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Effects of elevated CO_2 on growth and photosynthesis with three different cultivars of radish: which is the most limiting for maximal growth, source or sink capacity?

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Introduction

Because the present atmospheric CO_2 concentration imposes a limit to C3 photosynthesis, the predicted increase of atmospheric CO_2 concentration is expected to stimulate dry matter production of C3 plants. In the short-term, enhancement of CO_2 levels generally stimulates the net photosynthetic CO_2 fixation in C3 plants. Many studies have shown that this short-term gain can be offset, in the longer term, by negative acclimation of photosynthetic capacity, even though examples of no negative acclimation and even the positive acclimation of photosynthetic capacity have been reported (Bowes 1996). The underlying causes for acclimation of photosynthetic capacity after long-term treatment with elevated CO_2, have been the issue of experimentation and speculation, but they have been only partially identified (Bowes 1996). The negative acclimation might be related to an imbalance between source and sink capacity. One of the hypotheses is that over accumulation of carbohydrates regulates gene expression and results in down regulation of photosynthesis under elevated CO_2 (see, e.g. Bowes 1996). Indeed, White Cherrish (WC), a radish cultivar having a big storage root showed no down regulation of photosynthesis under increased atmospheric CO_2 concentration. CO_2 elevation resulted in an enhanced sink capacity that was responsible for absorbing higher level of photosynthates and preventing over accumulation of carbohydrates in source leaves. We suggested that decline of photosynthetic capacity under elevated CO_2 is due to accelerated senescence derived from accelerated ontogenesis (Usuda & Shimogawara 1998). In the present study three different cultivars of radish including WC were used to examine the effect of elevated CO_2 on growth and photosynthesis considering the role of sink capacity of storage root on photosynthetic acclimation under elevated CO_2. The two other cultivars were Cherry Belle (CB), with big storage root, which was reported to show down regulation of photosynthesis under elevated CO_2 (Moore et al. 1998) and Kosena (K) with a lower storage root being similar to the wild radish (Usuda & Rouhier 2001).

Materials and methods

Three cultivars of radish, *Raphanus sativus* L. (cv. White Cherrish, Cherry Belle and Kosena) were grown hydroponically in a growth chamber. The concentration of CO_2 in the chamber was maintained at 350 (normal) or 750 (elevated) µmol/mol and light condition was controlled with 10 or 14.5 h photoperiod. Plants were grown under four different conditions: at 350 µmol/mol of CO_2 and 10 h photoperiod (NCS), 350 µmol/mol of CO_2 and 14.5 h photoperiod (NCL), 750 µmol/mol of CO_2 and 10 h photoperiod (HCS), and 750 µmol/mol of CO_2 and 14.5 h photoperiod (HCL). Temperature was set 25 and 21˚C during light and dark period, respectively. The light intensity was 500~600 µmol/m^2s at plant height. The rate of photosynthesis was measured at CO_2 concentrations of 350 (designated as P_{350}) or 750 µmol/mol(designated as P_{750}), under light intensity of 550 µmol/m^2s and at 25°C with an infrared gas analyser (ADC LCA4, Analytical Development Corp., Hoddesdon, U.K.). Leaf disks were harvested from the first leaves of 22-day old plants at the end of dark period, frozen in liquid nitrogen and used for the determination of enzymatic determination of carbohydrates as described previously (Usuda & Shimogawara 1998). Seven plants were harvested at 22 days after sowing and separated into shoots, storage root and fibrous roots. The DW was determined after drying.

Results and Discussion

The effects of elevated CO_2 and prolonged photoperiod on growth, rate of photosynthesis and carbohydrate contents are summarized in Table 1. The rates of photosynthesis were compared with the first leaves of three cultivars of 2 and 3-week old plants grown under various conditions. With plants grown under normal CO_2 condition the ratio of P_{750} to P_{350} was 1.39± 0.053, 1.47±0.042 and 1.49±0.044 (mean ± SE, n=4) with K, WC and CB, respectively. With plants grown under elevated CO_2, it was 1.41±0.045, 1.42±0.055, and 1.40±0.018 (mean ± SE, n=4) with K, WC and CB, respectively. The mean value (± SE, n=24) for enhancement of photosynthesis by elevated CO_2 was 43±1.8%. Therefore, 45% prolonged photoperiod was chosen. Dry weight accumulation for Kosena was the highest for each growth conditions, although it partitioned only 2-3% of total dry matter into storage root. Vigorously growing shoots played at first the role of sink and then became source. With increasing CO_2 concentrations, the percentage enhancements (cv., photoperiod) in total DW after 3 weeks were 106% (K, 10 h), 37% (K, 14.5h), 52%(WC, 10hL), 60% (WC, 14.5h), 70% (CB, 10h) and 42% (CB, 14.5h). With increasing photoperiod, the percentage enhancements (cv., CO_2 condition) in total DW were 156% (K, NC), 70% (K, HC), 88% (WC, NC), 97% (WC, HC), 166% (CB, NC) and 121% (CB, HC). When the average values (± SE) of enhancement by the prolonged photoperiod (116±16%, n=6) and those obtained with elevated CO_2 (61±10%, n=6) were compared, the extension of the photoperiod showed significantly (p=0.017) bigger effect on DW accumulation than elevation of CO_2. Some trends of decline in the rate of photosynthesis were found only in the case of 3-week old Kosena grown under HCL, but no statistical significance of elevated CO_2 during growth on the rate of photosynthesis was observed (Table 1). Carbohydrates were accumulated highly in the first leaves of K, WC and CB grown under HCL and of K grown under HCS. A remarkable increase of 15 fold in the amount of glucose + fructose + sucrose + starch was found with Kosena grown under HCL compared to K grown under NCS. These results indicate that photosynthesis might be down regulated by elevated CO_2 only with K, cultivars that does not have big storage roots but presents the biggest shoots (see below for further discussion). The reasons for the discrepancy about down regulation of photosynthesis by elevated CO_2 with CB found in the present study from the previous one (Moore et al 1998) remain unclear at the moment.

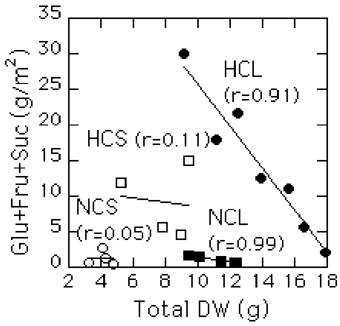
Table 1. Effects of elevated CO_2 on growth, rate of photosynthesis and level of carbohydrates with three different cultivars of radish.

CV[a]	Kosena				White Cherrish				Cherry Belle			
GC[b]	NCS	NCL	HCS	HCL	NCS	NCL	HCS	HCL	NCS	NCL	HCS	HCL
DW[c] (g)	4.0± 0.2	10.1±1.0	8.1± 0.6	13.8±1.2	2.3± 0.2	4.4± 0.7	3.6± 0.02	7.1± 0.3	1.2± 0.1	3.1± 0.4	2.0± 0.1	4.5± 0.3
SR[d] (%)	2.8± 0.2	2.5± 0.1	2.9± 0.4	2.1± 0.1	43± 2.7	53± 2.6	51± 1.3	47± 3.1	59± 1.7	57± 4.4	63± 1.1	62± 2.0
P_{350}[e]	10.8 ±0.3	12.2 ±0.5	11.6 ±0.4	11.8 ±0.3	11.8 ±0.2	12.9 ±0.4	11.4 ±0.3	12.0 ±0.8	12.9 ±0.4	14.1 ±0.2	13.3 ±0.2	13.5 ±0.7
P_{750}[f]	16.5 ±1.1	16.5 ±0.7	16.7 ±0.4	17.5 ±0.1	18.6 ±0.3	18.3 ±0.1	17.1 ±0.4	17.7 ±1.6	18.8 ±0.3	19.4 ±0.3	18.5 ±0.2	19.5 ±0.8
P_{350}[g]	11.2 ±0.7	10.4 ±0.8	10.9 ±0.4	8.7 ±1.0	11.4 ±0.1	10.4 ±0.6	12.9 ±0.4	10.6 ±1.2	14.1 ±0.8	13.1 ±0.9	13.7 ±0.5	13.7 ±0.2
P_{750}[h]	15.6 ±0.1	13.3 ±0.9	14.0 ±0.6	12.6 ±1.5	16.9 ±1.0	14.5 ±0.2	16.2 ±0.9	15.3 ±0.8	22.0 ±0.7	20.5 ±0.9	18.8 ±0.8	19.4 ±0.5
GFSS[i]	1.5± 0.6	1. 2± 0.3	13.9 ±0.9	22.3 ±5.9	0. 6± 0.03	1. 1± 0.8	2.1± 0.2	4.1± 1.5	0.7± 0.1	3.9± 1.7	1.3± 0.2	5.5± 2.6
GFS[j]	1.3± 0.5	1.1± 0.3	9.2± 2.5	14.4 ±3.6	0.5± 0.04	2.1± 0.7	0.9± 0.1	3.8± 1.4	0.7± 0.1	3.9± 1.7	1.3± 0.2	5.4± 2.5

[a] Cultivars (CV). [b] Growth condition (GC), see text for the abbreviations. [c] Dry weight (DW) of total plant (n=7). [d] Percentages of DW of storage root to total DW. [e] Rates of photosynthesis determined with the first leaves of 2–week old plants under 350 μmol/mol CO_2 (n=3-4). [f] Rates of photosynthesis determined with the first leaves of 2–week old plants under 750 μmol/mol CO_2 (n=3-4). [g] Rates of photosynthesis determined with the first leaves of 3–week old plants under 350 μmol/mol CO_2 (n=3-4). [h] Rates of photosynthesis determined with the first leaves of 3–week old plants under 750 μmol/mol CO_2 (n=3-4). [e-g] The rates were μmol $CO_2/m^2{\cdot}s$. [i] Content of glucose + fructose + sucrose + starch (GFSS) measured at dawn (g/m^2) in the first leaves of 3-week old plant (n=4-7). [j] Content of glucose + fructose + sucrose (GFS) measured at dawn (g/m^2) in the first leaves of 3-week old plant (n=4-7). All values were with ± SE.

We noticed big variations in total DW of K grown under HCL when plants should accumulate high amounts of photosynthates. We plotted the carbohydrates contents (glucose+fructose+sucrose) measured in the first leaves at dawn against the total DW at 22 days after sowing and found a significant negative relationship (Fig 1). These results strongly suggested that as long as sink capacity is important enough to absorb photosynthates which are increased by elevated CO_2 and/or prolonged photoperiod, plants are growing vigorously. No over accumulation of photosynthates occurs in the source leaves and the rate of photosynthesis might be sustained at normal level. In other words, sink capacity determines the maximal growth of K. These results also suggest that further analysis investigating the effects of elevated CO_2 on the rate of photosynthesis of K are needed, in particular when the plants are grown under HCL conditions. These conditions would be suitable for investigating the mechanisms for down regulation of photosynthesis by elevated CO_2 in relation to the significance of sink capacity. These studies will also assess the heterogeneity of maximum sink capacity for individual plants and the question previously raised in Usuda & Shimogawara (1998). What is crucial for down regulation of photosynthesis under elevated CO_2, regulation of gene expression by sugar level or accelerated senescence by enhanced ontogenesis?

Fig 1 Relationship between total dry weight and the level of glucose + fructose + sucrose measured in the first leaves at dawn with 22-day old Kosena grown under different conditions. Plants were grown under normal CO_2 with 10 h L (NCS, ○), normal CO_2 with 14.5 h L (NCL, ■), elevated CO_2 with 10 h L (HCS, □) and elevated CO_2 with 14.5 h L (HCL, ●).



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