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Effects of Doubled Atmospheric CO_2 Concentration on Apple Trees III. Carbohydrate Production

Auswirkungen einer Verdoppelung der atmosphärischen CO_2-Konzentration auf Apfel III. Bildung der Kohlenhydrate

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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. The elevated ambient CO_2 concentration increased carbohydrate production of apple trees. Both content and accumulation of non-structural carbohydrates, particularly starch and sucrose, rose in all organs of the trees under the doubled ambient CO_2 condition. Relative distribution of non-structural carbohydrates within the trees rose in leaves, shoots, and roots, but declined in stems due to the long-term atmospheric CO_2 enrichment. Carbohydrate proportions and starch/ sucrose ratio in different organs of the trees varied in line with the duration of the experiment. When compared with 350 ppm CO_2-treated trees, those grown at 700 ppm CO_2 increased non-structural carbohydrate-production efficiency of leaves by 48 %and 32 % in the first and the second 60 d of the CO_2 treatments, respectively. Long-term atmospheric CO_2 enrichment constantly improved non-structural carbohydrate-production efficiency of the apple trees, especially starch-production efficiency. A further increase of the global atmospheric CO_2 concentration in the future will promote carbohydrate production of apple trees and consequently enhance the fruit productivity.

Zusammenfassung

Zweijährige Apfelbäume (*Malus domestica* Borkh. cv. 'Golden Delicious') auf 'M9' wurden 120 Tage in Pflanzenkammern, die in einer Apfelplantage aufgestellt waren, der gegenwärtigen (350 ± 10 ppm) und der doppelten atmosphärischen CO_2-Konzentration (700 ± 10 ppm) ausgesetzt. Infolge der erhöhten CO_2-Konzentration stieg die Kohlenhydratproduktion der Apfelbäume. Sowohl der Gehalt als auch die Anreicherung von Stärke und Saccharose erhöhte sich in allen Organen der Bäume. Die relative Verteilung der Nicht-Struktur-Kohlenwasserstoffe stieg in den Blättern, Trieben und Wurzeln, sank aber in den Stämmen infolge der langfristigen CO_2-Anreicherung. Das Verhältnis der Kohlenwasserstoffe sowie das Stärke/Saccharose-Verhältnis variierte bei den verschiedenen Organen in Abhängigkeit von der Versuchsdauer. Im Vergleich zu Bäumen, die bei 350 ppm CO_2 wuchsen, stieg bei den unter 700 ppm CO_2 gehaltenen die Effizienz der Bildung von Nicht-Struktur-Kohlenwasserstoffen in den Blättern um 48 % und 32 % in den ersten bzw. zweiten 60 Tagen des Versuches.

Introduction

In the previous articles, we reported the effects of a doubled atmospheric carbon dioxide (CO_2) concentration on plant growth rate (CHEN et al. 2001) and dry mass production (CHEN et al. 2002) of apple trees. This study focuses on carbohydrate production of the trees, because carbohydrates are the primary products of plant photosynthesis (CURE et al. 1991, OLIVEIRA and PRIESTLEY 1988). They are the most important components of plant dry mass, essential to both vegetative and reproductive growth of trees (DUFFUS and DUFFUS 1984, ROGERS et al. 1983). Carbohydrate accumulation and allocation may be controlled by the rate of carbon fixation in mesophyll cells, rate of photoassimilate translocation, and biochemical partitioning forms of carbohydrates into different organs of the tree (DAIE 1985, WULLSCHLEGER et al. 1992). Carbohydrate-production efficiency of apple leaves is of central importance for tree growth and apple production (CEULEMANS and MOUSSEAU 1994, LENZ 1979). Little research, however, has been designed to investigate responses of apple trees to an elevated atmospheric CO_2 concentration with regard to their carbohydrate production. The objectives of the present study were, therefore,

- to investigate carbohydrate contents in different organs of apple trees grown under 350 or 700 ppm CO_2 conditions,
- to compare carbohydrate accumulation, relative distribution, proportion and starch/sucrose ratio in these trees, and
- to evaluate carbohydrate-production efficiency of apple leaves under long-term atmospheric CO_2 enrichment.

Materials and Methods

Sixteen two year old apple (*Malus domestica* Borkh.) trees cv. 'Golden Delicious' on 'M9' rootstocks grown in 10 l containers filled with quartz sand were exposed

to 350 ± 10 or 700 ± 10 ppm CO_2 for 4 months in growth chambers situated in an apple orchard near Bonn, Germany (CHEN et al. 2001). Environmental conditions in the chambers were maintained similar to those in the orchard using a closed air-circuit microclimate-control system (UKG 4000, Kälte-Klimatechnik, K. H. Spitzl GmbH, Bonn, Germany). 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.

Four trees of each treatment were harvested at a 2-months-interval. Samples of each tree were divided into leaves, shoots, stems, and roots. All organs were freeze-dried for a week in a TPYL-10 freeze-drying system (WKF GmbH, Heistenbach, Germany) to determine dry weight of different components. Each fraction was ground and homogenized into a mixed sample passing a 25 µ sieve and kept in an exsiccator for subsequent carbohydrate analyses. Total leaf area per tree was separately measured with a LI-COR 3100 area meter (LI-COR INC., Lincoln, Nebraska, USA).

Contents of starch, glucose, fructose, and sucrose were determined enzymatically as described by ANONYMOUS (1997) and expressed as percentages of dry mass in different organs. The carbohydrate analyses of each sample were replicated twice. The sum of starch and soluble sugars was considered as non-structural carbohydrates. Carbohydrate-production efficiency of leaves was evaluated as total amount of different carbohydrates produced per unit leaf area per tree during the CO_2 treatment.

The experimental data were analysed with the SPSS statistical package (SPSS INC., Chicago, USA). Student t-tests were adopted to examine significant differences between 350 and 700 ppm CO_2 treatments at $P<0.05$ or $P<0.01$.

Table 1. Carbohydrate content in different organs of apple trees as affected by doubled CO_2
Auswirkungen einer Verdoppelung der gegenwärtigen CO_2-Konzentration auf den Kohlenhydratgehalt verschiedener Organe von Apfelbäumen

Treatment		Starch	Glucose	Fructose	Sucrose	Non-structural CH_2O
CO_2 (ppm)	Duration (d)	(% dry weight)				
		Leaves				
350	60	1.09±0.05	0.85±0.03	0.48±0.01	0.95±0.04	3.37±0.13
700	60	6.27±1.25	0.72±0.02	0.55±0.06	1.45±0.11	8.98±1.44
Significance		**	*	*	*	**
350	120	0.64±0.03	0.39±0.03	0.23±0.02	0.86±0.04	2.12±0.11
700	120	1.91±0.28	0.76±0.03	0.44±0.04	1.23±0.07	4.33±0.28
Significance		**	**	**	*	**
		Shoots				
350	60	2.29±0.05	0.47±0.01	0.39±0.01	0.45±0.01	3.60±0.07
700	60	2.87±0.17	0.40±0.02	0.37±0.01	0.56±0.04	3.89±0.13
Significance		*	*	NS	*	*
350	120	4.58±0.07	0.24±0.01	0.20±0.01	0.44±0.01	5.46±0.08
700	120	5.18±0.12	0.32±0.01	0.32±0.02	0.52±0.04	6.35±0.14
Significance		*	**	**	*	*
		Stems				
350	60	5.93±0.14	0.41±0.02	0.50±0.01	0.24±0.05	7.07±0.18
700	60	7.81±0.40	0.42±0.01	0.44±0.01	0.30±0.01	8.97±0.37
Significance		*	NS	*	*	*
350	120	9.63±0.22	0.15±0.02	0.16±0.01	0.17±0.01	10.11±0.21
700	120	10.53±0.29	0.16±0.01	0.18±0.01	0.20±0.01	11.07±0.29
Significance		*	NS	*	*	*
		Roots				
350	60	9.27±0.21	0.83±0.01	0.87±0.02	0.45±0.04	11.42±0.28
700	60	11.32±0.28	0.67±0.04	0.81±0.03	0.55±0.07	13.36±0.34
Significance		*	*	NS	NS	*
350	120	19.76±0.11	0.23±0.02	0.22±0.03	0.35±0.04	20.57±0.16
700	120	25.26±0.15	0.22±0.03	0.20±0.02	0.38±0.03	26.06±0.17
Significance		**	NS	NS	NS	**
		The whole tree				
350	60	5.55±0.31	0.64±0.01	0.60±0.02	0.48±0.01	7.28±0.33
700	60	7.90±0.48	0.58±0.01	0.59±0.02	0.68±0.06	9.74±0.55
Significance		*	NS	NS	*	*
350	120	9.02±0.26	0.24±0.02	0.20±0.01	0.43±0.01	9.89±0.26
700	120	10.59±0.11	0.39±0.02	0.29±0.01	0.62±0.02	11.88±0.10
Significance		*	*	*	*	*

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

Results

Carbohydrate content in different organs

Contents of carbohydrates varied with the organs and the duration of the CO_2 treatment (Tab. 1). Non-structural carbohydrate content was always highest in roots, medium in stems, and lowest either in leaves or in shoots. Therefore, the doubled ambient CO_2 generally raised non-structural carbohydrate contents in all organs of the trees. This effect was particularly prominent for starch.

Starch content dominated the other non-structural carbohydrates in the trees whether at 350 or at 700 ppm CO_2 throughout the experiment (Tab. 1). Both starch and sucrose contents in the plants increased due to the doubled atmospheric CO_2 concentration in 60 and 120 d of the CO_2 treatments. Glucose and fructose contents were also higher in above-ground organs of 700 than 350 ppm CO_2-grown trees at the end of the experiment (Tab. 1).

Carbohydrate accumulation in different organs

Accumulation of different carbohydrates also varied with different organs of the trees and the CO_2 treatments (Tab. 2). Total accumulation of non-structural carbohydrates was highest in roots, medium in stems, and least either in shoots or in leaves. There was a similar pattern for starch accumulation in different organs of the trees. Sucrose accumulation, however, was leaves > roots > stems > shoots during the first 60 d of the experiment, and leaves > shoots > roots > stems after the second 60 d of the CO_2 treatment. As shown in Tab. 2, starch was the major component of non-structural carbohydrates within the trees, which accounted for 76-91 % and 81-89 % of non-structural carbohydrates in 350 and 700 ppm CO_2-treated trees, respectively.

High CO_2 promoted starch, glucose, fructose, and sucrose accumulation in all organs of the trees. The stimulatory effect was especially pronounced for starch

Table 2. Carbohydrate accumulation in different organs of apple trees as affected by doubled CO_2
Auswirkungen einer Verdoppelung der gegenwärtigen CO_2-Konzentration auf die Anreicherung von Kohlenhydraten in den verschiedenen Organen von Apfelbäumen

Treatment		Starch	Glucose	Fructose	Sucrose	Non-structural CH_2O
CO_2 (ppm)	Duration (d)			(mg tree^{-1})		
			Leaves			
350	60	98.8± 4.5	77.8±2.6	43.3± 0.6	86.9±3.9	306.8±11.6
700	60	1194.1±285.4	136.3±8.4	103.8±15.7	275.9±31.6	1710.2±341.2
Significance		**	*	*	*	**
350	120	89.8± 10.3	54.8±8.2	32.9±0.3	120.3±3.5	297.9±21.7
700	120	637.0±108.7	251.9±4.0	145.8±9.0	410.8±34.6	1445.6±130.3
Significance		**	**	**	**	**
			Shoots			
350	60	117.5±16.1	24.2±9.1	19.9±1.3	23.2±9.2	184.7±11.7
700	60	319.3±34.6	44.1±4.4	40.8±1.2	28.3±3.4	432.6±36.8
Significance		*	*	*	NS	**
350	120	559.6±27.9	29.3±0.5	24.1±1.4	53.9±3.6	666.8±33.4
700	120	1393.9±10.5	86.3±2.5	87.2±5.6	140.5±9.6	1707.9±12.0
Significance		**	**	**	**	**
			Stems			
350	60	904.8±148.3	61.6± 6.3	76.7±12.0	37.3±12.9	1080.3±179.5
700	60	1461.9± 77.3	78.1±10.9	82.8±10.9	56.7± 7.2	1679.5±106.2
Significance		**	NS	NS	NS	*
350	120	1888.5± 9.7	29.2±4.6	30.7±2.1	34.1±0.9	1982.5± 13.2
700	120	2716.4±250.2	42.4±1.8	47.0±1.4	51.6±5.2	2857.4±258.6
Significance		**	*	*	*	*
			Roots			
350	60	1287.6±88.5	114.7± 6.3	121.3±8.2	62.0± 7.9	1585.7±110.9
700	60	2922.7±46.6	173.6±12.4	210.0±7.2	143.0±17.4	3449.3± 58.7
Significance		**	*	*	*	**
350	120	2940.0± 34.7	34.1±2.6	33.3±4.2	51.9±6.7	3059.3± 43.0
700	120	7503.6±112.4	64.8±9.7	59.3±7.5	112.8±9.6	7740.5±119.8
Significance		**	*	*	*	**
			The whole tree			
350	60	2408.7±186.2	278.2± 0.9	261.2±12.2	209.4± 7.8	3157.5±207.1
700	60	5898.0±289.4	432.1±10.6	437.4±13.2	504.0±38.4	7271.5±330.4
Significance		**	**	**	**	**
350	120	5478.0± 13.2	147.4±15.9	121.0±5.2	260.2± 1.3	6006.6± 25.2
700	120	12250.9±460.8	445.4±9.4	339.3±5.4	715.7±39.9	13751.4±496.7
Significance		**	**	**	**	**

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

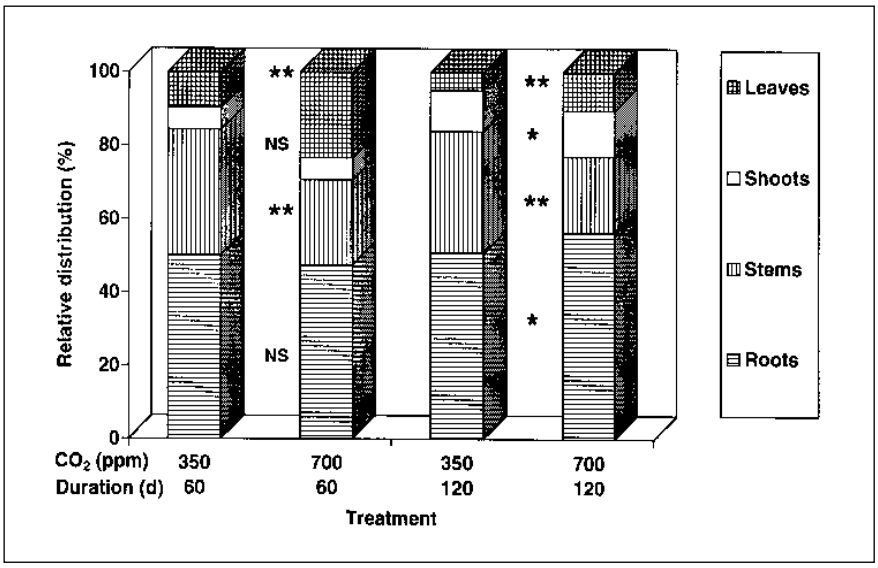


Fig. 1: Relative distribution of non-structural carbohydrates in different organs of apple trees as affected by doubled CO_2 (**, *, and NS denote significance of t-tests at $P<0.01$, $P<0.05$, and $P>0.05$, respectively.) *Auswirkungen einer Verdoppelung der CO_2-Konzentration auf die relative Verteilung der Nicht-Struktur-Kohlenhydrate in unterschiedlichen Organen von Apfelbäumen (**, * und NS kennzeichnen die Signifikanzen der T-Tests; $P<0.01$, $P<0.05$ und $P>0.05$.)*

and sucrose (Tab. 2). After 60 and 120 d of the CO_2 treatments, total accumulation of starch, glucose, fructose, sucrose, and non-structural carbohydrates per tree increased by 3489.3 and 6772.9 mg, 153.9 and 176.2 mg, 176.2 and 218.3 mg, 294.6 and 455.5 mg , and 4114.0 and 7744.8 mg due to the atmospheric CO_2 enrichment, respectively. Besides, total accumulation of starch, sucrose, and non-structural carbohydrates in the plants increased with the duration of the CO_2 treatment. Glucose in 350 ppm CO_2-treated trees and fructose in both 350 and 700 ppm CO_2-grown ones, however, decreased by the end of the experiment (Tab. 2). In comparison with trees grown at 350 ppm CO_2, those grown under 700 ppm CO_2 increased total accumulation of non-structural carbohydrates by 4.6 and 3.9 fold in leaves, 1.3 and 1.6 fold in shoots, 0.6 and 0.4 fold in stems, 1.2 and 1.5 fold in roots, and both 1.3 fold in the whole tree during the first and the second 60 d of the experiment, respectively.

Relative distribution of non-structural carbohydrates

Relative distribution of non-structural carbohydrates was highest in roots, followed by stems, and lowest either in leaves or in shoots (Fig. 1). After 120 d of the CO_2 treatments, relative distribution of non-structural carbohydrates increased in leaves, shoots, and roots, but declined in stems at 700 ppm CO_2. These effects were particularly prominent for leaves and stems (Fig. 1). Besides, relative distribution of non-structural carbohydrates was higher in leaves than in shoots during the first 60 d of the CO_2 treatment, but this pattern became reverse after 120 d of the experiment.

Carbohydrate proportion in different organs

Carbohydrate proportion varied with different organs as well as the duration of CO_2 treatment (Tab. 3). Among different carbohydrates, starch occupied the highest proportion in most organs of the trees. Doubled CO_2 increased the proportion of starch, but decreased those of glucose, fructose, and sucrose in leaves. During the first 60 d of CO_2 treatment, starch and sucrose proportions increased, whereas glucose and fructose proportions declined in trees grown under 700 ppm CO_2. At the end of the experiment, however, the starch proportion decreased, but glucose, fructose and sucrose proportions rose under the elevated ambient CO_2 condition due to the long-term acclimation in this CO_2-enriched environment (Tab. 3).

Starch/sucrose ratio

During the first 60 d of the experiment, the starch/sucrose ratio was highest in stems, followed by roots, shoots, and lowest in leaves (Fig. 2). After 120 d of the CO_2 treatment, however, it became highest in roots, followed by stems and shoots, and still lowest in leaves (Fig. 2). By the end of the experiment, high CO_2 concentration raised the starch/sucrose ratio not only in leaves, but also in roots. No significant difference in the starch/sucrose ratio, however, was observed in stems and shoots between 350 and 700 ppm CO_2-grown trees after 120 d of the atmospheric CO_2 treatment. As a whole, starch/sucrose ratio of the trees was higher in the second 60 d than in the first 60 d of the CO_2 treatment. Nevertheless, when compared with trees grown under 350 ppm CO_2, starch/sucrose ratio declined in those grown under 700 ppm CO_2 by the end of the experiment (Fig. 2).

Carbohydrate-production efficiency of leaves

Carbohydrate-production efficiency of leaves increased due to the long-term atmospheric CO_2 enrichment (Tab. 4). This effect was particularly prominent for starch and sucrose. As shown in Table 4, starch- and non-structural carbohydrate-production efficiency of leaves was higher during the second 60 d than the first 60 d of the CO_2 treatment. Glucose-, fructose-, and sucrose-production efficiency of leaves, however, showed just the opposite trend. In comparison with trees grown under 350 ppm CO_2, non-structural carbohydrate-production efficiency of leaves increased in those grown under 700 ppm CO_2 by 48 % and 32 % during the first 60 d and the second 60 d of the CO_2 treatment, respectively (Tab. 4).

Table 3. Carbohydrate proportion (%) in different organs of apple trees as affected by doubled CO_2
Auswirkungen einer Verdoppelung der gegenwärtigen CO_2-Konzentration auf das Verhältnis der Kohlenhydrate zueinander in den verschiedenen Organen von Apfelbäumen

Treatment		Starch	Glucose	Fructose	Sucrose
CO_2 (ppm)	Duration (d)		(%)		
		Leaves			
350	60	32.2±0.2	25.3±0.1	14.1±0.3	28.3±0.2
700	60	69.5±2.8	8.1±1.1	6.1±0.3	16.3±1.4
Significance		**	**	**	**
350	120	30.1±1.3	18.4±1.4	11.1±0.9	40.5±1.8
700	120	43.9±3.6	17.5±1.9	10.2±1.5	28.4±0.2
Significance		*	*	*	*
		Shoots			
350	60	63.6±0.2	13.1±0.2	10.8±0.2	12.5±0.1
700	60	73.7±1.7	10.2±0.1	9.5±0.5	6.6±1.4
Significance		*	NS	NS	*
350	120	83.9±0.1	4.4±0.1	3.6±0.1	8.1±0.1
700	120	81.6±0.1	5.1±0.2	5.1±0.4	8.2±0.5
Significance		*	NS	*	NS
		Stems			
350	60	83.8±0.2	5.7±0.4	7.1±0.1	3.4±0.6
700	60	87.1±0.9	4.6±0.4	4.9±0.3	3.4±0.2
Significance		NS	NS	*	NS
350	120	95.3±0.1	1.5±0.2	1.5±0.1	1.7±0.1
700	120	95.1±0.2	1.5±0.1	1.6±0.1	1.8±0.1
Significance		NS	NS	NS	NS
		Roots			
350	60	81.2±0.1	7.2±0.1	7.7±0.1	3.9±0.2
700	60	84.7±0.1	5.0±0.4	6.1±0.1	4.1±0.4
Significance		NS	NS	NS	NS
350	120	96.1±0.2	1.1±0.1	1.1±0.1	1.7±0.2
700	120	96.9±0.1	0.8±0.1	0.8±0.1	1.5±0.1
Significance		NS	NS	NS	NS
		The whole tree			
350	60	76.3±0.9	8.8±0.6	8.3±0.2	6.6±0.2
700	60	81.1±0.3	6.0±0.4	6.0±0.1	6.9±0.2
Significance		*	*	*	*
350	120	91.2±0.2	2.5±0.3	2.0±0.1	4.3±0.1
700	120	89.1±0.1	3.2±0.2	2.5±0.1	5.2±0.1
Significance		*	*	*	*

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

Discussion

Responses of plants to atmospheric CO_2 enrichment varies with different species (POORTER 1993). ARP (1991) observed that the long-term response to exposure to high levels of CO_2 was dependent in a large measure on the plant's abilities to initiate new sinks, to accelerate the growth of existing sinks, and/or to develop temporary storage capacity for excess carbohydrates. The extent to which a plant can expand its sink or storage capacity depends on both genetic factors (e.g. determinant vs. indeterminant growth habit) and environmental factors (e.g. sunlight, air temperature, water and nutrient availability). In this experiment, content and accumulation level of non-structural carbohydrates (Tab. 1 and 2) were both high in roots, medium in stems, and low either in shoots or in leave of the trial trees. The successively increased gradients of nonstructural carbohydrates from sources to sinks were particularly prominent for starch. These observations were just the opposite to the previous results on strawberry *(Fragaria x ananassa* Duch.) cv. 'Elsanta' in which content and accumulation of nonstructural carbohydrates were highest in leaves, and lowest in roots (CHEN and LENZ 1997, CHEN et al. 1997). These differences between the two species suggest that the sinks for non-structural carbohydrates are stronger in apple trees than in strawberry plants. In the present and the previous experiments on effects of a doubled atmospheric CO_2 concentration on apple and strawberry, the environmental factors were set to preferential conditions, which could not limited non-structural carbohydrate production and its accumulation in the plant organs. The major difference, thus, may be the growth potential of the two species. Apple trees can continuously produce new

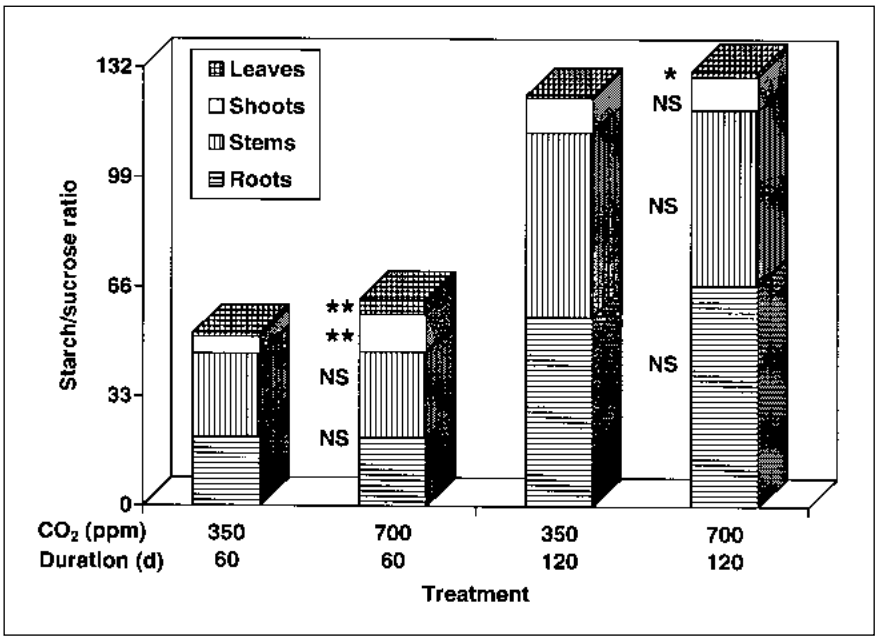


Fig. 2: Starch/sucrose ratio in different organs of apple trees as affected by doubled CO_2 (**; * and NS denote significance of t-test at $P<0.01$, $P<0.05$ and $P>0.05$, respectively.)
*Auswirkungen einer Verdoppelung der CO_2-Konzentration auf das Verhältnis Stärke/Saccharose in den verschiedenen Organen von Apfelbäumen (**, * und NS kennzeichnen die Signifikanzen der T-Tests; $P<0.01$, $P<0.05$ und $P>0.05$.)*

Table 4. Carbohydrate-production efficiency of apple leaves as affected by doubled CO_2
Auswirkungen einer Verdoppelung der gegenwärtigen CO_2-Konzentration auf die Effizienz der Kohlenhydratproduktion von Apfelbäumen

Treatment		Starch	Glucose	Fructose	Sucrose	Non-structural CH_2O
CO_2 (ppm)	Duration (d)	($g\,CH_2O\,m^{-2}$ leaf)				
350	60	18.77±1.51	2.17±0.01	2.03±0.10	1.63±0.07	24.60±1.69
700	60	29.58±0.91	2.17±0.09	2.19±0.03	2.53±0.15	36.47±0.99
Significance		**	NS	NS	*	**
350	120	32.62±0.88	0.88±0.07	0.72±0.05	1.55±0.04	35.77±0.90
700	120	42.15±1.41	1.53±0.04	1.17±0.01	2.46±0.13	47.31 ±1.51
Significance		**	*	*	*	**

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

shoots and leaves during the whole growing season. By contrast, growth of strawberry plants is more often limited by environmental conditions (e.g. high air temperature in summer). This may result in differences in sink strength for non-structural carbohydrates. The consequence should be a different pattern of carbohydrate accumulation in organs between apple trees and strawberry plants (DAIE 1985, POORTER 1993). WOLF (1995) also noticed that indeterminate species tended to respond more positively to atmospheric CO_2 enrichment than determinate types which have a more limited sink capacity of non-structural carbohydrate production.

DAIE (1985) concluded that a lack of correlation between net photosynthesis rates and economic yield at the whole plant level may result from the biochemical partitioning of carbohydrates mainly between starch and sucrose because they are both primary end-products of photosynthesis. Starch is a temporary storage carbohydrate which may accumulate in the chloroplast (DUFFUS and DUFFUS 1984). It is formed through photosynthesis during the day and degraded to transportable carbohydrates by respiration during the night. Under the doubled atmospheric CO_2 environment, the excessively produced starch may accumulate in the plants, especially in leaves (Tab. 1 and 2). Sucrose is also the major component of photosynthetic assimilates. In contrast to starch, it is a non-reducing and transportable carbohydrate as well as a temporary storage form of carbohydrate in the vacuole (DUFFUS and DUFFUS 1984). Sucrose can be translocated from assimilation organs (sources) to utilization or storage ones (sinks) within the plants (TOLBERT and ZELITCH 1983). The primary site of sucrose biosynthesis in the sources (leaves) is the cytoplasm of mesophyll cells. The rate of sucrose biosynthesis is a function of the carbon fixation rate, biochemical partitioning of carbohydrates between starch and sucrose, and the rate of sucrose export from the leaves (DAIE 1985). Biochemical partitioning patterns of carbohydrates depend on the competitive activity of various sinks and sources within the plants as well as their mobilizing abilities (TOLBERT and ZELITCH 1983). Growing sinks usually play a key role in determining the rate of sucrose export out of leaves. The sink's ability to acquire assimilates affects the rate and direction of biochemical partitioning of carbohydrates (DAIE 1985). In the present experiment, starch accumulation in the leaves (Tab. 2) indicated that sucrose transport out of leaves might be delayed behind the rate of net photosynthesis. Sucrose content (Tab. 1) and accumulation (Tab. 2) in leaves, on the contrary, were both highest in all organs of the trees. This indicated that sucrose biosynthesis rate was higher than its

transport rate within the trees because in apple there are some other translocated carbohydrates, such as sorbitol (OLIVEIRA and PRIESTLEY 1988). TOLBERT and ZELITCH (1983) also observed that long-term atmospheric CO_2 enrichment could enhance sucrose biosynthesis in leaves where sucrose production was in excess of the plant ability to transport it from sources to sinks. This could probably be the result of a reduced sink demand for assimilates or preferential control toward starch biosynthesis in apple trees. An increased starch/sucrose ratio of leaves in Figure 2 demonstrated that (i) sucrose synthesis declined, and (ii) a large part of the fixed CO_2 had been diverted into starch due to long-term CO_2 enrichment. WULLSCHLEGER et al. (1992) also observed an increased starch/sucrose ratio in *Liriodendron tulipifera* L. and *Quercus alba* L. leaves due to long-term high CO_2 treatments.

Carbohydrate production of apple leaves directly determines apple productivity (OZBUN 1978, LENZ 1979). Carbohydrate-production efficiency in this study represents the capacity of carbohydrate biosynthesis of apple leaves during the CO_2 treatment. The present results showed that long-term atmospheric CO_2 enrichment improved carbohydrate-production efficiency of leaves, especially starch-production efficiency (Tab. 4). In contrast to dry mass-production efficiency of leaves (CHEN et al. 2001b), long-term high CO_2 could successively enhance carbohydrate-production efficiency of apple leaves. This suggests that the continuous increase in CO_2 concentration of the global atmosphere will likely promote carbohydrate-production efficiency of the trees as well as apple productivity in the future.

Conclusion

Doubling the present atmospheric CO_2 concentration accelerated carbohydrate production of apple trees, mainly by improving carbohydrate-production efficiency of leaves. Atmospheric CO_2 enrichment promoted carbohydrate accumulation and allocation to all organs of the trees, especially to roots. Ambient CO_2 concentration also affected biochemical partitioning of carbohydrates into various organs within the trees. The predicated increase in global CO_2 concentration in the future atmosphere will likely enhance carbohydrate production of apple trees.

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