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Chapter 7

General Discussion

The impact of SO$_2$ on crops is ambiguous and complicates sulfur fertilization recommendations

Since the 1950's, the impact of SO$_2$ on plant metabolism has been studied in detail, however, the basis for differences in susceptibility between plant species and cultivars is still largely obscure (De Kok, 1990; De Kok and Tausz, 2001). Despite several studies, it remains unclear to what extent the observed changes in metabolism upon SO$_2$ exposure are the primary cause or the consequence of an already disturbed physiology or acute (pre-injury) effects. Furthermore, Thomas and co-workers established already more than 60 years ago that despite its potential phytotoxicity SO$_2$, upon its foliar absorption, might be metabolized (see ref. Thomas, 1951) and used as sulfur source for growth (Chapter 3, 4 and 5; De Kok, 1990; De Kok et al., 1998; De Kok and Tausz, 2001). The paradoxical effects of SO$_2$ on plants complicate the establishment of clear cause-effect relationships.

It has become evident that foliar deposition of atmospheric sulfur gases substantially contributes to sulfur nutrition of agro-ecosystems, since modern fertilizers are low in sulfur and supplemental sulfur fertilization is needed to prevent economic losses (Chapter 5 and 6; Schnug and Evans, 1992; Ceccotti and Messick, 1997; Zhao et al., 1999; Thomas et al., 2003). Also in China an imbalance of sulfur in relation to nitrogen, phosphorus and potassium in the fertilizers has resulted in a widespread sulfur deficiency of soils (Chapter 5 and 6). Even in the Beijing and Tianjin areas in China, which are highly industrialized, about 30% of the farmland appeared to be sulfur deficient. In these regions, Chinese cabbage is produced under intensive farming practice with a general use of low S or even S-free fertilizers, and additional sulfur fertilization was needed for optimal production (Chapter 6).

Most vegetable producing areas are located around the big cities, where the air pollutant levels are relatively high (Chapter 2). For instance, in the largest industrial city of southwest China, Chongqing, the annual average SO$_2$ level during 1995 was 0.13 µl l$^{-1}$, whereas the maximum daily average SO$_2$ level exceeded 0.36 µl l$^{-1}$. In 1996 the average level of SO$_2$ in the cities in China ranged from 0.001 to 0.16 µl l$^{-1}$ and in 2002, 22.4% of the cities had a higher annual average SO$_2$ concentration than 0.024 µl l$^{-1}$ (Chapter 4). These concentrations are close to the minimal effective concentration of SO$_2$ for plants, which minimum levels range from 0.01 to 0.03 µl l$^{-1}$ (Posthumus 1998) and exceed the maximum allowable concentration standards for crop protection in China (Table 1). For comparison, in Europe (EC) an annual mean of 0.008 µl l$^{-1}$ (20 µg m$^{-3}$) has been set for SO$_2$ (http://europa.eu.int/comm/environment/air/), as air quality standard for ecosystems. In the USA, there are both short- and long-term National Ambient Air Quality Standards for SO$_2$ (http://www.epa.gov/air/airtrends/sulfur2.html). The short-
term (24 h) standard of 0.14 µl l⁻¹ (365 µg m⁻³) is not to be exceeded more than once per year and the long-term standard specifies an annual arithmetic mean which may not exceed 0.030 µl l⁻¹ (80 µg m⁻³).

Table 1. Susceptibility of crop species and maximum allowable SO₂ concentration for crop protection in China (Derived from the "Environmental Standards" in "State Environmental Protection Administration of China" (www.sepa.gov.cn/)

<table>
<thead>
<tr>
<th>Susceptibility to SO₂</th>
<th>Average concentration during growing season</th>
<th>Average daily concentration</th>
<th>Peak concentration</th>
</tr>
</thead>
<tbody>
<tr>
<td>High</td>
<td>µg m⁻³ (µl l⁻¹)</td>
<td>µg m⁻³ (µl l⁻¹)</td>
<td>µg m⁻³ (µl l⁻¹)</td>
</tr>
<tr>
<td>alfalfa, apple, barley, buckwheat, cabbage, clover, cucumber, grape, lettuce, pear, potato, pumpkin, ryegrass, sesame, soybean, spinach, sugar beet, wheat</td>
<td>50 (0.02)</td>
<td>150 (0.06)</td>
<td>500 (0.19)</td>
</tr>
<tr>
<td>Medium</td>
<td>µg m⁻³ (µl l⁻¹)</td>
<td>µg m⁻³ (µl l⁻¹)</td>
<td>µg m⁻³ (µl l⁻¹)</td>
</tr>
<tr>
<td>apricot, carrot, cherry, corn, cotton, eggplant, oat, orange, peach, plum, rice, sorghum, tobacco, tomato</td>
<td>80 (0.03)</td>
<td>250 (0.10)</td>
<td>700 (0.27)</td>
</tr>
<tr>
<td>Low</td>
<td>µg m⁻³ (µl l⁻¹)</td>
<td>µg m⁻³ (µl l⁻¹)</td>
<td>µg m⁻³ (µl l⁻¹)</td>
</tr>
<tr>
<td>broccoli, horse bean, rape, strawberry, sunflower, taro</td>
<td>120 (0.05)</td>
<td>300 (0.12)</td>
<td>800 (0.31)</td>
</tr>
</tbody>
</table>

In northern China, the growing season of Chinese cabbage is from autumn to the beginning of winter, during the heating season, when atmospheric SO₂ levels are the highest (Chapter 2 and 4). It is evident that at chronic atmospheric SO₂ levels of 0.06 µl l⁻¹ and higher (levels which may arise in polluted areas in China, see above) Chinese cabbage may also suffer from the negative impact of chronic atmospheric SO₂, and levels as low as 0.06 µl l⁻¹ might already negatively affect growth (Fig. 1). On the contrary, these SO₂ levels may contribute substantially to the sulfur nutrition of Chinese cabbage, at least if the soil is not severely sulfate deficient (Fig. 1; Chapter 3, 4 and 5). These ambiguous effects of SO₂ complicate the establishment of cause-effect relationships for its phytotoxic effects on Chinese cabbage grown under field conditions, and the sulfur fertilizer recommendations for optimal production of this crop. Evidently, the latter needs not solely to be adapted to the local soil sulfur status but also adjusted to the local levels of SO₂ pollution.
There is hardly interaction between atmospheric and pedospheric sulfur nutrition

Similar to other *Brassica* species, Chinese cabbage is characterized by a high sulfur requirement for growth. Kasumi F1 (Dutch cultivar) and Beijing 3 (Chinese cultivar) had an estimated sulfur requirement of 5.1 and 4.7 \( \mu \text{mol g}^{-1} \text{ plant fresh weight day}^{-1} \), respectively, at the given experimental (sub-optimal) growth conditions (Chapter 4).

However, the greater proportion of the sulfur taken up by the roots was not directly assimilated and was present as sulfate in both roots and shoots (Fig. 2; Chapter 3, 4, 5 and 6; Blake-Kalff et al., 1998; Castro et al., 2003). Still it needs to be established whether the concept of sulfur requirement for growth needs to be re-defined as the sulfur requirement for structural growth, wherein the organic sulfur content would be the parameter in the calculation of sulfur requirement. At present it is unknown to what extent, the bulk fraction of the accumulated sulfate (present in the vacuole; De Kok et al., 2002, 2005), during further development of the plant is redistributed/remobilized and used as sulfur source for growth.

![Graph](image)

Fig. 1. \( \text{SO}_2 \) - nutrient of toxin for Chinese cabbage (*Brassica pekinensis*, cv. Beijing 3): Impact of \( \text{SO}_2 \) exposure and sulfate deprivation on growth. Ten-day-old seedlings were grown in a 25% Hoagland nutrient solution with or without sulfate and simultaneously exposed to of 0.06 \( \mu \text{l l}^{-1} \) \( \text{SO}_2 \) for two weeks. For experimental conditions, see Chapter 4 and 5. Data on shoot and root fresh weight represents the mean of 2 experiments with 10 measurements in each (± SD). Relative growth rate (RGR) of the plant was calculated on a fresh weight basis and was determined over the exposure period. S/R ratio, shoot to root ratio. Different letters indicate significant differences at \( p \leq 0.01 \) between different treatments.
Fig. 2. SO₂ - nutrient of toxin for Chinese cabbage (Brassica pekinensis, cv. Beijing 3): Common effects of SO₂ exposure and sulfate deprivation on sulfur metabolite content. Ten-day-old seedlings of Chinese cabbage (Brassica pekinensis, cv. Beijing 3) were grown in a 25% Hoagland nutrient solution with or without sulfate and simultaneously exposed to of 0.06 µl l⁻¹ SO₂ for two weeks. Data on total S and sulfate content of shoot and root (measured in freeze-dried material) represents the mean of 5 measurements with 9-12 plants in each (± SD). For analytical methods, see Chapter 4 and 5. Data on total water-soluble non-protein thiol content (µmol g⁻¹ FW) in shoot and root represents the mean of 3 measurements with 3 plants in each (± SD). Different letters indicate significant differences at p ≤ 0.01 between different treatments.
The shoot of Chinese cabbage formed a sink for SO₂ and similar to observations with other species there was a linear relation between the rate of uptake and the atmospheric SO₂ level (0.03 to 1.4 µl l⁻¹; Chapter 4; De Kok, 1990; Van Der Kooij and De Kok, 1998; De Kok and Tausz, 2001). SO₂ exposure resulted in an increase in the content of water-soluble non-protein thiols and total sulfur in the shoot. The latter increase could largely be ascribed to an accumulation of sulfate, whereas that of the root remained unaffected (Fig. 2; Chapter 3, 4 and 5). The increased content of thiols presumably reflected a slight overload of the sulfur supply to the shoots. Glutathione is usually the most abundant thiol compound present in plant tissue. However, if the regulation of the uptake of sulfate by the roots is by-passed and sulfur is directly supplied to foliar tissue in either oxidized or reduced form viz. SO₂ or H₂S, then not only the size but also the composition of the thiol pool changes and in addition to glutathione, high levels of cysteine and other thiols may occur (De Kok, 1990; De Kok et al., 1998; De Kok et al., 2002).

Based on the sulfur requirement to maintain structural growth and the SO₂ uptake kinetics, it could be estimated that an atmospheric SO₂ level of approximately 0.1 µl l⁻¹ should be sufficient to cover the sulfur requirement if Chinese cabbage were able to transfer from pedospheric sulfate to SO₂ as sulfur source for growth (Chapter 4). Upon sulfate deprivation it became evident that a level as low as 0.06 µl l⁻¹ SO₂ was already sufficient to cover the sulfur requirement for growth of Chinese cabbage (Chapter 3, 4 and 5). However, it became obvious that the ability of Chinese cabbage to utilize SO₂ as sulfur source strongly depended on the sulfur status, duration of the exposure and/or developmental stage of the plant (Chapter 5). Upon a prolonged period of sulfate-deprivation, Chinese cabbage benefited from SO₂ exposure to a limited extent (Fig. 1; Chapter 5) and solely leaves, which had been formed prior to the exposure, benefited from the absorbed SO₂. There was hardly any redistribution of the absorbed and assimilated SO₂ from the older to the developing new leaves. Apparently, new developing leaves relied directly on sulfur supplied by the root. It is often assumed that sulfate is solely reduced in the shoot, in the chloroplast. However, the root contains all enzymes of the sulfate assimilatory pathway, which are present in the plastids (Heiss et al., 1999; Lappartient et al., 1999; Lee and Leustek, 1999; Yonekura-Sakakibara et al., 2000). Their activity and expression, e.g. that of ATP sulfurylase and APS reductase responded to the sulfate supply (Lappartient et al. 1999) and sulfate reduction most likely occurs in the plastids of the root. Moreover, four decades ago Pate (1965) already demonstrated that roots were able to reduce sulfur, some of which was transported as methionine and to a lesser extent as cysteine and glutathione to the shoot. It needs to be assessed to what extent new developing leaves rely on sulfate or reduced sulfur compounds, e.g. methionine, assimilated in the root.

At a whole plant level, the uptake of sulfate by the root and its transport and assimilation in the shoot will be coordinated by and balanced with the actual sulfur requirement for growth (De Kok et al. 2002). Sulfate deprivation induced multiple responses facilitating increased sulfate uptake efficiency on a whole plant basis. In addition to a general fast induction of expression of the sulfate transporters (Buchner et al. 2004), and sulfate uptake capacity by the roots (Chapter 5; Buchner et al. 2004), more prolonged sulfate deprivation generally results in changes in plants' biomass partitioning
in favor of that of root production resulting in a decreased shoot/root ratio (Chapter 3, 4 and 5; Stuiver et al., 1997; Buchner et al., 2004). However, both the enhanced sulfate uptake capacity (Chapter 5) and the decreased shoot/root ratio in response to sulfate deprivation were not rapidly alleviated when the absorbed SO₂ by the shoot replaced sulfate taken up by the root as sulfur source for growth (Chapter 3, 4 and 5). Root biomass production upon SO₂ exposure was even higher than that of plants grown under sulfate-sufficient conditions (Chapter 4 and 5). Similar to the observations on the impact of H₂S on curly kale, another Brassica species (Buchner et al., 2004), there was a poor shoot to root signaling in the regulation of sulfate uptake and shoot to root biomass partitioning upon sulfate deprivation. If indeed sulfate is reduced and assimilated in the root, the level of sulfate and/or products or metabolites involved in sulfate reduction viz. cysteine, glutathione or O-acetylserine, formed in the root, might directly be involved in root to shoot signaling in response to changes in the pedospheric sulfate supply in order to facilitate optimal sulfate uptake efficiency at a whole plant level.

References


