Consequences of High CO_2-Concentrations in Air on Growth and Gas-Exchange Rates in Tobacco Mutants

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Wild type tobacco *N. tabacum* var. John William's Broadleaf and the tobacco aurea mutant Su/su were permanently grown under 700 ppm CO_2 in air. In comparison to plants grown under 350 ppm CO_2 in air but under otherwise identical conditions growth was substantially enhanced. Gas exchange measurements carried out by mass spectrometry show that the rate of photosynthesis in the wild type and in the mutant is increased by more than 100%. The photorespiratory rate in the wild type measured as $^{18}O_2$-uptake in the light in the "700 ppm CO_2-plants" is not reduced to the extent expected or deduced from experiments in which the 350 ppm system responds under *in vitro* conditions to 700 ppm CO_2. An analysis of the induction kinetics of room temperature fluorescence kinetics of the adapted (700 ppm CO_2) system and the control system (350 ppm CO_2) under various CO_2-partial pressures shows that permanent growth under the elevated CO_2-partial pressure leads to a structural modification of the photosynthetic apparatus.

Introduction

Since the beginning of the industrial aera the CO_2-concentration of the atmosphere has increased from 290 ppm to 350 ppm. It is expected that the CO_2-concentration of air will double within the next 50 years that is, the concentration might increase to 600–700 ppm. Beyond the known increase in temperature due to the high CO_2-concentration (greenhouse effect), the high CO_2-concentration will probably stimulate growth of C_3-plants. This stimulation, however, will depend on a series of factors such as nutrient availability, light conditions and the temperature really reached. This potential stimulation will relate to very defined plant species in particular, and will lead via selection mechanisms to alterations of ecosystems.

This paper investigates metabolic reactions of tobacco plants as a response to an increased atmospheric CO_2-concentration. Under *in situ* conditions the O_2-gas exchange of tobacco plants which have been grown under the high CO_2-concentration of 700 ppm are investigated via the isotope-technique ($^{18}O_2$) by means of mass spectrometry. With this method photosynthesis, potorespiration and mitochondrial respiration are analyzed simultaneously.

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Materials and Methods

Plant material: The green cigar tobacco variety *N. tabacum* var. John William's Broadleaf was used and the mutant set derived from it, described by Okabe *et al.* (1977), which originated from a selfed seed lot of the dominant tobacco aurea mutant Su/su discovered by Burk and Menser (1964).

Growth of the plants. The plants were grown in a fully climatized growth chamber. The light/dark cycle was 14 hrs/10 hrs, with the day temperature 27° C and night temperature 20° C. Relative humidity was kept at 60% during the day and 70% during night. Light intensity was 75 x 10^{18} quanta/$m^2 \cdot sec$ corresponding to 120 μ Einstein $\cdot m^{-2} \cdot sec^{-1}$. Plants were grown in glas compartments which were constantly gassed with air containing 700 ppm CO_2. The CO_2 content was verified by mass spectrometry (mass 44) (Schmid *et al.,* 1981; Ishii and Schmid, 1982). Controls were grown aside the "700 ppm-plants" under exactly the same temperature, humidity and light conditions but kept in normal air having a verified and regulated content of 350 ppm CO_2.

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Gas exchange measurements were carried out by mass spectrometry essentially as described earlier (Ishii and Schmid, 1982 and 1983; Bader *et al.*, 1992). Measurements were carried out with the Stable Isotope Ratio Mass Spectrometer "delta" from Finnigan MAT (Bremen, Germany). The device operates with a two directional focussing Nier type ion source.

Leaves and leaf sections of the plants were analyzed in a home made cell (described by Bader *et al.*, 1987). *Fast responses of the detector* to changes in the partial pressure of the gas phase were achieved by direct connection of the reaction chamber to the main vacuum of the ion source bypassing the usual inlet system (Budzikiewicz *et al.*, 1969; Bader *et al.*, 1987).

Calibration of the system is explictly described by Bader *et al.* (1992) and also earlier by Ishii and Schmid (1982). Calculation of oxygen exchange rates was done essentially as described by Peltier and Thibault (1985).

Fluorescence measurements, i.e. the induction kinetics of room temperature fluorescence were carried out with leaves and leaf sections of the tobacco plants using the PAM-2000 Fluorometer from Waltz (Effeltrich, Germany).

Results

Growth of the tobacco plants, cultivated under the two CO_2-concentrations, differs remarkably in the sense that the high CO_2-concentration of 700 ppm enhances the growth of the wild type *N. tabacum* var. John William's Broadleaf (Fig. 1a) and that of the aurea mutant Su/su (Fig. 1b). Starting from identical conditions, after 3 weeks of growth the plants differ substantially in size (Fig. 1a and b). The biggest relative difference is seen with the aurea mutant Su/su. Concerning the growth conditions it should be noted that the light intensity used in the growth chamber is saturating for the green tobacco but is not saturating for the yellow mutant (Schmid and Gaffron, 1966; Schmid, 1967). The reason lies in the reduced antenna size of the photosynthetic apparatus of the Su/su mutant, a fact which is characterized and fully described by Homann and Schmid (1967) and Okabe *et al.* (1977).

According to the principal CO_2-dependence of photosynthesis an increase of the CO_2-concentration in the air is supposed to enhance photosynthesis. In C_3-plants another factor which should respond to the high CO_2-concentration is photorespiration. The only way to measure this phenomenon under *in situ* conditions is mass spectometry, using the isotope $^{18}O_2$. Only with this method the phenomenon can be measured *in situ*. No other method permits to measure photosynthesis and photorespiration simultaneously. If photorespiration is measured in leaves of plants grown under the normal CO_2-content of air (350 ppm), the diagram shown in Fig. 2 demonstrates that $^{18}O_2$-up-

a

b

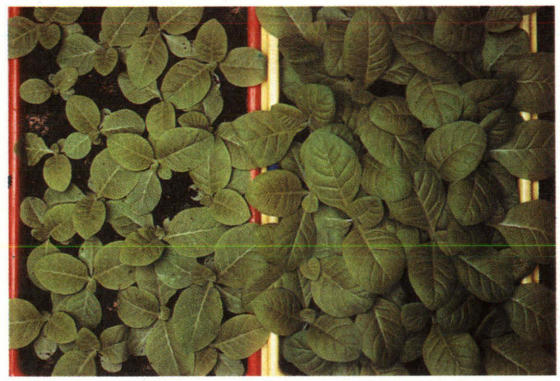

Fig. 1a. *Nicotiana tabacum* var. John William's Broadleaf grown in 350 ppm CO_2 in air (left) and 700 ppm CO_2 in air (right). Age of the plants: 6 weeks after sowing and 3 weeks after transplantation.
Fig. 1b. *Nicotiana tabacum* aurea mutant Su/su grown in 350 ppm CO_2 in air (left) and 700 ppm CO_2 in air (right). Age of the plants: 6 weeks after sowing and 3 weeks after transplantation.

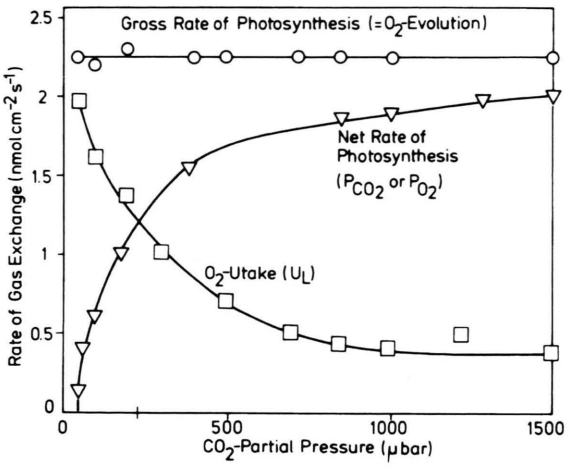

Fig. 2. Oxygen gas exchange in leaves of *N. tabacum* var. John William's Broadleaf. Dependence of $^{16}O_2$-evolution in the light (photosynthesis) and of $^{18}O_2$-uptake in the light (photorespiration) on the CO_2-concentration in air. Measurements have been carried out simultaneously by mass spectrometry at a light intensity of 250 μ Einstein $m^{-2} \cdot sec^{-1}$.

take decreases with increasing CO_2-concentration, and photosynthesis increases at the same time. Only $^{18}O_2$-uptake responding to the CO_2-concentration is photorespiration proper. The curve represents the analysis of the substrate affinity of the bifunctional enzyme ribulose bisphosphate carboxylase/oxygenase. This dependence has been observed not only for tobacco (Ishii and Schmid, 1982) but also for other C_3-plants (Gerbaud and André, 1979; Radmer and Kok, 1976). If plants are grown under high CO_2-concentration, adaptations and even alterations in the composition of the photosynthetic apparatus or metabolic changes are to be expected. If tobacco plants grown for 3 weeks under 700 ppm are analyzed for photosynthesis and compared in this analysis for a control to plants grown under 350 ppm, it is seen of course that plants grown under 700 ppm perform better than plants grown under 350 ppm (Table I). From what has been said above and from what is shown in Fig. 1a and b, this is a trivial statement. But plants grown under 700 ppm and analyzed in 350 ppm also perform better than plants grown permanently under normal air and which are analyzed under the defined light condition as before (Table I). This indicates a structural alteration of the photosynthetic apparatus in such plants. As a following paper will show, such plants have an altered structure of photosystem I (Makewicz *et al.*, in press). At any rate, photosynthesis measured in "350 ppm CO_2-grown plants" as $^{16}O_2$-evolution in

Table I: CO_2- and O_2-gas exchange rates in *Nicotiana tabacum* var. John William's Broadleaf (JWB) in normal air (350 ppm CO_2) or in air enriched in CO_2 (700 ppm).

	Rates of photosynthesis (μmol CO_2 or O_2)				Ratio	$^{18}O_2$-uptake (μmol O_2) in light (U_L)		Ratio
	P_{CO_2}		P_{O_2}		P_{O_2}/P_{CO_2}			U_L/P_{O_2}
	mg Chl^{-1} h^{-1}	dm^{-2} h^{-1}	mg Chl^{-1} h^{-1}	dm^{-2} h^{-1}		mg Chl^{-1} h^{-1}	dm^{-2} h^{-1}	
Control plants measured under 350 ppm CO_2	15.3 ± 1.3	79.6 ± 4	21.3 ± 2.8	109.9 ± 15	1.4 ± 0.12	17.7 ± 2.2	64,2 ± 8.6	.83 ± 0.22
Control plants measured under 700 ppm CO_2	22.9 ± 1.3	124.9 ± 8.7	26.0 ± 5.6	142.6 ± 23.6	1.1 ± 0.18	11.7 ± 1.9	42.4 ± 8	.45 ± 0.23
"700 ppm plants" measured at 350 ppm CO_2	26.4 ± 7.5	126.5 ± 22.8	34.6 ± 10.5	164.9 ± 32	1.3 ± 0.03	13.7 ± 2.4	49.0 ± 10.2	.400 ± 0.07
"700 ppm plants" measured at 700 ppm CO_2	43.9 ± 4	215.1 ± 5	45.0 ± 12.2	216.0 ± 36	1.03 ± 0.17	10.9 ± 1.9	39.2 ± 8.2	.243 ± 0.03

Age of the tobacco plants: 3 weeks after transplantation, i.e. 6 weeks after sowing. Control plants are grown in normal air containing 350 ppm CO_2. "700 ppm plants" are grown all the time under air having a CO_2-content of 700 ppm. Measured at 350 ppm CO_2 or 700 ppm CO_2 means that the leaves have been conditioned before the gas exchange measurement in the measuring cell in the respective atomosphere. The values are averages of 3 independent measurements on different leaves. The variations given represent absolute variations inherent to the performance of different leaves tested. The mass spectrometric technique itself works with an internal precision of less than 0.5 per cent.

350 ppm CO_2 under our light conditions used is 21 μmol mg $Chl^{-1} \cdot h^{-1}$, whereas the rate in "700 ppm CO_2-grown plants" measured in 700 ppm CO_2 amounts to 45 μmol O_2 evolved · mg $Chl^{-1} \cdot h^{-1}$ which is a difference of 110% (Table I). A the same time in this tobacco plant the CO_2-dependent O_2-uptake (see also Fig. 2) is approx 11 μmol O_2 mg $Chl^{-1} \cdot h^{-1}$, hence does not change much when the values are compared between control plants tested at 700 ppm CO_2 and "700 ppm plants" tested at the CO_2 concentration of 700 ppm under which they have been grown (Table I). This means that photosynthesis increases and photorespiration is *not* or not much reduced in the plant when grown under 700 ppm CO_2 and when analyzed under the condition of 700 ppm CO_2 in air. When the aurea mutant Su/su is tested, it is seen that under the light and temperature conditions used which are identical to those shown for the wild type tobacco in Table I, the mutant plant grown at 350 ppm CO_2 exhibits a rate of photosynthesis of 63 μmol $^{16}O_2$ evolved · mg $Chl^{-1} \cdot h^{-1}$ (Table II). These plants transferred under *in vitro* conditions to 700 ppm exhibit an evolution rate of 116 μmol $^{16}O_2$ evolved · mg $Chl^{-1} \cdot h^{-1}$ which is practically the same value which plants exhibit that have been grown under 700 ppm under *in vivo* conditions (Table II). It is interesting to note that the plants grown under 700 ppm but analyzed under *in vitro* conditions under 350 ppm CO_2 do not exhibit substantially more photosynthesis than the plants that have been grown under 350 ppm (Table II). This is an important observation since it shows that the Su/su mutant has apparently a photosynthetic system that does not adapt further under the high CO_2 concentrations. In contrast, the wild type tobacco, as many other green plants, shows the phenomenon that photosynthesis of the high CO_2-grown plants exhibits, also when measured under normal 350 ppm CO_2, a higher rate than the plants grown at 350 ppm CO_2 (Table I).

At this point it should be noted that the Su/su mutant, originally introduced by Schmid (1966) and Schmid and Gaffron (1967) has been shown to exhibit an unusual photorespiratory behaviour as demonstrated by many laboratories (Zelitch and Day, 1968; Ishii and Schmid, 1982 and 1983). Besides its reduced light antenna the mutant has a ribulose 1,5-bisphosphate carboxylase/oxygenase system which is characteristically different from that of the wild type (Okabe, 1977) which was demonstrated by immunological means (Beuttenmüller *et al.*, 1990; Nespoulous *et al.*, 1988). In the present paper it is observed that the rate of $^{18}O_2$ uptake in response to the CO_2 concentration (i.e. photorespiration) decreases under *in vivo* conditions from 33 μmol O_2 · mg $Chl^{-1} \cdot h^{-1}$ in plants grown at 350 ppm to 11 μmol O_2 · mg $Chl^{-1} \cdot h^{-1}$ in

Table II. CO_2- and O_2-gas exchange rates in the *Nicotiana tabacum* aurea mutant Su/su in normal air (350 ppm CO_2) or in air enriched in CO_2 (700 ppm).

	Rates of photosynthesis (μmol CO_2 or O_2) P_{CO_2}		P_{O_2}		Ratio P_{O_2}/P_{CO_2}	$^{18}O_2$-uptake (μmol O_2) in light (U_L)		Ratio U_L/P_{O_2}
	mg Chl^{-1} h^{-1}	dm^{-2} h^{-1}	mg Chl^{-1} h^{-1}	dm^{-2} h^{-1}		mg Chl^{-1} h^{-1}	dm^{-2} h^{-1}	
Control plants measured under 350 ppm CO_2	63.3 ± 4.4	58.9 ± 11.8	65.5 ± 0.8	62.1 ± 5.4	1.04 ± 0.08	33.5 ± 6.1	31.2 ± 6.1	.511 ± 0.086
Control plants measured under 700 ppm CO_2	116.7 ± 13	107.6 ± 28	124.0 ± 13.6	119.0 ± 25	1.119 ± 0.049	22.0 ± 2.5	20.7 ± 0.6	.181 ± 0.033
"700 ppm plants" measured at 350 ppm CO_2	90.0 ± 12.7	105.3 ± 11	79.9 ± 6.7	95.9 ± 6.4	.939 ± 0.14	16.3 ± 4.5	20.6 ± 8.5	.211 ± 0.075
"700 ppm plants" measured at 700 ppm CO_2	120.2 ± 4.6	145.3 ± 16.5	132.7 ± 1.4	161.1 ± 22.8	1.105 ± 0.03	10.8 ± 2	14.4 ± 4	.082 ± 0.053

Age of the tobacco plants: 3 weeks after transplantation, i.e. 6 weeks after sowing. Control plants are plants that are grown in normal air containing 350 ppm CO_2. "700 ppm Plants" are grown all the time under air having a CO_2-content of 700 ppm. Measured at 350 ppm CO_2 or 700 ppm CO_2 means that the leaves have been conditioned before the gas exchange measurement in the measuring cell in the respective atomosphere. Three independent measurements from three different plants are shown.

plants grown at 700 ppm (Table II). It is interesting to see that if these plants are tested under *in vitro* conditions that is the 350 ppm grown plants under 700 ppm CO_2 and the 700 ppm grown plants under 350 ppm, an intermediate value (practically the same in both cases) of 22/16 μmol $O_2 \cdot$ mg $Chl^{-1} \cdot h^{-1}$ is observed which shows only a limited structural adaptation of the mutant to the changed CO_2 conditions, in contrast to the green wild-type. The mutant apparently stays as it is.

A further method to analyze photosynthetic performance in a non-invasive way is to measure the Kautsky effect, i.e. the room temperature induction kinetics of fluorescence in leaves of plants grown under 350 ppm CO_2 and in leaves of those grown under 700 ppm CO_2. Room temperature fluorescence originates almost exclusively from photosystem II and reflects ultimately the poising and capacity of photosynthetic electron transport.

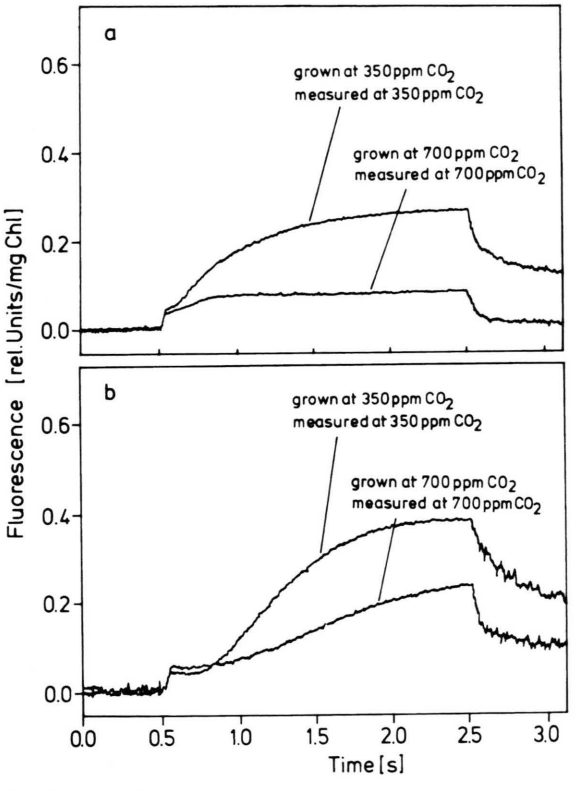

Fig. 3a,b. Induction kinetics of room temperature fluorescence: a) in leaves of green wild type tobacco (JWB), b) in leaves of the tobacco aurea mutant Su/su. Plants were grown either at 350 ppm CO_2 or at 700 ppm CO_2 in air.

If fluorescence induction is measured in leaves of the green wild type tobacco (JWB) from plants grown under normal CO_2-conditions (350 ppm) and from those grown under 700 ppm CO_2 in air, a large difference is seen (Fig. 3a). Fluorescence in the "700 ppm CO_2-grown plants" is much lower than in "350 ppm CO_2-grown plants". Obviously, in plants grown under the higher CO_2-concentration energy trapping and electron transport are more efficient. Of course, the CO_2 conditioning of the leaves used for fluorescence measurements corresponded to the CO_2-partial pressure under which the plants were grown. The observation with the green wild type was also verified with the aurea mutant Su/su (Fig. 3b). If, however, the fluorescence induction in 700 ppm plants is compared to the fluorescence induction which is observed in plants grown under 700 ppm CO_2 but which are exposed to 350 ppm CO_2 then the difference is striking (Fig. 4, curve 4). In curve 4 of Figure 4 the observed fluorescence is considerably higher than in plants grown at 350 ppm (and also measured at this partial pressure) showing that structural changes probably on the level of photosystem II and photosystem I have taken place which is of no use when the system is exposed to 350 ppm instead of to the adapted 700 ppm, (compare curve 2 and

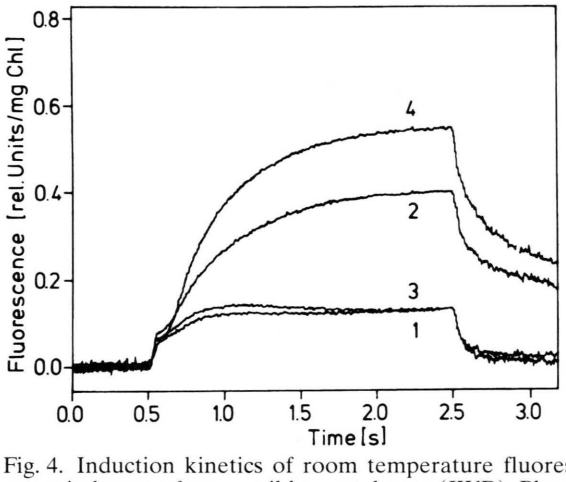

Fig. 4. Induction kinetics of room temperature fluorescence in leaves of green wild type tobacco (JWB). Plants are shown in figure 1a. Curve 1: plants grown at 350 ppm CO_2, leaves were conditioned at 700 ppm CO_2 with fluorescence measured; curve 2: plants grown at 350 ppm with fluorescence measured at 350 ppm CO_2; curve 3: plants grown at 700 ppm CO_2 and measured at 700 ppm; curve 4: plants grown at 700 ppm CO_2 but measured at 350 ppm CO_2.

4 of Figure 4). Thus, it appears that plants grown under high CO_2 adapt their electron transport capacity to the higher acceptor concentration. If the Su/su mutant is tested under the same conditions practically the same observation as with the green wild type is made.

Discussion

In the context with plant production an enrichment of the CO_2-content in the atmosphere of green houses is used since quite some time in order to increase plant development. In laboratory and greenhouse tests it is usually seen that CO_2-fixation is greatly stimulated during the first hours after the increase of the CO_2-concentration. This stimulation of photosynthesis is explained by the activation of Rubisco, the enzyme which fixes CO_2 at the actual CO_2-concentration of air with only 30% of its maximal speed. Nevertheless, most reports say that after a few days of adaptation to the high CO_2-content a much weaker stimulation (if at all) is seen, clearly showing other limitations in context with plant growth. With the aim to have access to the functional characteristics of photosynthesis and in particular to Rubisco, we have analyzed the O_2-and CO_2-gas exchange in tobacco plants that have grown and developed from its germination in an atmosphere of 700 ppm CO_2 in air. The effect of the increased CO_2-concentration on growth is spectacular in comparison to plants grown under normal CO_2-content and is demonstrated in Fig. 1a and b. Three weeks after transplantation to buckets and starting at that time with plants which were visually very similar in size, these plants have grown in the high CO_2-content all the time faster than their controls. One obvious question relates immediately to photorespiration. Photorespiration is initiated by the oxygenase activity of Rubisco. The "fixation" of O_2 on ribulosebisphosphate produces phosphoglycolate which is metabolized leading to the formation of glycine and serine. When photorespiration is active, the plant cell produces CO_2 in the light and consumes per CO_2-molecule fixed twice as much energy than in the absence of this activity. Only mass spectrometry permits to measure photorespiration (Fig. 2). All other methods that try to measure this activity such as the postillumination burst of CO_2 and others (Zelitch, 1968; Mahon *et al.*, 1977) underestimate photorespiration without exception. The method of mass spectrometry is actually the only method which permits to quantify in a more or less direct manner under steady state conditions photosynthetic oxygen production and hence the activity of the linear electron transport chain. The method allows to see that under the experimental conditions used in a C_3-plant like tobacco under the normal CO_2-content of air practically half of the reducing power goes into the reduction of O_2 and the other half into that of CO_2. This is manifested by an O_2-evolution of 21 μmol $O_2 \cdot$mg $Chl^{-1} \cdot h^{-1}$ and a simultaneously occurring O_2-uptake rate (U_L) of 18 μmol·mg $Chl^{-1} \cdot^{-1}$ (Table I). This is already known from the literature although only the laboratories that use mass spectrometry can reliably measure it. Under the same growth conditions with respect to temperature, light intensity and humidity under 700 ppm CO_2 in air the rate of photosynthetic O_2-evolution (P_O2, i.e. $^{16}O_2$) is 45 μmol $O_2 \cdot$mg $Chl^{-1} \cdot h^{-1}$ and the simultaneously occurring O_2-uptake (U_L, i.e. $^{18}O_2$) is only 11 mg $O_2 \cdot$mg $Chl^{-1} \cdot h^{-1}$ (Table I). This shows that due to the higher CO_2-concentration photosynthesis increases stronger than photorespiration decreases. The "Bonus-effect" i.e. the rate difference 45/11 and 21/18 (Table I) is obviously due to a structural change of the photosynthetic apparatus which seems to occur when plants grow permanently under the high CO_2-concentration. It appears now that the structure of the photosystems is altered in such plants. Among others in photosystem I the ratio of LHCPI and CPI appears decreased. Moreover, the relative amount of lipids with respect to the photosystem I peptides in the region of the reaction core is changed and so is the pigment ratio of the complex with respect to carotenoids (Makewicz *et al.*, 1995). From the present mass spectrometric data this inherent change of the photosynthetic system might also be deduced. If the plants grown at the high CO_2-concentration of 700 ppm and are then conditioned at the normal CO_2-content of 350 ppm, the steady rate of photosynthetic O_2 evolution Po_2 (measured via the evolution of $^{16}O_2$) is 35 μmol $O_2 \cdot$mg $Chl^{-1} \cdot h^{-1}$ which is a 66 per cent higher performance than that of a plant grown under 350 ppm CO_2 and measured under 350 ppm CO_2 (Table I). Under these conditions the photorespiratory activity

barely changes from 18 to 11 μmol $O_2 \cdot$mg $Chl^{-1} \cdot h^{-1}$, showing that the principal CO_2-dependence of photosynthesis and the specificity factor of Rubisco for CO_2 are not the only factors that become effective. By the simple experiments presented in the present paper it becomes clear that the increase of the CO_2-concentration in air from 350 ppm to 700 ppm will have overall and very complex consequences in the plant system. Studies in the past followed the principle that photorespiration decreased with higher CO_2-concentration (or with lower O_2-levels). It was overlooked that what has been measured was in fact the reaction of a system adapted to 350 ppm CO_2 to these parameters. A system adapted to another CO_2-concentration will show changed dependencies. As the fluorescence measurements also show, altered CO_2-concentrations obviously lead to altered quantum yields of photosystem II. The combination of the experiments shown in Figs 3 and 4 leave no doubt that in these plants the structure of photosystem II has, due to the higher CO_2-content undergone a substantial modification.

The Su/su mutant is a plant with particular photosynthetic and photorespiratory characteristics. At high light intensity photosynthetic efficiency per chlorophyll and per leaf area is greater than in the green control (Schmid *et al.*, 1966; Schmid, 1967; Homann and Schmid, 1967; Canaani *et al.*, 1985; Okabe *et al.*, 1977). However, the plant exhibits also a high photorespiratory activity (Zelitch and Day, 1968; Ishii and Schmid, 1982 and 1893). It is astonishing that all the time that this plant was under investigation, the idea did not come up to grow these plants under elevated CO_2. This has been done here and as Fig. 1b shows, the effect of 700 ppm on growth is impressing. It should be emphasized again that the light intensity in the growth chamber is not saturating for the mutant but is for the wild type. Future experiments with plants adapted to high light conditions will show the maximum performance of this plant.

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