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Effects of Doubled Atmospheric CO_2 Concentration on Apple Trees II. Dry Mass Production

Auswirkungen einer Verdoppelung der atmosphärischen CO_2-Konzentration auf Apfel II. Trockenmassebildung

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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. Long-term atmospheric CO_2 enrichment enhanced dry weight in all organs of the trees, particularly in leaves and shoots. Relative distribution of dry mass within the trees increased in leaves and shoots, declined in stems, and remained unchanged in roots under the doubled CO_2 concentration. Dry mass increment and daily gain of dry mass in different components of the trees rose concomitantly with the ambient CO_2 enrichment. The proportion of dry mass allocated to different organs varied with the doubled atmospheric CO_2 concentration. High CO_2 promoted both total leaf area development and total dry mass increment of the trees. When compared with the 350 ppm CO_2 treatment, 700 ppm CO_2-grown trees increased dry mass-production efficiency of leaves by 51 % during the first 60 d of the CO_2 treatment, but this stimulatory effect diminished in the second 60 d of the experiment due to the tree's adaptation to the atmospheric CO_2 enrichment. The physiological mechanisms for the increments in dry mass production of apple trees by doubled atmospheric CO_2 concentration were related to the promoted source activity by increases of total dry mass and daily gain of dry mass in the plants, as well as to the enlarged source size by development of total leaf area of the plants.

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. Die langfristige CO_2-Anreicherung erhöhte das Trockengewicht in allen Organen der Bäume, besonders in den Blättern und den Trieben. Bei einer Verdoppelung der CO_2-Konzentration nahm der Anteil der Trockenmasse an der Gesamttrockenmasse pro Pflanze in Blättern und Trieben zu, im Stamm ab und in den Wurzeln blieb er unverändert. Die Zunahme der Trockenmasse und der tägliche Zugewinn an Trockenmasse in den verschiedenen Pflanzenteilen stieg bei einer Zunahme der atmosphärischen CO_2-Konzentration an. Die tägliche Trockengewichtszunahme der Pflanzenteile stieg in der CO_2-Behandlung. Eine hohe CO_2-Konzentration stimulierte sowohl die Blattflächenzunahme pro Baum als auch die Trockenmassezunahme der Bäume. Im Vergleich zum Ansatz mit 350 ppm CO_2, erhöhte sich die Effizienz der Trockenmasseproduktion der in 700 ppm CO_2 angezogenen Bäume um 51 % in den ersten 60 Tagen des Experimentes, aber dieser stimulierende Effekt verschwand in den folgenden 60 Tagen infolge einer Anpassung der Bäume an die Umweltbedingungen mit erhöhtem CO_2-Gehalt in der Luft.

Introduction

Plant responses to elevated atmospheric carbon dioxide (CO_2) concentrations have been extensively investigated (Bazzaz 1990, Culotta 1995). Many of the previous studies have sought to examine dry mass productivity of plants at different levels of atmospheric CO_2 enrichment (Eamus and Jarvis 1989, Rogers et al. 1983). Poorter (1993) estimated that a doubled ambient concentration of atmospheric CO_2 enhanced dry mass production by a mean of 41 % in 50 woody species with C_3 pathway of photosynthesis. Dry mass increment represents plant primary production of biological yield because more than 90 % of the dry mass in a plant directly results from leaf photosynthesis (Arp 1991, Cannell 1985). Dry mass increment is the physiological basis of plant growth and productivity, particularly for regulation and improvement in photosynthate distribution within the trees and dry mass-production efficiency of leaves (Ceulemans and Mousseau 1994, Lenz 1979). On the other hand, both net photosynthesis and dry mass production vary remarkably among different species (Ozbun 1978, Poorter et al. 1996). There is no published report on dry mass production of apple trees as affected by long-term atmospheric CO_2 enrichment. The objectives of this study were (i) to determine dry weight of different organs in 350 and 700 ppm CO_2-grown apple trees, (ii) to examine the effects of long-term atmospheric CO_2 enrichment on dry mass increment and relative distribution in different components of the trees, (iii) to in-

vestigate daily gain and allocation of dry mass in the plants due to changes of the atmospheric CO_2 concentration, and (iv) to evaluate dry mass-production efficiency of apple leaves under ambient and doubled atmospheric CO_2 conditions.

Materials and Methods

Two year old apple (*Malus domestica* Borkh. cv. 'Golden Delicious') trees, grafted on 'M9' rootstocks, were individually planted in 10 l plastic pots with 0.7-1.2 mm Ø quartz sand in the middle of April, 1996. After a two-month preculture in the fields, they were exposed separately to 350 ± 10 or 700 ± 10 ppm CO_2 in growth chambers situated in an apple orchard for 120 d (CHEN et al. 2001). Other environmental conditions in the chambers were maintained similar to those in the apple orchard using a closed air-circuit and microclimate-control system (UKG 4000, Kälte-Klimatechnik, K. H. Spitzl GmbH, Bonn, Germany). The trees were supplied with 500 ml Hoagland nutrient solution (HOAGLAND and ARNON 1938) twice a week and irrigated with tap water 5 times per day throughout the experiment.

Four trees of each treatment were destructively harvested at 60-d-intervals. The plant components were separately grouped into leaves, shoots, stems, and roots. They were freeze-dried for a week in a TPYL-10 freeze-drying system (WKF GmbH, Heistenbach, Germany) to determine dry weight of different organs, dry mass increment and allocation as well as relative distribution of dry mass in each component of the trees. Total leaf area of each tree was measured with a LI-COR 3100 area meter (LI-COR INC., Lincoln, Nebraska, USA) to evaluate leaf area increment of the trees between the two harvests. Dry mass increment represented the net increase in dry weight of each organ during the experiment. Daily gain of dry mass was estimated as the mean increment of dry mass in different organs per day. Dry mass allocation was assessed as a proportion of net dry mass partitioning into different organs. Dry mass-production efficiency of leaves was calculated by dividing total dry mass increment by total leaf-area increment of each tree.

The experimental data were analysed with the SPSS statistical package (SPSS INC., Chicago, USA). They were tested for normal distribution and variance homogeneity, and compared by student t-tests at a 5 % or 1 % significance level.

Results

Dry weight of different organs

Dry weight in all organs consistently increased during the experiment (Tab. 1). At the beginning of CO_2 treatments, dry weight of different organs was stems > roots > leaves > shoots. After 60 d and 120 d of the CO_2 treatments, trees grown under 350 ppm CO_2 condition still kept the same order of dry weight in the above organs. Whereas dry weight of those grown at 700 ppm CO_2 concentration became roots > leaves > stems > shoots after 60 d of the CO_2 treatment, and leaves > roots > shoots > stems by the end of the experiment (Tab. 1). Atmospheric CO_2 enrichment significantly increased dry weight in all organs of the trees, especially in leaves, shoots and roots. In comparison with the 350 ppm CO_2 treatment, the doubled ambient CO_2 concentration increased total dry weight of the trees by 72 % and 90 % after 60 and 120 d of the experiment, respectively (Tab. 1).

Relative distribution of dry mass

Relative distribution of dry mass in different organs varied with ambient concentration of atmospheric CO_2 and the duration of the CO_2 treatment (Tab. 2). At the beginning of the experiment, stems had the highest percentage of dry mass in all organs. After 60 d and 120 d of the CO_2 treatments, the percentage of dry mass distributed to leaves and shoots rose dramatically, while it declined in stems and roots. Atmospheric CO_2 enrichment, on the other hand, also enhanced relative distribution of dry mass in leaves and shoots, and reduced that in stems (Tab. 2). As a result, relative distribution of dry mass significantly increased in leaves and shoots, and decreased in stems of the trees grown under 700 CO_2 concentration by the end of the experiment. However, no significant difference was observed between 350 and 700 ppm CO_2 treatments for relative distribution of dry mass in roots throughout the experiment (Tab. 2).

Dry mass increment

Dry mass increment in different organs of the trees was higher during the first than the second 60 d of the experiment (Fig. 1). During the first 60 d of the CO_2 treatment, dry mass increment was leaves > roots > shoots

Table 1: Dry weight of different organs of apple trees as affected by doubled CO_2
Auswirkungen einer Verdoppelung der CO_2-Konzentration auf das Trockengewicht verschiedener Organe bei Apfel

Treatment		Leaves	Shoots	Stems	Roots	Total
CO_2 (ppm)	Duration (d)	(g dry mass in the organs per plant)				
Ambient	60	2.59±0.25	0.87±0.11	11.94±1.23	8.43±2.12	23.83±2.15
350	60	9.11±0.01	5.11±1.89	15.25±2.14	13.88±0.64	43.34±0.91
700	60	18.98±0.76	11.11±0.57	18.76±1.95	25.83±0.22	74.67±0.85
Significance		**	*	*	**	**
350	120	14.07±1.00	12.21±0.42	19.62±0.54	14.88±0.09	60.77±1.88
700	120	33.34±0.84	26.89±0.72	25.78±1.67	29.70±0.27	115.71±3.20
Significance		**	**	*	**	**

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

Table 2: Relative distribution of dry mass in different organs of apple trees as affected by doubled CO_2
Auswirkungen einer Verdoppelung der CO_2-Konzentration auf die relative Verteilung der Trockenmasse in die verschiedenen Organe bei Apfel

Treatment		Leaves	Shoots	Stems	Roots
CO_2 (ppm)	Duration (d)			(%)	
Ambient	60	10.9±0.3	3.6±0.25	50.1±4.1	35.4±2.5
350	60	21.0±0.4	11.8±4.6	35.1±4.2	32.0±0.8
700	60	25.4±1.3	14.9±0.9	25.1±2.3	34.6±0.1
Significance		*	*	**	NS
350	120	23.1±0.9	20.1±0.1	32.3±0.1	24.5±0.9
700	120	28.8±0.1	23.2±0.3	22.3±0.8	25.7±0.5
Significance		**	*	**	NS

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

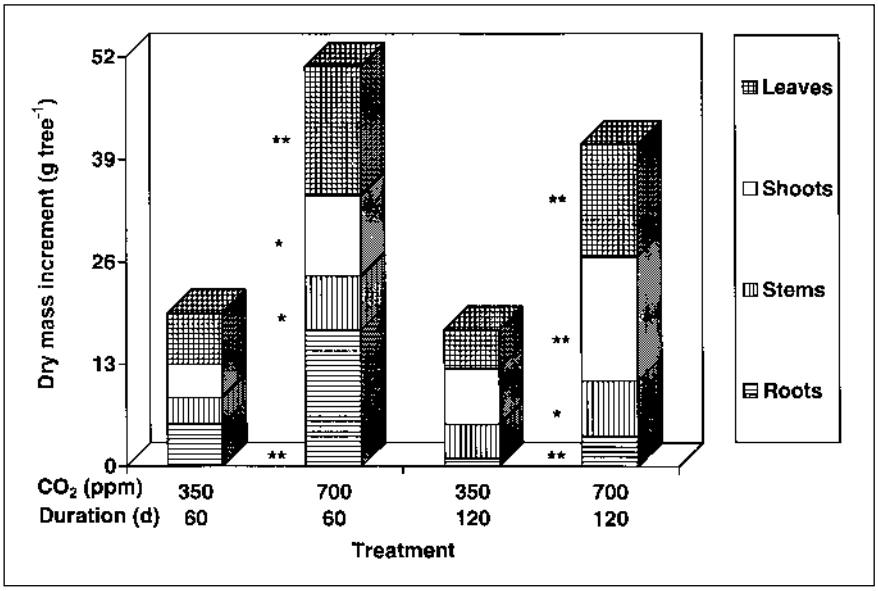


Fig. 1: Dry mass increment in different organs of apple trees as affected by doubled CO_2 (** and * denote significances of t-tests at $P<0.01$ and $P<0.05$, respectively.)
*Auswirkungen einer Verdoppelung der CO_2-Konzentration auf die Trockenmassezunahme verschiedener Organe von Apfel (** und * kennzeichnen signifikante Unterschiede der T-Tests bei $P<0.01$ und $P<0.05$.)*

> stems for trees grown under 350 ppm CO_2, and roots > leaves > shoots > stems for those grown at 700 ppm CO_2 concentration. After 120 d of the CO_2 treatment, however, the order changed to shoots > leaves > stems > roots in both 350 and 700 ppm CO_2 treatments. Atmospheric CO_2 enrichment accelerated dry mass increment in all organs of the trees, especially in leaves, shoots, and roots (Fig. 1). In comparison with 350 ppm CO_2-treated trees, those grown at 700 ppm CO_2 enhanced total dry mass increment by 9.9 and 9.4 g per tree in leaves, 6.0 and 8.7 g per tree in shoots, 3.5 and 2.7 g per tree in stems, and 12.0 and 3.0 g per tree in roots during the first and the second 60 d of the experiment, respectively.

Daily gain of dry mass

High CO_2 promoted daily gain of dry mass in all organs of the trees (Fig. 2). This effect was particularly prominent for roots and leaves in the first 60 d, and for shoots and leaves in the second 60 d of the CO_2 treatment. When compared with 350 ppm CO_2-grown trees, 700 ppm CO_2-treated ones increased daily gain of dry mass in leaves, shoots, stems, and roots by 151 %, 140 %, 106 %, and 219 % during the first 60 d, and by 189 %, 122 %, 61 %, and 291 % in the second 60 d of the CO_2 treatment, respectively (Fig. 2). As a consequence, daily gain of dry mass in the whole plant increased by 0.52 and 0.39 g per tree due to a doubled ambient CO_2 level during the first and the second 60 d of the experiment, respectively.

Dry mass allocation

The proportion of dry mass allocated to different organs also varied with the atmospheric CO_2 concentration as well as the duration of the CO_2 treatment (Fig. 3). In the first 60 d of the experiment, no significant differences in dry mass allocation to leaves, shoots, and stems, except more to roots, were observed between trees grown at 350 or 700 ppm CO_2. During the second 60 d of the experiment, however, the doubled ambient CO_2 concentration promoted dry mass allocation to leaves and roots, and reduced that to stems (Fig. 3).

Dry mass-production efficiency of leaves

Both total leaf area increment and total dry mass increment per tree were larger in the first than in the second

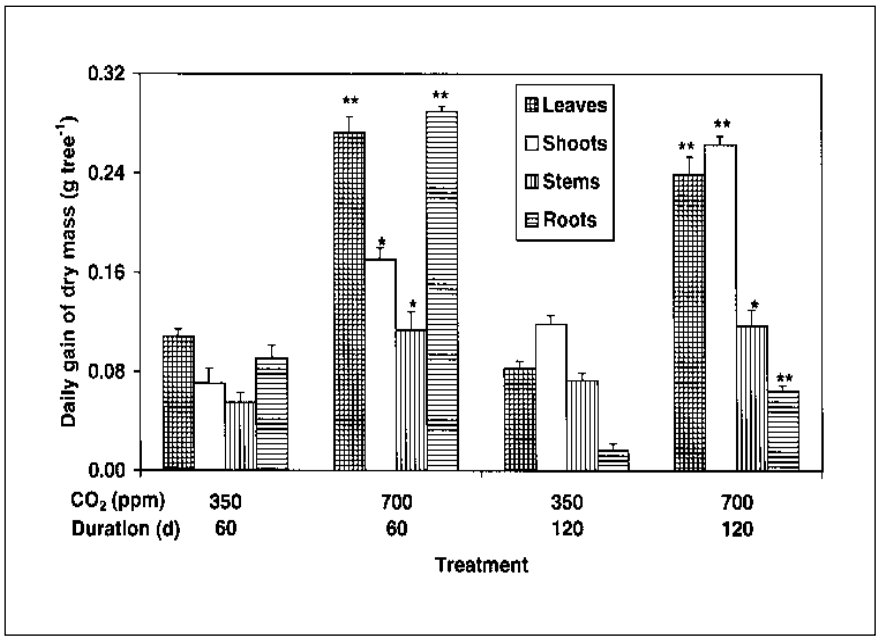


Fig. 2: Daily gain of dry mass in different organs of apple trees as affected by doubled CO_2 (** and * denote significances of t-tests at $P<0.01$ and $P<0.05$, respectively.)
*Auswirkungen einer Verdoppelung der CO_2-Konzentration auf den täglichen Zugewinn an Trockenmasse verschiedener Organe von Apfel (** und * kennzeichnen signifikante Unterschiede der T-Tests bei $P<0.01$ und $P<0.05$.)*

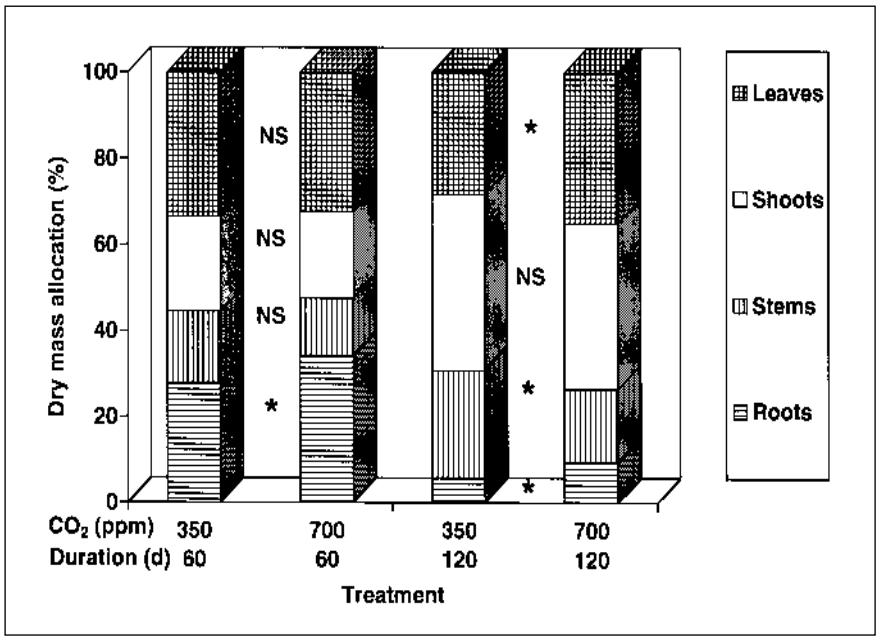


Fig. 3: Proportion of dry mass allocation to different organs of apple trees as affected by doubled CO_2 (* and NS denote significances of t-tests at $P<0.05$ and $P>0.05$, respectively.)
Auswirkungen einer Verdoppelung der CO_2-Konzentration auf die Verteilung der Trockenmasse zu verschiedenen Organen von Apfel (und NS kennzeichnen die Signifikanzen der T-Tests bei $P<0.05$ und $P>0.05$.)*

60 d of the experiment, whereas dry mass-production efficiency of leaves showed just the opposite tendency (Tab. 3). Atmospheric CO_2 enrichment accelerated not only total leaf area increment, but also total dry mass increment of the trees (Tab. 3). In comparison with the 350 ppm CO_2 treatment, 700 ppm CO_2-grown trees increased total leaf area by 73 % and 130 %, and total dry mass by 161 % and 136 % after 60 d and 120 d of the atmospheric CO_2 treatments, respectively. As a result, dry mass-production efficiency of leaves was enhanced by 51 % due to the doubled ambient CO_2 concentration in the first 60 d of the CO_2 treatment. However, there was no significant difference in dry-mass production efficiency of the plant leaves between 350 and 700 ppm CO_2 treatments by the end of the experiment (Tab. 3).

Discussion

Dry mass production of an apple tree is an accumulative process of biological yield, which is closely related to fruit productivity (CANNELL 1985, POORTER et al. 1996). Atmospheric CO_2 enrichment increased the strength of the carbon source for the plants and enhanced leaf photosynthesis of the trees (CEULEMANS and MOUSSEAU 1994, CURE et al. 1986). In the present experiment on apple trees, the doubled atmospheric CO_2 concentration not only promoted source activity as indicated by an increase of total dry mass (Fig. 1) and daily gain of dry mass (Fig. 2), but also increased source size indicated by the enhanced increment of total leaf area (Tab. 3). The increase of plant dry weight in trees grown under doubled CO_2 might be attributed primar-

Table 3: Total leaf area and dry mass increment per tree and dry mass-production efficiency of apple leaves as affected by doubled CO_2

Auswirkungen einer Verdoppelung der CO_2-Konzentration auf die gesamte Blattfläche und die Trockenmassezunahme pro Baum sowie die Effektivität der Trockenmassebildung bei Apfel

Treatment		Total leaf area	Total dry mass	Dry mass-production
CO_2 (ppm)	Duration (d)	increment per tree (cm^2)	increment per tree (g)	efficiency of leaves (g dry mass m^{-2} leaf)
350	60	970.4±3.8	19.5±0.9	201.1±10.1
700	60	1680.4±36.4	50.8±0.8	302.7±11.6
Significance		**	**	**
350	120	396.3±49.2	17.4±1.9	440.0± 7.1
700	120	913.0±12.0	41.0±3.2	449.3±29.2
Significance		**	**	NS

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

ily to an extra amount of photosynthetic CO_2 uptake (EAMUS and JARIVS 1989, POORTER et al. 1996). These results were in good agreement with previous observations of effects due to a doubled atmospheric CO_2 concentration on net assimilation rate and relative growth rate of the trees (CHEN et al. 2001).

Elevated atmospheric CO_2, on the other hand, altered dry mass allocation (Fig. 3) and relative distribution (Tab. 2) in different organs of the trees. FIELD et al. (1992) noticed that plants responded to changes of resource balance (e.g., C/N ratio) mainly by increasing dry mass allocation to the organs acquiring more strongly limited resource. In this experiment, adjustments in dry mass allocation to different organs were observed in long-term high CO_2-treated trees (Fig. 3), suggesting that they compensated for changes in carbon supply. Doubled atmospheric CO_2 promoted dry mass allocation to leaves and roots, but limited it to stems (Fig. 3). This indicated that high CO_2 might increase apple productivity by the change of dry mass allocation to both productive and structural components of the trees (CANNELL 1985, CEULEMANS and MOUSSEAU 1994). Leaves and roots are major sources and sinks of photosynthates in apple trees, respectively. The elevated atmospheric CO_2 concentration accelerated dry mass production and partitioning within the trees, because it enhanced both sides of sources and sinks (ARP 1991, LENZ 1979). In addition, the increased dry mass allocation to roots will enable the trees to absorb more nutrients and water more efficiently, which may in turn promote dry mass production (FIELD et al. 1992, ROGERS and RUNION 1994). Thus, both dry mass production and allocation of the trees depend on the balance between CO_2 supply for leaf photosynthesis and nutrient and water uptake of the roots (EAMUS and JARVIS 1989, ROGERS and DAHLMER 1993). These observations are in line with our previous results on *Fragaria x ananassa* Duch. cv. 'Elsanta' as affected by doubled CO_2 and phosphorus deficiency (CHEN and LENZ 1997).

Dry mass-production efficiency of leaves reflects productivity of biological yield per unit leaf area of the trees (OZBUN 1978). It can be factorized into total dry mass increment and total leaf area increment per tree during the same period of the CO_2 treatment. The mechanisms for diminished total dry mass increment and dry mass-production efficiency of leaves between 350 and 700 ppm CO_2-grown trees with the experiment time can be explained in at least four different ways. It may be caused by pot size, which might restrict growth volume and activity of root systems. As the trial trees were grown in volume-limited pots, their roots might get pot-bound (FIELD et al. 1992, ROGERS and RUNION 1994).

It may result from the limited chamber volumes as well (CEULEMANS and MONSSEAU 1994). The mutual shading among the trial apple trees occurred when they were growing closely together in the volume-limited chambers. Because the trees treated by 700 ppm CO_2 grew faster than those at 350 ppm CO_2 concentration (CHEN et al. 2001), they would probably suffered more from growth limitations as well as self-shading at an earlier stage than those grown under 350 ppm CO_2. Similarly, both net assimilation rate and relative growth rate of the trees also declined more rapidly during the second 60 d of the CO_2 treatment (CHEN et al. 2001).

It can also be attributed to the rapid change of plant size. As high CO_2-treated trees grew faster and became taller, they had to invest more biomass in supporting tissues (BAZZAZ 1990, CANNELL 1985). Thus, the stimulation in dry mass increment of the trees and dry mass-production efficiency of leaves due to atmospheric CO_2 enrichment can be partly offset by the increased size of the doubled CO_2-grown trees after a certain period of CO_2 treatment (CURE and COCK 1986, EAMUS and JARVIS 1989).

The above limitations in expansion of sink capacity may lead to the down-regulated acclimation in net photosynthesis rate per unit leaf area as a consequence of the feed-back inhibition in leaf photosynthetic efficiency under long-term CO_2 enrichment (CEULEMANS and MOUSSEAU 1994, CURE et al. 1991). These effects deserve further attention.

Conclusion

Atmospheric CO_2 enrichment promoted both total leaf area increment and dry mass production of apple trees. It increased dry weight, dry mass increment, and daily gain of dry mass in all organs of the trees. High CO_2 also accelerated dry mass allocation to leaves and roots, while reduced that to stems. Doubled atmospheric CO_2 improved dry mass-production efficiency

of leaves, but this effect diminished with the duration of the CO_2 treatment.

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