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Effects of Doubled Atmospheric CO_2 Concentration on Apple Trees I. Growth Analysis

Auswirkungen einer Verdoppelung der atmosphärischen CO_2-Konzentration auf Apfel I. Wachstumsanalyse

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Summary

Two year old apple (*Malus domestica* Borkh. cv. 'Golden Delicious') trees on 'M9' were exposed to ambient (350 ± 10 ppm) and doubled (700 ± 10 ppm) atmospheric CO_2 for 120 d in growth chambers situated in an apple orchard. Doubled CO_2 promoted tree growth, indicated by more leaves and shoots, a larger average leaf area, and total leaf dry weight per tree, as well as a wider canopy and trunk diameter. Average shoot length and diameter, shoot length per tree, tree height, and total leaf area increased, whereas specific leaf area and leaf area ratio of the trees decreased at 700 ppm CO_2. When compared to trees grown under 350 ppm CO_2, 700 ppm CO_2-treated trees stimulated the mean daily growth rate of total leaf area by 73–130 %, total shoot length by 161–162 %, and plant dry mass by 134–158 %, respectively. Impacts of long-term atmospheric CO_2 enrichment on dry weight ratio in different components of the trees were more prominent in above-ground organs than in roots. High CO_2 raised leaf and shoot dry weight ratio, but reduced stem dry weight ratio, whereas root dry weight ratio and root/shoot ratio of the trees were not affected throughout the experiment. On average, net assimilation rate and relative growth rate were 0.6–1.7 g $m^{-2}d^{-1}$ and 1.2–3.9 g $kg^{-1}d^{-1}$ higher in trees grown at 700 than in those at 350 ppm CO_2, but tended to decline with the duration of CO_2 treatment. The physiological and morphological mechanisms for the increased apple tree growth and plant development by the doubled atmospheric CO_2 concentration were associated with net assimilation rate and relative growth rate of the plants as well as cell differentiation and elongation of the plant organs. The adjustment of plant growth under long-term atmospheric CO_2 enrichment resulted from the plant adaptation to high CO_2 conditions, which was affected by carbon sink/source availability and strength.

Zusammenfassung

Zwei Jahre alte Apfelbäume (*Malus domestica* Borkh. cv. 'Golden Delicious') auf 'M9' wurden der derzeitigen atmosphärischen CO_2-Konzentration (350 ± 10 ppm) und der doppelten (700 ± 10 ppm) für 120 Tage in Pflanzenkammern, die in einer Apfelplantage aufgestellt waren, ausgesetzt. Eine Verdoppelung der atmosphärischen CO_2-Konzentration stimulierte das Wachstum der Bäume. Es wurden mehr Blätter und Triebe ausgebildet, die mittlere Blattfläche war größer, ebenso das gesamte Blattrockengewicht pro Baum, der Kronen- und der Stammdurchmesser. Der mittlere Durchmesser und die mittlere Länge der Triebe, die Trieblänge pro Baum, die Baumhöhe und die gesamte Blattfläche nahmen zu, während die spezifische Blattfläche und das Blattflächenverhältnis der Bäume bei 700 ppm CO_2 abnahmen. Im Vergleich zu Bäumen, die bei 350 ppm CO_2 wuchsen, förderte 700 ppm CO_2 die mittlere tägliche Wachstumsrate der gesamten Blattfläche um 73–130 %, der gesamten Trieblänge um 161–162 % und der Pflanzentrockenmasse um 134–158 %. Die Auswirkungen der langfristigen CO_2-Anreicherung auf den Trockenmasseanteil der unterschiedlichen Baumfraktionen war in den oberirdischen Organen deutlicher als in der Wurzelfraktion. Eine erhöhte CO_2-Konzentration steigerte den Anteil der Blätter und der Triebe an der Trockenmasse, verringerte jedoch den Stammanteil. Allerdings nahm das Wurzel/Sproß-Verhältnis im Verlauf des Versuches ab. Im Mittel war die Nettoassimilationsrate um 0.6–1.7 g $m^{-2}d^{-1}$ und die relative Wachstumsrate um 1.2–3.9 g $kg^{-1}d^{-1}$ größer bei Bäumen, die bei 700 ppm CO_2 wuchsen, aber die Unterschiede zwischen den beiden Ansätzen wurden um so geringer, je länger die CO_2-Applikation dauerte.

Introduction

Since the past century, carbon dioxide (CO_2) concentration in the global atmosphere has been continuously increasing from 280 ppm before the Industrial Revolution to the present level of 350 ppm (KIMBALL 1983). Recent trends suggest that it will probably come up to 700 ppm by the end of this century (CEULEMANS and MOUSSEAU 1994, CURE and COCK 1986). Atmospheric CO_2 is the major carbon source for plants growing on earth. Plants obtain carbon from the air through photosynthetic CO_2 uptake. At present ambient CO_2 concentration in the global atmosphere is far below the CO_2 saturation point of most C_3 plant photosynthesis (CULOTTA 1995, POORTER et al. 1996). Fertilizing effects of an increased atmospheric CO_2 concentration on plant growth and productivity have been observed in numerous studies on various C_3-plant species (CHEN and LENZ 1997, KIMBALL 1983). The response of various

species to high atmospheric CO_2 concentrations differ remarkably (BAZZAZ 1990, EAMUS and JARVIS 1989). POORTER (1993) observed that the stimulation in relative growth rate of plants ranged from 1.3 to 9.4 g $kg^{-1}d^{-1}$ in 50 woody C_3 species. HAMACHER et al. (1994) investigated diurnal fluctuations of atmospheric CO_2 concentration in an experimental apple orchard. But no data are available for the long-term effects of atmospheric CO_2 enrichment on apple trees growing under field conditions. The objectives of this study, therefore, were to examine whether doubling the present ambient atmospheric CO_2 level will increase plant growth and canopy development of apple trees, to evaluate net assimilation rate and relative growth rate of the trees under 350 and 700 ppm CO_2 conditions, and to predict the consequence of long-term CO_2 enrichment in the global atmosphere on apple productivity in the future.

Materials and Methods

The experiments were carried out in the Institute of Fruit and Vegetable Sciences at the University of Bonn in 1996. In the middle of April, two year old apple (*Malus domestica* Borkh. cv. 'Golden Delicious') trees on 'M9' rootstocks were planted individually in 10 l plastic pots filled with 0.7–1.2 mm Ø quartz sand and precultured in an apple orchard for 2 months. Each tree was supplied with 500 ml Hoagland nutrient solution (HOAGLAND and ARNON 1938) twice a week, and irrigated with sufficient tap water 5 times per day throughout the experiment. On June 18, 16 uniform plants were selected for the experiment, moved into 2 growth chambers situated in the orchard and fumigated with CO_2 concentrations of 350 ± 10 (the control) or 700 ± 10 ppm (the doubled ambient CO_2 level). Each chamber was 3 m in height, 1.6 m in diameter and exposed to sunlight as well as the natural day/night rhythm. The chambers were equipped with a closed air-circuit microclimate-control system (UKG4000, Kälte-Klimatechnik, K. H. Spitzl GmbH, Bonn, Germany). The air flow rate was set to 100 m^3h^{-1}. Air temperature and relative air humidity within the chambers were maintained similar to the conditions in the apple orchard. The chambers were made of transparent, 0.1 mm thick polyethylene cover and sealed airtight at the bottom by water barriers. The CO_2 concentration in each chamber was monitored continuously by an URAS 2-T infrared gas analyser (IRGA, Hartmann und Braun AG Meß- und Regeltechnik, Frankfurt/Main, Germany) and controlled automatically. When the CO_2 concentration in the chamber was 10 ppm lower or higher than the preset values, industry CO_2 gas (Technisches Gas, Linde AG, Düsseldorf, Germany) was automatically injected from a concentrated CO_2 cylinder into the chamber or the injection was stopped.

The CO_2 treatment lasted for 120 days. At the beginning (June 18), middle (August 17), and end (October 16) of the experiment, 4 trees of each CO_2 treatment were destructively harvested and individually separated into leaves, shoots, stems and roots. Leaf area was measured with an area meter (Model 3100, LI-COR, INC., Lincoln, Nebraska, USA) with a precision of ± 0.01 cm^2. Dry weight of different organs was determined with a precision of ± 0.01 g after freeze-drying (WKF GmbH, TPYL-10 freeze-drying system, Heistenbach, Germany) to constant weight. Daily growth of leaf area, shoot length, and dry mass of each tree was separately calculated as a mean of net increment per day. Dry weight ratio of individual organs was expressed as a fraction of plant dry mass allocated to each component (LAMBERS and POORTER 1992). Leaf area ratio (LAR) was defined as the amount of leaf area per plant dry mass. It was the product of leaf dry weight ratio (LDWR) and specific leaf area (SLA), the amount of leaf area per leaf dry mass.

$$LAR = LDWR \times SLA \quad (1)$$

Net assimilation rate (NAR) of the trees represented net increment in plant dry mass per leaf area during the experiment. Relative growth rate (RGR) of the trees was the product of LAR and NAR (LAMBERS and POORTER 1992).

$$RGR = LAR \times NAR \quad (2)$$

The experimental data were evaluated by student t-tests using the SPSS statistical package (SPSS INC., Chicago, USA). A probability of 5 % or 1 % was used to define significant or very significant differences between 350 and 700 ppm CO_2 treatments. In this study, all data were reported on a per tree basis.

Results

Leaf growth

CO_2 enrichment promoted leaf growth of apple trees (Tab. 1, Fig. 1). In comparison with the control, the doubled ambient CO_2 accelerated leaf development as

Table 1: Leaf growth of apple trees as affected by doubled CO_2.
Auswirkungen einer Verdoppelung der CO_2-Konzentration auf das Blattwachstum bei Apfel.

Treatment		Total leaf number per tree	Total leaf area per tree (cm^2)	Average leaf area (cm^2)	Specific leaf area (m^2kg^{-1})	Leaf area ratio (m^2kg^{-1})
CO_2 (ppm)	Duration (d)					
Ambient	60	12±1	313.3±16.8	26.1±2.2	12.1±0.7	1.31±0.05
350	60	45±3	1283.6±37.9	28.9±3.7	14.1±0.6	2.96±0.07
700	60	65±4	1993.6±36.4	30.7±4.1	10.5±0.2	2.67±0.08
Significance		**	**	*	**	*
350	120	81±6	1680.0±49.2	20.7±2.4	12.0±0.5	2.76±0.04
700	120	115±8	2906.6±12.0	25.3±2.1	8.7±0.2	2.51±0.06
Significance		**	**	**	**	*

Values are means ± SD. ** and * denote significance of t-test at $P<0.01$ and $P<0.05$, respectively.

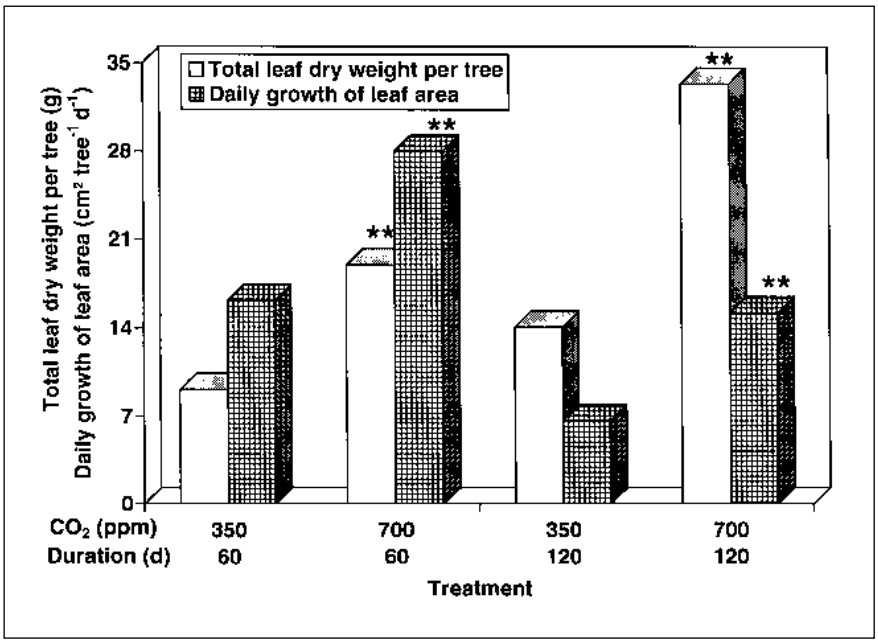


Fig. 1: Total leaf dry weight per tree and daily growth of leaf area of apple trees as affected by doubled CO_2 (** denotes significance of t-tests at $P<0.01$.)
*Auswirkungen einer Verdoppelung der CO_2-Konzentration auf das Trockengewicht aller Blätter pro Baum und die tägliche Zunahme der Blattfläche bei Apfel (** gibt die Signifikanz der T-Tests an; $P<0.01$.)*

indicated by a 3–5 d earlier leaf appearance and a faster leaf expansion. As a result, CO_2-enriched trees not only had more leaves, but also developed a larger average leaf area (Tab. 1). Comparing with 350 ppm CO_2 treated plants, total leaf area per tree increased by 55 % and 73 % for those grown under 700 ppm CO_2 concentration after 60 and 120 d of the CO_2 treatment, respectively. Doubling ambient CO_2 concentration, on the other hand, decreased both specific leaf area and leaf area ratio of the trees (Tab. 1). Consequently, total leaf dry weight per tree increased by 108–137 % due to the atmospheric CO_2 enrichment (Fig. 1). Mean daily growth of leaf area was larger in the first than the second 60 d of the CO_2 treatment at 350 as well as at 700 ppm CO_2 (Fig. 1). On average, 700 ppm CO_2-treated trees increased mean daily growth of leaf area by 73–130 % in comparison with 350 ppm CO_2-grown ones.

Shoot growth

Similarly, high CO_2 accelerated shoot growth of the trees (Tab. 2). Shoot growth started 5–7 d earlier, and the shoot developed fast and lasted for a longer period at 700 than 350 ppm atmospheric CO_2 concentration. As a consequence, doubled atmospheric CO_2 not just increased shoot number per tree, but enhanced average shoot length and diameter (Tab. 2). In comparison with 350 ppm CO_2 treatment, total shoot length and daily growth of shoot length per tree increased by 103–131 % and 161–162 %, respectively, in 700 ppm CO_2-grown trees (Tab. 2).

Plant growth

High CO_2 boosted plant growth and canopy development of apple trees (Tab. 3). In consequence, 700 ppm CO_2 increased tree height by 14 % after 60 d and by 18 % after 120 d of the CO_2 treatment, in comparison with 350 ppm CO_2-grown trees, respectively. Canopy diameter and trunk diameter were not significantly affected by the doubled CO_2 concentration in the first 60 d, but distinctly increased during the second 60 d of the CO_2 treatment (Tab. 3). Root/shoot ratio of the trees tended to decline during the experiment. Significant differences in root/shoot ratio between trees grown at 350 and 700 ppm CO_2 conditions were not observed after 60 d and 120 d CO_2 treatments. Daily

Table 2: Shoot growth of apple trees as affected by doubled CO_2
Auswirkungen einer Verdoppelung der CO_2-Konzentration auf das Triebwachstum bei Apfel

Treatment		Shoot	Total shoot	Average	Average	Daily growth
CO_2 (ppm)	Duration (d)	number per tree	length (cm tree^{-1})	shoot length (cm)	shoot diameter (mm)	of shoot length (cm tree^{-1} d^{-1})
Ambient	60	1.0±0.0	29.5± 8.2	29.5±8.2	3.8±0.1	–
350	60	2.5±0.3	157.6±57.6	62.3±5.4	4.3±0.2	2.13±0.96
700	60	4.5±0.5	363.3±69.7	80.5±2.8	4.7±0.2	5.56±1.16
Significance		*	*	*	*	*
350	120	3.5±0.4	262.7±39.2	75.5±4.0	5.2±0.6	1.75±0.65
700	120	5.5±0.7	533.1±57.4	97.1±2.1	8.0±0.3	2.83±0.96
Significance		*	*	*	*	*

Values are means ± SD. * denotes significance of t-test at $P<0.05$.

Table 3: Plant growth of apple trees as affected by doubled CO_2
Auswirkungen einer Verdoppelung der CO_2-Konzentration auf das Baumwachstum bei Apfel.

Treatment		Tree	Canopy	Trunk	Root /	Daily growth
CO_2 (ppm)	Duration (d)	height (cm)	diameter (cm)	diameter (cm)	shoot ratio	of dry mass (g tree^{-1}d^{-1})
Ambient	60	73.1±3.5	45.6±1.8	1.4±0.2	0.55±0.06	–
350	60	92.3±3.8	56.8±2.9	1.9±0.2	0.47±0.02	0.33±0.02
700	60	105.5±4.6	62.1±3.4	2.2±0.3	0.53±0.03	0.85±0.01
Significance		*	NS	NS	NS	**
350	120	115.7±4.0	61.0±3.2	2.4±0.1	0.32±0.02	0.29±0.03
700	120	136.6±5.2	73.2±4.6	3.1±0.2	0.35±0.01	0.68±0.05
Significance		*	*	*	NS	**

Values are means ± SD. **, * and NS denote significance of t-test at $P<0.01$, $P<0.05$ and $P>0.05$, respectively.

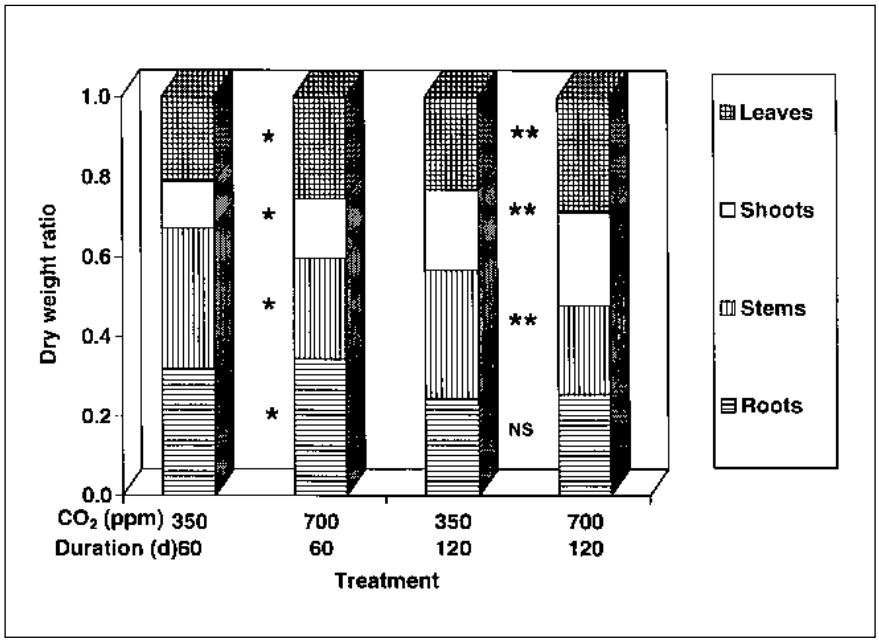


Fig. 2 : Dry weight ratio of different organs of apple trees as affected by doubled CO_2 (**, *, and NS denote significances of t-tests at $P<0.01$, $P<0.05$ and $P>0.05$, respectively.)
*Auswirkungen einer Verdoppelung der CO_2-Konzentration auf das Verhältnis der Trockengewichte verschiedener Organe bei Apfel (**, * und NS geben die Signifikanzen der T-Tests an; $P<0.01$, $P<0.05$ bzw. $P>0.05$.)*

growth of dry mass per tree was higher at 700 than 350 ppm atmospheric CO_2 concentration. The differences were very significant after 60 d and 120 d of the CO_2 treatments (Tab. 3). When compared with 350 ppm CO_2-grown trees, 700 ppm CO_2-treated ones increased daily growth of dry mass by 158 % during the first 60 d and by 134 % in the second 60 d of the atmospheric CO_2 treatment.

Dry weight ratio

The atmospheric CO_2 concentration also influenced the dry weight ratio in different organs of the trial apple trees (Fig. 2). As shown in Fig. 2, atmospheric CO_2 enrichment enhanced leaf dry weight ratio and shoot dry weight ratio, but reduced stem dry weight ratio. Root dry weight ratio, however, was not significantly different between 350 and 700 ppm CO_2 treatments by the end of the experiment. Consequently, the differences in dry weight ratio between 700 and 350 ppm CO_2-treated trees were more prominent in aboveground organs than in roots (Fig. 2). In addition, dry weight ratio of different organs also varied with the duration of the CO_2 treatment (Fig. 2). Stem dry weight ratio was always highest in trees grown under 350 ppm CO_2. In 700 ppm CO_2-treated ones, root dry weight ratio and leaf dry weight ratio became highest in the first 60 d and the second 60 d of the CO_2 treatments, respectively. Shoot dry weight ratio was lowest in all treatments, although it tended to increase with the duration of the experiment.

Net assimilation rate and relative growth rate

Both net assimilation rate and relative growth rate of the trees were higher during the first than the second 60 d of the CO_2 treatment (Fig. 3). High CO_2 promoted not only net assimilation rate, but also relative growth rate of the trees. When compared with trees grown under 350 ppm CO_2, those grown under 700 ppm CO_2 increased net assimilation rate by 1.7 and 0.6 g m^{-2}d^{-1}, and relative growth rate by 3.9 and 1.2 g kg^{-1}d^{-1} in the first and the second 60 d of the experiment, equivalent to a 36–68 % and 24–51 % increase in net assimilation rate and relative growth rate, respectively (Fig. 3).

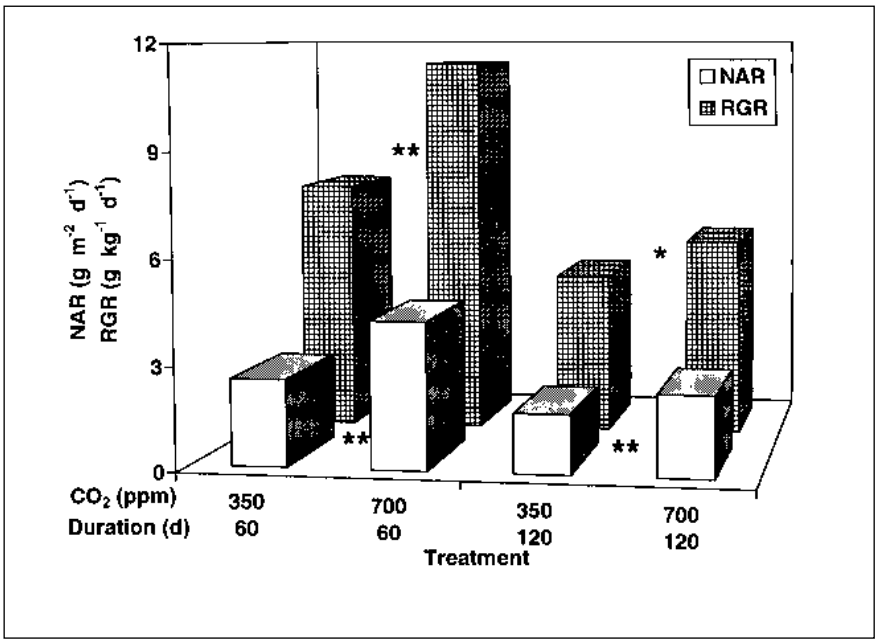


Fig. 3: Net assimilation rate (NAR) and relative growth rate (RGR) of apple trees as affected by doubled CO_2 (**and * denote significances of t-tests at $P<0.01$ and $P<0.05$, respectively.) *Auswirkungen einer Verdoppelung der CO_2-Konzentration auf die Nettoassimilationsrate (NAR) und die relative Wachstumsrate (RGR) bei Apfel (** und * geben die Signifikanzen der T-Tests an; $P<0.01$ bzw. $P<0.05$.)*

Discussion

Elevating the ambient CO_2 concentration from 350 to 700 ppm increased total leaf area (Fig. 1), total shoot length (Tab. 2), and plant dry mass (Tab. 3) of apple trees by factors of 1.73, 2.61, and 2.58 in the first 60 d, and factors of 2.30, 1.62, and 2.34 in the second 60 d of the experiment. COLEMAN and BAZZAZ (1992) also reported that plant harvest date might significantly affect the interpretations of CO_2 experiments. The effects of the atmospheric CO_2 enrichment on growth of apple trees presented here are consistent with our previous observations in *Fragaria x ananassa* Duch. cv. 'Elsanta' (CHEN and LENZ 1997, CHEN et al. 1997). According to ARP (1991) and CURE et al. (1991), the physiological basis of the enhanced plant growth rate may be associated with the increased carbon sink-strength due to atmospheric CO_2 enrichment at the growing sites, because high CO_2 may lead to a so-called „luxury consumption of carbon" (BAZZAZ 1990, CULOTTA 1995). An increased turgor and the enhancement of cell differentiation and elongation have been observed in plants grown under high CO_2 concentrations (CEULEMANS and MOUSSEAN 1994, EAMUS and JARVIS 1989). This may accelerate leaf expansion, shoot prolongation, canopy development and dry mass increment of the trees. The present experiment, on the other hand, showed that a doubled CO_2 level affected neither root dry weight ratio (Fig. 2), nor root/shoot ratio (Tab. 3). The results support our previous observations (CHEN and LENZ 1997, CHEN at al. 1997), and also tally with the suggestions of RETUERTO and WOODWARD (1992) who reported no effect of a high atmospheric CO_2 concentration on partitioning of assimilates to root and shoot. The root/shoot ratio depends on the equilibrium of dry mass allocation to above-ground organs and to roots as well (BAZZAZ 1990, CHEN and LENZ 1997). The present experiment was conducted under the natural field conditions of daylight, air temperature, and relative air humidity. The effects of these factors on plant growth and dry mass allocation to different organs of the trees cannot be discounted. The results obtained in this study, thus, are thought to represent realistic effects of atmospheric CO_2 enrichment on apple trees under the actual field conditions.

The response of apple to changes of the atmospheric CO_2 environment also interacts with the ontogenetic stage of tree development. If a doubled CO_2 concentration could enhance plant growth each day, then the 120 d experiment should show a larger stimulation in relative growth rate of the trees than the 60 d treatment. To enlighten the mechanisms controlling growth stimulation in apple trees by a long-term atmospheric CO_2 enrichment, the technique of plant growth analysis described by LAMBERS and POORTER (1992) was adopted in the present study. Plant growth was expressed as the net increment in total dry weight per plant dry weight already present and per duration of the CO_2 treatment, i.e. as relative growth rate, which can be factorized into net assimilation rate (the increment in total plant dry weight per leaf area per time) and leaf area ratio (the amount of leaf area per total plant dry weight). Net assimilation rate and leaf area ratio may represent physiological and morphological components of a tree. In addition, the increase in relative growth rate was positively correlated with a 68 % and 36 % stimulation of net assimilation rate during the first and the second 60 d of the CO_2 treatment (Fig. 3). This increase, however, was counterbalanced by a 10 % and 9 % reduction in leaf area ratio (Tab. 1). It suggested that the increased photosynthetic assimilation was not used for investment in new actively growing leaf area (source), but rather was accumulated as storage starch in the trees, because the source-sink balance of the plants may play a crucial role in determining to what extent a growth stimulation can take place (ARP 1991, CURE et al. 1991). The stimulation in relative growth rate of 700 ppm CO_2-treated trees mainly resulted from the enhanced net assimilation rate of the trees. In comparison with 350 ppm CO_2 treatment, the relative growth rate of apple trees increased by 1.2–3.9 g kg^{-1} d^{-1} at the 700 ppm CO_2 environment in this study (Fig. 3). It is in

line with the results of POORTER (1993) who reported a mean increase of relative growth rate of 3.7 g kg^{-1} d^{-1} based on 50 woody C_3 species.

The leaf area ratio, moreover, can be further factorized into the specific leaf area and leaf dry weight ratio. The reduction in leaf area ratio of trees grown at 700 ppm CO_2 could primarily be attributed to a declined proportion of dry mass allocated per leaf area rather than changes in dry mass per leaf area (POORTER et al. 1996). The reduced specific leaf area under the elevated atmospheric CO_2 conditions has previously been reported in *Fragaria x ananassa* Duch. cv. 'Elsanta' as well (CHEN and LENZ 1997, CHEN et al. 1997). The present experiment demonstrated that leaf area ratio of apple trees was significantly lower at 700 ppm than at 350 ppm CO_2 (Tab. 1). Similar results have also been obtained by RETUERTO and WOODWARD (1992) in *Sinapis alba* L., who suggested that most of the variation of leaf area ratio could be attributed to a large reduction in specific leaf area. In this experiment, the decrease in leaf area ratio of apple trees also resulted from a very significant reduction of specific leaf area (Tab. 1). The decreased specific leaf area of trees grown at high CO_2 could be to a large extent explained by the accumulation of non-structural carbohydrates (especially starch) in leaves (CHEN et al. 1997, WONG 1990), and/or by the dilution of essential nutrients in the plant organs (BAZZAZ 1990, EAMUS and JARVIS 1989).

Finally, plant growth analysis for effects of the duration of CO_2 treatment revealed that the initial enhancement of plant growth due to the atmospheric CO_2 enrichment declined in time although this may also resulted partly from the time of growing season (Tab. 1–3, Fig. 3). The differences between trees grown under 350 and 700 ppm CO_2 resulted from noticeable effects on net assimilation rate and relative growth rate of the whole plants (Fig. 3). Such an adjustment of plant growth under long-term atmospheric CO_2 enrichment can be considered as an adaptation of the trees to the elevated atmospheric CO_2 concentration (EAMUS and JARVIS 1989), influenced by sink and/or source availability within the plants (BAZZAZ 1990). Although the physiological mechanisms are unknown, several causes of this responses may be proposed. They include (i) the down-regulation of photosynthesis due to limitations of enzyme activity and photosynthetic efficiency (EAMUS and JARVIS 1989) as well as starch accumulation in the leaves (CHEN and LENZ 1997), (ii) an imbalance in the supply and demand of photosynthates as a result of the feedback inhibition of photosynthesis (CEULEMANS and MOUSSEAN 1994, COLEMAN and BAZZAZ 1992), (iii) a limitation of daytime photosynthate export from sources to sinks (CURE et al. 1991, DELUCIA et al. 1985), and (iv) insufficient resource availability of the trees (ARP 1991, POORTER et al. 1996), because the plant growth response to CO_2 enrichment will be depressed under low levels of other resources such as nutrients (BAZZAZ 1990, POORTER 1993). These effects need further attention in future studies.

Conclusion

Long-term atmospheric CO_2 enrichment accelerated leaf area expansion, shoot prolongation, canopy enlargement, and dry mass increment of apple trees. Specific leaf area and leaf area ratio decreased due to the doubled ambient CO_2 concentration. Net assimilation rate and relative growth rate of the trees rose at the high CO_2 environment in the earlier growth period, but declined when the CO_2 treatment continued. Dry weight ratio increased in leaves and shoots, decreased in stems, and remained similar in roots under the elevated CO_2 conditions. Atmospheric CO_2 enrichment strongly affected dry mass allocation to above-ground organs rather than to roots. The predicted increase of global atmospheric CO_2 concentration in the future will likely be beneficial to pomiculture, although the effect of the doubled present atmospheric CO_2 concentration on the tree growth is time-dependent.

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