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The Basis for Different Sensitivities of Photosynthesis to SO_2 in Two Cultivars of Pea

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ABSTRACT

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The response of several physiological parameters to exposure to SO_2 (0·8 ppm and 0·6 ppm) was studied in two cultivars of *Pisum sativum* in which photosynthesis showed a different sensitivity to SO_2. Leaf conductance was slightly reduced during exposure to SO_2 in the sensitive but not the insensitive cultivar. More sulphite accumulated in the leaves of the sensitive than in those of the insensitive cultivar. Total leaf content of reduced glutathione in the insensitive cultivar increased during exposure to SO_2, while in the sensitive cultivar there was no increase until the post-exposure period. The activities of fructose 1,6-*bis*phosphatase and glyceraldehyde-3-phosphate dehydrogenase did not decrease greatly in either cultivar, although activities of enzymes from the sensitive cultivar were more affected by SO_2 than were those of the insensitive cultivar. Exposure to SO_2 also had little effect on either coupled or uncoupled electron transport of isolated thylakoids from the leaves of either cultivar. Increased glutathione in the insensitive cultivar may protect the photosynthetic apparatus against SO_2

Key words—SO_2, photosynthesis, light modulation, glutathione.

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INTRODUCTION

Under certain conditions, exposing plants to SO_2 reversibly inhibits net photosynthesis (McLaughlin, Shriner, McConathy, and Mann, 1979). Both chloroplast metabolism and the stomatal apparatus have been implicated in this inhibition (Hallgren, 1978). At the pH within the chloroplast (8·0; Werdan, Heldt, and Milancev, 1975), SO_2 is mainly in the form of sulphite. In isolated chloroplasts and/or thylakoids, sulphite can influence carbon fixation (Libera, Ziegler, and Ziegler, 1973), the activity of light-activated enzymes (Alscher-Herman, 1982; Anderson and Duggan, 1977), ribulose *bis*phosphate carboxylase (Parry and Gutteridge, 1984; Khan and Malhotra, 1982), photophosphorylation (Cerovic, Kalezic, and Plesnicar, 1982), and the phosphate translocator (Mourioux and Douce, 1979).

There is, however, a lack of information relating sulphite accumulation in the leaf to SO_2 exposure and to its effects on leaf physiology and only one reported attempt to measure sulphite accumulated in leaf tissue *in vivo* through exposure to SO_2 (Miller and Xerikos, 1978).

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Abbreviations: FbPase, fructose-1,6-*bis*phosphatase; GAPDH, glyceraldehyde-3-phosphate dehydrogenase (NADP); GSH, reduced glutathione; GSSG, oxidized glutathione; SOD, superoxide dismutase.

Exposing intact spinach plants to relatively high levels of SO_2 (2·0 ppm) inhibited photosystem II function (Shimazaki and Sugahara, 1980; Shimazaki, Nakamachi, Kondo, and Sugahara, 1984) and the activity of -SH containing light-activated enzymes of the chloroplast (Tanaka, Otsubo, and Kondo, 1982). An SO_2-induced decrease in enzyme activity in spinach leaves was associated with inhibited net photosynthesis and with an accumulation of hydrogen peroxide (Tanaka, Kondo, and Sugahara, 1982). Photosynthesis did not recover fully after the exposure to SO_2, whereas the activities of the light-activated enzymes showed a rapid increase immediately after the plants were removed from the SO_2 atmosphere. The authors suggested that an irreversible impairment of photosystem II function by SO_2 was probably responsible for the lack of recovery of photosynthesis.

Alscher, Jeske, and Rogers (1983) found two cultivars of *Pisum sativum* with different responses to SO_2 exposure. CO_2 uptake in cv. 'Nugget' was more inhibited by exposure to SO_2 than in cv. 'Progress'. The effect of SO_2 was fully reversible in both cultivars, although the recovery times differed. We report here an investigation of the possible relationships between SO_2 effects on CO_2 uptake *in vivo*, stomatal response, thylakoid function, and the activity of -SH containing light-activated enzymes in leaf extracts obtained from the two cultivars. Tanaka, Kondo *et al.* (1982) showed that H_2O_2 is generated in leaves exposed to SO_2. Because glutathione is involved in the light-dependent removal of H_2O_2 generated in the chloroplast (Nakano and Asada, 1980, 1981) we also measured the effect of SO_2 on GSH levels in leaves of the two cultivars.

MATERIALS AND METHODS

Experimental plants

Seeds of cv. 'Progress' (Agway, Ithaca, N.Y.) and cv. 'Nugget' (Asgrow, Mechanicsburg, PA) were planted and grown in Cornell mix (Bing and Boodley, 1981) and watered daily in an air-conditioned greenhouse using supplemental light (16 h photoperiod) during the winter months. Greenhouse temperatures ranged from a night-time minimum of 21 °C to a daytime maximum of 25–27 °C. Thirteen- or fourteen-day-old plants were used for all experiments.

SO_2 exposure and net photosynthesis determination

Plants were placed in controlled environment chambers 2–4 d before exposure to SO_2. Light (approximately 400 μmol m^{-2} s^{-1} *PAR* at plant level) was provided by two General Electric MV400U multivapour lamps and two Lucalux LU400 lamps. Radiant heating of the chamber was decreased by water baths, keeping chamber temperatures between 23 °C and 27 °C. Relative humidity varied between 50% and 80% over a 24-h period. SO_2 exposure began 3·5 h after the onset of illumination and lasted 45 min after the target SO_2 level was attained. SO_2 was measured by a fluorescent analyser (Model 8850, Moniter Labs Inc., San Diego, CA). Stomatal conductance was measured using a steady-state porometer (Model LI-1600, Li-Cor Inc., Lincoln, NE).

Net photosynthetic rates were determined from the CO_2 differential measured by an infrared gas analyser (Model 705D, Infrared Industries Inc., Santa Barbara, CA), and the dry weight of the plant material remaining in the chamber after the experiment. The flow rate through the controlled environment chamber was measured by a pressure sensor (Model 590D-10-T-2P1-V1X-4D. Datametrics Inc., Wilmington, MA).

Leaf extracts

Samples of 10–12 leaves (0·6–0·8 g fr. wt.) were wrapped in aluminium foil and immediately frozen in liquid nitrogen. Each sample was ground in a Brinkman homogenizer at setting #9 for 10 s in 10 cm^2 of cold grinding buffer described by Leegood and Walker (1982), using 0·1 mol m^{-3} fructose 1,6-*bis*phosphate instead of 1·0 mol m^{-3}. The brei was filtered through four layers of 'Rag-on-a-Roll' (Kimberly-Clark Corp., Roswell Park, GA). Aliquots were removed for the measurement of chlorophyll (0·5 cm^3), GSH (1·8 cm^3) and sulphite (0·25 cm^3). The remaining filtrate was used for enzyme assays.

Measurement of chlorophyll, sulphite and reduced glutathione

Chlorophyll was determined by the method of Arnon (1949). Sulphite was determined by a fuchsin colorimetric method (Grant, 1949) as modified by Rothermel and Alscher (1985). Sulphite present in control extracts was subtracted and thus the concentrations reported represent sulphite accumulated as a consequence of exposure to SO_2. The procedure included a mercuric chloride precipitation step to remove free amino acids and GSH as well as proteins. Sulphite levels down to 10 mmol m^{-3} were detectable using this method. TCA was added to the sample reserved for the glutathione determination to precipitate proteins. GSH was determined by measuring the change in absorbance at 412 nm obtained on reaction of 10 mol m^{-3} DTNB with TCA-soluble material (Chiment, Alscher, and Hughes, 1986). A correction was made for sulphite present. Chiment *et al.* (1986) showed that *c.* 96% of the DTNB reactive material present in such extracts is reduced glutathione, the remainder is cysteine. Addition of 0·05, 0·075, and 0·1 mg authentic GSH to leaf homogenates gave a linear increase in A_{412} in the DTNB assay, with recovery calculated to be 92%. ΔA_{412} was linear with respect to GSH from 10^{-1} mol m^{-3} to 4×10^{-4} mol m^{-3}. Concentrations were calculated on a per mg chlorophyll basis.

Enzyme assays

The filtrate was centrifuged at $15\,000 \times g$ for 5 s in an Eppendorf Microfuge. The supernatant was assayed for GAPDH by the method of Anderson, Ng, and Park (1974) and FbPase by the method of Rosa (1981). The reaction rates were measured by following changes in absorbance at 340 nm using a Gilford 250-1 single-beam, or a Perkin-Elmer Lambda 5 split-beam, spectrophotometer. Results are expressed as μmol substrate consumed per mg chlorophyll per hour.

Isolation of thylakoids and measurement of electron transport

Thylakoids were isolated by the method of Alscher and Strick (1984). Intact chloroplasts were purified by centrifuging through a 40% Percoll solution. The chloroplasts were lysed to obtain the thylakoids. Uncoupled electron transport was measured by ferricyanide-dependent oxygen evolution using NH_4Cl (5·0 mol m^{-3}) and gramicidin (0·5 mmol m^{-3}) added together as uncouplers. ADP-stimulated electron transport was measured by ferricyanide-dependent O_2 evolution, prior to uncoupling, in the presence of 200 mmol m^{-3} ADP.

Sampling times

Leaf samples were taken during the pre-exposure (#1—0 min) exposure, (#2—10 to 80 min), and two post-exposure periods (#3—80 to 130 min and #4—130 to 150 min).

RESULTS

The effect of exposure to SO_2 at 0·8 ppm on apparent photosynthesis in *Pisum sativum* cv. 'Progress' and cv. 'Nugget' is shown in Fig. 1. Apparent photosynthesis in cv. 'Nugget' was more sensitive to SO_2, showing a greater decrease during the exposure period. After the plants were removed from the SO_2 atmosphere photosynthesis regained its pre-exposure value within 60 min in cv. 'Progress', and 125 min in cv. 'Nugget'.

Stomatal conductance, initially higher in cv. 'Nugget' ($0{\cdot}72 \pm 0{\cdot}09$ cm s^{-1}) than cv. 'Progress' ($0{\cdot}52 \pm 0{\cdot}09$ cm s^{-1}), was similar in both cultivars after the first 30 min of SO_2 exposure (Fig. 2). In both cultivars, conductance decreased during the first post-exposure period (#3), and did not change during the second post-exposure period (#4).

Exposure to SO_2 increased the sulphite content of leaves of both cultivars. However, the sulphite content of cv. 'Nugget' leaves increased more rapidly as a consequence of exposure and reached higher levels than in cv. 'Progress' leaves (time period 2) (Fig. 3, Table 1). During the post-exposure period sulphite levels returned to control levels in a shorter time in cv. 'Progress' than they did in cv. 'Nugget' (74 min to fall to control levels in cv. 'Progress' versus 125 min in cv. 'Nugget' for 0·8 ppm; 57 min versus 42 min for 0·6 ppm).

Exposing cv. 'Progress' to 0·8 ppm SO_2 increased the GSH content above the pre-exposure concentration with a further increase occurring during the recovery period (Table 2). In cv. 'Nugget' exposed to the same SO_2 concentration, GSH levels remained at pre-exposure

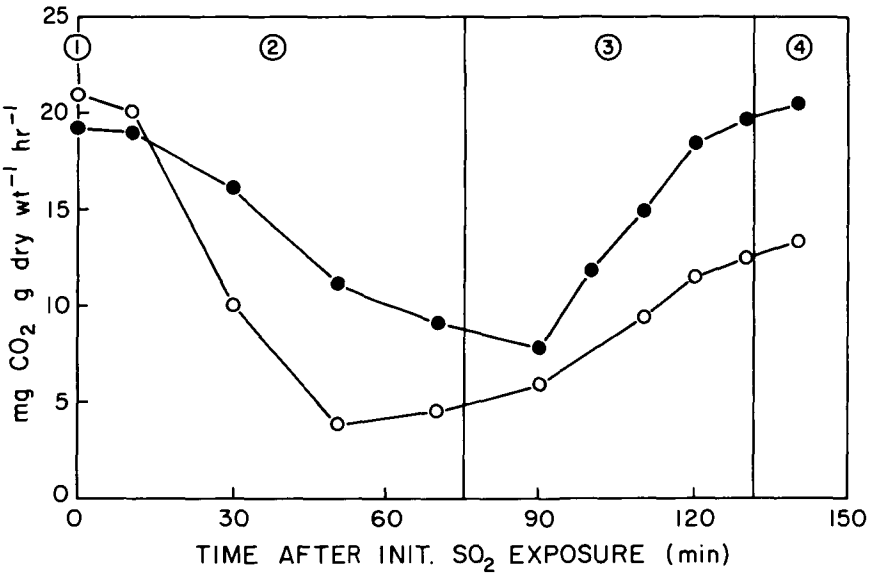

FIG. 1. Effect of exposure to SO_2 on net photosynthesis in *Pisum sativum* cv. 'Progress' and cv. 'Nugget'. Plants were exposed to SO_2 as described in Materials and Methods. —●— = cv. 'Progress' exposed to 0·8 ppm SO_2; —○— = cv. 'Nugget' exposed to 0·8 ppm SO_2. Measurements of CO_2 uptake were made with an infrared gas analyser and carbon fixation rates were calculated as described in Materials and Methods. Pre-exposure values were obtained immediately before onset of fumigation and end of exposure values were obtained at the end of the 80 min exposure period. Time periods 1, 2, 3 and 4 correspond to (1) pre-exposure (0 min), (2) exposure (10–80 min), (3) post-exposure (80–130 min), and (4) post-exposure (130–150 min). Results reported here are the means of values obtained on four separate occasions.

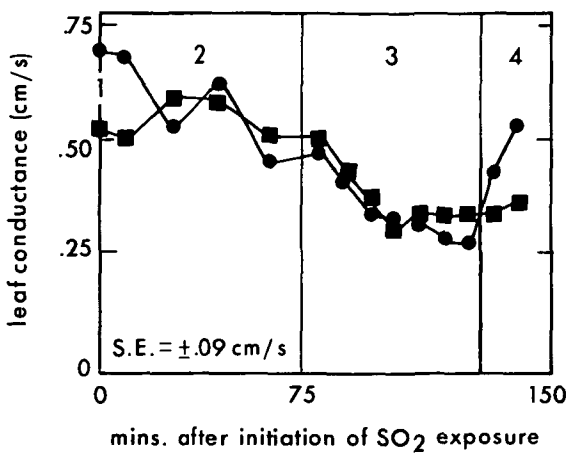

FIG. 2. Effect of exposure to 0·8 ppm SO_2 on leaf conductance in *Pisum sativum* cv. 'Progress' and cv. 'Nugget'. Conductance was determined as described in Materials and Methods. —■— = cv. 'Progress' exposed to 0·8 ppm SO_2; —●— = cv. 'Nugget' exposed to 0·8 ppm SO_2. Time periods as described for Fig. 1.

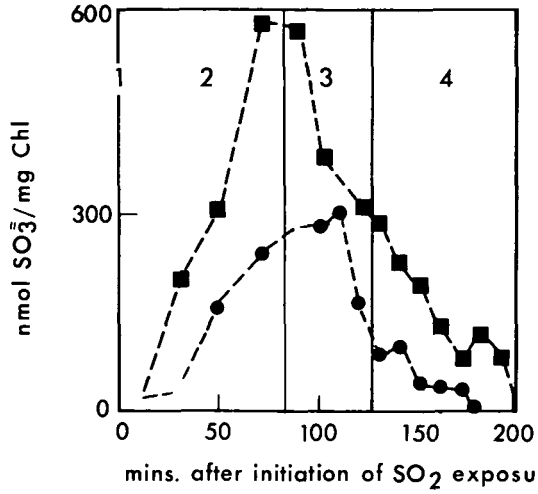

FIG. 3. Effect of exposure to SO_2 on the accumulation of sulphite in the leaves of *Pisum sativum* cv. 'Progress' and cv. 'Nugget'. Sulphite was determined using the fuchsin method described in Materials and Methods. Values shown are the means of results obtained from four separate experiments. —●— = cv. 'Nugget' exposed to 0·8 ppm SO_2; —■— = cv. 'Progress' exposed to 0·8 ppm SO_2. Time periods as described for Fig. 1.

TABLE 1. *The effect of exposure to 0·6 and 0·8 ppm SO_2 on sulphite accumulation and net photosynthesis in* Pisum sativum *cvs 'Progress' and 'Nugget'*

Cultivar treatment	% Inhibition photosynthesis at end of exposure	Highest sulphite level (nmol SO_2 mg^{-1} chl)	Sulphite return to control level (min)
'Nugget' 0·8 ppm	82	599 ± 7·8	125
'Progress' 0·8 ppm	64	301 ± 12·7	74
'Nugget' 0·6 ppm	72	280 ± 52	57
'Progress' 0·6 ppm	65	175 ± 18	42

Measurements of CO_2 uptake were made with an infrared gas analyser as described in Materials and Methods. Pre-exposure values were obtained immediately before the onset of fumigation and end of exposure values were obtained at the end of the exposure period. Results reported here are the means of values obtained on four separate occasions. Photosynthetic rates in the pre-exposure period were as shown in Fig. 1.

Sulphite levels were determined by the fuchsin method described by Rothermel and Alscher (1985) and in Materials and Methods. 'Highest sulphite level' is defined as the mean of the two highest consecutive sulphite levels measured ± standard deviation. 'Return to control level' is defined as the time taken for sulphite to return to the pre-exposure level from the highest level.

levels. This was associated in time with the extensive inhibition of CO_2 uptake shown in Fig. 1. After cv. 'Nugget' was removed from the SO_2 atmosphere its GSH concentration increased, although more slowly than in cv. 'Progress' exposed to the same conditions. The GSH eventually increased to significantly above the pre-exposure levels in both cultivars.

The effect of exposure to 0·6 ppm and 0·8 ppm SO_2 on the activities of GAPDH and

TABLE 2. *Effect of exposure to 0·8 ppm SO_2 on GSH levels in the leaves of* Pisum sativum *cvs 'Progress' and 'Nugget'*

Cultivar	Condition			
	Pre-exposure	Exposure	Post-exposure 1	Post-exposure 2
		GSH (μmol mg^{-1} chl)		
'Progress'	0·322 ± 0·048 (n = 8)	0·469 ± 0·068* (15)	0·667 ± 0·064* (18)	0·564 ± 0·088* (12)
'Nugget'	0·334 ± 0·036 (8)	0·318 ± 0·034 (16)	0·356 ± 0·037 (19)	0·522 ± 0·037* (20)

Significant differences are indicated by a * ($P < 0·05$). Comparisons were made within each row only. All values are followed by the standard error of the mean (95% confidence interval). n = Number of samples. Pre-exposure samples were harvested immediately before SO_2 exposure. Exposure, Post- exposure 1 and Post-exposure 2 correspond to time periods 2, 3 and 4 respectively in Fig. 1.

TABLE 3. *Effect of exposure to 0·8 ppm SO_2 on (a) GAPDH and (b) FbPase activities in the leaves of* Pisum sativum *cvs 'Progress' and 'Nugget'*

Cultivar	Condition						
	Pre-exposure	Exposure			Post-exposure 1		
(a) GAPDH activity (μmol substrate mg^{-1} chl h^{-1})							
		Control	0·6 ppm	0·8 ppm	Control	0·6 ppm	0·8 ppm
'Progress'	588 ± 60 (n = 21)	735 ± 90* (20)	597 ± 70 (12)	541 ± 62 (20)	573 ± 54 (18)	611 ± 55 (24)	482 ± 60 (26)
'Nugget'	536 ± 51 (20)	604 ± 41 (16)	448 ± 68 (17)	291 ± 29* (11)	693 ± 54* (13)	521 ± 61 (29)	253 ± 22* (16)
(b) FbPase activity (μmol substrate mg^{-1} chl h^{-1})							
		Control	0·6 ppm	0·8 ppm	Control	0·6 ppm	0·8 ppm
'Progress'	69·8 ± 7·2 (22)	56·7 ± 6·7 (19)	76·8 ± 10·3 (13)	70·4 ± 3·1 (24)	54·8 ± 6·6 (18)	78·9 ± 9·0 (24)	67·2 ± 4·1 (29)
'Nugget'	71·7 ± 6·7 (19)	74·1 ± 9·8 (16)	72·5 ± 8·1 (18)	51·5 ± 3·8* (21)	90·4 ± 7·3* (14)	72·0 ± 6·3 (28)	49·0 ± 2·2* (23)

Samples were obtained and assayed for GAPDH and FbPase activity as described in Materials and Methods. Values shown are followed by the standard error of the mean (95% confidence interval). Values obtained for exposure and post-exposure conditions were compared with the pre-exposure value in each case. Significant differences are indicated by a * ($P < 0·05$). n = Number of samples. Exposure and post-exposure 1 correspond to time periods 2 and 3 in Fig. 1.

FbPase is shown in Table 3. GAPDH activity decreased significantly in cv 'Nugget' in both cases and remained low during the post-exposure period. The same pattern is apparent in cv. 'Progress' for the 0·8 ppm exposure, although the decreases measured were not statistically significant. GAPDH activities were not affected by the exposure to 0·6 ppm SO_2. FbPase activities rose as a result of exposure to 0·6 ppm SO_2 in cv. 'Progress'. They fell during

the exposure and post-exposure periods in cv. 'Nugget' after exposure to 0·8 ppm SO_2 and were unaltered by exposure to 0·6 ppm SO_2.

Table 4 shows results obtained for effects of exposure to SO_2 (0·8 ppm) on the electron transport capacities, both coupled and uncoupled, of thylakoids isolated from the leaves of cv. 'Progress' and cv. 'Nugget'. Values obtained over the same time period for thylakoids isolated from untreated leaves are shown for comparison. Exposure to SO_2 had little effect on thylakoid function. During the period of recovery of CO_2 uptake, also (Fig. 1, 80-120 min, ♯3) there was no indication of large increases in capacity for electron transport in either cultivar.

TABLE 4. *Effect of exposure to 0·8 ppm* SO_2 *on (a) uncoupled and (b) ADP-stimulated electron transport in thylakoids from* Pisum sativum *cvs 'Progress' and 'Nugget'*

Sampling period	'Progress' control	'Progress' exposed	'Nugget' control	'Nugget' exposed
	μmol O_2 mg^{-1} chl h^{-1}			
(a) Pre-exposure (0 min)	368±27 (n = 18)		422±43 (25)	
Exposure (10-80 min)	369±46 (14)	353±40 (8)	379±88 (11)	370±(54) (18)
Post-exposure (90-140 min)	365±46 (13)	360±43 (12)	335±40 (14)	339±37 (18)
(b) Pre-exposure (0 min)	211±26 (17)		194±28 (23)	
Exposure (10-80 min)	190±20 (11)	180±45 (9)	176±35 (10)	184±30 (14)
Post-exposure (90-140 min)	192±30 (13)	214±29 (12)	174±30 (17)	176±26 (23)

n = Number of samples. Values shown are means followed by s.e.m. (95% confidence interval). Thylakoids were obtained as described in Alscher and Strick (1984) and in Materials and Methods. Time periods were as described in Materials and Methods and Fig. 1.

DISCUSSION

Our results show that one cause for the different sensitivities to SO_2 of photosynthesis in the two cultivars of pea of 0·6 ppm and 0·8 ppm is their relative abilities to detoxify exogenous sulphite. Thus, more sulphite accumulated in the sensitive cultivar during exposure to SO_2. The mechanism by which sulphite decreased photosynthesis was not through an effect on stomatal conductance since, during the rapid recovery of photosynthesis, leaf conductance continued to decrease to below pre-exposure levels.

Furthermore, Table 3 shows evidence that the inhibition of carbon fixation by SO_2 was not by inactivation of FbPase or GAPDH. Miszalski and Ziegler (1979) demonstrated a stimulation of activation of GAPDH by light in spinach leaves exposed to SO_2. Leegood and Walker (1980) show that CO_2 and FbPase act as competitors for reductant generated as a result of photosynthetic electron transport. The results of Table 4 show that thylakoid

function is not greatly affected by exposure to SO_2. Thus, since sulphite in the leaves inhibited carbon fixation by a mechanism distinct from the light inactivation of activated enzymes, more reductant from electron transport would become available for the reductive activation of enzymes such as FbPase. FbPase activities increased or were unaffected under all but the severest condition ('Nugget' at 0·8 ppm). Tanaka, Otsubo *et al.* (1982) reported decreased activity of FbPase and NADP-GAPDH in spinach leaves which had been exposed to 2·0 ppm SO_2. Our exposure of 'Nugget' at 0·8 ppm SO_2 approaches, perhaps, the severity of the conditions used by Tanaka, Otsubo *et al.* (1982) since we observed decreased enzyme activities during the exposure and post-exposure periods. The high concentrations of sulphite present in the leaves of cv. 'Nugget' as a consequence of exposure to 0·8 ppm SO_2 may cause the oxidation of FbPase at such a rate that the net effect is a decrease in activity. Since the data reported here are enzyme activities obtained *in vitro*, however, it is possible that other factors may contribute to inhibition *in vivo*.

Our results obtained for GAPDH activities during the exposure period are in agreement with those of Tanaka, Otsubo *et al.* (1982). Decreases occurred during the exposure periods in the leaves of each cultivar, although the decrease was not statistically significant in the case of cv. 'Progress'. However, with 0·8 ppm SO_2, activities remained low during the post-exposure period. Thus, the activity of this enzyme adjusts to the prevailing rate of photosynthesis rather than the converse, since GAPDH rates were low during those post-exposure periods when CO_2 uptake was recovering rapidly. Control levels of GAPDH in cv. 'Progress' increased during the exposure period. During the post-exposure periods in cv. 'Nugget' both GAPDH and FbPase activities increased.

Exposure to SO_2 resulted in higher reduced glutathione concentrations in leaves of cv. 'Progress' than in those of cv. 'Nugget'. Increased foliar GSH levels as a result of exposure to SO_2 and other forms of stress have been reported before (Chiment *et al.*, 1986; deKok and Oosterhuis, 1983; Guri, 1983; Grill, Esterbauer, and Hellig, 1982). Because extracts of whole leaves were analysed, it is impossible to assign the GSH produced under stress to any subcellular compartment. GSH is normally present in the vacuole and cytosol in micromolar amounts (Rennenberg, 1982) but in millimolar amounts in the chloroplast, where it may function to remove hydrogen peroxide produced as a consequence of pseudocyclic electron transport and the chloroplast's response to stress (Edwards and Walker, 1983; Foyer and Halliwell, 1976; Nakano and Asada, 1980, 1981). Other sites of hydrogen peroxide detoxification cannot be ruled out, however, and, in fact, Foyer, Rowell, and Walker (1983) have reported that *c.* 70% of total cellular ascorbate and glutathione reductase are located outside the chloroplast. As a result of this finding, they have suggested that the entire SOD/GSH/ascorbate cycle may be present in the cytosol as well as in the chloroplast. Since hydrogen peroxide has been shown to accumulate in spinach leaves exposed to SO_2 (Tanaka, Kondo *et al.*, 1982), it is possible that the changes in GSH reported here are due to increases in levels of the compound which took place in response to the stress imposed by SO_2. The greater response in cv. 'Progress' compared with cv. 'Nugget' may reflect the relative resistance to SO_2 of their respective H_2O_2 detoxification systems, regardless of their respective subcellular locations. The highest GSH levels were obtained during recovery, and not during exposure. Perhaps a portion of the GSH produced at the period of greatest stress was quickly converted to GSSG and was, therefore, not detectable as GSH.

We propose that our results are the expression of an inhibition by SO_2 of photosynthesis at a site within the chloroplast which is not associated with electron transport and which is more sensitive to SO_2/sulphite than is the light activation pathway. This additional proposed site of SO_2 action is as yet unknown. RubisCo is one possibility (Parry and Gutteridge, 1984; Marques and Anderson, 1986). Another possible site is the transport of intermediates across

the chloroplast envelope (Mourioux and Douce, 1979; Marques and Anderson, 1986). The sulphite levels which accumulated in the leaves of both cultivars were, we propose, not sufficiently high to affect light activated enzymes to an extent that would have resulted in an inhibition of photosynthesis. The same difference in susceptibilities between cv. 'Progress' and cv. 'Nugget' seen in photosynthesis (Fig. 1) was expressed, however, in a differential response of FbPase and GAPDH to SO_2. The stress-induced increases in reduced glutathione, which we report here to be correlated with differential resistance to SO_2, have been reported elsewhere (deKok and Oosterhuis, 1983; Grill *et al.*, 1982; Grill, Esterbauer, and Klosch, 1979; Guri, 1983) for other stresses. Taken together with the demonstration by Tanaka, Kondo *et al.* (1982) of SO_2-induced increases in H_2O_2 our results point to the H_2O_2 scavenging system as a plausible candidate for the role of differential resistance to metabolic stresses such as SO_2.

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