Chapter 1

General introduction

Sulfur in plants - uptake and assimilation of sulfate taken up by the root

Sulfur is one of the essential nutrients required for plant growth and is considered as the fourth major important nutrient after nitrogen, phosphorous and potassium for agricultural crop production. The plants’ sulfur content strongly varies between species and ranges from 0.03 to 2 mmol g\(^{-1}\) dry weight (0.1 - 6%; Tabatabai 1986; De Kok et al., 2002, 2005). The predominant proportion of the organic sulfur is present in proteins as methionine and cysteine residues, which are highly significant for protein structure, conformation and function. Plants contain a large variety of other sulfur metabolites, e.g. glutathione, sulfolipids and secondary sulfur compounds, which play an important role in plant functioning and adaptation to the environment (De Kok et al., 2002, 2005). The sulfur supply to the plant has a decisive effect on the yield and quality of crops.

Sulfate taken up by the root is the predominant sulfur source for growth (De Kok et al., 2002, 2005). The sulfate is loaded into the xylem and transported to the shoot, where it is reduced in the chloroplast prior to its assimilation into organic sulfur compounds. First the sulfate is activated by ATP to APS (adenosine 5' phosphosulfate), catalyzed by ATP-sulfurylase and subsequently reduced by APS reductase to sulfite and then to sulfide by sulfite reductase (Fig. 1). The sulfide is incorporated into cysteine by \(O\)-acetyl-L-serine (thiol)lyase. Cysteine is used as sulfur donor for the synthesis of methionine and both amino acids are incorporated into proteins. Cysteine is also the precursor for several other sulfur compounds including glutathione (De Kok et al., 2002, 2005). The sulfate uptake by the roots and its transport to the shoots are mediated by specific sulfate transporters (Hawkesford and Wray, 2000). The regulation and expression of sulfate transporters is controlled by the plant’s sulfur nutritional status (Bucher et al., 2004). Sulfate itself, or a metabolic product of sulfate assimilation, such as cysteine or glutathione etc. may be involved as signals in the regulatory control of uptake and transport of sulfate.

Uptake of SO\(_2\) by the shoot - metabolism and toxicity

It is evident that in addition to sulfate taken up by the root plants are able to metabolize sulfur gases, viz. H\(_2\)S, SO\(_2\), absorbed by the shoot (De Kok, 1990; De Kok et al., 1998; Buchner et al., 2004). The uptake of these sulfur gases by the shoot proceeds via the stomata, since the cuticle is hardly permeable for these gases (Lendzian 1984). The rate of uptake depends on the stomatal and mesophyll conductance towards the gas and the atmospheric concentration; the uptake can be described by Fick’s law for diffusion (Fig. 2; Baldochi, 1993; De Kok et al., 1998; De Kok and Tausz, 2001). The mesophyll
conductance towards SO₂ is very high since SO₂ is highly soluble in the aqueous phase of the mesophyll cells (in either apoplast or cytoplasm). Furthermore it is rapidly hydrated/dissociated yielding bisulfite and sulfite (\( \text{SO}_2 + \text{H}_2\text{O} \rightarrow \text{H}^+ + \text{HSO}_3^- \rightarrow 2 \text{H}^+ + \text{SO}_3^{2-} \)), which either may be reduced in the chloroplast or are enzymatically or non-enzymatically oxidized to sulfate (Fig. 1; De Kok, 1990; De Kok and Tausz, 2001). The stomatal conductance is generally the limiting factor for the foliar uptake of SO₂, which is reflected by a nearly linear relation between the uptake and the atmospheric SO₂ concentration (Tausz et al., 1998; Van der Kooij et al., 1998; De Kok and Tausz, 2001).

Fig. 1. Metabolism of sulfate and SO₂ in the plant (adapted from De Kok et al., 2002). APS, adenosine 5’-phosphosulfate; Fd_red, Fd_ox, reduced and oxidized ferredoxin; RSH, RSSR, thiol compound (reduced and oxidized, presumably glutathione).
SO₂ is potentially phytotoxic and its ambient air concentration may exceed values, which negatively affect plant growth and functioning. The minimal effective concentration of SO₂ air pollutants at which plant injury may occur is 0.01 µl l⁻¹ for chronic injury and 0.03 µl l⁻¹ for acute injury, respectively (Posthumus, 1998). Doubtlessly the physical/biochemical background of the phytotoxicity of SO₂ can be ascribed to the negative consequences of acidification of tissue/cells upon the dissociation of SO₂ in the aqueous phase of the mesophyll cells and/or the direct reaction of the formed (bi)sulfite with cellular constituents and metabolites (De Kok, 1990; De Kok and Tausz, 2001). However, the physiological basis for the wide variation in susceptibility between plants species and cultivars for atmospheric sulfur gases is still largely obscure (De Kok, 1990; De Kok et al., 1998; De Kok and Tausz, 2001).

![Fig. 2. Foliar gas exchange, where J_gas represents the gas exchange rate, g_gas the diffusive conductance of the foliage, representing the resultant of the stomatal and mesophyll conductance to the gas and Δ_gas the gas concentration gradient between the atmosphere and leaf interior (derived from Baldochi 1993; De Kok et al. 1998; De Kok and Tausz 2001).](image)

The impact of SO₂ on plants is ambiguous, since despite its potential toxicity it may also be metabolized and contribute to the plants’ sulfur nutrition (De Kok, 1990; Van der Kooij et al., 1997; Stulen et al., 1998). The absorbed SO₂ in the mesophyll cells of the shoot may enter the sulfur reduction pathway as either sulfite or, after oxidation, sulfate (Fig. 1). Excessive absorbed SO₂ is presumably transferred into the vacuole as sulfate, where it is only slowly accessible for metabolism (Cram, 1990; Clarkson et al., 1993). Generally, SO₂ exposure results in an enhanced sulfur content of the foliage, mainly because of an accumulation of sulfate presumably in the vacuole, even at relatively low atmospheric concentrations (De Kok, 1990; De Kok and Tausz, 2001).
Outline of this thesis

The economic growth, industrialization and urbanization of rapid developing countries viz. China, are associated with a strong increase in energy demand and emissions of gaseous pollutants including SO$_2$ (Kesselmeier, 2005). Consequently, agricultural crops are at most risk from current levels of sulfurous air pollutants, viz. SO$_2$, since they are grown close to sources of emissions. The paradoxical effects of SO$_2$ complicate the establishment of cause-effect relationships and its acceptable atmospheric concentrations in agro-ecosystems. Furthermore, it is still unclear to what extent metabolism contributes to the detoxification of the absorbed sulfur gases. The latter may have practical significance, especially in agro-ecosystems, where during recent years sulfur deficiency of soils has become a major problem in various areas in the world due to an imbalance of sulfur in relation to nitrogen, phosphorus and potassium in the fertilizers (Haneklaus et al., 2003).

Chinese cabbage (Brassica pekinensis) is a very important high-yield vegetable crop in China. It is cultivated throughout the country, because of its rapid biomass accumulation, cold resistance and short growing period. Chinese cabbage is often grown around big cities, and in northern China its growing season is from autumn to the beginning of winter. During this period, the SO$_2$ pollution levels are usually high because of the heating season (October to March). It is yet unclear to what extent atmospheric SO$_2$ affects Chinese cabbage production under intensive farming practice with a general use of low sulfur or even sulfur-free fertilizers. In this thesis, the interaction between atmospheric SO$_2$ and pedospheric sulfate nutrition was studied in order to evaluate whether SO$_2$ may be considered as toxin or nutrient for Chinese cabbage, and to what extent sulfur fertilization in the field needs to be adjusted to the level of atmospheric SO$_2$ pollution.

Chapter 2 presents an overview of air pollution problems in China and their impact on agriculture. Although some air pollution control measures are adopted in China, the emission of SO$_2$ is still one of the biggest in the world. Vegetables, fruit trees and agricultural/horticultural crops, which are grown close to the densely populated areas, appear at the highest risk. Chapter 3 reports on the interaction between atmospheric SO$_2$ deposition and pedospheric sulfate nutrition in a Dutch variety of Chinese cabbage. Chapter 4 describes the impact of various levels of SO$_2$ on growth, sulfur and nitrogen metabolism and the relevance of toxic and nutritional effects of SO$_2$ for Chinese cabbage. Subsequently in Chapter 5, the ability of Chinese cabbage to utilize SO$_2$ as sulfur source in relation to the sulfur status of the plant is investigated by exposure of seedlings at various stages of sulfate deprivation and re-supply. Furthermore, the interaction between SO$_2$ exposure and pedospheric sulfate nutrition is studied. In Chapter 6, the sulfur status of Chinese soils and the response of Chinese cabbage to sulfur fertilization in field experiments in the Beijing area are presented. In Chapter 7, the relevance of toxicity versus metabolism of SO$_2$ for Chinese cabbage and the significance of shoot to root signaling in sulfur uptake and assimilation are discussed.
References


nitrogen deposition on plant functioning. New Phytologist 139: 61-70.