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Growth and root respiration of C4 plants under CO_2 enrichment

Rast in dihanje korenin C4 rastlin pri povečani koncentraciji CO_2

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Abstract. Respiratory measurements of apical root parts of several C4 plant species (*Echinochloa crus-galli* var. *crus-galli*, *Setaria pumila* and *Zea mays* DK 312 (Dekalb, USA) subjected to an elevated CO_2 regime during growth in climatic chambers or at natural CO_2 springs were performed.

Biomass production, root respiratory potential and root respiration of *Echinochloa* was not significantly changed by high atmospheric CO_2 treatment in the climatic chambers, compared to ambient CO_2 treatment.

Root respiratory potential of C4 weeds (*Echinochloa crus-galli* and *Setaria pumila*) growing in natural CO_2 spring area was not significantly affected by extremely high CO_2 in the rhizosphere. Yet, respiratory potential of one and a half month old sown maize seedlings was significantly lower in the roots exposed to naturally elevated CO_2 concentrations.

Key words: root respiration, ETS activity, respiratory potential, C4 plants, *Echinochloa crus-galli*, *Zea mays*, *Setaria pumila*, elevated CO_2, natural CO_2 springs, CO_2 mofette

Izvleček. V pričujoči raziskavi smo merili dihalno aktivnost apikalnih delov korenin nekaterih C4 vrst (navadne kostrebe *Echinochloa crus-galli* var. *crus-galli*, sivozelenega muhviča *Setaria pumila* in koruze *Zea mays* DK 312 (Dekalb, ZDA), izpostavljenih povečani koncentraciji CO_2 med rastjo v klimatskih komorah ali ob naravnih izvirih CO_2.

Pri navadni kostrebi povečana koncentracija CO_2 v klimatskih komorah ni značilno vplivala na produkcijo biomase, dihalni potencial in dihanje korenin.

Ekstremno povečana koncentracija CO_2 v rizosferi rastlin (navadne kostrebe in sivozelenega muhviča) ob naravnih izvirih CO_2 ni značilno vplivala na dihalni potencial v koreninah. Ta je bil značilno manjši le pri mesec in pol stari sejani koruzi rastoči na področju naravnih izvirov CO_2.

Ključne besede: dihanje korenin, aktivnost ETS, dihalni potencial, C4 rastline, *Echinochloa crus-galli*, *Zea mays*, *Setaria pumila*, povečana koncentracija CO_2, naravni izviri CO_2, CO_2 mofeta

Introduction

An elevated atmospheric CO_2 concentration can have a significant effect on growth and carbon metabolism of many plant species. On a daily basis, more than 50% of the photosynthates produced, may be simultaneously respired by roots (LAMBERS et al. 2002). Compared to the number of papers on inhibition of aboveground shoot respiration by elevated CO_2 (e.g. AMTHOR 1991, DRAKE et al. 1997, TJOELKER et al. 2001), very little information on the effects of elevated CO_2 on root respiration has been published so far. Furthermore, the reported CO_2 effects on root respiration are rather heterogeneous, limited to only few plant species and differently discussed among authors (e.g. BURTON et al. 1997, YODER et al. 2000, LAMBERS et al. 2002). LAMBERS et. al. (1996) report that there is insufficient evidence to state that root respiration is inhibited by the $[CO_2]$ around roots in a similar manner as leaf respiration is inhibited by elevated CO_2 in the atmosphere. Moreover, there is no convincing evidence for a direct effect of elevated atmospheric CO_2 on the specific rate of root respiration or the fraction of carbon required for root respiration. However, there are probable indirect effects of elevated CO_2 on the carbon requirement of plants in natural systems.

The partial pressure of CO_2 in soil may differ from the CO_2 partial pressure above ground and it seems to be more variable. The concentration of CO_2 in soil rapidly increases after rainfall because its diffusion through the gas phase is restricted by the water saturation of the soil. Thus, plant roots are frequently exposed to relatively high CO_2 concentrations. Water flooding can also present a longer exposure of roots to elevated CO_2 and consequently hypoxic environment. Plants growing near CO_2 springs are exposed to extreme CO_2 regimes that can also lead to hypoxic conditions in the rhizosphere. Vegetation at CO_2 springs has been exposed to such conditions for long periods, giving time for acclimation, and perhaps also genetic adaptation of plants (VODNIK et al. 2002). Thus, natural CO_2 springs may represent a good model ecosystem to study effects of elevated CO_2 on plants (RASCHI et al. 1997, BADIANI et al. 1999).

Our work was performed on three C4 plant species *Echinochloa crus-galli* var. *crus-galli*, *Setaria pumila* and *Zea mays* DK 312 (Dekalb, USA) subjected to an elevated CO_2 regime during growth in climatic chambers as well as in a CO_2 spring-area Stavešinci in NE Slovenia.

Material and methods

Seedlings of *Echinochloa*, the offsprings of plants growing near the CO_2 springs, were grown in climatic chambers under ambient (368.4 ± 15.6 µmol CO_2 mol^{-1}) and elevated (1906.2 ± 195.0 µmol CO_2 mol^{-1}) CO_2 for seven weeks at the temperature 25 °C during the light (14 h) and 16 °C during the dark period (10 h) of the day. The fumigation started two weeks after seed germination. After the growth period plant roots were sampled for respiratory measurements.

In the July 2002, root samples were also collected for natural growing *Echinochloa*, *Setaria* and one and a half month old plants of sown maize (*Zea mays* DK 312, Dekalb, USA) growing in the natural CO_2 spring area Stavešinci in NE Slovenia (for detailed information on the site characteristics and other details see VODNIK et al. in press). The plants were chosen according to their height and the preliminary measured soil CO_2 concentration in the rooting zone by a gas analyzer GA 2000 (Ansyco, FRG). A significant correlation between plant height and plant exposition to elevated CO_2 from CO_2 springs is known from our previous studies (VODNIK et al. 2002[a,b], TURK et al. 2002).

Root respiration rates were measured as oxygen consumption on root tip segments (1 cm length) using Clark-type oxygen electrodes (Hansatech, Norfolk, UK). Measurements were performed in 50 mM MES (morpholinoethanesulfonic acid) buffer solution pH 6 at 20 °C.

The root respiratory potential - electron transport system (ETS) activity was determined on root tip segments (1 cm length) using the iodonitrotetrazolium salt (INT) method described by KENNER & AHMED (1975).

Statistical analyses were performed by Statgraphic Plus 4.0 (Statistical Graphics Corp.).

Results and discussion

In the fumigation experiment no significant impact of high atmospheric CO_2 concentration on biomass production of *Echinochloa* was found (Tab. 1). In general, the growth response of C4 plants to elevated [CO_2] is inconsistent and depends on various environmental factors (GHANNOUM et al. 2000). For *Echinochloa* the increase of plant biomass under elevated CO_2 concentration (690 µmol mol^{-1}) was documented by ZISKA et al. (1997).

Measurements of root oxygen consumption revealed no significant differences in root respiration of elevated CO_2 chamber-grown *Echinochloa* plants. There was also no significant difference in root respiratory potential (Tab. 1).

Table 1: Biomass production, root respiration and root respiratory potential of *E. crus-galli* var. *crus-galli* subjected to elevated atmospheric CO_2 in climatic chambers, (avg ±SD).

	Ambient CO_2 (368.4 ± 15.6 µmol CO_2 mol^{-1})	Elevated CO_2 (1906.2 ± 195.0 µmol CO_2 mol^{-1})
Dry weight of shoot (g) $^{(1)}$	0.95 ± 0.26	1.15 ± 0.26
Dry weight of root (g) $^{(1)}$	0.83 ± 0.16	0.89 ± 0.33
Root respiration$^{(2)}$	1.5 ± 0.6	1.8 ± 0.5
ETS roots$^{(3)}$	1.0 ± 0.2	1.0 ± 0.2

$^{(1)}$By ANOVA, n = 24. $^{(2)}$Given as nmol O_2 g^{-1} fresh wt s^{-1}, by ANOVA, n = 15. $^{(3)}$Given as µg O_2 g^{-1} fresh wt h^{-1}, by ANOVA, n = 15

In addition to these findings, measurements of *Echinochloa* exposed to different CO_2 regimes at the natural CO_2 spring Stavešinci showed no significant effects of high rhizospheric CO_2 concentration on root respiratory potential of the root-tip segments. The same was true for another C4 plant *Setaria pumila* (Tab. 2). It is to conclude that both species are relatively insensitive to high CO_2. A high tolerance of *E. crus-galli* to hypoxia is known from different studies and is especially well documented for its variety *E. crus-galli* var. *oryzicola* (BUCHANAN & al. 2000). Germination of *E. crus-galli* could be stimulated by elevated CO_2 as it was shown by YOSHIOKA & al. (1998). In this study germination was stimulated by exposure to 30 mmol mol^{-1} CO_2 and it was concluded that soil CO_2 is responsible for causing intermittent flushes of seed germination of this species after heavy rainfall. This could also explain the presence of germinating and growing *Echinochloa* plants at the sites with extreme CO_2 concentrations in the natural CO_2 spring Stavešinci as reported by KALIGARIČ (2001). No similar reports have been published on *Setaria pumila*.

Table 2: Shoot height and root respiratory potential of *E. crus-galli* var. *crus-galli*, *S. pumila* and *Z. mays* subjected to elevated soil and atmospheric CO_2 at a natural CO_2 spring (avg ± SD).

Plant species	CO_2 exposure[1]	Mean height (cm)[2]	ETS[3]
Echinochloa crus-galli	Low (0.4%)	62.3 ± 11.7	1.52 ± 0.19
	High (26%)	15.9 ± 1.8	1.55 ± 0.18
Setaria pumila	Low (0.4%)	51.0 ± 6.8	0.34 ± 0.05
	High (26%)	28.0 ± 5.6	0.32 ± 0.06
Zea mays	Low (0.1–0.4%)	239.0 ± 21.0	1.12 ± 0.13
	High (over 10%)	114.2 ± 7.9	0.95 ± 0.13

(1)Measured as soil CO_2 concentration (25 cm depth) by a gas analyzer GA 2000 (Ansyco, FRG). (2)By ANOVA, n = 10. (3)Given as $\mu g\ O_2\ g^{-1}$ fresh wt h^{-1}, by ANOVA, n = 12.

Results on *Echinochloa* and *Setaria*, could indicate a general low sensitivity of root respiration to a high CO_2 concentration, which is suggested by LAMBERS et al. (1996, 2002). Yet, root respiratory potential in root tips of *Zea mays* measured in our study was significantly lower in the roots exposed to high soil CO_2 than in those growing in the low CO_2 environment (Tab. 2). Different results obtained for native species (*Echinochloa*, *Setaria*) and sown maize suggest that plants growing as a part of natural vegetation could be adapted to extreme conditions. This however, has to be confirmed in the future work.

Conclusions

At natural CO_2 springs, the growth of *Echinochloa* and *Setaria* can be decreased by high CO_2 concentrations and physiological processes in shoots can be severely affected. Despite this, no significant impact of CO_2 exposure on root respiratory potential of the root-tip segments was found for the same species. More detailed physiological studies on root respiration are needed, regarding to the different parts of the root system, different ontogenetic development and measurements on different plant species. Further research is also needed in connection to different environmental factors affecting root respiration.

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