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Compensating effects to growth of carbon partitioning changes in response to SO_2-induced photosynthetic reduction in radish

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Summary. Exposure of plants to SO_2 reduced their photosynthetic performance due to reductions in carboxylating capacity. Although the reduced carbon gain resulted in a lower growth rate of SO_2-exposed plants over that of controls, their loss of potential growth was minimized because of proportional increases in allocation to new leaf material.

Key words: Carbon allocation – Photosynthetic performance – SO_2 inhibition – Growth analysis – Radish

The detrimental effects of sulphur dioxide on plant metabolic capacity have been long known and well documented as has been the generally depressing effects of this toxic gas on plant growth (reviewed in Winner et al. 1985). However the links between metabolic events, which are observed in time spans of seconds and minutes, and plant growth which integrates these events over longer time periods are often tenuous. For example, projections of growth inhibition based simply on the degree of depression of photosynthesis measured after short-term exposure of a leaf to a gaseous pollutant may be in error due to acclimation of the leaves, as well as to shifts in allocation which enhance proportional dry weight accumulation (Walmsley et al. 1980).

Here we examine the quantitative link between plant metabolism and growth reduction utilizing radish (*Raphanus sativus*, cultivar "Cherry Belle"). Although this plant has not been extensively explored with gas exchange studies, a number of growth analysis studies show its growth rate and allocation are sensitive to stress treatments. Plants raised with SO_2 and O_3 weighed less than control plants and growth of below-ground tissues (root and hypocotyl) was suppressed more than growth of shoots (Tingey et al. 1971). This was surprising since these gaseous pollutants were thought to act directly on foliage and that roots were protected from these pollutants by soils. Following these earlier studies with radishes, subsequent experiments have verified this growth response of radishes to gaseous pollutants (Reinert et al. 1982), and have shown other plants to have similar growth responses to SO_2, NO_2, and O_3 (e.g. Oshima et al. 1978; Jones and Mansfield 1982; Whitmore and Mansfield 1983).

The physiological mechanisms that account for these shifts in acclimation and allocation are unknown. Acclimation to a stress which inhibits photosynthesis can occur via a number of changes in leaf biochemistry. Carbon allocation patterns also reflect stress-induced changes in photosynthetic parameters; those factors which reduce carbon gain, such as low light, SO_2, O_3, etc., shift allocation to favor shoots (Davidson 1969). In this study we use gas exchange techniques to evaluate the mechanisms of SO_2-caused changes in radish photosynthetic capacity. These techniques allow measurement of SO_2 absorption (Winner and Mooney 1980a), partitioning of SO_2-caused photosynthetic change between stomatal and non-stomatal factors (Winner and Mooney 1980b), and assessment of the functional capacity of Rubisco and the RuBP regeneration system (Sharkey 1985). The joint assessment of SO_2-caused changes in photosynthetic properties and growth parameters of radish suggests changes in photosynthesis alone cannot account for changes in growth.

Material and methods

Radish plants were grown hydroponically for a period of 35 days in growth chambers under a thermoperiod of 15/10° C and a 10 h photoperiod. Daytime humidity was 60% and plant-level photon flux density was 800 µmol m-2 s-1. Atmospheric CO_2 concentration was controlled at 330 ppm. The hydroponically-supplied nutrients (controlled at 15° C were non-limiting with the exception of nitrate which was supplied continuously at a growth-limiting concentration of 5 μM. The chambers were fumigated during the light period with SO_2 concentrations of 0 (control), 0.24 and 0.40 ppm respectively. Forty plants, each transplanted to a separate growth tube four days after germination, were grown in each chamber. Starting 15 days after germination six plants were harvested from each chamber every five days until the final harvest at day 35. Each plant was separated into roots, hypocotyl, and leaves for dry weight and leaf area analysis. Details of the growth chamber system including nutrient and gas control and monitoring, as well as plant handling, are given by Koch et al. (1987).

The remaining plants of the control and 0.4 ppm SO_2 treatments were utilized for measurements of photosynthesis and respiration. Plants were removed from the growth chambers at periodic intervals and measurements made on leaves in clean air at 25° C at a series of CO_2 concentrations and quantum flux densities. These measurements were made to determine if photosynthetic rates were impaired

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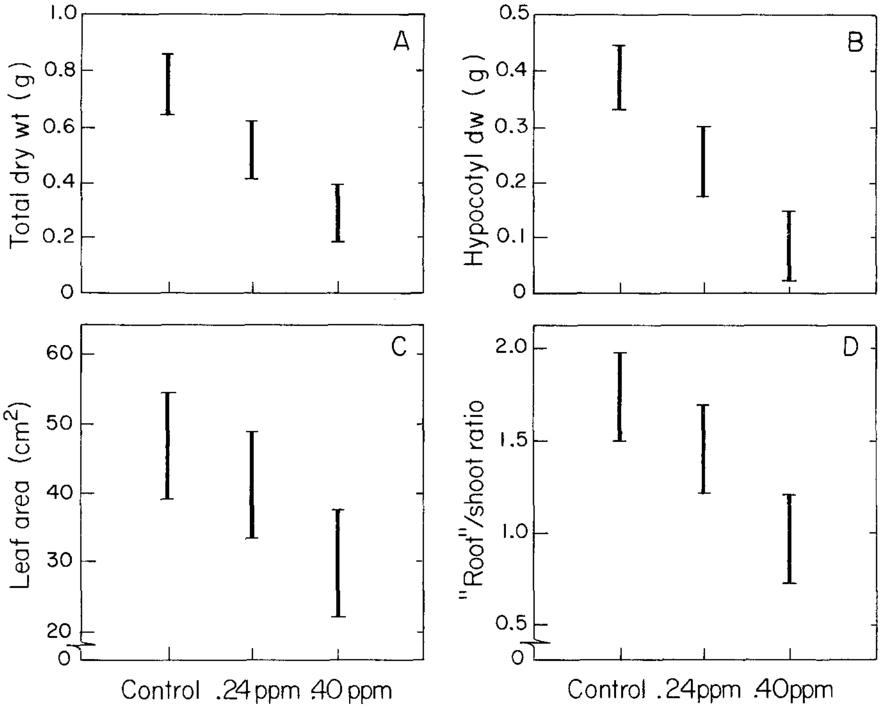

Fig. 1. 95% least significant difference intervals for mean total plant dry weight, (**A**), hypocotyl dry weight, (**B**), leaf area, (**C**) and "root"/shoot ratio (**D**), of plants harvested after 35 days from germination under the treatments indicated

by the SO_2 treatments and, if so, whether the electron transport or carboxylating capacity or both were affected. The system utilized for these measurements has been described by Winner and Mooney (1980a).

Results

Growth analysis

End of harvest. At harvest time the dry weights of the SO_2-treated plants were significantly lower, less than one half in the case of the 0.4 ppm treatment, than the controls (Fig. 1 A). The plant part that had the greatest proportional weight loss by the SO_2 treatments was the hypotcotyl, which under the highest SO_2 level attained only a quarter of the weight of the control plants (Fig. 1 B). Leaf area was also reduced by treatment (Fig. 1 C). The SO_2-treated plants had a great proportional allocation to shoots (lower "root"/shoot ratio, Fig. 1 D) than the controls.

Time course. Utilizing data from all harvests the time course of change in growth functions was calculated according to Hunt and Parsons (1974). In response to the highest treatment of SO_2 the leaf area ratio (LAR), or amount of leaf area per weight of plant, overtook that of control (Fig. 2). In spite of this, the amount of dry weight accumulated per leaf area (NAR) appeared to be less in the SO_2 treatment and the relative growth rate (RGR) was consistently lower, although not significantly so.

The patterns of change in allocation varied in a consistent manner among treatments (Fig. 3). The controls increased allocation to the hypocotyl at an earlier age and total dry weight than did the 0.24 ppm or the 0.4 ppm grown plants. This time gradient in hypocotyl filling may be related to the time at which the plant attains a given whole plant carbon flux rate (O. Bjorkman, unpublished). Equivalent canopy carbon-gaining capacity occurred about two days later on the 0.24 ppm plants than the controls and 5 days later on the 0.4 ppm plants (Fig. 4).

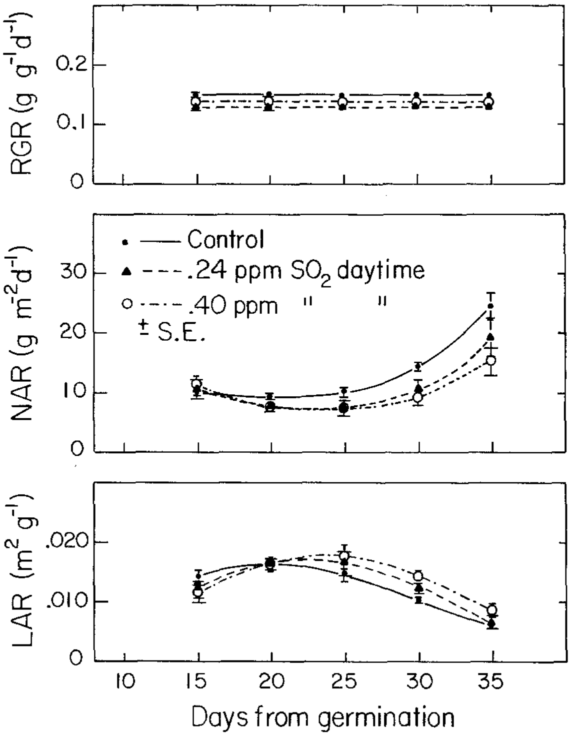

Fig. 2. Time-course for fitted values of relative growth rate (*RGR*), net assimilation rate (*NAR*) and leaf area ratio (*LAR*) of radish grown under three conditions. The *bars* indicate SE

In summary then the SO_2 treated plants accumulated less dry matter than control plants but in response to the treatments they shifted their allocation such as to produce proportionately more leaf material and thus reduced some of the potential loss in carbon gaining capacity. The quantitative nature of this compensation is discussed below.

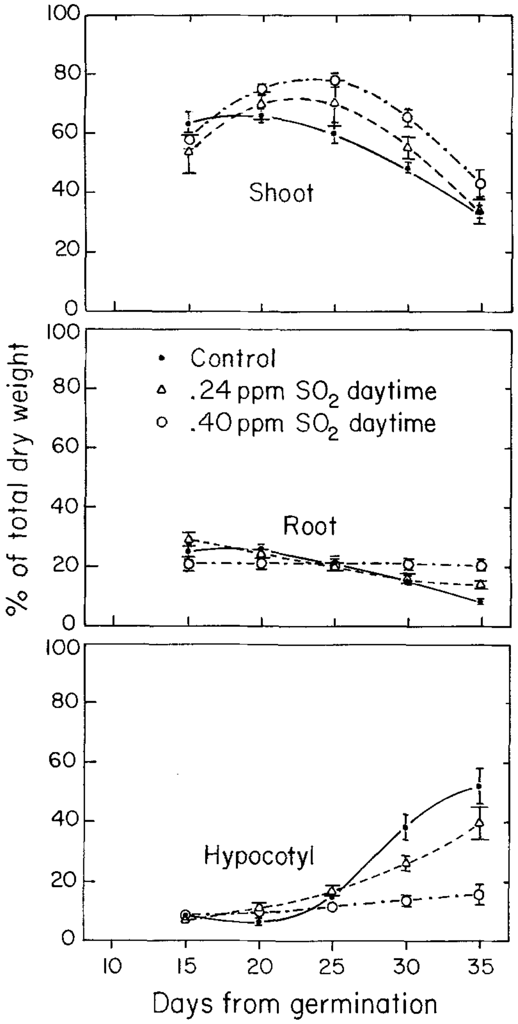

Fig. 3. Time-course for fitted values of the proportional allocation to shoot, root, and hypocotyl of radish plants grown under three conditions. *Bars* indicate SE

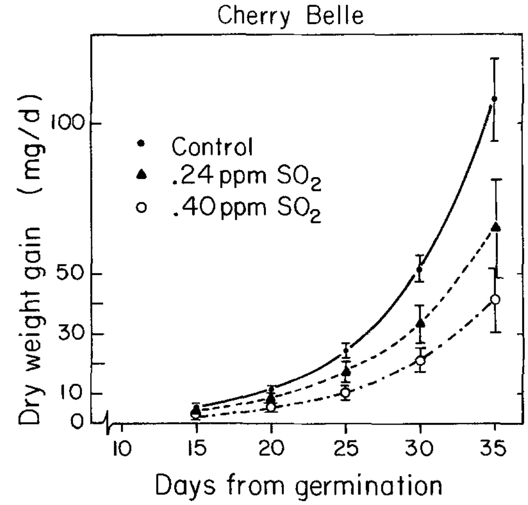

Fig. 4. Fitted values for the time-course of whole plant canopy carbon gain (net assimilation rate times leaf area) of radish plants grown under three conditions. Bars indicate estimates of standard errors calculated from factor SE's by the delta method (Miller 1986)

Photosynthesis

A summary of the results of the photosynthesis measurements is given in Table 1. The mean maximum photosynthetic performance measured at growth CO_2 concentrations (A_{max}) was reduced by about a quarter on the SO_2-treated plants versus the controls. Stomatal conductance changed proportionately with photosynthesis (g, at A_{max}) so that internal CO_2 concentrations (C_i) remained constant between treatments. The incident quantum yields (µmol CO_2/µmol photon) was reduced in the SO_2-treated plants, as was the carboxylating efficiency (delta photosynthesis/delta CO_2 internal). Dark respiration rates averaged the same between the control and treatment plants. Representative light and CO_2 photosynthetic response curves for control and treatment leaves are shown in Fig. 5.

Discussion and conclusions

Photosynthetic capacity of the leaves of radish plants was impaired by exposure to SO_2. The principal effect was on the leaf carboxylating capacity rather than electron transport. These conclusions are based on reductions in the response (of fumigated over control plants) to increased CO_2 concentrations, but the lack of differences in their quantum yields. Maximum photosynthetic capacity at the growth CO_2 and light conditions was reduced by about one quarter in the exposed (0.4 ppm) plants over the control plants.

Table 1. Photosynthetic characteristics of leaves at their maximum light-saturated net photosynthetic rates. (A_{max}: maximum photosynthetic performance; gA_{max}: leaf conductance at A_{max}; c_i: intercellular CO_2 concentration at A_{max} and ambient CO_2 concentration in the air; A_{c80}: photosynthetic capacity at an intercellular CO_2 concentration of 80 Pa; R: dark respiration rate at similar environmental conditions as for A_{max}; QY: incident quantum yield; $\Delta A/\Delta c_i$: carboxylation efficiency; A_{perf}: net photosynthetic rate at growth conditions corrected for temperature and light according to the model of Küppers and Schulze (1985). Two control plants and three SO_2-treated plants were measured repetitively over time (2–9 measurements per plant); values represent means (standard deviations) of plant means

Treatment	$*A_{max}$	$g_{(A_{max})}$	c_i	$*A_{c80}$	R	*QY	$*\Delta A/\Delta c_i$	*A perf
Control	29.1	750	25.1	46.9	−2.9	0.048	1.59	24.7
	(3.0)	(174)	(0.9)	(2.5)	(0.3)	(0.001)	(0.19)	(2.5)
SO_2-treated	22.3	512	24.6	40.2	−2.7	0.045	1.23	18.9
(0.4 ppm)	(1.1)	(36)	(0.3)	(1.0)	(0.1)	(0.001)	(0.03)	(1.0)

A_{max}, A_{c80}, R, A_{perf} in (µmol $m^{-2}s^{-1}$); $g_{(A_{max})}$ in (mmol $m^{-2}s^{-1}$); c_i in (Pa); QY in (µmol CO_2/µmol photon); $\Delta A/\Delta c_i$ in (µmol $m^{-2}s^{-1}$ Pa^{-1})

* Treatment significantly different than control ($P < 0.05$, *t*-test)

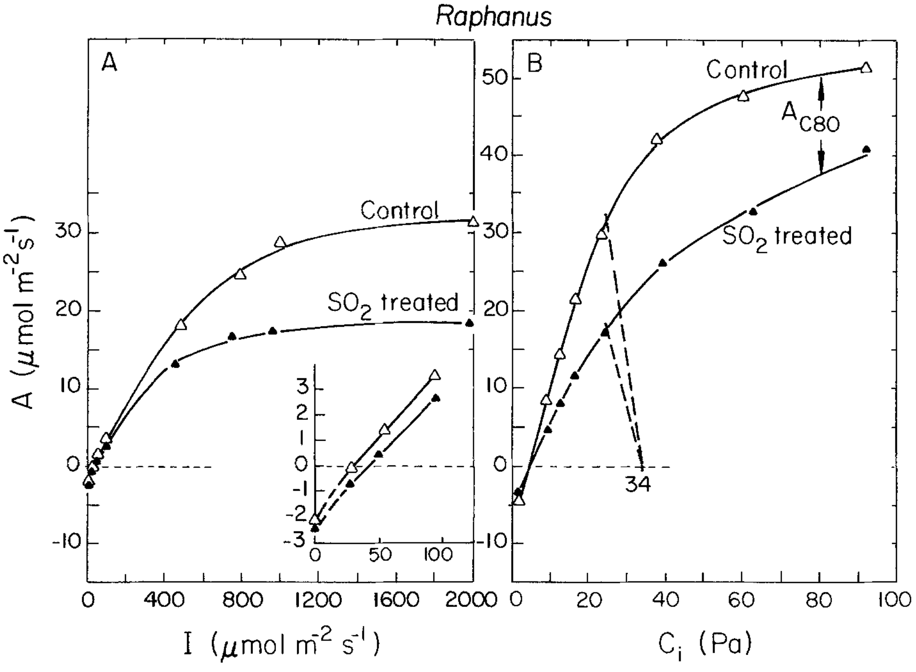

Fig. 5. Photosynthetic response to light (**A**), and CO_2 internal leaf concentration (**B**) of control and SO_2-treated (0.40 ppm SO_2) radish plants. Curves represent measurements on single plants from each treatment intended to be representative

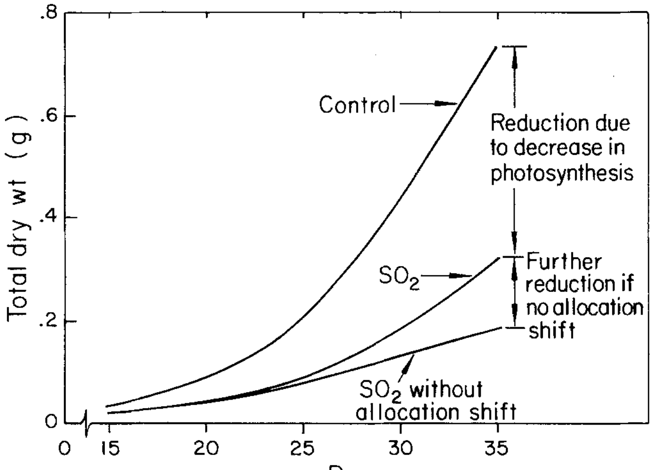

Fig. 6. Simulated growth of radish under control, 0.4 ppm SO_2, and 0.4 ppm SO_2 without an allocation shift

Dry weight accumulation was reduced by over one half by the end of 35 days. Dry weight accumulation would have been reduced even further if there had not been compensating effects due to allocation shifts. The treatment plants allocated more of their dry matter to new leaf production thus enhancing their potential dry weight accumulation.

To compare effects on growth of the decreased photosynthesis and delayed hypocotyl enlargement in the SO_2 treated plants, a model simulating dry-weight accumulation of radish was used. Model input parameters included: rates of net photosynthesis, shoot and root respiration, specific leaf weight, elemental carbon content, and shoot, root, and hypocotyl partitioning ratios.

Daily net CO_2 gain was calculated by 24 h integration of measured rates of root respiration, shoot net photosynthesis and dark respiration, and the estimated hypocotyl respiration, all of which were assumed constant for the duration of one growth simulation period. CO_2 gain was converted to a biomass increment by multiplying the weight of CO_2 by 0.716, based on a carbon content of 38% for radish (Mooney, unpublished data). This procedure was then iterated over the entire experimental period.

Values of CO_2 exchange parameters used in the model were obtained by measurements of whole shoot and root gas exchange of wild-type radish plants grown under similar conditions of light, photoperiod, and nitrate availability to those of the present control treatment. Gas exchange parameter values were: whole-shoot photosynthesis, 20.4 and 15.3 $\mu mol\ m^{-2}s^{-1}$ for control and SO_2-treated respectively; shoot respiration, 2.2 and 1.7 $\mu mol\ m^{-2}s^{-1}$ for control and SO_2-treated plants; root respiration, 3.1 $\mu mol\ CO_2\ g^{-1}min^{-1}$; hypocotyl respiration, 2.0 $\mu mol\ CO_2\ g^{-1}min^{-1}$. Previous studies of comparative leaf CO_2 exchange characteristics have found the wild-type and Cherry Bell cultivar to be nearly identical when grown under the same conditions (Mooney et al., unpublished work). As root gas exchange has been measured only for the wild-type radish thus far, the simulations used root respiration rates measured for the wild-type, with hypocotyl respiration adjusted until the simulated growth matched that fit by growth analysis. Changes in shoot, root, and hypocotyl allocation ratios over time were input as polynomials obtained from growth analysis (Fig. 3). Specific leaf weight in both treatments was 50 $g\ m^{-2}$.

Figure 6 shows simulated dry weight accumulation curves for the control and the 0.4 ppm SO_2 treatment (upper two curves), as well as that predicted for plants having the photosynthetic rate of the SO_2-treated plants and the partitioning functions of the control plants (lower curve). The simulated and observed dry weights for control plants were similar. This match was obtained when hypocotyl respiration rate was set to 2/3 of the root respiration rate. Subsequently, to evaluate the model's prediction of growth in the SO_2 treatment, photosynthesis was decreased by 25%, as was found for leaf gas exchange (Fig. 5), with shoot night respiration decreased proportionately. The allocation schedule and SLW used were those observed in the SO_2

treatment. Root and hypocotyl respiration were given the same values as in the control treatment simulation. The day 35 dry weight predicted by the model with these new input parameters was 0.32 g, very close to the actual value (from growth analysis) of 0.31 g. Thus, the model produced a reasonable simulation of growth for both the control and SO_2-treated plants. The model was then used to address the question: what would growth have been in the SO_2 treatment if the allocation schedule had remained the same as in the control treatment? Under these conditions, the model predicted a day 35 dry weight of only 0.18 g or 57% of that observed for the SO_2-treated plants. This may indicate that the increased shoot partitioning associated with the SO_2 stress partially compensated for the growth depression resulting from decreased photosynthesis. Without reference to a mechanism for such a compensation, it is of interest to note that when photosynthesis is decreased by growth at low light, a qualitatively similar increase in shoot allocation and delay of hypocotyl expansion is found (C. Deweirdt, unpublished).

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