneficial when sulfate supply to the root was limited and an atmospheric level as low as 0.06 µl l^−1 appeared to be sufficient to cover the plants’ sulfur requirement for growth (Yang et al., 2003). Similar to observations on H2S with other species (De Kok et al., 1997, 2000; Buchner et al., 2004), the decrease in shoot to root ratio of Chinese cabbage upon sulfate deprivation was not rapidly alleviated when SO2 was used as sulfur source for growth (Yang et al., 2003).

The aim of the present paper was to investigate the ability of a local cultivar of Chinese cabbage (Brassica pekinensis cv. Beijing 3), which has a higher sulfur requirement for growth than the Dutch cultivar Kasumi F1 (Yang et al., 2005), to utilize SO2 as sulfur source for growth in relation to the sulfur status of the plant. The sulfur status of the plant was manipulated by subjecting seedlings to various treatments of sulfate deprivation at two developmental stages, directly after germination and one week after growth on sulfate, in combination with subsequent sulfate (re)-supply and exposure to SO2. The interaction between atmospheric SO2 utilization and the uptake and
metabolism of pedospheric sulfate in Chinese cabbage is discussed in relation to plant
development and root to shoot partitioning.

Materials and methods

Plant material and growth conditions

Seeds of Chinese cabbage (Brassica pekinensis, cv. Beijing 3, BVRC, China) were
germinated in vermiculite in a climate-controlled room for 10 days. Day and night
temperatures were 19 and 16 °C, respectively, with a relative humidity of 60-70%. The
photoperiod was 14 h at a photon fluence rate of 400 ± 50 µmol m⁻² s⁻¹ (PAR 400-700
nm). 10-day-old seedlings were transferred to 30-l tanks (60 plants per tank) containing a
25% Hoagland nutrient solution with 0 (sulfate-deprived) or 0.5 mM sulfate (sulfate-
sufficient) for one week in the climate-controlled room. At 0 mM sulfate, MgCl₂
replaced MgSO₄, and their respective Cl⁻ salts replaced all micronutrient SO₄²⁻ salts.
Subsequently the sulfate-deprived and sulfate-sufficient plants were transferred to 12-l
stainless steel containers (30 plants per tank) filled with freshly prepared 25% Hoagland
nutrient solution containing 0 or 0.5 mM sulfate (see above), and simultaneously
exposed to SO₂.

SO₂ exposure

Plants were exposed to SO₂ in cylindrical stainless steel cabinets (65 cm diameter, 185 l
volume) with polycarbonate tops. Day and night temperatures were 21 and 18 ± 1°C
respectively, relative humidity was 40-50% and the photoperiod was 14 h at a photon
fluence rate of 325 ± 25 µmol m⁻² s⁻¹ (PAR 400-700 nm) at plant height, with a Philips
HPL(R)N (400W) as light source. Adjusting the cabinet wall temperature controlled the
air temperature of the cabinets, the air exchange was 40 l min⁻¹ and a ventilator stirred
the air inside the cabinets continuously. Pressurized SO₂ diluted with N₂ (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). SO₂ level in the cabinets was
measured by a SO₂ analyzer (model 9850, Lear Siegler Measurement Controls
Corporation, Englewood, USA).

Analyses of plant growth, metabolite contents and the uptake of sulfate and nitrate

Plants were harvested, shoot and root separated, weighted and analyzed (water-soluble
non-protein thiols) or freeze-dried (Heto LyolaB 300 freeze dryer (Heto-Holten A/S,
Allerød, Denmark). Fresh shoot and root biomass production was calculated by
subtracting pre-exposure weight from that after exposure. RGR of plant (% day⁻¹) was
calculated on a fresh weight basis and determined from the exposure time interval using
the ln-transformed plant fresh weight as described by Hunt (1982).

Powdered freeze-dried material was used for total S, total N, sulfate, nitrate and amino
acids assays. Total S was determined with the barium sulfate precipitation method after
Durenkamp and De Kok (2002), and total N with the Kjeldahl method according to Barneix et al. (1988). Sulfate and nitrate were determined refractometrically after HPLC separation (Tausz et al., 1996; Durenkamp and De Kok, 2002). The organic S content was derived by subtracting the sulfate content from the total S content. Free amino acids were measured by colorimetric determination of the ninhydrin-reactive groups (Stuiver et al., 1997). Water-soluble non-protein thiols were extracted from fresh material according to Stuiver et al. (1992) and the DTNB-reactive compounds were measured as described by De Kok et al. (1988).

For measurement of the sulfate uptake capacity and nitrate uptake rate, 3 or 4 sets of plants (3 plants per set) per treatment were transferred to beakers with 1 l 25% Hoagland solution (containing 0.5 mM sulfate). After 24 h, the nutrient solution was adjusted to its initial volume by weighing. Aliquots were taken from the nutrient solution and the sulfate and nitrate contents were determined by HPLC as described above. Sulfate and nitrate uptake was calculated from the differences in ion content (µmol) of the nutrient solution at the start and after 24 h, and expressed on a fresh weight basis (µmol g⁻¹ FW 24 h⁻¹).

Statistical analysis was performed with an unpaired Student’s t-test.

Results

Impact of sulfate deprivation on growth, sulfur and nitrogen metabolites

Seedlings of Chinese cabbage, transferred to sulfate-deprived nutrient solution directly after germination, became rapidly sulfur deficient. Shoot biomass production was strongly reduced (by 40% and 82% upon 7 and 13 days of exposure, respectively; Table 1, Fig. 1). RGR of the plant and shoot biomass production were reduced (Fig. 1). Shoot development was affected as well, since less new leaves were formed and leaves became slightly yellow due to a loss of pigments (Fig. 2). Shoot biomass production was more rapidly affected than that of the root upon sulfate deprivation, as reflected by a substantial decrease in shoot to root ratio, which decreased from 5.8 for sulfate-sufficient to 3.2 for sulfate-deprived plants upon a 7-day exposure (Table 1). Sulfate deprivation resulted in increased dry matter content of the shoot but did not affect that of the root (Table 1; Fig. 1). Furthermore, sulfate deprivation resulted in a substantial decrease in the total S, sulfate, organic S and water-soluble non-protein thiol contents of both shoot and root (Table 1, Fig. 3). Prolonged sulfate deprivation (-S-S) resulted in a strong decrease in nitrate content of the shoot, whereas that of the root was slightly increased. The amino acid content was strongly increased in both shoot and root upon prolonged sulfate deprivation (Fig. 3).

If seedlings after germination were first grown on a sulfate-containing nutrient solution for 7 days and subsequently transferred to a sulfate-deprived nutrient solution for 6 days (+S-S), the sulfur deficiency symptoms started to appear but were less pronounced than in 13-day sulfate-deprived plants (Fig. 1, 2 and 3). The shoot biomass production was reduced by 32% (Fig. 1), though the number of developed leaves was
similar to that of sulfate-sufficient leaves (Fig. 2). The plant’s RGR was decreased but root biomass production was not yet affected, resulting in a decrease in shoot to root ratio upon sulfate deprivation (Fig. 1). Changes in all metabolites in shoot and root were quite similar to those observed after prolonged sulfate deprivation (13 days), but to a lesser extent (Fig. 3).

Table 1. Effect of sulfate deprivation on growth and sulfur metabolites contents of Chinese cabbage. 10-day-old seedlings were grown on a 25% Hoagland nutrient solution with and without sulfate for 7 days. The data of biomass production and dry matter content represent the mean of 30 measurements with 3 plants in each (± SD). The shoot /root ratio of 7-day sulfate-deprived and sulfate-sufficient plants was 3.2 ± 0.4 and 5.8 ± 0.9, respectively. Total S and sulfate content represent the mean of 6 measurements with 15 shoots in each and 3 measurements with 30 roots in each (± SD). The total water-soluble non-protein thiol content represents the mean of 5 measurements with 3 plants in each (± SD). Different letters indicate significant differences at p ≤ 0.01 between different treatments.

<table>
<thead>
<tr>
<th></th>
<th>Shoot</th>
<th>Root</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>-Sulfate</td>
<td>+Sulfate</td>
</tr>
<tr>
<td>Biomass production (g)</td>
<td>0.32 ± 0.06a</td>
<td>0.67 ± 0.13b</td>
</tr>
<tr>
<td>Dry matter content (%)</td>
<td>13.4 ± 0.2b</td>
<td>10.3 ± 0.5a</td>
</tr>
<tr>
<td>Total S (µmol g⁻¹ DW)</td>
<td>50 ± 3a</td>
<td>367 ± 8b</td>
</tr>
<tr>
<td>Sulfate (µmol g⁻¹ DW)</td>
<td>9 ± 1a</td>
<td>259 ± 25b</td>
</tr>
<tr>
<td>Organic S (µmol g⁻¹ DW)</td>
<td>42 ± 1a</td>
<td>107 ± 16b</td>
</tr>
<tr>
<td>Thiols (µmol g⁻¹ FW)</td>
<td>0.06 ± 0.01a</td>
<td>0.56 ± 0.04b</td>
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Impact of sulfate re-supply on growth, sulfur and nitrogen metabolites

If 7-day sulfate-deprived plants were transferred to sulfate-containing nutrient solution for 6 days (-S+S), plant biomass production, dry matter content, shoot to root ratio and leaf formation were quite similar to those of plants grown at sulfate-sufficient conditions for 13 days (Fig. 1; Fig. 2). The 7-days sulfate-deprived plants were characterized by low contents of total S, sulfate, organic S and water-soluble non-protein water-soluble non-protein thiols in both shoot and root (Table 1). However, upon 6-days sulfate re-supply (-S+S), the shoot contained a substantially higher total sulfur content than plants grown at sulfate-sufficient conditions for 13 days (Fig. 3). This was primary due to the strongly increased shoot sulfate content. The contents of the other metabolites in sulfate re-supplied plants were similar to those of sulfate-sufficient plants (Fig. 3). Clearly, upon re-supply of sulfate the onset of sulfur deficiency symptoms was prevented and growth was restored.
Fig. 1. Effect of sulfate deprivation, sulfate re-supply and SO₂ exposure on growth of Chinese cabbage. 10-day-old seedlings were grown on a 25% Hoagland nutrient solution with and without sulfate for 7 days and subsequently transferred to fresh nutrient solution with and without sulfate and exposed to 0 (white bars) and 0.12 µl l⁻¹ (grey bars) SO₂ for 6 days. +S+S, plants were grown on a nutrient solution with sulfate for 13 days; -S-S, plants were grown without sulfate for 13 days; +S-S, plants were grown with sulfate for 7 days and then without sulfate for 6 days; -S+S, plants were grown without sulfate for 7 days and then with sulfate for 6 days. Data on biomass production of shoot and root (g) represent the mean of 2 experiments with 3 measurements and 6 plants in each (± SD). RGR of plant (% day⁻¹) was calculated on a fresh weight basis and was determined over the 6-day time exposure. Different letters indicate significant differences at p ≤ 0.01 between different treatments.
Impact of SO₂ exposure on growth, sulfur and nitrogen metabolites as affected by sulfate nutrition

Exposure of sulfate-sufficient plants (+S+S) or plants which were sulfate deprived for 7 days, subsequently transferred to sulfate-containing nutrient solution for 6 days (-S+S), to 0.12 µl l⁻¹ SO₂ for 6 days neither affected plant biomass production, dry matter content, shoot to root ratio, leaf development nor sulfur and nitrogen metabolites content of shoot and root (Fig. 1, 2 and 3). Upon the latter treatment (-S+S), SO₂ exposure had a minor effect on nitrate content. In the shoot it was slightly reduced and in the root slightly increased (Fig. 3). Evidently, a short-term 6-day exposure of sulfate-sufficient plants to 0.12 µl l⁻¹ SO₂ affected neither plant growth nor sulfur and nitrogen metabolism substantially.

Exposure of prolonged sulfate-deprived plants (-S-S) to SO₂ resulted in a slightly increased shoot biomass production and RGR of the plant, whereas root growth and shoot to root ratio were hardly affected (Fig. 1). SO₂ exposure did not enhance leaf formation, since the number of leaves of exposed plants remained less than that of sulfate-sufficient plants (Fig. 2). SO₂ exposure did affect dry matter content of the shoot, which was decreased (Fig. 1). The amino acid content of the shoot, which was strongly enhanced upon sulfate deprivation, was substantially decreased by SO₂ (Fig. 3). Evidently, the contribution of SO₂ as sulfur source was rather limited for plants subjected
to prolonged sulfate deprivation. Apparently only the leaves, which were already present at the start of the exposure to SO\textsubscript{2} benefited from the atmospheric sulfur source.

If seedlings were first grown on a sulfate-containing nutrient solution for 7 days and subsequently transferred to a sulfate-deprived nutrient solution for 6 days (+S-S) and simultaneously exposed to SO\textsubscript{2}, then both shoot and root biomass production were enhanced (Fig. 1), whereas the number of formed leaves was similar to that of sulfate-sufficient plants (+S+S). The dry matter content of the shoot decreased (Fig. 1) and the amino acid content of the shoot, which was enhanced upon sulfate-deprivation, was decreased upon SO\textsubscript{2} exposure (Fig. 3). Upon SO\textsubscript{2} exposure the root biomass production was even higher than that of sulfate-sufficient plants (+S+S). The shoot to root ratio was hardly affected by SO\textsubscript{2} and was still substantially lower than that of plants at sulfate-sufficient conditions. Apparently, the foliarly absorbed SO\textsubscript{2} was able to replace sulfate taken up by the root as sulfur source for the synthesis of essential sulfur compounds necessary for growth. Upon SO\textsubscript{2} exposure the shoot of these plants (+S-S) contained a higher total sulfur content, due to an enhanced sulfate content, and an enhanced water-soluble non-protein thiol content (Fig. 3).

**Effect of sulfate deprivation, sulfate re-supply and SO\textsubscript{2} on sulfate and nitrate uptake**

Sulfate deprivation of Chinese cabbage (-S-S, +S-S) resulted in an increased sulfate uptake capacity expressed on a root basis (up to 2-fold). The increase was even more pronounced when expressed on a plant basis (up to 3-fold; Fig. 4). The latter was due to an increase in the actual sulfate uptake capacity of the root itself, in combination with a change in shoot to root ratio in favor of that of the root, which explains the more pronounced increase in sulfate uptake when expressed on a plant basis. There was no direct relation between the uptake of sulfate and nitrate, since the latter was depressed upon sulfate-deprivation (Fig. 4). The sulfate uptake capacity of plants, which were sulfate-deprived for 7 days and subsequently transferred to sulfate-containing nutrient solution for 6 days (-S+S), was still slightly higher and the nitrate uptake was still slightly lower than that of sulfate-sufficient plants (+S+S; Fig. 4).

Exposure to 0.12 µl l\textsuperscript{-1} SO\textsubscript{2} of sulfate-sufficient plants (+S+S) or plants which were sulfate-deprived for 7 days and subsequently transferred to sulfate-containing nutrient solution for 6 days (-S+S), did neither substantially affect the sulfate uptake capacity nor the nitrate uptake by the root (Fig. 4). If plants were sulfate deprived for 13 days (-S-S) and simultaneously exposed to 0.12 µl l\textsuperscript{-1} SO\textsubscript{2} for the last 6 days, it resulted in a further

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Fig. 3. Effect of sulfate deprivation, sulfate re-supply and SO\textsubscript{2} exposure on sulfur and nitrogen metabolites contents of Chinese cabbage. For details see legend Fig. 1. Data on the total S, sulfate, nitrate and amino acids represent the mean of 2 experiments 3 measurements with 3 to 6 plants in each (± SD). Data on total water-soluble non-protein thiol content represent the mean of 3 measurements with 3 plants in each (± SD). Different letters indicate significant differences at p ≤ 0.01 between different treatments. Undoubtedly, part of the foliarly absorbed SO\textsubscript{2} was metabolized, as illustrated by the enhanced total S, organic S and water-soluble non-protein thiol contents of the shoot of the sulfate-deprived plants upon SO\textsubscript{2} exposure.
increment of the sulfate uptake capacity and in an increase in nitrate uptake on both root and plant basis. This might be explained by the beneficial effect of SO₂, which is used as sulfur source for growth to a low extent (see above), resulting in a slight recovery of severe sulfur deficiency upon prolonged sulfate deprivation. It likely resulted in a healthier root system and sulfate and nitrate uptake rates comparable to those of plants moderately suffering from sulfur deficiency (+S-S). However, exposure of these plants (+S-S) to SO₂ did not further affect the sulfate uptake, whereas the nitrate uptake was increased (Fig. 4).

Discussion

Plants generally utilize sulfate as primary sulfur source for growth. Sulfate is taken up with high affinity by the root, subsequently loaded into the xylem and transported to the shoot by the transpiration stream, where it is reduced in the chloroplast prior to its metabolism into organic sulfur compounds (Hell, 1997; Leustek and Saito, 1999; De Kok et al., 2002b, 2005). The remaining sulfate in plant tissue appears to be predominantly present in the vacuole. Under normal conditions the uptake and assimilation of sulfur is in tune with the actual plant’s sulfur requirement for growth, and the uptake of sulfate by the root and its transport to the shoot appear to be major sites of regulation (Hawkesford and Wray, 2000; De Kok et al., 2002b, 2005). The root and shoot of Brassica contain distinct sulfate transporter proteins, which mediate the uptake, transport and subcellular distribution of sulfate. According to their cellular and subcellular expression, and possible functioning, the sulfate transporter gene family has been classified in different groups (Buchner et al., 2004). Generally sulfate deprivation of plants induces multiple responses that increase the efficiency of sulfate uptake on a plant basis. Initially there is a rapid increase in expression of genes encoding sulfate transporters in the roots and in the rest of the plant, which is accompanied by an enhanced sulfate uptake capacity of the root (Hawkesford, 2000, 2003; Hawkesford and Wray, 2000; Buchner et al., 2004). Secondly, upon more prolonged sulfate deprivation there is a change in shoot to root biomass partitioning in favor of that of root (Stuiver et al., 1997; Westerman et al. 2000a; Yang et al., 2003; Buchner et al., 2004).

Similar to other observations upon sulfate deprivation there were changes in sulfur and nitrogen metabolite contents of Chinese cabbage, which are characteristic for the onset of sulfur deficiency, e.g. a strongly decreased sulfate, thiol and organic sulfur content and an increased amino acid content, in general more pronounced in the shoot than in the root (Stuiver et al., 1997; Westerman et al., 2000a; Yang et al., 2003, Buchner et al., 2004). In addition, sulfate-deprived plants had a higher sulfate uptake capacity, whereas the nitrate uptake was substantially decreased. The latter could be related to the decrease in plant growth upon sulfate deprivation, since the net nitrate uptake is closely linked to the growth rate (Muller et al., 1995, Ter Steege et al., 1999; Westerman et al., 2000a). Similar to previous observations, root growth of Chinese cabbage was less affected upon sulfate deprivation that of the shoot, resulting in a decrease in shoot to root
ratio (Stuiver et al., 1997; Westerman et al., 2000a; Yang et al., 2003; Buchner et al., 2004)

![Graphs showing sulfate and nitrate uptake](image)

Fig. 4. Effect of sulfate deprivation, sulfate re-supply and SO₂ exposure on sulfate and nitrate uptake by Chinese cabbage. For details see legend Fig. 1. After the 6 day-fumigation exposure, plants were transferred to a fresh 25% Hoagland nutrient solution containing 0.5 mM SO₄²⁻ exposed to 0 and 0.12 µl l⁻¹ SO₂. The uptake of sulfate and nitrate calculated on plant and root fresh weight basis was measured over a 24-h period. Data represent the mean of 2 experiments with 4 measurements on 3 plants in each (± SD). Different letters indicate significant differences at \( p \leq 0.01 \) between different treatments.

Evidently, Chinese cabbage was able to transfer from sulfate taken up by the root to SO₂ absorbed by the shoot as sulfur source for growth under sulfate deprivation (Yang et al., 2003). However, from the present results it is obvious that the ability of Chinese cabbage to utilize SO₂ as sulfur source strongly depends on the sulfur status and/or developmental stage of the plant. For example, prolonged sulfate-deprived plants benefited only little from SO₂ exposure, even though previous experiments with Chinese cabbage showed that atmospheric levels as low as 0.06 µl l⁻¹ SO₂ are in principle sufficient to cover the sulfur requirement for growth (Yang et al., 2003). From the changes in the sulfur and nitrogen metabolites upon exposure to SO₂, it was clear that the absorbed SO₂ was metabolized and sulfur-deficiency symptoms in sulfate-deprived plants were partly alleviated, viz. a slightly restored shoot growth, an increase in organic sulfur and thiol content and a decrease in amino acid content of the shoot. However, SO₂ exposure of the sulfate-deprived plants did not support development of new leaves. Solely leaves, which had been formed prior to the exposure benefited from the absorbed SO₂. Apparently there was hardly any redistribution of sulfur from the older to the
developing new leaves. The latter completely relied on the supply of sulfur taken up as sulfate by the roots, since upon re-supply of sulfate to sulfate-deprived plants, leaf development of Chinese cabbage in presence and absence of SO$_2$, was quite similar to that of sulfur-sufficient plants. Moreover, Chinese cabbage, which was first grown under sulfate-sufficient conditions for 7 days and was then sulfate deprived for 6 days, fully benefited from the absorbed sulfur. Upon SO$_2$ exposure, shoot growth and development were quite similar to those of sulfate-sufficient plants and root biomass production was even substantially higher than that of sulfur-sufficient plants. Apparently, the level of sulfate present in the plant prior to the deprivation was sufficient to fully support the development of new leaves to such extent that all leaves were able to benefit optimally from the absorbed atmospheric sulfur as sulfur source. The data are in agreement with observations of Anderson and co-workers (Anderson and Fitzgerald, 2003) that the distribution of sulfate taken up by the roots and the redistribution of sulfur between leaves strongly depends on the developmental stage of plant and the degree of leaf expansion.

In curly kale (Brassica oleracea L.) there was a direct interaction between foliar H$_2$S deposition and the uptake and metabolism of pedospheric sulfate. The total sulfur content and the total N/S ratio of both shoot and root were hardly affected upon prolonged H$_2$S exposure and atmospheric levels, which exceeded the sulfur requirement of this species (De Kok et al., 2002a; Westerman et al., 2000a,b, 2001a). H$_2$S exposure resulted in a negative feedback regulation of the uptake and assimilation of pedospheric sulfate and it induced a reduction of sulfate uptake by the roots (Westerman et al. 2000a,b, 2001a), and a substantial decrease in the activity of APS reductase, the rate-limiting enzyme in the sulfate reduction pathway in shoot (Westerman et al., 2001b). Peculiarly, the strong increase in the sulfate uptake capacity of root and the decrease in shoot to root biomass ratio of curly kale upon sulfate deprivation were hardly affected by H$_2$S exposure (Westerman et al., 2000a; Buchner et al., 2004).

Despite the ability of Chinese cabbage to utilize absorbed SO$_2$ as sulfur source, SO$_2$ did not affect the sulfate uptake of sulfate-sufficient plants. Neither the sulfate uptake of sulfate-sufficient nor the enhanced sulfate uptake capacity upon sulfate deprivation was decreased upon SO$_2$ exposure. Upon prolonged sulfate deprivation, the sulfate uptake capacity was even more enhanced. In addition, the shoot to root partitioning in favor of roots was unaffected upon SO$_2$ exposure. Even after a 6-day sulfate re-supply of previously sulfate-deprived plants, the sulfate uptake capacity was still higher and the shoot to root ratio lower than those of sulfate-sufficient plants, both in absence and presence of SO$_2$. Apparently, the increased sulfate uptake capacity on a whole plant basis is the cause of the extremely high sulfate content of their shoot upon the sulfate re-supply. The present results with Chinese cabbage exposed to SO$_2$ support the conclusions based on previous observations with curly kale exposed to H$_2$S, that there is apparently no strict and direct shoot to root signaling in the tuning of the sulfate uptake by the root and its transport to the shoot in relation to the need for growth via down-regulation of the sulfate uptake capacity, and normalizing the shoot to root biomass partitioning (Buchner et al., 2004).
References


