Interactive effects of high CO2 and SO2 on growth and antioxidant levels in wheat

Rao, M.V.; De Kok, L.J.

Published in:
Phyton-Annales rei botanicae

Publication date:
1994

Phyton (Horn, Austria)	**Vol. 34**	Fasc. 2	279–290	29. 12. 1994

Interactive Effects of High CO_2 and SO_2 on Growth and Antioxidant Levels in Wheat

By

Mulpuri V. Rao*) & Luit J. de Kok**)

With 3 Figures

Received May 20, 1994

Key words: *Triticum aestivum*, ascorbic acid, chlorophyll fluorescence, glutathione, high CO_2, photosynthesis, SO_2.

Summary

Rao M. V. & de Kok L. J. 1994. Interactive effects of high CO_2 and SO_2 on growth and antioxidant levels in wheat. - Phyton (Horn, Austria) 34 (2): 279–290, 3 figures. – English with German summary.

The impact of elevated CO_2 and/or SO_2 on the growth and antioxidant levels of wheat (*Triticum aestivum* L. cv. Urban) plants has been studied. High CO_2 (0.7 ml l^{-1}) significantly enhanced shoot biomass and photosynthetic capacity, while exposure to SO_2 (0.14 µl l^{-1}) resulted in a decreased shoot biomass and in an injured photosynthetic aparatus, illustrated by a loss of chlorophyll and a decreased ratio of variable to maximal fluorescence (F_v/F_m) and A_{max}. However, combined exposure of plants to high CO_2 and SO_2 eliminated the negative effects of SO_2. Sulfate accumulation was almost equal in plants exposed to SO_2 and, high CO_2 and SO_2. A significant increase in ascorbate, glutathione and their redox state was observed in plants exposed to high CO_2 and SO_2, compared to that of plants exposed to solely SO_2. The absence of the negative effects of SO_2 in the presence of high CO_2 might be related to a high redox state of ascorbate and glutathione.

Abbreviations: A_{max}, maximum rate of oxygen evolution at saturated light and CO_2 (µmol m^{-2} s^{-1}); ASA, reduced ascorbic acid; DHA, dehydroascorbic acid; F_m, maximum emission of photosystem-II chlorophyll fluorescence; F_v, variable component of F_m; GSH, reduced glutathione; GSSG, oxidized glutathione.

*) Dr. M. V. Rao, Department of Horticulture Science, University of Guelph, Guelph, Ontario, Canada N1G 2W1.

**) Dr. L. J. de Kok, Department of Plant Physiology, University of Groningen, P.O. Box 14, 9750 AA Haren, The Netherlands.

Zusammenfassung

RAO M. V. & DE KOK L. J. 1994. Wechselwirkungen von hohem CO_2 und SO_2 auf Wachstum und Antioxidantiengehalt in Weizen. – Phyton (Horn, Austria) 34 (2): 279–290, 3 Abbildungen. – Englisch mit deutscher Zusammenfassung.

Es wurde der Einfluß von erhöhtem CO_2 und/oder SO_2 auf das Wachstum und den Antioxidantiengehalt von Weizenpflanzen (*Triticum aestivum* L. cv. Urban) untersucht. Hohes CO_2 (0,7 ml l^{-1}) erhöht signifikant die Sproßbiomasse und die Photosynthesekapazität, während eine Begasung mit SO_2 (0,14 µl l^{-1}) zu einer Verminderung in der Biomasse und zu einem beeinträchtigten Photosyntheseapparat führt, was durch einen Verlust an Chlorophyll und ein vermindertes Verhältnis von variabler zu maximaler Fluoreszenz (F_v/F_m) und A_{max} verdeutlicht wird. Eine Begasung von Pflanzen mit hohen CO_2- und SO_2-Mengen jedoch verhindert die negativen Einflüsse von SO_2. Die Sulfatanreicherung in den Pflanzen war ziemlich gleich bei SO_2 und hohem CO_2 und SO_2-Einfluß. Ein signifikanter Anstieg an Ascorbat, Glutathion und deren Redoxzustand wurde in Pflanzen beobachtet, welche mit hohem CO_2 und SO_2 behandelt wurde gegenüber solchen, welche bloß SO_2 ausgesetzt waren. Das Fehlen von negativen Effekten durch SO_2 in Anwesenheit von hohem CO_2 dürfte auf einen hohen Redoxzustand von Ascorbat und Glutathion zurückzuführen sein.

Introduction

Due to the increasing energy needs of an expanding human population, atmospheric levels of carbon dioxide (CO_2) are expected to double during 21st century (LONG & al. 1993). This, in turn, has prompted the evaluation of many plant species for their response to elevated CO_2 concentrations (EAMUS & JARVIS 1989, SAGE & al. 1989, YELLE & al. 1989, ZISKA & al. 1991, LONG & DRAKE 1991, BOWES 1993). Although there is a wide variation in the response of plant species, generally high CO_2 levels result in an enhanced plant yield. Stimulation of growth by high CO_2 is usually temporary and strongly dependent on the level of mineral nutrition (STULEN & DEN HERTOG 1993, STULEN & al. 1993). In industrialized and populated areas, high CO_2 levels are accompanied with gaseous pollutants like NO_x, SO_2 and O_3 (CARLSON & BAZZAZ 1985, ROZEMA 1993). This has prompted wide spread concern to evaluate the impact of high CO_2 and air pollutants (CARLSON 1983, BARNES & PFIRRMAN 1992, MULCHI & al. 1992).

Exposure of plants to high CO_2 usually enhances photosynthesis while transpiration is often decreased, due to a reduced stomatal opening (ALLEN 1990). It is generally considered that the partial stomatal closure in response to elevated CO_2 will reduce the impact of toxic air pollutants like SO_2 and O_3 (ALLEN 1990). However, the present experimental data on the combined effects of CO_2 and air pollutants are too inconsistent for the support of this assumption. Recent studies on the impact of high CO_2 and air pollutants have suggested that the elimination of air pollutant toxicity at high CO_2 levels to be due largely to the internal detoxification mechanisms rather than to a reduced pollutant uptake (KROPFF 1987, MULCHI & al. 1992, BARNES & PFIRRMANN 1992).

The physiological processes underlying the phytotoxicity of SO_2 are rather unclear. Sulfite ions formed due to the hydration of SO_2 in cell sap are very reactive and the reaction with various cellular compounds is believed to be the major cause of SO_2 phytotoxicity (De Kok 1990). On the other hand, it has been proposed that the toxicity of SO_2 is due to the formation of superoxide anions and hydrogen peroxide (H_2O_2) generated during the oxidation of sulfite to sulfate (Madamanchi & Alscher 1991, Rao 1992). In this view, plants tolerate SO_2 by scavenging the toxic oxygen free radicals through a sequence of events involving metabolites like ascorbate and glutathione and the enzymes like glutathione reductase, ascorbate peroxidase and dehydroascorbate reductase (Rao & Dubey 1993).

It has been suggested that the higher availability of carbohydrates in plants exposed to high CO_2 would detoxify air pollutants (Carlson & Bazzaz 1985, Long & al. 1993). However, this assumption lacks experimental evidence. Synthesis of ascorbic acid, a major antioxidant, depends on carbohydrate availability (Loewus & al. 1990). Since plants growing under elevated CO_2 have high production of carbohydrates (Yelle & al. 1989), we hypothesized that growth under elevated CO_2 and SO_2 would enhance ascorbic acid to detoxify SO_2. A series of experiments were conducted to investigate the effects of high CO_2 and/or SO_2 on biomass production, A_{max}, ascorbic acid, glutathione and their redox state in an attempt to test the hypothesis and to offer physiological explanations for the observed protection in wheat plants, if any.

Materials and Methods

Winter wheat (*Triticum aestivum* L. cv. Urban) was germinated in plastic pots (1 l; five seeds per pot) containing commercial soil (Florafleur Potting Soil, Nevema, Zwolle,The Netherlands). Day and night temperatures were 19 and 15 °C, respectively, RH was 60–70 % and the photopheriod was 14 h at a fluence rate of 200 µmol m^{-2} s^{-1} (400–700 nm). Seven day old seedlings were thinned to three plants per pot and were transferred to the experimental cabinets.

Plants were exposed to high CO_2 and/or SO_2 in 150 l cylindrical stainless steel cabinets with polycarbonate tops (for a description see Maas & al. 1987). Pressurized CO_2 and/or SO_2 diluted with nitrogen (1 ml l^{-1}) were mixed with air to obtain desired concentrations (715 µl l^{-1} CO_2 and or 0.138 µl l^{-1} SO_2) by ASM electronic mass flow controllers (Bilthoven, The Netherlands) and injected into the cabinets through a teflon pipe system. The air exchange in the cabinets was 50 l min^{-1} and the air inside the cabinets was continuously circulated by a ventilator (air movement capacity 20 l s^{-1}) to reduce the boundary layer surrounding the leaves. The air temperature was 24 ± 2 / 18 ± 2 °C (day/night) and the RH was 68 ± 4 / 55 ± 6 % (day/night). The photoperiod was 14 h and the light intensity at plant height was in the range of 275–300 µmol m^{-2} s^{-1} (within the 400–700 nm range). A Philips HPI-T 400 W lamp was used as a light source.

CO_2 concentrations in the air stream were measured periodically with an IRGA (ADC Model 225, MK 3, Hoddesdon, UK) and the SO_2 con centrations in the cabinets

were estimated according to MAAS & al. (1987). The mean day/night CO_2 concentrations in the cabinets were 365/374 (ambient) and 715/726 µl l^{-1} (high). The mean SO_2 concentrations were 0.004 (ambient) and 0.138 µl l^{-1} (high) which remained constant during day and night. Plants were irrigated daily with tap water and on alternate days with half strength Hoagland nutrient solution (for composition see SMAKMAN & HOFSTRA 1982). To minimize spatial effects, within a cabinet, plants were randomly relocated on alternate days. A total of four cabinets were employed in the present investigation and the experiment was repeated in another set of four cabinets.

To determine whether the growth of wheat plants under high CO_2 for four weeks resulted in photosynthetic desensitization, the maximal photosynthetic capacity (A_{max}) was measured with an oxygen electrode (Model LD-2. Hansatech, Kings Lynn, Norfolk, UK). The details of the method are described elsewhere (DIJKSTRA & LAMBERS 1989). Measure ments were made at 25 °C at a saturating light intensity of 1600 µmol m^{-2} s^{-1} in the presence of 5 % CO_2 (from a 1 M Na_2CO_3/$NaHCO_3$ buffer, 1:19 v/v). PPFD values greater than 1600 µmol m^{-2} s^{-1} did not increase the rates of O_2 evolution; consequently 1600 µmol m^{-2} s^{-1} was considered as saturating. O_2 evolution measurements were made on 4 leaf discs sampled from recently developed leaf (70–80 % of total leaf area). Chlorophyll was determined in the leaf discs used in O_2 evolution measurements according to LICHTENTHALER & WELLBURN 1983. Whole shoot dry weight was determined after drying for 36 h at 70 °C.

Chlorophyll fluorescence ratio (F_v/F_m) was determined from the upper leaf surfaces of 15 min dark adapted leaves using a pulse amplitude modulation fluorescence meter (PAM-101, H. Walz, Effel trich, FRG). The PPFD of modulation light was about 0.2 µmol m^{-2} s^{-1}. After measuring F_0, F_m was measured by exciting the surface with white light of 300 µmol m^{-2} s^{-1}. No further increases in the ratio of F_v/F_m were noted when the length of dark adaptation was increased beyond 15 min or if the actinic excitation beam increased above 300 µmol m^{-2} s^{-1}. F_v/F_m measurements were made on 4–6 leaves sampled from plants exposed to different CO_2 and/or SO_2 concentrations.

Sulfate was estimated refractometrically after separating the anions by HPLC as described by MAAS & al. 1986. The HPLC system consisted of a Kratos spectroflow pump, model 400 (Ramsey, NJ 07446, USA), provided with a Rheodyne sample injector, model 7175 (loop volume 20 µl; Cotati, CA 94928, USA) and a Knauer differential refractometer, model 9800 (Bad Homburg, Germany). The anions are separated on an Ionospher^{tm}-A anion exchange column (250 × 4.6 mm) with guard column (75 × 2.1 mm) (Chrompack, Middelburg, The Nether lands). Potassium biphthalate (30 mM, pH 4.0) was used as a mobile phase. The flow rate was 1 ml min^{-1} and the column and detector are thermostated at 24 °C by a water bath. The HPLC was connected with a Shimadzu Chromtopac C-RIB data processor (Kyoto, Japan). Analyses of sulfate and nitrate were made by extracting three individual whole shoots (1 g 4 ml^{-1} extraction medium) from each treatment and each extract yielded five observations.

Ascorbate (ASA) and dehydroascorbate (DHA) and glutathione (GSH and GSSG) were determined as described by LAW & al. 1983 and SMITH 1985, respectively. Foliar samples (0.2 g) frozen in liquid nitro gen were extracted in 2 ml of 10 % TCA (w/v). The pH of the extract was brought to 5.6 with 10 % sodium citrate (w/v) before analyses were made. All measurements were made on recently developed leaves (70–80 % of total leaf area) of six plants from each treatment.

Results and Discussion

Substantial changes were evident in the shoot biomass of plants transferred into the cabinets enriched with CO_2 and/or SO_2 when compared to that of plants exposed to ambient CO_2 (Fig. 1). Exposure of plants to high CO_2 or SO_2 for one week had no significant effect on whole shoot fresh weight. Exposure to high CO_2 for four weeks enhanced fresh weight by 24 %, while exposure to SO_2 resulted in a decreased shoot fresh weight by 42 % (Fig. 1). However, when plants were exposed to high CO_2 and SO_2 in combination, the toxic effects of SO_2 were eliminated and the shoot fresh weight was almost equal to that of plants exposed to high CO_2 (23 %

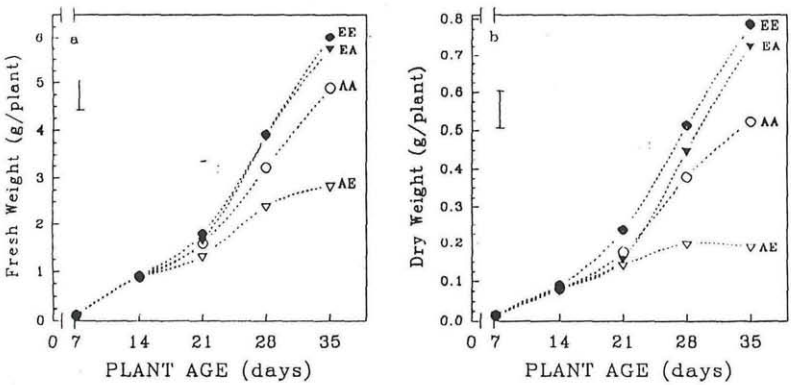

Fig. 1. Shoot growth of wheat plants upon exposure to high CO_2 and SO_2. Error bars indicate LSD ($P < 0.05$). Gas composition: AA, 365 $\mu l\ l^{-1}$ CO_2 + 0.004 $\mu l\ l^{-1}$ SO_2; EA, 715 $\mu l\ l^{-1}$ CO_2 + 0.004 $\mu l\ l^{-1}$ SO_2; AE, 365 $\mu l\ l^{-1}$ CO_2 + 0.138 $\mu l\ l^{-1}$ SO_2; EE, 715 $\mu l\ l^{-1}$ CO_2 + 0.138 $\mu l\ l^{-1}$ SO_2.

higher than that of plants exposed to ambient CO_2) (Fig. 1). Similarly, data on the dry matter production presented in Fig. 1b also indicated the deleterious effect of SO_2 as well the absence of SO_2 effect on the dry matter production of wheat plants exposed to high CO_2 and SO_2 in combination.

The observed increases and decreases were consistent with previous results obtained at high CO_2 (YELLE & al. 1989, HOCKING & MEYER 1991) and at high SO_2 (SOLDATINI & al. 1992, RAO & DUBEY 1993). Also, the observation that exposure of plants to a combination of high CO_2 and SO_2 may eliminate negative effects of SO_2 is consistent with the results reported earlier by CARLSON & BAZZAZ 1982 and SANDHU & al. 1992.

The negative effects of SO_2 on biomass production may partly be explained by negative and injurious effects of SO_2 on the photosynthetic apparatus. The chlorophyll content of SO_2 exposed plants decreased by

42 % compared to plants exposed to ambient CO_2. However, the chlorophyll content of plants exposed to combination of high CO_2 and SO_2 was almost equal to that of plants exposed to ambient or high CO_2 (Tab. 1).

Similarly, the chlorophyll fluorescence ratio, F_v/F_m, a measure of photochemical efficiency, was significantly lower in plants exposed to high SO_2, while it remained unaffected in plants exposed to high CO_2 or to a combination of CO_2 and SO_2 (Tab. 1). Apparently, the decreases in F_v/F_m ratio in SO_2 exposed plants appears to be directly related to the decreases in chlorophyll content (ADAMS & al. 1989, SCHMIDT & al. 1990). The injurious effects of SO_2 exposure were also evident from the measurements on maximum photosynthetic capacity (A_{max}). The A_{max} of plants exposed to either high CO_2 or to a combination of high CO_2 and SO_2 was significantly higher (20 %) compared to plants exposed to ambient CO_2, while in SO_2 exposed plants, A_{max} was decreased by 40 % (Tab. 1).

Table 1

Effect of high CO_2 and SO_2 on chlorophyll content, chlorophyll fluorescence ratio (F_v/F_m), maximal photosynthetic capacity (A_{max}) and sulfate content (μmol g^{-1} fr. wt.) of wheat leaves. Data represent the mean of three to six measurements (±SD). Plants were exposed for 30 days.

TREATMENT	AA	EA	AE	EE
Chlorophyll (mg g^{-1} f.wt.)	1.83 ± 0.12	1.86 ± 0.15	1.06 ± 0.15	1.79 ± 0.14
F_v/F_m	0.82 ± 0.06	0.85 ± 0.07	0.70 ± 0.09	0.82 ± 0.08
A_{max} (μmol O_2 m^{-2} s^{-1})	29.5 ± 2.6	35.4 ± 2.8	16.5 ± 1.6	33.9 ± 3.1
Sulfate (μmol g^{-1} f.wt.)	3.8 ± 0.4	3.7 ± 0.4	13.3 ± 3.1	11.3 ± 2.3

AA, 365 μl l^{-1} CO_2 + 0.004 μl l^{-1} SO_2
EA, 715 μl l^{-1} CO_2 + 0.004 μl l^{-1} SO_2
AE, 365 μl l^{-1} CO_2 + 0.138 μl l^{-1} SO_2
EE, 715 μl l^{-1} CO_2 + 0.138 μl l^{-1} SO_2

Generally, high CO_2-induced stomatal closure has been largely believed to reduce pollutant flux and protect plants from pollutant injury (ALLEN 1990). In general, SO_2 exposure results in increased sulfate levels of the leaf tissue and is largely dependent on the SO_2 concentration and duration of the exposure (DE KOK 1990). Sulfate levels in the plant are a reflection of various dynamic parameters, e.g. sulfate uptake by the root, its translocation to the shoot, and the rate of its assimilation (DE KOK

1990). Therefore, increases in sulfate levels upon SO_2 exposure can not directly be used as a measure for SO_2 uptake by the plant, yet they have an indicative value. Exposure of wheat plants to high SO_2 or to a combination of high CO_2 and SO_2 resulted in a three-fold increase in sulfate levels compared to that of plants exposed to ambient or high CO_2 (Tab. 1). From these results, it is clear that the absence of toxic effects of SO_2 at high CO_2 can not solely be attributed to the decreased pollutant flux and that the protection is dependent on the internal detoxification mechanisms.

It is assumed, generally, that the ascorbate-glutathione cycle plays an active role in protecting plant chloroplasts from oxygen free radicals. Enhanced sulfite levels in SO_2 exposed plants are believed to strongly induce oxygen free radicals. However, the significance of sulfite-induced formation of oxygen species *in situ* at realistic SO_2 levels remain unclear as well the role of ascorbate-glutathione cycle (De Kok & Stulen 1993). Yet, it has been proposed that high levels of ascorbate and glutathione would have adaptive value in protecting plants from the harmful effects of SO_2 enhanced oxygen free radicals (Rao & Dubey 1993). In addition, the ability of plants to maintain high ASA/DHA and GSH/GSSG ratios have been reported to determine the plant response to various oxidative stresses (Creissen & al. 1994).

Total ascorbic acid level (ASA + DHA) was slightly higher in plants exposed to high CO_2 compared to plants exposed to ambient CO_2 (Fig. 2A). Although the ASA + DHA level tended to be slightly higher in plants exposed to high CO_2 than in plants exposed to ambient CO_2, there were no significant changes in the ASA/DHA ratio (Fig. 2B). Although there was an initial increase in the ASA + DHA level of plants exposed to SO_2 for one week ($P < 0.05$), four week exposure decreased the ASA + DHA

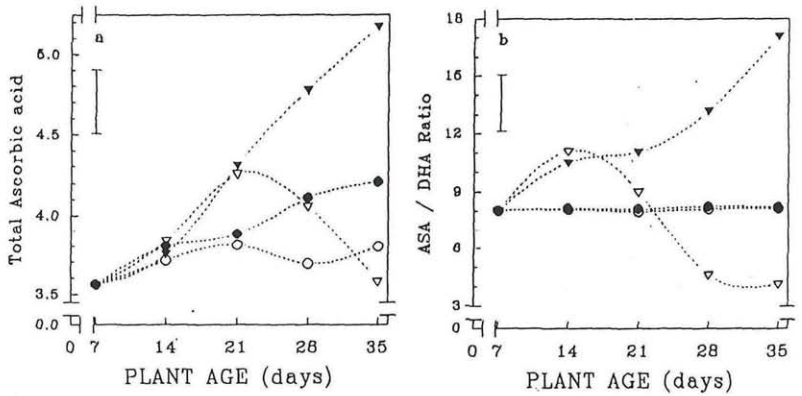

Fig. 2. Total ascorbic acid content (μmol g^{-1} f.wt.) (a) and its redox state (b) in wheat leaves upon exposure to high CO_2 and SO_2. For legends see Fig. 1.

level by 10 % compared to that of plants exposed to ambient CO_2 (Fig. 2A). However, exposure to high CO_2 and SO_2 in combination enhanced the ASA + DHA level by 23 % compared to that of plants exposed to ambient CO_2 (Fig. 2A). In addition to changes in the ASA + DHA level, significant changes were apparent in the ASA/DHA ratio in plants exposed to CO_2 and or SO_2 (Fig. 2B). The ASA/DHA ratio was significantly lower (4.1) in wheat plants exposed to SO_2 for four weeks when compared to that of plants exposed to ambient or high CO_2 (8.1). However, an exposure of to high CO_2 and SO_2 in combination enhanced the ASA/DHA ratio to 17.1 (Fig. 2B).

Exposure to SO_2 and, CO_2 and SO_2 in combination enhanced the total glutathione (GSH + GSSG) content by 19 and 23 %, respectively, when compared to that of plants exposed to ambient or high CO_2 (Fig. 3A). Simi-

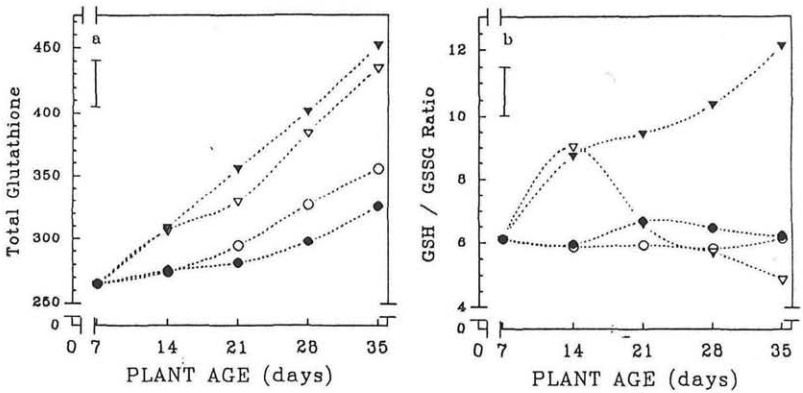

Fig. 3. Total glutathione content (nmol g^{-1} f.wt.) (a) and its redox state (b) in wheat leaves upon exposure to high CO_2 and SO_2. For legends see Fig. 1.

lar to ascorbic acid, significant changes were also apparent in the redox state of glutathione of plants exposed to high SO_2 and, CO_2 and SO_2 in combination. The GSH/GSSG ratio of wheat plants exposed to high SO_2 was significantly lower (4.9) when compared to that of plants exposed to ambient or high CO_2 for four weeks (6.1). However, growth under high CO_2 and SO_2 in combination increased the GSH/GSSG ratio to 12.1 when compared to that of plants exposed to ambient or high CO_2 (Fig. 3B).

Even though the antioxidant levels and their redox states were affected by SO_2 and high CO_2, the observed results do not provide a clear picture whether the changes are the cause or consequence of altered metabolism. For instance, recently it has been demonstrated that thiol accumulation in foliar tissue is a general phenomenon when the sulfate is directly supplied to leaves by-passing the sulfate uptake by roots (De Kok 1990, De Kok & Stulen 1993, Stulen & De Kok 1993). In addition to gluta-

thione, substantial amounts of cysteine and γ-glutamyl-cysteine (in darkness) may accumulate upon the direct supply of sulfur to leaves, which is likely due to the lack of strict regulation of the size and composition of the thiol pool under these conditions (DE KOK 1990, DE KOK & STULEN 1993). Therefore, the observed accumulation of glutathione in wheat leaves may be explained by the direct assimilation of the part of deposited SO_2, rather than it has adaptive value in the protection of plants against the toxic effects of SO_2 (DE KOK 1990, DE KOK & STULEN 1993).

Impact of SO_2 exposure on plant ascorbate levels are rather inconsistent. In general, ascorbic acid upon SO_2 exposure may either increase (RAO & DUBEY 1993), decrease or remain unchanged (MADA MANCHI & ALSCHER 1991). Recently, BADIANI & al. 1993 reported decreased levels of ascorbate in soybean growing at a natural site with strongly elevated CO_2 levels. From the present study it is evident that SO_2 exposure may result in enhanced ascorbate levels, especially upon combined exposure with high CO_2. However, the ascorbic acid remained unaltered in plants exposed to high CO_2 alone. Therefore, the physiological significance of increased levels of ascorbate upon exposure to high CO_2 and SO_2 is rather unclear.

The observed changes in the redox state of ascorbate and glutathione may be more or less the consequence of an altered metabolism. Interpretation of changes in the redox state of ascorbate and glutathione are complexed by the lack of information on the subcellular localization of accumulated ascorbate and glutathione. Although the observed decreases and increases in the redox state of ascorbate and glutathione in plants exposed to high SO_2 or high CO_2 and SO_2, in combination, appear to be related to the changes in plant sensitivity, further indepth studies are required to establish the fact.

Acknowlegdements

We wish to thank Dr. Ineke STULEN, University of Groningen, for critical reading of the manuscript. The research was supported by the Netherlands Organization for Scientific Research (NWO). We wish to acknowledge Mrs. C. E. E. STUIVER, Mr. J. M. A. M. CLEMENT, Mr. T. A. W. VAN DER KOOIJ and Mr. G. P. TELKAMP, University of Groningen for their helpful assistance.

References

ADAMS W. W. III, WINTER K. & LANZL A. 1989. Light and the maintenance of photosynthetic competence in leaves of *Populus balsa mifera* L. during short-term exposure to high concentrations of SO_2. – Planta 177: 91–97.

ALLEN L. H. 1990. Plant response to rising carbon dioxide and potential interactions with airpollutants. – J. Environ. Quality 19: 15–34.

BADIANI M., D'ANNIBALE A., PAOLOCCI A. R., MIGLIETTA F. & RASCHI A. 1993. The antioxidant status of soybean *(Glycine max)* leaves grown under natural CO_2 enrichment in the field. – Aust. J. Plant Physiol. 20: 275–284.

BARNES J. D., PFIRRMANN P. J. 1992. The influence of CO_2 and O_3, singly and in combination, on gas exchange, growth and nutrient status of radish (*Raphanus sativus* L.). – New Phytol. 121: 403–412.

BOWES G. 1993. Facing the inevitable: Plants and increasing at mospheric CO_2. – Ann. Rev. Plant Physiol. Mol. Biol. 44: 309–332.

CARLSON R. W. 1983. The effect of SO_2 on photosynthesis and leaf resistance at varying concentrations of CO_2. – Environ. Pollut. 30: 309–321.

— & BAZZAZ F. A. 1982. Photosynthetic and growth response to fumigation with SO_2 at elevated CO_2 for C_3 and C_4 plants. – Oecologia 54: 50–54.

— & — 1985. Plant responses to CO_2 and SO_2. In: WINNER W. E., MOONEY H. A. & GOLDSTEIN R. A. (eds.), Sulphur dioxide and vegetation, pp. 222–223. – Stanford University Press, Stanford, California, USA.

CREISSEN G. P., EDWARDS E. A. & MULLINEAUX P. M. 1994. Glutathione reductase and ascorbate peroxidase. In: FOYER C. H. & MULINEAUX P. M. (eds.), Causes of photooxidative stress and amelioration of defense systems in plants, pp. 343–364. – CRC Press, Boca Raton, Florida, USA.

DE KOK L. J. 1990. Sulfur metabolism in plants exposed to atmospheric sulfur. In: RENNENBERG, H., BRUNOLD C., DE KOK, L. J. & STULEN I. (eds.), Sulfur nutrition and sulfur assimilation in higher plants: Fundamental, environmental and agricultural aspects, pp. 111–130. – SPB Academic Publishing, The Hague, The Netherlands.

— & STULEN I. 1993. Role of glutathione in plants under stress. In: DE KOK L. J., STULEN I., RENNENBERG H., BRUNOLD C. & RAUSER W. E. (eds.), Sulfur nutrition and assimilation in higher plants: regulatory, agricultural and environmental aspects, pp. 125–138. – SPB Academic Publishing, The Hague, The Netherlands.

DIJKSTRA P. & LAMBERS H. 1989. Analysis of specific leaf area and photosynthesis of two inbred lines of *Plantago major:* differences in relative growth rate. – New Phytol. 113: 283–290.

EAMUS D. & JARVIS P. G. 1989. The direct effects of increases in global atmospheric CO_2 concentration on natural and commercial temperate trees and forests. – Adv. Ecol. Res. 19: 1–55.

HOCKING P. J. & MEYER C. P. 1991. Effects of CO_2 enrichment and nitrogen stress on growth, partitioning of dry matter and nitrogen in wheat and maize. – Aust. J. Plant Physiol. 18: 339–356.

KROPFF M. J. 1987. Physiological effects of sulphur dioxide. 1. The effect of SO_2 on photosynthesis and stomatal regulation in *Vicia faba* L. – Plant Cell & Environ. 10: 753–760.

LAW M. Y., CHARLES S. A. & HALLIWELL B. 1983. Glutathione and ascorbic acid in spinach *(Spinacia oleracea)* chloroplasts. – Biochem. J. 210: 899–903.

LICHTENTHALER H. L. & WELLBURN A. R. 1983. Determination of carote noids and chlorophylls a and b of leaf extracts in different solvents. – Biochem. Soc. Trans. 603: 591–592.

LOEWUS M. W., BEDGAR D. L., SAITO K. & LOEWUS F. A. 1990. Conversion of L-sorbonose to L-ascorbic acid by a NADP dependent dehydrogenase in bean and spinach leaves. – Plant Physiol. 94: 1492–1495.

LONG S. P. & DRAKE B. G. 1991. Effect of long-term elevation of CO_2 concentration in the field on the quantum yield of photosynthesis of the C_3 sedge, *Scripus olneyi*. – Plant Physiol. 96: 221–226.

— , BAKER N. R. & RINES C. A. 1993. Analysing the response of photosynthetic CO_2 assimilation to long-term elevation of atmospheric carbon dioxide concentration. – Vegetatio 104/105: 33–45.

MADAMANCHI N. R. & ALSCHER R. G. 1991. Metabolic bases for differences in the sensitivity of two pea cultivars to SO_2. – Plant Physiol. 97: 88–93.

MAAS F. M., HOFFMANN I., VAN HARMELEN M. J. & DE KOK L. J. 1986. Refractometric determination of sulphate and other anions in plants by high performance liquid chromatography. – Plant & Soil 91: 129–132.

— , DE KOK L. J., STRIK-TIMMER W. & KUIPER P. J. C. 1987. Plant response to H_2S and SO_2 fumigation. II. Differences in metabolism of H_2S and SO_2 in spinach. – Physiol Plant. 70: 722–728.

MULCHI C. L., SLAUGHTER L., SALEEM M., LEE E. H., PAUSCH R. & ROWLAND R. 1992. Growth and physiological characteristics of soybean in open top chambers to ozone and increased atmospheric carbon dioxide. – Agric. Ecosys. & Environ. 38: 107–118.

RAO M. V. 1992. Cellular detoxifying mechanisms determine age dependent injury in tropical plants exposed to SO_2. – Plant Physiol. 140: 733–740.

— & DUBEY P. S. 1993. Response of hydrogen peroxide scavenging system in two soybean cultivars. Experimental evidence for the detoxification of SO_2 by enhanced H_2O_2 scavenging system. – Environ. Pollut. 82: 99–105.

ROZEMA J. 1993. Plant response to atmospheric carbon dioxide enrichment: interactions with some soil and atmospheric conditions. – Vegetatio 104/105: 173–190.

SAGE R. F., SHARKEY T. D. & SEEMAN J. R. 1989. Acclimation of photo synthesis to elevated CO_2 in five C_3 species. – Plant Physiol. 89: 590–596.

SANDHU R., LI Y. & GUPTA G. 1992. Sulphur dioxide and carbon dioxide induced changes in soybean physiology. – Plant Science 83: 31–34.

SCHMIDT W., NEUBAUER C., KOLBOWSKI J., SCHREIBER U. & URBACH U. 1990. Comparison of effects of air pollutants (SO_2, O_3, NO_2) on intact leaves by measurements of chlorophyll fluorescence and P700 absorbance changes. – Photosynth. Res. 25: 241–248.

SMAKMAN G. & HOFSTRA J. J. 1982. Energy metabolism of *Plantago lanceolata*, as affected by change in root temperature. – Physiol. Plant. 56: 33–37.

SMITH I. K. 1985. Stimulation of glutathione synthesis in photorespiring plants by catalase inhibitors. – Plant Physiol. 79: 1044–1047.

SOLDATINI G. F., RANIERI A., LENCIONI L. & LORENZINI G. 1992. Effects of continuous SO_2 fumigation on SH-containing compounds in two wheat cultivars of differing sensitivity. – J. Exp. Bot. 43: 797–801.

STULEN I. & DE KOK L. J. 1993. Whole plant regulation of sulfur metabolism - a theoretical approach and comparison with current ideas on regulation of nitrogen metabolism. In: DE KOK L. J., STULEN I., RENNENBERG H., BRUNOLD C. & RAUSER W. E. (eds.), Sulfur nutrition and assimilation in higher plants: re-

gulatory, agricultural and environmental aspects, pp. 77–91. – SPB Academic Publishing, The Hague, The Netherlands.

— & Den Hertog J. 1993. Root growth and functioning under atmospheric CO_2 enrichment. – Vegetatio 104/105: 99–115.

— , — & Jansen C. M. 1993. The influence of atmospheric CO_2 enrichment on allocation patterns of carbon and nitrogen in plants from natural vegetations. In: Abrol Y. P., Mohanty P. & Govindjee (eds.), Photosynthesis – Photoreactions to plant productivity, pp. 509–524. – Oxford & IBH Publishing Co., New Delhi, India.

Yelle S., Beeson R. C. Jr., Trudel M. J. & Gosselin A. 1989. Acclimation of two tomato species to high atmospheric CO_2. I. Sugar and starch concentrations. – Plant Physiol. 90: 1465–1472.

Ziska L. H., Hogan K. P., Smith A. P. & Drake B. G. 1991. Growth and photosynthetic response of nine tropical species with long-term exposure to elevated CO_2. – Oecologia 86: 383–389.

Phyton (Horn, Austria) 34 (2): 290 (1994)

Recensio

Ruppert Verena 1993. Einfluß blütenreicher Feldrandstrukturen auf die Dichte blütenbesuchender Nutzinsekten insbesondere der Syrphinae (Diptera: Syrphidae). – In: Nentwig W. & Poehling H.-M. (Eds.), Agrarökologie, Band 8. – 8°, 149 Seiten, 44 Abbildungen, 12 Tabellen; brosch. – Verlag Paul Haupt Bern, Stuttgart, Wien. – DM 35,–, sFr 30,–. – ISBN 3-258-04785-5.

Vertreter der Fliegenfamilien Syrphidae, Hybotidae und Dolichopodidae wurden, ebenso wie Coccinellidae und die Entwicklung der Blattlauspopulation 1989 und 1990 auf Versuchsflächen in der Nähe von Darmstadt, an den nördlichen Ausläufern des Odenwaldes, untersucht. Ackerschonstreifen (= Ackerrandstreifen; Streifen im Acker ohne Herbizid- und Insektizidbehandlung) und Feldraine, 1988 auch Wildkrautparzellen, und Winterweizen- bzw. Wintergerstenfelder wurden mittels Blütenbeobachtung, Fallenfang und Transektzählungen bearbeitet. Mit verschiedenen Methoden ermittelte Dominanzverhältnisse werden verglichen. Die sechs häufigsten Syrphidenarten waren Episyrphus balteatus, Eupeodes corollae, Platycheirus clypeatus, Sphaerophoria spp. (meist S. scripta), Melanostoma mellinum und M. scalare. Die Blüten mit den höchsten Besucherfrequenzen waren diejenigen von *Sonchus arvensis, Papaver rhoeas, Pastinaca sativa, Heracleum sphondylium, Cichorium intybus* und *Convolvulus arvensis* (*Papaver* ein Ackerwildkraut, alle übrigen Feldrainpflanzen). Besonders im Frühjahr, für den Reifungsfraß vor der Eiablage (Mai) erwiesen sich aber vor allem Ackerwildkräuter, im Sommer mehr die Pflanzen der Feldraine als wichtige Nahrungsgrundlage für die Schwebfliegen. Über Syrphidae vgl. auch die Rezensionen in Phyton 31 (2): 207–208 und 32 (1): 175–176.

H. Teppner