Gas Exchange Characteristics in Leaves of the *Euphorbiacea Aleurites montana* as Consequence of Growth under 700 ppm CO_2 in Air
A Study on Photosynthesis and Photorespiration in the Chinese Tung-Oil Tree

P. He[a], K. P. Bader[b], A. Radunz[b], U. Kahmann[c], G. H. Ruppel[c] and G. H. Schmid[b]

[a] Central South Forestry University, Zhuzhou/Hunan 41206, People's Republic of China
[b] Lehrstuhl für Zellphysiologie, Fakultät für Biologie, Universität Bielefeld, Germany
[c] Abteilung für Morphologie der Pflanzen und Feinbau der Zelle, Fakultät für Biologie, Universität Bielefeld, Germany

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Three months old plants of the Chinese tung-oil tree *Aleurites montana* (Euphorbiaceae) were cultivated for 4 months in air containing 700 ppm CO_2. These plants, which grow substantially better in the CO_2-enriched atmosphere, were analyzed by mass spectrometry for photosynthesis and photorespiration together with control plants grown all the time in normal (350 ppm CO_2) air. Thereafter part of the plants was subjected for two weeks to 0.3 ppm SO_2 in the atmosphere and again analyzed for photosynthesis and photorespiration. *Aleurites montana* exhibits a strongly CO_2-dependent photosynthesis which partially explains the observed stimulatory effect of 700 ppm CO_2 on growth of the plant. In control plants grown in normal air, photorespiration measured simultaneously with photosynthesis via the uptake of $^{18}O_2$ in the light, is much lower than in C_3-plants like tobacco (He *et al.*, 1995, Z. Naturforsch. **50c**, 781–788). In *Aleurites* grown in 700 ppm CO_2, however, photorespiration is completely absent in contrast to tobacco when grown under 700 ppm CO_2. In tobacco, photorespiration is not inhibited to the extent of the *in vitro* experiments in which plants grown at 350 ppm CO_2 are measured under the increased CO_2 content of 700 ppm. Gas exchange measurements carried out by mass spectrometry show that the ratio of O_2 evolved to CO_2 fixed is about 0.5. Apparently, part of the CO_2 fixed is channelled into a metabolic path without concomitant O_2-evolution. Although the plant has no succulent appearance (its leaves somehow resemble maple leaves) apparently a *Crassulacean* type metabolism is performed. When *Aleurites* plants grown all the time in normal air with 350 ppm, are exposed for two weeks to 0.3 ppm SO_2 the treatment **completely** inhibits this CO_2-fixing portion which is tentatively attributed to a *Crassulacean* type of metabolism. This is demonstrated by a normal C_3-type ratio O_2 evolved/CO_2 fixed of 1. When *Aleurites* plants, grown for 4 months in a CO_2-enriched atmosphere of 700 ppm CO_2, are subjected for two weeks to 0.3 ppm SO_2, the features of control plants show up again. When these plants are **tested** under 350 ppm CO_2 the *Crassulacean* type CO_2-fixation apparently is not inhibited by SO_2. Photorespiration, although low, is present in the same activity as in the controls. Seemingly, an increased level of CO_2 in air tends to alleviate the impact of the SO_2 at least in the Chinese tung-oil tree.

Introduction

The Chinese tung-oil tree has been extensively studied in recent years (He *et al.*, 1995; He *et al.*, 1996a; He *et al.*, 1996b). In China seeds of the tung-oil tree represent an important crop (Fang *et al.*, 1985), Fang and Que, 1981). The CO_2-content of air as well as the content of gas pollutants as SO_2 is constantly increasing. Thus, it is generally anticipated that the CO_2-content of the atmosphere will increase within the next 50 years from actually 350 ppm CO_2 to 700 ppm CO_2. Air pollutants as SO_2 play an augmenting role in particular in China where the expansion of industries and growing private energy demands dramatically increase this air pollutant. It appears now that the tung-oil tree is particularly sensitive and is more and more endangered by air pollution. The pre-

Abbreviations: CAM, *Crassulacean* Acid Metabolism, TEM, Transmission Electron Microscope.

Reprint requests to Prof. Dr. Georg H. Schmid.
Universität Bielefeld, Fakultät für Biologie, Lehrstuhl Zellphysiologie, Postfach 10 01 31, D-33501 Bielefeld.
Fax: (0521) 106-6410.
E-mail: G.Schmid@Biologie.Uni-Bielefeld.DE.

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sent study includes the aspect of future changes in the composition of the atmosphere namely the increase in CO_2 content. Plants (i.e. small trees) were grown under normal conditions in air and under the CO_2-content of 700 ppm (He *et al.*, 1996). In both conditions the plants were exposed additionally to 0.3 ppm SO_2 for two weeks and then analyzed. The present study presents novel characteristics of *Aleurites montana* which belongs to the family of *Euphorbiaceae,* most of its members are succulent plants. Although the tung-oil tree rather looks like a maple tree, and leaves have no succulent appearance, the gas exchange characteristics seem to indicate that *Aleurites* might be a C_3-CAM intermediate.

Materials and Methods

Cultivation of Aleurites-plants

Aleurites montana was cultivated in a fully climatized growth chamber in a light/dark cycle of 14 h/10 h at a day temperature of 27 °C and a night temperature of 22 °C at 60% relative humidity. Seeds came from the Central South Forestry University, Zhuzhou, Hunan. Voucher specimens of *Aleurites montana* and *Aleurites fordii* are available in the laboratories of Bielefeld. Cultivation of plants under increased CO_2- and/or SO_2-content was carried out in glass compartments in the same growth chamber. In the glass compartments the plants were otherwise exposed to the same conditions as in the uncompartmented growth chamber. *CO_2*-plants were grown at 700 ppm CO_2 in the gas phase and SO_2-plants with 0.3 ppm. Dosage was achieved with a peristaltic pump (Perimax 12) from Spectec GmbH, 85435 Erdingen and a suitable valve system (Schmid *et al.*, 1981; Ishii and Schmid, 1982).

The plant growth protocol was as follows: Small trees of *Aleurites montana* were grown for 3 months in the fully climatized growth chamber in normal air as described above. After this 3 months period the plants were transferred in the compartments where the CO_2-content of air was set at 700 ppm. In two months intervals the gas exchange measurements were carried out, hence after the 5th month and after the 7th month. After this experimental period part of the plants, namely the control plants which were grown in normal air (350 ppm) over the entire 7 months period and the *CO_2*-plants which were grown for 5 months in an atmosphere with increased CO_2 (700 ppm), were exposed for two weeks under the otherwise unchanged conditions to an atmosphere which contained 0.3 ppm SO_2. After this two weeks period gas exchange measurements were carried out.

Measurements of the gas exchange

were carried out by mass spectrometry with intact leaves as described recently for the characteristics of the gas exchange of tobacco leaves by He *et al.* (1995). The method used is described in detail by Ishii and Schmid (1982 and 1983) and Bader *et al.* (1992). The 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). Calibration of the system is described by Bader *et al.,* (1992). Calculation of the oxygen exchange rates was done as described by Peltier and Thibault (1985).

Results

The first general observation when *Aleurites montana* is grown in air containing 700 ppm CO_2 is that growth is constantly improved. The response to the increased CO_2-content is a long term effect and is visually superior to what is seen with other plants e.g. tobacco (He *et al.*, 1995). Fig. 1 shows the influence of 700 ppm CO_2 in air on growth. All plants are 7 months old. The 3 plants on the left of Fig. 1 have grown all the time in normal air with 350 ppm CO_2 whereas the 3 plants on the right have grown 3 months in normal air and then for the following 4 months in air containing 700 ppm CO_2. The difference in size is spectacular. Due to CO_2-dependence of photosynthesis, an increase in CO_2-concentration in air obviously enhances photosynthesis. The quantitative analysis of the photosynthetic performance of the plants shown in Fig. 1 is shown in Table I. Leaves of control plants grown during 7 months in normal air under the used growth chamber conditions exhibit photosynthetic rates of 8 μmol $CO_2 \cdot$ mg $Chl^{-1} \cdot h^{-1}$ which is relatively low in comparison to tobacco under the same conditions (He *et al.*,

Fig. 1. 7 ½ months old plants of *Aleurites montana* (*Euphorbiaceae*).
Plants in the 3 pots on the left have been grown for 7 months and 2 weeks in normal air (350 ppm CO_2). The plants in the 3 pots on the right hand side have been first grown for 3 months in normal air, then transferred to air containing 700 ppm CO_2 and kept in this atmosphere for 4 months two weeks. All other conditions are identical (see Materials and Methods).

1995). It should be noted that the photosynthetic performance is measured here under the CO_2-partial pressure of 350 ppm. If these control plants are exposed to 700 ppm CO_2 and then measured the value increases to 12 μmol CO_2 · mg Chl^{-1} · h^{-1}. *CO_2*-plants grown during 4 months (the plants on the right hand side of Fig. 1) under the increased CO_2-content of 700 ppm in air give when the performance is measured under control conditions (which are 350 ppm CO_2 in air), 18 μmol CO_2 fixed · mg $chlorophyll^{-1}$ · h^{-1}. The same plants, measured under the CO_2-partial pressure of 700 ppm, which is the concentration under which they have been grown for 4 months, have a photosynthetic rate of ≈ 25 μmol CO_2 fixed · $chlorophyll^{-1}$ · h^{-1} (Table I). This clearly demonstrates the long known CO_2-dependence of the rate of photosynthesis but also the adaptation of the photosynthetic system to the higher CO_2-concentration. When photosynthesis is measured as O_2-evolution, measured as the evolution of $^{16}O_2$ by mass spectrometry, it is clearly seen that less O_2 is evolved than CO_2 is fixed (Table I). The P_{O_2}/P_{CO_2} ratio is generally about 0.5. The difference in performance between the control plants and the *CO_2*-plants measured under the respective conditions is the same as for the CO_2-fixation. It should be noted that the ratio of oxygen evolved/CO_2 fixed (P_{O_2}/P_{CO_2}) for typical C_3-plants like tobacco is in the range of 1 (He *et al.*, 1995). The figure of 0.5 found for *Aleurites* indicates that half of the fixed

Table I. CO_2- and O_2-gas exchange rates in leaves of *Aleurites montana* in normal air (350 ppm CO_2) and in air enriched in CO_2 (700 ppm).

Plants and CO_2 atmosphere	Rates of photosynthesis (μmol CO_2 or O_2)				Ratio	$^{18}O_2$-uptake (μmol O_2)		Ratio
	P_{CO_2}		P_{O_2}		P_{O_2}/P_{CO_2}	in light (U_L*)		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 at 350 ppm CO_2	8.3 ± 0.34	67.1 ± 3.6	4.25 ± 0.59	33.65 ± 2.5	0.51 ±0.4	0.97 ± 0.2	7.8 ± 1.6	0.23 ±0.04
Control plants measured at 700 ppm CO_2	12.0 ± 3.0	95.8 ± 15.7	4.8 ± 0.9	38.46 ± 4.4	0.40 ±0.3	0	0	0
"700 ppm plants" measured at 350 ppm CO_2	18.4 ± 0.4	89.6 ± 14.1	9.6 ± 1.0	46.42 ± 1.1	0.52±0.05	0	0	0
"700 ppm plants" measured at 700 ppm CO_2	24.9 ± 2.1	120.98 ± 11	11.4 ± 1.4	55.02± 2.02	0.46±0.07	0	0	0

Age of the *Aleurites* plants: *Control plants* were grown for 7 months in normal air containing 350 ppm CO_2. "700 ppm plants" were grown for 3 months in normal air and then transferred in an atmosphere containing air with an increased CO_2-content of 700 ppm and grown for 4 months in this atmosphere. Measured at 350 ppm or 700 ppm CO_2 means that the leaves have been conditioned before the gas exchange measurements in the measuring cell in the respective atmosphere. Values are averages of at least 3 independent measurements on different leaves. The variations given represent absolute variations due to the performance of the different leaves tested. Mass spectrometry itself works with practically no error with an internal precision of less than 0.5 per cent. *U_L = uptake in the light.

CO_2 is channelled into a pathway without concomitant O_2-evolution. Seemingly, a metabolism like the *Crassulacean* acid metabolism (CAM) is partially active and used in this plant. The plant has no bundle sheath cells but contains a palisade parenchyma (Fig. 2a). In the vicinity of the chloroplasts microbodies are visible with protein cristalloids (Fig. 2b) which consist of catalase shown by immuno-gold labelling (Ruppel and Kahmann, manuscript in preparation). Hence, microbodies of the type seen in Fig. 2b are to be considered as peroxisomes.

In a typical C_3-plant like tobacco the activity of photorespiration is of the same order of magnitude as photosynthesis itself and in general 50 per cent of the photosynthetic performance (Ishii and Schmid, 1982; Schmid *et al.*, 1981; He *et al.*, 1995). Only by means of mass spectrometry and the use of the isotope $^{18}O_2$ the phenomenon can be measured correctly *in situ*. No other method permits to measure photosynthesis and photorespiration simultaneously. Photorespiration of C_3-plants grown under the normal CO_2-content of air, i.e. 350 ppm, shows that the $^{18}O_2$ uptake decreases with increasing CO_2 concentrations (Ishii and Schmid, 1982; He *et al.*, 1995) while photosynthesis increases at the same time. Only the $^{18}O_2$-uptake responding to the CO_2 concentration is photorespiration proper (see Fig. 2 in He *et al.*, 1995). The $^{18}O_2$-uptake in the light by *Aleurites montana* leaves is low (Table I). The sensitivity of our technique allows to measure reliably such values which in *Aleurites* are $\approx$ 1 μmol O_2 · mg Chl^{-1} · h^{-1} that is less than 10% of that observed in tobacco ($\approx$ 15 μmol $^{18}O_2$ · mg Chl^{-1} · h^{-1}) (He *et al.*, 1995). When leaves coming from the plant grown all the time in normal CO_2 (350 ppm) are subjected to the increased CO_2-content of 700 ppm, the phenomenon disappears entirely, hence absolutely no $^{18}O_2$-uptake is measured anymore (Table I). So the observed $^{18}O_2$-uptake is indeed due to photorespiration. Hence, *Aleurites* plants grown under 700 ppm CO_2 exhibit no photorespiration anymore (Table I). This is in contrast to tobacco which is a typical C_3-plant. Tobacco grown ("long term" adapted) in 700 ppm still shows photorespiration which is not decreased to the extent expected from the *in vitro* response (in the unadapted system) to the increased CO_2-content of 700 ppm (He *et al.*, 1995). The observation has a bearing on the long accepted notion that photorespiration would disappear or be greatly reduced when the CO_2-content in air is substantially increased. This is not generally the case (He *et al.*, 1995). In the tested C_3-plants adapted to high CO_2 (e.g. 700 ppm in He *et al.*, 1995), photorespiratory activity persists, maybe due to changes in the substrate affinity of ribulose-1.5-bisphosphate carboxylase/oxygenase (Rubisco) (Okabe, 1977). Only in *Aleurites* the anticipated suppression of photorespiration by the high CO_2 partial pressure is really observed. Here, photosynthesis is substantially enhanced (Fig. 1 and Table I) **and** photorespiration is completely suppressed. This makes *Aleurites* a suitable plant

Table II. CO_2- and O_2-gas exchange rates in leaves of *Aleurites montana* in normal air and in air supplemented with 0.3 ppm SO_2.

Plants and CO_2 atmosphere	Rates of photosynthesis (μmol CO_2 or O_2)				Ratio	$^{18}O_2$-uptake (μmol O_2)		Ratio
	P_{CO_2}		P_{O_2}		P_{O_2}/P_{CO_2}	in light (U_L*)		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	15.7 ± 3.4	138.5 ±10.8	9.5 ± 2.9	79.9 ± 17.7	0.598±0.05	0.58 ± 0.2	5.0 ± 1.1	0.64 ± 0.09
"SO_2-plants" measured under 350 ppm CO_2	9.12 ± 1.4	65.3 ± 8.5	8.4 ± 1.1	59.7 ± 6.6	0.915± 0.08	0.99 ± 0.3	7.2 ± 1.8	0.124 ± 0.05

Age of the *Aleurites* plants: *Control plants* were grown for 7 months and 2 weeks in normal air containing 350 ppm CO_2. "SO_2 plants" were grown for 7 months in normal air and then subjected for 2 weeks to normal air containing 0.3 ppm SO_2. Mass spectrometric measurements were carried out with leaves conditioned in normal air (350 ppm CO_2). The deviations given represent absolute variations due to the performance of the different leaves tested.

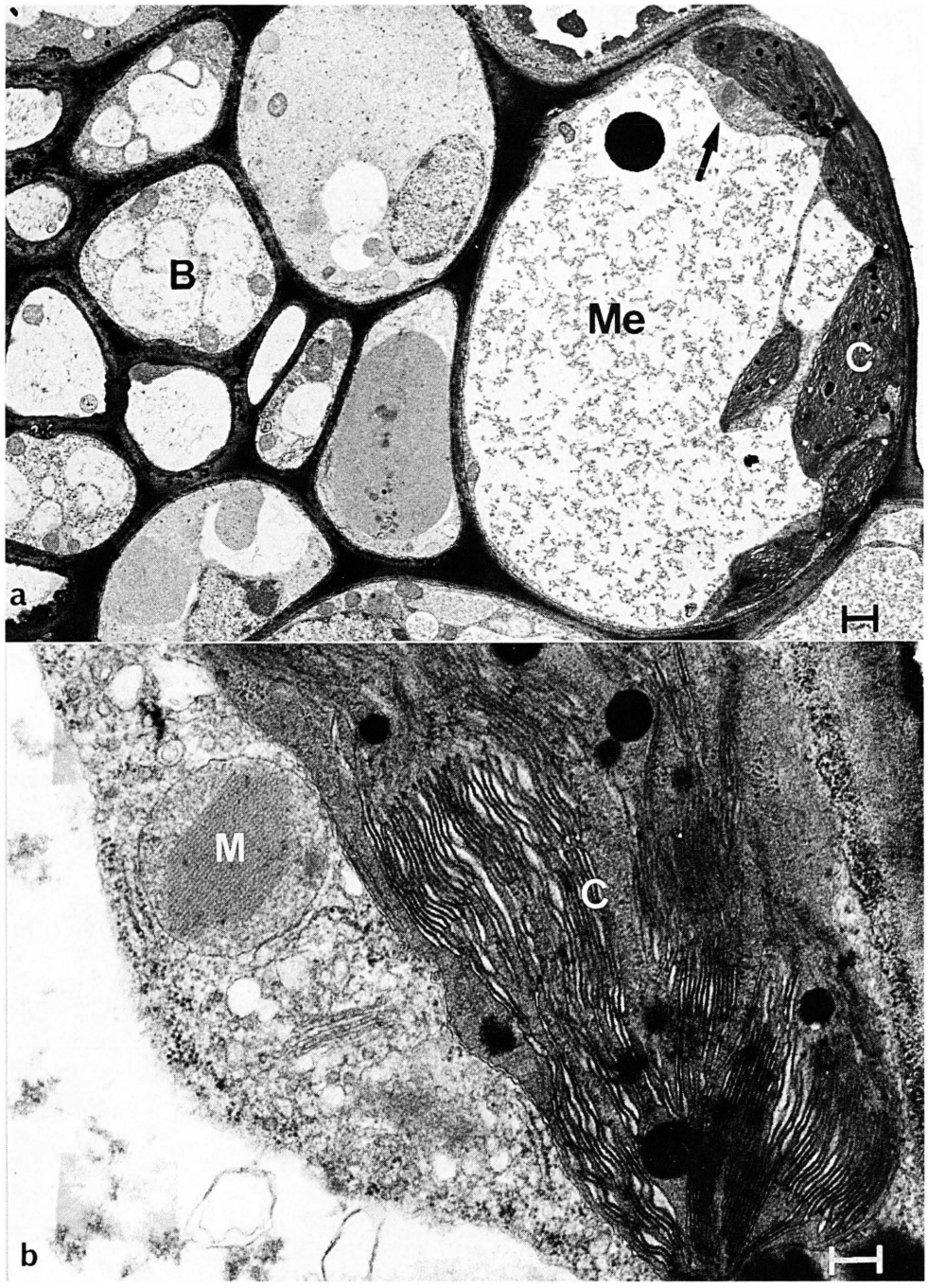

Fig. 2. Transmission electron micrographs of an ultrathin section of a leaf from *Aleurites montana.*
a) Shows the vascular bundle region with tracheary elements and mesophyll cells; the bar represents 1.5 μm;
b) shows an enlarged part of the region near the chloroplast indicated by an arrow in a), the bar represents 0.2 μm.
M = microbody with a protein cristalloid; c = chloroplast; Me = mesophyll cell; B = tracheary elements.

for future studies on the regulation of photorespiratory activity, that is the regulation of Rubisco activity. It should be noted that *Aleurites* is a plant with a peculiar lipid/fatty acid metabolism (He *et al.*, 1996 and 1997).

When a 7 months old *Aleurites* plant is subjected to a two weeks treatment with 0.3 ppm SO_2 in air (Fig. 1), the effect on photosynthetic performance and photorespiration is remarkable. Photosynthesis measured as CO_2 fixation decreases from ≈ 15.7 to 9.1 μmol CO_2 fixed · mg chlorophyll^{-1} · h^{-1}. Concomitantly oxygen evolution decreases from ≈ 9.5 to only 8.4 μmol O_2-evolved. The decrease in CO_2-fixation is about 50% whereas that of oxygen evolution, although decreased, is only between 10–20% (Table II). At the same time photorespiration measured as $^{18}O_2$-uptake in the light increases from ≈ 0.58 μmol mg Chl^{-1} · h^{-1} (which is low for a control) to 0.99 μmol mg Chl^{-1} · h^{-1}. In addition the formerly low P_{O_2}/P_{CO_2} ratio of 0.5 (Tables I and II) **increased** to a normal value of ≈ 1 (exactly 0.915) (Table II). Accordingly, the effect of SO_2 deals exclusively with that part of CO_2 fixation which is not related to O_2-evolution (Table I) and which we tentatively attribute to a CAM-type activity. Only this activity seems to be affected by the SO_2-treatment and is fully inhibited. In conclusion, the SO_2-treatment restores the O_2/CO_2 gas exchange properties of *Aleurites* to those of a typical C_3-plant (Table II). It should be kept in mind that a low photorespiratory value of 0.58 μmol $^{18}O_2$-uptake · mg chlorophyll^{-1} · h^{-1} can be enhanced to about 1 μmol O_2-uptake · mg Chl^{-1} · h^{-1} which is normal for *Aleurites* (Table I and II). If it is grown under 700 ppm CO_2 according to the protocol described above (meaning that the plants which have been kept for 4 months in air containing 700 ppm CO_2) are exposed for 2 weeks to an atmosphere of 0.3 ppm SO_2, the inhibitory effect of SO_2 on the portion of *Crassulacean* type CO_2-fixation (shown in Table II) has disappeared (Table III). This becomes evident by a normal P_{O_2}/P_{CO_2} ratio of about 0.5 (Table III) just as for the control and CO_2-plants shown in Table I. Hence, an increased CO_2-content in the atmosphere attenuates the effect of SO_2 on plant growth and metabolism of *Aleurites montana* as already shown earlier for other metabolic parameters (see Table IV in He *et al.*, 1996). The most striking feature is that photorespiration which is completely suppressed by any increase of CO_2 in the short-term experiment as well as in the long-term experiment (Table I) reappears under the impact of SO_2 although the plant has been kept in air with 700 ppm CO_2 for 4 ½ months (Table III). Here, photorespiration observed is at the maximum value of the control grown under 350 ppm (Table I). Evidently, SO_2 interferes with the carbon metabolism of photosynthesis. In context with the *Crassulacean* type metabolism in *Aleurites montana* it should be noted that the CAM-type metabolism is not strictly genetically fixed (Grams *et al.*, 1995; Gehrig *et al.*, 1995).

Table III. Effect of 0.3 ppm SO_2 on CO_2- and O_2 gas exchange rates in leaves of *Aleurites montana* grown in air with an increased CO_2-content of 700 ppm.

Plants and CO_2 atmosphere	Rates of photosynthesis (μmol CO_2 or O_2)				Ratio	$^{18}O_2$-uptake (μmol O_2)		Ratio
	P_{CO_2}		P_{O_2}		P_{O_2}/P_{CO_2}	in light (U_L*)		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}	
700 ppm plants measured at 350 ppm CO_2	13.4 ± 1.6	94.3 ± 17.3	6.2 ± 1.6	45.6 ± 7	0.46 ± 0.3	0	0	0
"SO_2-plants" measured under 350 ppm CO_2	13.17 ± 0.9	91.7 ± 4.1	5.03 ± 0.53	34.98 ± 1.6	0.38 ± 0.11	0.96 ± 0.11	6.7 ± 0.3	0.19 ± 0.007

Age of the *Aleurites* plants: *Control plants* were grown for 3 months in normal air containing 350 ppm CO_2 and then transferred to an atmosphere of air enriched with 700 ppm CO_2 and grown for 4 months and two weeks under these conditions. SO_2-plants were grown 3 months in normal air, transferred to air enriched with 700 ppm CO_2 and grown for 4 months under these conditions and then subjected for two weeks to this atmosphere supplemented with 0.3 ppm SO_2. The variations given represent absolute variations due to the performance of the different leaves tested.

Discussion

Photorespiration is considered as the decisive process which limits plant productivity (Zelitch and Day, 1968; Böger, 1983). A CO_2-dependence of photorespiration, which occurs **during** photosynthesis, is experimentally difficult to determine (Ishii and Schmid, 1982). Only a few laboratories are equipped to measure this dependence. (Gerbaud and André, 1979; Ishii and Schmid, 1982; He *et al.*, 1995). Generally, leaves from plants that had been grown under normal atmospheric conditions of 350 ppm CO_2 were exposed *in vitro* for a short time to different CO_2-concentrations and photorespiration was subsequently measured by mass spectrometry. The results of such studies were not simple but reasonable (see for example, Fig. 2 in He *et al.*, 1995). The interpretation followed the hypothesis that photorespiration essentially depended on the bifunctional ribulose-1,5-bisphosphate carboxylase/oxygenase activity and therefore was diminished by an increased CO_2-partial pressure and stimulated by an increased O_2-partial pressure. The data thus obtained (i.e. Gerbaud and André, 1979; Ishii and Schmid, 1982; He *et al.*, 1995) and other measurements with less appropriate methods led to the conclusion that photorespiration in the investigated C_3-type plants in a 700 ppm CO_2 atmosphere, would be practically suppressed. It was overlooked that the plant system could adapt to a modification of its atmospheric environment. The plant, e.g. tobacco can overcome these changes by a structural modification of its photosynthetic apparatus (He *et al.*, 1995). Tobacco plants which have been grown under 700 ppm CO_2 develop a smaller light antenna in photosystem I (Makewicz *et al.*, 1995). Moreover, the pigment-lining is changed with particular respect to carotenoids and the lipid-lining of the peptides of the reaction core of photosystem I (Makewicz *et al.*, 1995). Not only the lipid composition of the photosynthetic membrane is changed but also that of all functional membranes such as that of mitochondria, the cell membranes of the tonoplast, the plasmalemma and of the endoplasmatic reticulum (He *et al.*, 1997). The plant response is a change of membrane fluidity, achieved not necessarily by an alteration of the lipid type of the membrane but by a different saturation degree of the fatty acids within the respective lipid (Radunz *et al.*, 1997). As far as the present studies permit to conclude, photosystem II also undergoes changes in the macrostructure of the photosystem II complex, namely in the region of the light antenna (Alfermann and Schmid, in preparation). Since such structural adaptations have been neglected, measured dependencies such as the CO_2-dependence of photorespiration under *in vitro* conditions of the unadapted plant system are worthless with respect to an answer of the question what would happen if the CO_2-concentration of air is durably increased. The results with tobacco exposed to 700 ppm CO_2 in air show that photorespiration is not abolished with plants that have been grown all the time under 700 ppm CO_2 in air (He *et al.*, 1995). As demonstrated with *Aleurites montana* photorespiration occurs in this C_3/CAM intermediate but here photorespiration just as in the old dependencies measured with tobacco in the artificial system is absent with plants grown under 700 ppm CO_2 in air. The important result of this observation is that **different plants** will react to changes of the atmospheric composition **in different ways**. This implies that today's plant ecosystems will be changed with increasing the CO_2 content of air. The fact that with *Aleurites montana* photorespiration under 700 ppm is restored when the plant is temporarily exposed to an increased SO_2 content of the atmosphere (Table II and III) shows that adaptation constraints take course as interactions. Thus, to the adaptation coercion of an increased CO_2 content, the interaction with higher temperatures, light intensity, air pollutants (e.g. SO_2) and water stress will incurably belong. That the plants take all this into account, if exposed to the increased CO_2-content, is seen from the fact that growth in increased CO_2 leads to a structural change of the photosynthetic apparatus in which the light antenna is diminished (Makewicz *et al.*, 1995). The plant apparently awaits also higher light intensities. It will be necessary to understand the system-complex of these interactions.

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