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## Photosynthetic Acclimation in Plants Growing Near a Carbon Dioxide Spring

By

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### Summary

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Photosynthesis of several plant species (*Phleum pratense*, *Echinochloa crus-galli*, *Juncus effusus*, *Plantago major*), grown under naturally elevated CO<sub>2</sub> at the Stavešinci mofette area, NE Slovenia, was studied. Plants were selected for photosynthetic measurements according to soil CO<sub>2</sub> concentration measured within the rooting zone and/or according to their height. Plant height was in good agreement with soil CO<sub>2</sub>. Differences in several decisive photosynthetic parameters (photosynthesis measured at different CO<sub>2</sub> concentrations, carboxylation efficiency and CO<sub>2</sub> compensation point) were affected in various C3 species and also in the C4 grass *E. crus-galli*. Results show that both C3 and C4 plants had adapted to extreme CO<sub>2</sub> conditions and had adjusted respiration and photosynthetic carbon assimilation according to the CO<sub>2</sub> exposure.

### Introduction

Atmospheric carbon dioxide concentration has a significant impact on leaf photosynthesis in C3 (BOWES 1993) and also in C4 plants (ZISKA & BUNCE 1997). Elevated CO<sub>2</sub> concentrations usually result in a significant increase in leaf photosynthesis and vegetative growth (BOWES 1993, CONSTABLE & al. 1992, DRAKE & al. 1997, ZISKA & BUNCE 1997). This has been shown in many short-term experiments, mainly related to the problem of increasing atmospheric CO<sub>2</sub> concentrations. Extending the duration of elevated (e.g. doubled) CO<sub>2</sub> to weeks or years, however, often leads to down-regulation of photosynthesis, i.e. to a

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reduction or even a loss of the initial photosynthetic response. This long-term response can vary with species, developmental stage, temperature, resource availability and internal factors, such as source-sink balance. Despite much effort in dissecting physiological, metabolic, and even molecular features of acclimatory down-regulation of photosynthesis among species, functional types and ecosystems, its implications and consequences are still matters of intensive debate (see BADIANI & al. 1999).

Natural CO<sub>2</sub> springs offer a good method to study the effects of long-term CO<sub>2</sub> exposure on ecosystems (RASCHI & al. 1997, BADIANI & al. 1999). Vegetation at springs has been exposed to high CO<sub>2</sub> for long periods, allowing time for acclimation, and perhaps genetic adaptation. The main reason for increased research activity at these sites is the expected increase of atmospheric CO<sub>2</sub> concentration (WMO 1990, BOWES 1993). However, investigation of ecophysiological processes at CO<sub>2</sub> springs can be related also to other issues than global change. Plants growing close to CO<sub>2</sub> springs are temporarily exposed to extreme (toxic) CO<sub>2</sub> concentrations and have to cope with huge and frequent diurnal fluctuations of local CO<sub>2</sub> conditions. There is little information on plant physiological responses at such conditions and present knowledge is limited to few plant species (e.g. COOK & al. 1998). In our study photosynthetic performance of different C3 and C4 species growing at different CO<sub>2</sub> regimes (high, medium or low CO<sub>2</sub> exposure) was studied at mofette Stavešinci, NE Slovenia.

## Material and Methods

The study was conducted between 1999 and 2001 at the geothermal mofette field near Stavešinci, Slovenia (see KALIGARIČ 1999, TURK & al. 2001). At this site very pure CO<sub>2</sub> is released into the atmosphere by several vents in a flat area of ca. 3000 m<sup>2</sup>. CO<sub>2</sub> concentrations in air strongly depended on weather (wind) conditions and fluctuated from 0.036% to at least 1%. Plants of different species were found growing at locations with soil CO<sub>2</sub> ranging from 0.4 to 26% (w/v) (PFANZ & al. unpublished). The soil is a reduced gley on quaternary alluvium, consisting of silty clay material derived from different parent rocks. The vegetation at the study area at which agriculture was stopped in 1998 consists of C3 and C4 grasses and several (pioneer) herbs. The CO<sub>2</sub> exposure of plants differs according to irregular distribution of the gas releasing vents and cracks. Individual plant height is highly variable, the smallest plants can be found in the close neighborhood to the vents.

For our research the following plant species were selected: *Phleum pratense* L., *Juncus effusus* L., *Echinochloa crus-galli* (L.) P.B. and *Plantago major* L. Plants differently exposed to CO<sub>2</sub> were selected at different distances from the gas releasing vents according to their height and/or soil CO<sub>2</sub> concentration measured within the rooting zone using a landfill gas analyzer GA 2000 (Ansyco, FRG). Holes of 10, 25 and 40 cm depth were drilled into the soil with a borer and the gas-piping tubing of the analyzer was immediately inserted and values recorded.

Gas exchange measurements of intact leaves that were still attached to the plants were made with a portable porometer system (LI-6400, LI-COR Inc., Lincoln, USA). Light response curves were obtained under constant climatic conditions (20°C, 65-70% relative humidity; 24°C, 50-55% relative humidity for E- c.g.) and a controlled CO<sub>2</sub> supply (350 µmol mol<sup>-1</sup>). CO<sub>2</sub> response curves were performed at 20°C, 75% RH (24°C, 50-55% RH E. c.-g.) and 800-1000 µmol photons m<sup>-2</sup> s<sup>-1</sup>. The response of net CO<sub>2</sub>-exchange (A) to changing intercellular CO<sub>2</sub> concentrations (C<sub>i</sub>) were conducted at 20°C, 65% rel. humidity (24°C, 55% RH E. c.-g.) and light-saturating conditions (800 µmol photons m<sup>-2</sup> s<sup>-1</sup>). Statistical analysis showed that the relationship can be described most

appropriately by the exponential functions  $y = y_0 + A \cdot (1 - \exp(-B \cdot x))$  or  $y = A \cdot (1 - \exp(-B \cdot (x - y_0)))$  (E. c.-g.),  $r^2 = 0,99$ . Net  $\text{CO}_2$ -exchange was measured 10-15 min after  $\text{CO}_2$ -supply when all parameters and the total coefficient of variation (CV, %) indicated stable leaf chamber conditions.

The carboxylation efficiencies (CE,  $\text{mol m}^{-2} \text{s}^{-1}$ ) equivalent to the initial slope (B) of the  $A/C_i$ -response curves were read. Saturating external  $\text{CO}_2$  concentrations for maximal photosynthesis (SEC, %) were calculated from the individual hyperbolic equation of the  $A/C_i$ -response curves. Statistical analysis and calculations were performed using Sigma Plot 5.0 (SPSS Science Software) and Statgraphics Plus 4.0 (Statistical Graphics Corp.).

## Results and Discussion

Simultaneous measurements of  $\text{CO}_2$ , CO,  $\text{O}_2$ ,  $\text{CH}_4$  and  $\text{H}_2\text{S}$  in the soil or in the air revealed that the  $\text{CO}_2$  spring in Stavešinci is emitting very pure  $\text{CO}_2$ . No significant influence of contaminating gases on the plants could therefore be expected. The soil  $\text{CO}_2$  measured at the depth of 20 cm was thought to be indicative for the  $\text{CO}_2$  conditions during plant growth. When plant height and average soil  $\text{CO}_2$  concentration were compared, a strong correlation can be found (data not shown). Plants growing at higher soil  $\text{CO}_2$ , which is closer to the vents, were smaller. This indicates that gaseous regime directly or indirectly influences plant growth.

Gas exchange measurements revealed a significant influence of the  $\text{CO}_2$  growth conditions on several decisive photosynthetic parameters. For *Phleum pratense*, a C3 grass, maximum net photosynthesis measured at 2%  $\text{CO}_2$ , net photosynthesis measured at 0.7 and 0.35% were higher in low  $\text{CO}_2$  grown plants than in plants exposed to elevated  $\text{CO}_2$  (Table 1). In addition a lower carboxylation efficiency was found for plants exposed to elevated  $\text{CO}_2$ . Similar differences were found for other C3 plants *Juncus effusus* and *Plantago major* (data not shown) but not for the C4 plant *Echinochloa crus-galli*. For the species studied literature data on elevated  $\text{CO}_2$  effects are limited to growth responses in short term experiments. Although the results of these studies vary, at least a transient growth stimulation under doubled ambient  $\text{CO}_2$  was observed for *Phleum pratense* (NORTON & al. 1999, MORTENSEN 1999, WILSEY 2001), *Plantago major* (THOMAS & al. 1999, FONSECA & STULEN 2000) and *Echinochloa crus-galli* (ZISKA & BUNCE 1997). Information on the growth response of *Juncus effusus* is scarce (KANG & al. 2001). The photosynthetic response in these plant species has not been studied in detail with the exception of *Plantago major* growing at a  $\text{CO}_2$  spring (FORDHAM & BARNES 1999). Results of this study suggest that long-term adaptation at elevated  $\text{CO}_2$  does not appear to be linked to the intrinsic capacity for photosynthesis. In our case a clear decrease in carboxylation efficiency was found for *Plantago major*, as also for *P. pratense* and *Juncus effusus*. Hence it is concluded that a decreased activity/efficiency of Rubisco (MOORE & al. 1999) is involved in down-regulation of photosynthesis.



Table 1. Photosynthetic parameters of *Phleum pratense* and *Echinochloa crus-galli* at the CO<sub>2</sub> spring Stavešinci. Means and SE are presented (n = 4-5 for soil gas and gas exchange measurements and 6-20 for the plant height).

Plant	CO <sub>2</sub> exposure <sup>(1)</sup>	Mean height (cm)	A <sub>350</sub> <sup>(2)</sup>	A <sub>700</sub> <sup>(3)</sup>	A <sub>2000</sub> <sup>(4)</sup>	CE <sup>(5)</sup>	CO <sub>2</sub> compensation point <sup>(6)</sup>
<i>Phleum pratense</i>	Low (0.4%)	135 ± 15	16.9	21.6	23.0	4.2	36
	Medium (3.3%)	47 ± 7	8.9	15.2	20.4	2.2	93
	High (26%)	23 ± 5	7.8	14.9	20.3	2.3	144
<i>Echinochloa crus-galli</i>	Low	66 ± 2	14.3 ± 1	15.7 ± 1.3	17.3 ± 1.2	19 ± 3	5.1 ± 3.1
	Medium	34 ± 2	11.1 ± 1.0	13.8 ± 1.0	15.8 ± 1.0	15 ± 2	7.2 ± 2.5
	High	15 ± 3	12.4 ± 1.8	15.3 ± 2.1	18.0 ± 1.8	13 ± 3	9.0 ± 5.9

<sup>(1)</sup>Plants were selected at different distances from the gas releasing vents according to their height and soil CO<sub>2</sub> concentration at the rooting zone (*P. pratense* only). For soil CO<sub>2</sub> values in % are given in parentheses. <sup>(2-4)</sup>Net assimilation rates measured at 350 (A<sub>350</sub>), 700 (A<sub>700</sub>) or 2000 (A<sub>2000</sub>) µmol CO<sub>2</sub> mol<sup>-1</sup> in (µmol CO<sub>2</sub> fixed m<sup>-2</sup> s<sup>-1</sup>). <sup>(5)</sup>Carboxylation efficiency (µmol m<sup>-2</sup> s<sup>-1</sup>). <sup>(6)</sup>CO<sub>2</sub> compensation point (µmol mol<sup>-1</sup>).

In general, studies of photosynthetic acclimation at natural CO<sub>2</sub> springs revealed inconsistent results (BADIANI & al. 1999, VAN GARDINGEN & al. 1997). In spite of acclimation-promotive conditions, which are typical for spring sites, poor availability of mineral nutrients for example, photosynthetic down-regulation, in terms of photosynthetic capacity, carboxylation efficiency, and Rubisco content was rarely found. In the work of COOK & al. 1998 photosynthesis of the sub-Arctic grass *Nardus stricta* was studied. Comparisons between plants growing at elevated CO<sub>2</sub> (estimated mean air CO<sub>2</sub> ≅ 790 µmol mol<sup>-1</sup>) and plants growing in adjacent areas exposed to ambient CO<sub>2</sub> concentrations (≅ 360 µmol mol<sup>-1</sup>) showed reductions in photosynthetic capacity, reductions in the content, activity and activation state of Rubisco and decreased chlorophyll content under elevated CO<sub>2</sub>. On the other hand no acclimation of photosynthesis has been reported for grasses from temperate regions, or grassland species of agricultural importance (BADIANI & al. 1999). In *Agrostis canina* for example, no change in light saturated photosynthesis, carboxylation efficiency and the content of Rubisco was found (FORDHAM & al. 1997). Our research at Stavešinci however, suggests a general tendency to photosynthetic acclimation in C3 species. A plausible rationale for down-regulation is that it optimizes carbon gain with respect to the lower capacity of the plant for carbon utilization. This lower capacity is a direct (CO<sub>2</sub> toxic action) or indirect result (anoxia in the soil and concomitant effects on the roots,

absorption of mineral nutrients etc.) of CO<sub>2</sub> exposure. There is no evidence for similar acclimation in C4 plant *E. crus-galli*. Still, a slight but not significant decrease in CE under elevated CO<sub>2</sub> can be observed.

In all plant species measured the CO<sub>2</sub> compensation point of the ACI curves strongly depended on the prevailing CO<sub>2</sub> conditions (Table 1). In *Phleum* CO<sub>2</sub> compensation point was at 48, 97 and 170  $\mu\text{mol mol}^{-1}$  CO<sub>2</sub> for low-, medium- and high-CO<sub>2</sub> grown plants, respectively. A similar trend was observed for *Plantago* and *Juncus* (data not shown). Interestingly, a shift in the CO<sub>2</sub> compensation point was observed in C4 plant *E. crus-galli*, too. Values 5.2, 7.2 and 9.0  $\mu\text{mol mol}^{-1}$  CO<sub>2</sub> were recorded for low-, medium- and high-CO<sub>2</sub> exposure, respectively. Results show that both C3 and C4 plants adapted to extreme CO<sub>2</sub> conditions and had adjusted photosynthetic carbon assimilation and respiration according to the CO<sub>2</sub> exposure. There is abundant evidence that a reduction in dark respiration occurs when atmospheric CO<sub>2</sub> is increased (DRAKE & al. 1999) and similar effect can be described for photorespiration. However, no data on changes in photorespiration are available from natural CO<sub>2</sub> springs and information on dark respiration is very scarce indicating stage-specific increase (see BADIANI & al. 1999). More detailed physiological and biochemical studies of vegetation at the mofette Stavešinci are therefore needed to explain the observed effects.

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