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Effect of Elevated Atmospheric CO_2 on Carbohydrate Partitioning and Plant Growth

By

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Summary

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The effect of elevated CO_2 on changes in shoot and root soluble carbohydrate and starch content, and various growth parameters was investigated in an apoplastic (*Bellis perennis*) and a symplastic loader (*Epilobium hirsutum*). Comparison with data on other plant species, grown under the same climatic conditions, showed that the way of phloem loading might not be the decisive factor to explain differences in shoot carbohydrate pool between various plant species. We speculate that the growth strategy of a plant is the major factor in explaining differences in carbohydrate partitioning and magnitude of growth stimulation by elevated CO_2.

Introduction

In the next century a doubling of the current atmospheric CO_2 concentration (approximately 350 $\mu l\ l^{-1}$) can be expected (HOUGHTON & al. 1990). Growing plants at double the atmospheric CO_2 concentration can result in changes in chemical composition, as a higher soluble carbohydrate and a lower nitrogen concentration, physiological processes as photosynthesis and nutrient uptake, and dry matter partitioning between plant organs. However the magnitude and/or the direction of

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the responses is often variable and may be dependent on the developmental stage of the plant, the experimental set up and the accumulation of nonstructural carbohydrates (ref. in STULEN & al. 1998).

Exposure of herbaceous plants to elevated atmospheric CO_2 usually results in an increase in biomass production (POORTER 1993, STULEN & al. 1998), which is often the result of a transient stimulation of the relative growth rate (RGR) at the beginning of the experiment. The transient nature of the stimulation of the RGR has been ascribed to a number of factors as accelerated plant development resulting in increased self-shading (POORTER 1993), earlier depletion of nutrients (ARP 1991), photosynthetic acclimation, viz. a decrease in photosynthetic rate due to a negative feedback of carbohydrates on the rate of photosynthesis (BESFORD 1993, VAN OOSTEN & al. 1994) and changes in partitioning of carbohydrates (FONSECA & al. 1997).

Exposure to elevated CO_2 increased nonstructural carbohydrate content in the shoot of many plant species (BAZZAZ 1990, DEN HERTOG & al. 1996, FONSECA & al. 1996, 1997, POORTER & al. 1988, VAN DER KOOIJ & DE KOK 1996, WONG 1990, YELLE & al. 1989). It has been postulated that plants with apoplastic phloem loading might exhibit less accumulation of total nonstructural carbohydrates (TNC) in the shoot than plants with symplastic phloem loading; the difference might become greater at elevated CO_2 (KÖRNER & al. 1995). Shoot nonstructural carbohydrate pool shows daily fluctuations (FONSECA & al. 1997) and is dynamic as the result of changes in input by photosynthesis, and output for structural shoot growth and export to other parts of the plant. The aim of this paper was to investigate the effect of elevated CO_2 on changes in shoot and root TNC content in combination with growth parameters in an apoplastic and a symplastic loader, grown under the same climatic conditions.

Materials and Methods

Seeds of the apoplastic loader *Bellis perennis* and the symplastic loader *Epilobium hirsutum* were germinated and transferred into nutrient solution (17 days after sowing) as described by FONSECA & al. 1996, 1997. Seeds of the apoplastic loader *Valeriana officinalis* and the symplastic loader *Origanum vulgare* were transferred into potting soil, 13 and 16 days after sowing, respectively. Ten days thereafter the plants were randomly divided over two climate controlled rooms, kept at 350 and 700 $\mu l\ l^{-1}$ CO_2, a temperature of 20° C, a relative humidity of 60-65 %, and a light intensity of 300 - 350 $\mu mol\ m^{-2}\ s^{-1}$ for 12 h.

Sugar and starch contents were determined in dried material as described in FONSECA & al. 1996, 1997. In the roots of *B. perennis* inuline was also present, which was determined by extracting the 80% ethanol insoluble pellet in boiling demineralized water, followed by the assay of FALES 1951. For *B. perennis* and *E. hirsutum* carbohydrates in shoot and root were measured 6 and 12 days after the plants were exposed to elevated CO_2. In *V. officinalis* and *O. vulgare* shoot carbohydrates were measured 7 days after transfer to elevated CO_2. The plants were all harvested at 10.00 h. In another experiment with *B. perennis* and *E. hirsutum* carbohydrates were determined 3 days after transfer to elevated CO_2, at the end of the light period (18.00 h), and the beginning of the light period (6.00 h) the next day. The results were analyzed by Student t-test.

At both atmospheric CO_2 concentrations a growth analysis was carried out with *B. perennis* and *E. hirsutum*, by harvesting 10 plants of each species every 3 days. Fresh and dry weight of shoot and root were determined separately (FONSECA & al. 1996, 1997). The growth parameters,

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relative growth rate (RGR; after POORTER 1989), and root weight ratio (RWR; after HUNT 1990) were all determined on a fresh weight basis to avoid interference of accumulation of TNC in the interpretation of the results (STULEN & al. 1998). The results were analyzed by Student t-test.

Results and Discussion

The analysis of nonstructural carbohydrates showed a difference between *B. perennis* and *E. hirsutum*. At day 6, soluble sugars and starch were increased in shoot as well as root of the apoplastic loader, *B. perennis*, while in the symplastic loader, *E. hirsutum*, only shoot starch content was increased. At day 12, only shoot soluble sugar was increased in *B. perennis*, while in shoot as well as root of *E. hirsutum* both fractions were higher at elevated CO_2 (Table 1).

Table 1. Soluble sugar and starch[1] content in shoot (S) and root (R) of *B. perennis* (*B.p*) and *E. hirsutum* (*E.h.*), in mg glucose g FW^{-1}. Significant differences between the CO_2 treatments are indicated with [a] ($P < 0.001$), [b] ($P < 0.01$) and [c] ($P < 0.05$). Inulin is included in the starch fraction of the root of *B. perennis*.

			Soluble sugar (mg g FW^{-1})		Starch[1] (mg g FW^{-1})	
		Day	350 µl l^{-1}	700 µl l^{-1}	350 µl l^{-1}	700 µl l^{-1}
B.p.	S	6	15.4 ± 3.4	31.2 ± 9.9[c]	12.0 ± 1.0	20.6 ± 4.0[c]
	R		8.5 ± 2.1	14.2 ± 3.0[c]	10.3 ± 1.1	13.1 ± 0.8[c]
	S	12	25.0 ± 1.0	39.1 ± 5.5[b]	14.1 ± 1.6	16.5 ± 4.8
	R		19.2 ± 4.1	20.3 ± 6.8	17.5 ± 5.6	19.6 ± 2.6
E.h.	S	6	6.5 ± 0.4	6.0 ± 1.8	14.1 ± 1.8	28.6 ± 2.1[a]
	R		2.8 ± 1.1	2.3 ± 0.2	3.4 ± 0.8	4.2 ± 0.3
	S	12	7.1 ± 0.6	8.7 ± 0.6[c]	15.3 ± 0.8	23.9 ± 2.0[c]
	R		2.3 ± 0.2	3.3 ± 0.6[b]	2.8 ± 0.5	4.5 ± 0.1[b]

Table 2. Soluble sugar and starch[1] content in shoot (S) and root (R) of *B. perennis* (*B.p*) and *E. hirsutum* (*E.h.*), in mg glucose g FW^{-1}, measured at day 3 (18.00 h) and day 4 (6.00 h) after transfer to elevated CO_2. Significant differences between data of 18.00 and 6.00 are indicated with * ($P < 0.05$). [1] Inulin is included in the starch fraction of the root of *B. perennis*.

			Soluble sugar (mg g FW^{-1})		Starch[1] (mg g FW^{-1})	
		Time	350 µl l^{-1}	700 µl l^{-1}	350 µl l^{-1}	700 µl l^{-1}
B.p.	S	18.00	17.5 ± 0.8	35.2 ± 1.1	18.6 ± 0.3	32.0 ± 1.3
	R		11.8 ± 0.2	17.7 ± 0.3	13.1 ± 1.3	15.2 ± 1.2
	S	6.00	9.7 ± 0.7 *	28.8 ± 1.4 *	11.9 ± 0.1 *	17.7 ± 1.0 *
	R		12.0 ± 0.5	13.3 ± 0.5 *	14.3 ± 0.4	16.3 ± 0.7
E.h.	S	18.00	5.1 ± 0.1	5.0 ± 0.5	25.9 ± 0.3	41.6 ± 2.0
	R		1.3 ± 0.1	1.1 ± 0.2	4.5 ± 0.3	4.7 ± 0.2
	S	6.00	11.0 ± 0.0*	4.9 ± 0.1	9.1 ± 0.1 *	25.9 ± 0.4 *
	R		2.2 ± 0.3 *	2.2 ± 0.2 *	4.6 ± 0.1 *	4.5 ± 0.5 *

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Changes in non structural carbohydrates between the end and the beginning of the light period were also different for *B. perennis* and *E. hirsutum* (Table 2). During the night both soluble sugars and starch were decreased in the shoot of *B. perennis*, while in the root no changes were found. This pattern was not changed by elevated CO_2. During the night soluble sugar content was increased, and starch content was decreased in the shoot of *E. hirsutum*, while in the root soluble sugar content was increased. At elevated CO_2 there was no change in sugar content, while the increase in starch content was less.

The effect of elevated CO_2 on carbohydrate contents in the shoot of the apoplastic loader *V. officinalis* and the symplastic loader *O. vulgare* was similar. In both species the starch fraction was increased most (Table 3).

Table 3. Soluble sugar and starch[1] content in the shoots of *V. officinalis* (*V.o.*) and *O. vulgare* (*O.v.*), in mg glucose g FW^{-1}, measured at day 7 after transfer to elevated CO_2. Significant differences between the CO_2 treatments are indicated with [a] ($P < 0.001$), [b] ($P < 0.01$) and [c] ($P < 0.05$).

	Soluble sugar (mg g FW^{-1})		Starch[1] (mg g FW^{-1})	
	350 µl l^{-1}	700 µl l^{-1}	350 µl l^{-1}	700 µl l^{-1}
V.o.	9.6 ± 0.5	13.3 ± 1.2[b]	15.1 ± 0.7	36.2 ± 2.1[a]
O.v	8.0 ± 0.4	10.4 ± 0.2[a]	23.8 ± 0.8	51.5 ± 1.0[a]

Compilation of the data found in the present experiments showed no significant difference in TNC content between the apoplastic loaders and the symplastic loaders, grown at 350 or 700 µl l^{-1} CO_2. At ambient CO_2 the average TNC content on a dry matter basis was19.2 and 19.6% for the apoplastic loaders *B. perennis* and *V. officinalis* resp. and 17 and 19.9 % for *E. hirsutum* and Origanum vulgare resp. This is not in agreement with the findings of KÖRNER & al. 1995, who found an average TNC content of 19% of dry matter for the apoplastic loaders (n=9), and 41% for the symplastic loaders (n=11). Especially in *O. vulgare* TNC content was much lower in the present experiments. At elevated CO_2 no significant differences in average TNC content on a dry matter basis were found between the apoplastic loaders and the symplastic loaders, viz. 31.0 and 33.6% for the apoplastic loaders *B. perennis* and *V. officinalis* resp. and 25.2 and 22.6 % for *E. hirsutum* and *O. vulgare* resp. These data are not in agreement with the findings of KÖRNER & al. 1995, who found that herbaceous symplastic loaders accumulated significantly more TNC at any given CO_2 level. Before any general conclusion can be drawn, it should be kept in mind that in our experiments only two apoplastic- and two symplastic loaders were used. However, it should also be noted that the list of symplastic species used by KÖRNER & al. 1995 contains a relatively large number of horticultural species, which have the highest TNC contents. The absolute increase in TNC content at elevated CO_2 was lower under our conditions, viz. 12 and 14% for the apoplastic *B. perennis* and *V. officinalis* resp., and 8 and 3% for the symplastic *E. hirsutum*

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and *O. vulgare* resp., compared to the 29% and 14% for the herbaceous apoplastic and symplastic species in the experiments of KÖRNER & al. 1995. The difference between the apoplastic- and symplastic loaders was not significant, which is in agreement with the findings of KÖRNER & al. 1995. In conclusion, although the way of xylem loading is one of the factors influencing shoot TNC pool, without data on photosynthetic input, and output for structural growth and storage it is not possible to draw a firm conclusion on the relationship between way of phloem loading and shoot TNC pool.

Plotting RGR versus ln FW, to correct for ontogenetic drift (FONSECA & al. 1996, STULEN & al. 1998) showed that elevated CO_2 caused a transient increase in RGR, which lasted approximately 9 days in *B. perennis*, and 18 days in *E. hirsutum* (Fig. 1A,B). Experiments performed under the same experimental conditions in our laboratory showed that stimulation of RGR may last from only a day for *Arabidopsis thaliana* (VAN DER KOOIJ & DE KOK 1996) to 6 and 14 days for *Plantago major* ssp. *pleiosperma* and *Urtica dioica* resp. (DEN HERTOG & al. 1993, 1996, FONSECA & al. 1996). Apparently the period of stimulation of RGR lasted longer in the spe

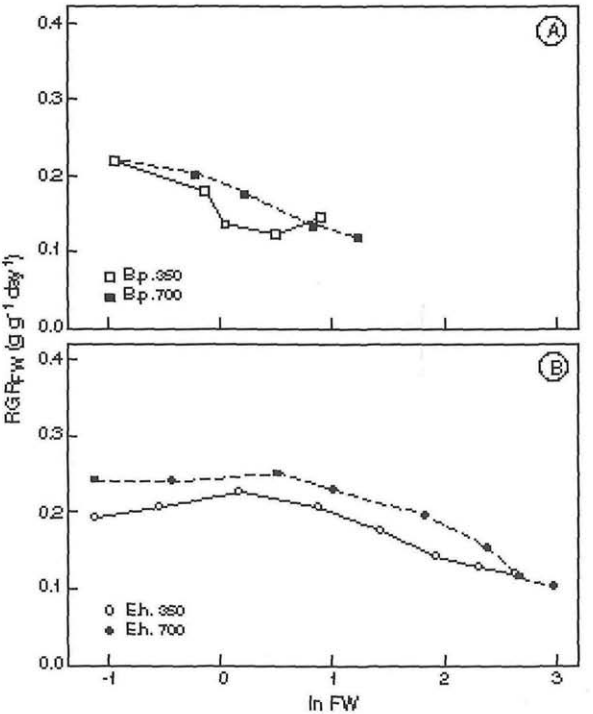

Fig. 1. Relative growth rate (RWR) on a fresh weight basis of A) *B. perennis* (*B.p.*) and B) *E. hirsutum* (*E.h.*), grown at 350 and 700 µl l^{-1} CO_2.

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cies with the more indeterminate growth pattern (*U. dioica* and *E. hirsutum*) compared to the species with the more determinate growth pattern (*A. thaliana*, *P. major* and *B. perennis*).

In neither *B. perennis* nor *E. hirsutum* RWR was affected by elevated CO_2, which is in agreement with data from many other species grown at non limiting nutrient conditions (STULEN & DEN HERTOG 1993). RWR of *B. perennis* was significantly ($P < 0.001$) higher than RWR of *E. hirsutum* over the whole experimental period (Fig. 2).

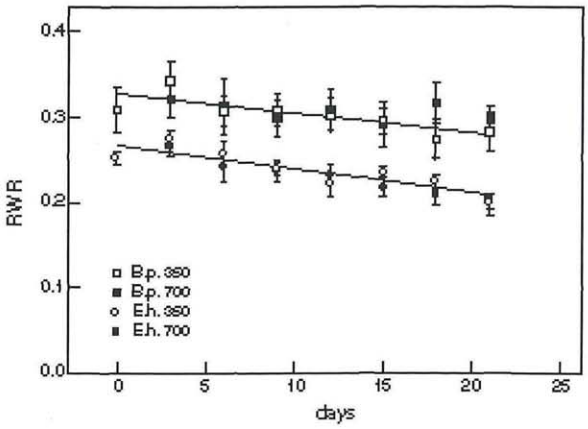

Fig. 2. Root weight ratio (RWR) on a fresh weight basis of *B. perennis* (*B.p.*) and *E. hirsutum* (*E.h.*), grown at 350 and 700 $\mu l\ l^{-1}$ CO_2.

The present experiments showed that period of transient increase in RGR was longer in the species with the more indeterminate growth pattern. Experiments with the determinate species *P. major* showed that the end of the transient increase in RGR and the simultaneously occurring stimulation of root metabolism coincided with the formation of secondary shoots (FONSECA & al. 1996, STULEN & al. 1998). This was interpreted by hypothesizing that the development of secondary shoots changed the sink:source balance, so that partitioning of the extra carbohydrates to these new sinks, placed along the transport pathway from shoot to root, took precedence over partitioning to the root. Whether growth at elevated CO_2 leads to an accumulation of TNC in the shoot is dependent on the capacity to 1) use the extra carbohydrates formed for structural growth, and 2) the storage capacity in the leaf as well as in other parts of the plant (ref. in STULEN & al. 1998). The development of new sinks can be regarded as a way to increase sink strength for structural growth.

Between the species used in the present experiments many difference were found in shoot soluble sugar and starch contents. This is not surprising, given the

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fact that species with different growth patterns were used, with different demands for use of photosynthetic carbohydrates for structural growth, different RWR and different storage capacity. Since the key factor that determines the response of a species to elevated CO_2 seems to be the ability to make or maintain sufficient sink strength, plants with a high genotypic plasticity in this respect might profit most from the expected rise in atmospheric CO_2.

References

ARP W.J. 1991. Effects of source-sink relations on photosynthetic acclimation to elevated CO_2. - Plant Cell Environ. 14: 869-875.

BAZZAZ F.A. 1990. The response of natural ecosystems to the rising global CO_2 levels. - Annu. Rev. Ecol. Syst. 21: 167-196.

BESFORD R.T. 1993. Photosynthetic acclimation in tomato plants grown in high CO_2. - Vegetatio 104/105: 441-448.

DEN HERTOG J., STULEN I. & LAMBERS H. 1993. Assimilation, respiration and allocation of carbon in *Plantago major* as affected by atmospheric CO_2 levels. - Vegetatio 104/105: 369-378.

— , — , FONSECA F. & DELEA P. 1996. Modulation of carbon and nitrogen allocation in *Urtica dioica* and *Plantago major* by elevated CO_2: Impact of accumulation of non-structural carbohydrates and ontogenetic drift. - Physiol. Plant. 98: 77-88.

FALES F.W. 1951. The assimilation and degradation of carbohydrates by yeast cells. - J. Biol. Chem. 193: 113-124.

FONSECA F., DEN HERTOG J. & STULEN I. 1996. The response of *Plantago major* ssp. *pleiosperma* is modulated by the formation of secondary shoots. - New Phytol. 133: 627-635.

— , BOWSHER C.G. & STULEN I. 1997. Impact of elevated atmospheric CO_2 on nitrate reductase transcription and activity in leaves and roots of *Plantago major*. - Physiol. Plant. 100: 940-948.

HOUGHTON J.T., JENKINS G.J. & EPHRAUMS J.J. 1990. Climate Change. - The IPCC Scientific Assessment. Cambridge University press, Cambridge.

HUNT R. 1990. Basic growth analysis, plant growth analysis for beginners. - Unwin Hyman Ltd. London.

KÖRNER C.H., PELAEZ-RIEDL S. & VAN BEL A.J.E. 1995. CO_2 responsiveness of plants: A possible link to phloem loading. – Plant, Cell and Environment 18: 595-600.

POORTER H. 1989. Plant growth analysis: Towards a synthesis of the classical and the functional approach. - Physiol. Plant. 75: 237-244.

— 1993. Interspecific variation in the growth response of plants to an elevated ambient CO_2 concentration. - Vegetatio 104/105: 99-115.

— , POT S. & LAMBERS H. 1988. The effect of an elevated atmospheric CO_2 concentration on growth, photosynthesis and respiration of *Plantago major*. - Physiol. Plant. 73: 553-559.

STULEN I. & DEN HERTOG J. 1993. Root growth and functioning under atmospheric CO_2 enrichment. - Vegetatio 104/105: 99-115.

— , — , FONSECA F., POSTHUMUS F., VAN DER KOOIJ T.A.W. & DE KOK L.J. 1998. Impact of elevated atmospheric CO_2 on plants. - In: DE KOK L.J. & STULEN I. (Eds.), Responses of plant metabolism to air pollution and global change, pp. 167-179. - Backhuys Publishers, Leiden.

VAN DER KOOIJ T.A.W. & DE KOK L.J. 1996. Impact of elevated CO_2 on growth and development of *Arabidopsis thaliana* L. - Phyton 36: 173-184.

VAN OOSTEN J.-J., WILKINS D. & BESFORD R.T. 1994. Regulation of the expression of photosynthetic nuclear genes by CO_2 is mimicked by regulation by carbohydrates: A mechanism for the acclimation of photosynthesis to high CO_2? - Plant Cell Environ. 17: 913-923.

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WONG S.C. 1990. Elevated atmospheric partial pressure of CO_2 and plant growth. II. Non-structural carbohydrate content in cotton plants and its effect on growth parameters. - Photosynth. Res. 23: 171-180.

YELLE S., BEESON R.C. JR., TRUDEL M.J. & GOSSELIN A. 1989. Acclimation of two tomato species to high atmospheric CO_2. I. Sugar and starch concentrations. - Plant Physiol. 90: 1465-1472.

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