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Autumn photosynthesis of 'Golden Delicious' apple trees – the effects of picking and fertilisation treatment

Der Einfluss von Ernte und Düngung auf die Herbstphotosynthese bei 'Golden Delicious' Apfelbäumen

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Summary

The influence of the foliar application of the mineral nutrients phosphorus and potassium on the photosynthesis and leaf and bark carbohydrates (sorbitol, sucrose, fructose and glucose) was studied in *Malus domestica* cv. 'Golden Delicious'. The research was done on 12-year old trees on M9 rootstocks (unpicked or picked trees either sprayed or not with the PK fertilizer Hascon M 10 AD) in the year 2000. Measurements of photosynthesis showed high photosynthetic activity (A_{350}) and photosynthetic capacity (A_{2000}) of apple trees in the late season. Results of the measurements of photosynthetic activity indicate that sink regulation of apple leaf photosynthesis was dependent on the fertilisation treatment. Photosynthesis measured at 350 ppm was the highest in the PK sprayed unpicked trees and the lowest in the PK sprayed trees without the crop. The sink removal effect was not observable two days after fruit picking, but was significant 5 and 20 days later. All trees showed a high photosynthetic capacity which decreased slowly until the end of October. The onset of senescence could be seen also from the foliar phosphorus content. Eight days after fruit removal trees without fruits showed significantly higher contents of sorbitol, sucrose, and fructose in the leaves. Sink dependent translocation of carbohydrates can be seen from the analyses of bark carbohydrates as well. The unpicked trees sprayed with PK had a significantly lower content of sorbitol and high photosynthetic rate when compared to the sprayed and picked trees. Nutritional dependency on sink/source effect could not be supported by foliar analyses.

Zusammenfassung

Der Einfluss der Blattdüngung mit Phosphor und Kalium auf die Photosynthese und die Kohlenhydratgehalte (Sorbitol, Sacharose, Fructose) der Blätter und Rinde der Bäume wurden bei der Apfelsorte 'Golden Delicious' untersucht. Durchgeführt wurde der Versuch im Jahr 2000 an zwölfjährigen, auf M9-Unterlagen veredelten Bäumen. Die fruchtbehangenen oder bereits abgeernteten Bäume wurden als Versuchsvarianten in den Versuch einbezogen. Die Blattdüngung erfolgte mit dem PK-Dünger Hascon M 10 AD, wobei die unbehandelten Bäume die Kontrollvariante darstellten. Die Apfelbäume wiesen in Spätsommer sowohl eine hohe photosynthetische Aktivität (A_{350}) als auch eine hohe photosynthetische Kapazität (A_{2000}) auf.
Die Abhängigkeit der vom Verbrauch („sink") regulierten Apfelblattphotosynthese von der Düngerbehandlung konnte durch die Messung der photosynthetischen Aktivität festgestellt werden. Die höchsten Werte der Photosynthese, gemessen bei 350 ppm erreichten die gedüngten fruchtbehangenen Bäume und die niedrigsten Werte die gedüngten abgeernten Bäume. Der Einfluss des Entfernens des Verbrauchers konnte zwei Tage nach der Ernte noch nicht festgestellt werden, war aber nach 5 und 20 Tagen signifikant nachweisbar. Alle Bäume zeigten eine hohe photosynthetische Kapazität, die bis Ende Oktober langsam abnahm. Der Beginn der Seneszenz konnte auch anhand der Phosphorgehalte in den Blättern festgestellt werden. Die Gehalte an Sorbitol, Saccharose und Fructose in den Blättern der abgeernten Bäume stiegen acht Tage nach der Ernte signifikant an. Die vom Verbrauch abhängige Verlagerung der Kohlenhydrate kann außerdem noch an den Ergebnissen der Kohlenhydratanalysen der Rinde beobachtet werden. Die fruchtbehangenen mit PK behandelten Bäume zeigten signifikant niedrigere Sorbitolgehalte und höhere photosynthetische Raten als die ebenso behandelten, abgeernteten Bäume. Die Abhängigkeit der Sink/Source-Wirkung vom Ernährungszustand konnte anhand der Blattanalysen nicht festgestellt werden.

Introduction

Fruits influence different physiological processes in the plant (WIBBE and BLANKE 1995). Due to increased photosynthesis and commensurate or reduced dark respiration fruiting trees are supposedly more efficient with respect to their carbon budget (WIBBE et al. 1993). Fruits represent sinks which regulate photosynthesis through signal transduction pathways that co-ordinate the plant carbon : nitrogen balance, which match photosynthetic capacity to growth and storage capacity and underpin and can override the direct short-term controls of photosynthesis by light and CO_2 (PAUL and FOYER 2001). With the removal of fruits the plant meets an imbalance between source and sink, which results in down regulation of photosynthesis. Decreased leaf net photosynthetic rate after removal of fruits has been found in several tree fruit species, including apple (*Malus domestica* Borkh.) (GUCCI et al. 1994, WIBBE and

BLANKE 1995, GIULIANI et al. 1997a, b). In field-grown apple trees cv. 'Golden Delicious' the inhibition of photosynthesis was positively correlated with crop sink strength, but it was not correlated with fruit relative growth rate or crop load (GUCCI et al. 1994). At saturating irradiances defruiting decreased assimilation in cv. 'Golden Delicious' (GUCCI et al. 1994) and cv. 'Smoothee' (GIULIANI et al. 1997b). On the other hand, the apparent quantum yield of single leaves was found to be independent of the presence of fruits (GUCCI et al. 1994). The effect of defruiting is dependent on the time of fruit-removal as shown in cv. 'Golden Delicious' (WIBBE and BLANKE 1995). Although the reduction in net photosynthesis occurred irrespective of the month of defruiting it was the most pronounced in October, when the date of defruiting resembled that of the commercial picking (WIBBE and BLANKE 1995).

At least some studies have shown that the rate of photosynthesis can be directly dependent on crop load (PALMER et al. 1997, WÜNSCHE et al. 2000). In cv. 'Braeburn' a clear correlation was found. A large response to crop load was observed at the time when accumulation of carbohydrates in the fruit was high and when shoot growth ceased (PALMER et al., 1997). After fruit harvest, the previous crop loads had no effect on leaf photosynthesis (WÜNSCHE et al. 2000).

The removal of fruits as major sink organs influences also the partitioning of carbohydrates from leaves (CHALMERS et al. 1975). Defruiting allocated the leaf assimilates to sinks other than fruit (shoot and root) resulting in large content in transport carbohydrates in the leaves (WIBBE and BLANKE 1995). In peach (*Prunus persica* L.) the content of total sugars in the leaves was higher in the fruiting trees than in non-fruiting. The same was true for sorbitol which increased one day after removal of fruit in parallel with accumulation of starch. On the other hand the sucrose content in the leaves did not change markedly upon removal of fruit (NII 1997). In apple cv. 'Golden Delicious' defruiting increased leaf starch and sucrose content but decreased glucose, fructose and sorbitol (WIBBE and BLANKE 1995).

Sink regulation of photosynthesis is highly dependent on different physiological processes. Among other factors mineral nutrition is of crucial importance for the sink/source balance (PIETERS et al. 2001). Although generally well known, photosynthetic dependency upon nutrient supply has not been extensively studied in apple. For different apple cultivars SCIBISZ and LENZ (1993) found that the total CO_2-uptake was strongly reduced as the result of low nutrient supply. The average photosynthetic rates of leaves however, were not affected by the nutrient deficiency. In York Imperial apple seedlings it was shown that potassium, applied as spray, did not significantly affect photosynthesis and stomatal conductance (SWIETLIK et al. 1982). On the other hand increased K supply increased net photosynthesis in cv. 'Golden Delicious' under salt stress (SCHREINER and LÜDDERS 1996).

Phosphorus and potassium are used in foliar sprays in orchard management (STAMPAR et al. 1999) due to their important role in different physiological and developmental processes (MARSCHNER 1995, FRIEDRICH and FISCHER 2000). The goal of our study was to estimate the possible combined effects of defruiting and the foliarly applied phosphorus and potassium on leaf photosynthesis and leaf carbohydrates in apple cv. 'Golden Delicious'. We were particularly interested to monitor changes of some physiological parameters (photosynthesis, carbohydrate levels) of the tree at commercial picking time of fruits.

Materials and Methods

Plant material

The measurement were carried out in autumn 2000. 12-year old 'Golden Delicious' apple trees on M9 rootstock, grown in the experimental orchard of the University of Ljubljana, central Slovenia, were used for the experiment. The treatments encompassed unpicked or picked trees either sprayed or not with the PK fertiliser Hascon M 10 AD (15 % P_2O_5, 20 % K_2O). Each treatment involved four trees (4 x 4).

The foliar fertiliser was added on September 27, 2000. The previous day fruits from one half of trees were picked (a picked tree treatment). For experimental orchard the commercial picking time of the cv. 'Golden Delicious' in the year 2000 was in the last week of September.

Photosynthesis, transpiration and water use efficiency (WUE)

The photosynthetic activity and transpiration of the leaves were measured with a portable measuring system Li-6400 (LICOR). Measurements were taken at PPFD of 1500 µmol m^{-2} s^{-1} (6400-02B light source) and at two CO_2 concentrations; namely, 350 ppm (A_{350}) or 2000 ppm (A_{2000}, photosynthetic capacity). Leaf temperature was adjusted to 22–23 °C. The measurements were carried out on spur leaves. The first measurement was performed four days prior to the application of fertiliser, other four were carried out 1, 5, 13 and 20 days after the application. Photosynthetic activity (A) of leaves was expressed in µmol CO_2 m^{-2} s^{-1}, transpiration (E) in mmol H_2O m^{-2} s^{-1}. Water use efficiency was calculated as A/E and expressed mmol/mol.

Sugar analysis

Leaves and bark for sugar analysis were sampled three times, the first sampling was carried out on the same day as picking the fruits from on half of the trees, the second one was performed 7 days after applying foliar PK sprays and the third sampling was done 30 days after the application of PK sprays. Leaves and bark for sugar analyses were sampled from one-year shoots with mature leaves at 10 a.m. each time. For analysis only the lamina of leaves without pedicle was taken. Leaves and bark were shock frozen in liquid nitrogen immediately after excision from the tree. After freeze drying samples were ground and prepared for sugar and sorbitol determination by HPLC (High Performance Liquid Chromatography) according to the DOLENC and STAMPAR (1997) method. This method was slightly modified because only 1 g (leaves) or less (bark) of the sample was used and diluted with bi-distilled water to 30 or 50 ml in regard to the sample amount.

Foliar nutrient analysis

Samples were taken at the same time as for the sugar analysis. One sample per tree was composed out of 10 mature leaves sampled from different type of one-year shoots. Plant samples were dried at 40 °C till constant weight. The samples were grind to powder. 1g of sample was taken for analysis. It was burned at 550 °C to ash. The ash was diluted with HCl, HNO_3 and distilled water to 50 ml. The samples were analysed according to Analytical methods: Analysis of plant tissue: Dry ashing (1982). The amount of P was estimated with molecular absorption spectrometry (Perkin-Elmer, LAMBDA 2) and the amount of K with emission technique on flame photometer (Carl Zeis, FLAPHO 40)

Statistical evaluation

The significance of both factors (picking and spraying with P and K) and also the interaction between them was tested. Results were statistically analysed with the program Statgraphics plus 4.0 using the nested analysis of variance (ANOVA). Differences between treatments were estimated with a multiple range test using least significant difference (LSD) or Duncan test at $\alpha < 0{,}05$.

Results

Photosynthesis

Pre-treatment measurements of leaf photosynthesis showed no differences among selected trees (Table 1). This proved that the source material was uniform regarding the photosynthetic activity of the leaves. In all measurements photosynthesis measured at 350 ppm CO_2 (A_{350}) varied between 14 and 17 µmol CO_2 m^{-2} s^{-1}. For the same leaf photosynthesis measured at 2000 ppm (A_{2000}) was in the range of 27-33 µmol CO_2 m^{-2}\$$s^{-1}$. At the second measurement which was performed two days after picking of the fruits and one day after the first application of PK fertiliser, no significant effects of treatments on photosynthetic efficiency (A_{350}) were observed. Presence of fruits affected A_{350} 6 days after fruit removal (3rd measurement) when photosynthetic rate was enhanced compared to the activity in non-fruiting trees. ANOVA revealed also statistically significant interaction between fruit presence and application of fertiliser. In fertilised non-picked trees photosynthesis was the highest and differed from fertilised picked trees. At fourth measurement (A_{350}) spraying of PK significantly influenced photosynthesis of the leaves. PK sprayed trees had lower photosynthesis than the trees in the control treatment. 20 days after fruit removal (5th measurement) the interaction between crop and spraying of PK fertiliser influenced leaf photosynthesis. Again sprayed and picked trees had lower rates of photosynthesis than other treatments .

For photosynthetic capacity of leaves (A_{2000}) there were less significant differences between the treatments (Table 1). Only at the second measurement fruiting trees showed higher rates of photosynthesis compared to non-fruiting ones. In all treatments A_{2000} was the highest at the first measurement and a clear decrease was observed to the fifth measurement.

Transpiration and water use efficiency (WUE)

Transpiration of the leaves showed some differences among treatments (Table 2). Only at 3rd measurement at the CO_2 concentration 350 ppm the interaction of spraying PK and defruiting the trees resulted in significantly lower transpiration than unsprayed picked treatment. There were no differences in transpiration when measured at 350 and 2000 ppm of CO_2.

Water use efficiency (WUE) was mostly affected by defruiting of trees at 350 ppm CO_2. 2, 6 and 14 days after defruiting (2nd, 3rd and 4th measurements respectively) this resulted in significantly lower WUE of defruited trees compared with fruiting trees. At 3rd measurement also spraying of PK fertiliser influenced leaf WUE.

Table 1. Photosynthesis (A_{350}) and photosynthetic capacity (A_{2000}) of apple 'Golden Delicious' leaves. CON-F=non-fertilised trees with crop, CON-E=non-fertilised picked trees, PK-F=PK-fertilised trees with crop, PK-E=PK-fertilised picked trees. Measurements were taken 4 days prior (1) and 1(2), 5 (3), 13 (4), 20 (5) days after PK spraying. Means and standard errors are presented, two-way ANOVA, N=4.
Photosynthese (A_{350}) und photosynthetische Kapazität (A_{2000}) bei Blättern der Apfelsorte 'Golden Delicious'. CON-F=nicht gedüngte Bäume mit Behang, CON-E=nicht gedüngte geerntete Bäume, PK-F=PK-gedüngte Bäume mit Behang, PK-E=PK-gedüngte geerntete Bäume. Messungen wurden 4 Tage vor dem ersten und 1 (2), 5 (3), 13 (4), 20 (5) Tagen nach PK-Behandlung durchgeführt. Ergebnisse und Standardfehler sind dargestellt in two-way ANOVA, N=4.

		Photosynthesis (µmol CO_2 m^{-2} s^{-1})				factors		
Photos.	**date**	**CON-F**	**CON-E**	**PK-F**	**PK-E**	**crop**	**spray**	**c x s**
A_{350}	1	16.6±1.2	14.0±1.0	16.9±0.6	16.7±1.6	NS	NS	NS
ppm	2	15.6±1.1	15.5±0.7	16.4±0.7	12.5±1.4	NS	NS	NS
	3	14.6±1.0	14.5±0.8	16.3±0.8	12.3±1.0	*	NS	*
	4	15.4±0.8	15.9±0.4	14.6±0.8	12.5±0.7	NS	*	NS
	5	13.8±0.9	14.2±0.5	15.4±1.0	10.9±1.0	NS	NS	*
A_{2000}	1	32.7±3.1	29.9±2.0	27.7±2.0	29.3±2.2	NS	NS	NS
ppm	2	29.8±0.9	27.0±1.0	29.0±0.8	23.3±2.2	*	NS	NS
	3	26.1±0.9	25.6±1.1	25.5±1.1	21.2±1.4	NS	NS	NS
	4							
	5	22.2±1.0	23.4±0.9	23.2±1.5	19.9±1.8	NS	NS	NS

Table 2. Transpiration and water use efficiency of apple 'Golden Delicious' leaves. Measurements were taken at 350 and 2000 ppm CO_2. CON-F=non-fertilised trees with crop, CON-E=non-fertilised picked trees, PK-F=PK-fertilised trees with crop, PK-E=PK-fertilised picked trees. Measurements were taken 4 days prior (1) and 1(2), 5 (3), 13 (4), 20 (5) days after PK spraying. Means and standard errors are presented, two-way ANOVA, N=4.
Transpiration und 'water use efficiency' von Blättern der Apfelsorte 'Golden Delicious'. Messungen wurden bei 350 und 2000 ppm CO_2 durchgeführt. CON-F=nicht gedüngte Bäume mit Behang, CON-E=nicht gedüngte geerntete Bäume, PK-F=PK-gedüngte Bäume mit Behang, PK-E=PK-gedüngte geerntete Bäume. Ergebnisse und Standardfehler sind dargestellt in two-way ANOVA, N=4.

CO_2 conc.	date	Transpiration (mmol H_2O m^{-2} s^{-1})				factors		
		CON-F	CON-E	PK-F	PK-E	crop	spray	c x s
350	1	5.6±0.4	5.2±0.3	5.7±0.4	5.8±0.4	NS	NS	NS
ppm	2	5.2±0.5	5.9±0.2	5.9±0.2	5.7±0.1	NS	NS	*
	3	5.4±0.4	6.0±0.2	5.7±0.2	5.6±0.2	NS	NS	*
	4	5.1±0.3	5.8±0.1	5.2±0.2	5.3±0.2	NS	NS	NS
	5	5.0±0.4	5.3±0.2	5.6±0.1	5.0±0.2	NS	NS	NS
2000	1	5.5±0.4	5.2±0.3	5.7±0.4	5.6±0.3	NS	NS	NS
ppm	2	5.2±0.5	6.0±0.2	5.8±0.1	5.5±0.1	NS	NS	NS
	3	5.4±0.4	5.8±0.2	5.4±0.2	5.0±0.3	NS	NS	NS
	4							
	5	5.1±0.4	5.3±0.2	5.6±0.1	4.8±0.4	NS	NS	NS
CO_2 conc.	date	Water use efficiency (mmol/mol)				factors		
		CON-F	CON-E	PK-F	PK-E	crop	spray	c x s
350	1	3.0±0.2	2.7±0.2	3.0±0.2	2.9±0.2	NS	NS	NS
ppm	2	3.1±0.1	2.6±0.1	2.8±0.1	2.2±0.2	*	NS	NS
	3	2.7±0.2	2.4±0.1	2.9±0.1	2.4±0.1	*	NS	NS
	4	3.1±0.2	2.8±0.1	2.8±0.2	2.4±0.1	*	*	NS
	5	2.8±0.1	2.7±0.1	2.7±0.2	2.2±0.2	NS	NS	NS
2000	1	6.0±0.3	5.8±0.4	5.0±0.6	5.2±0.2	NS	NS	NS
ppm	2	6.0±0.5	4.6±0.1	5.0±0.1	4.2±0.4	*	NS	NS
	3	5.1±0.5	4.5±0.3	4.7±0.2	4.3±0.2	NS	NS	NS
	4							
	5	4.4±0.3	4.5±0.2	4.1±0.3	4.3±0.5	NS	NS	NS

Carbohydrates in leaves and bark

At the beginning of the trial no differences in leaf sugars, sucrose, sorbitol, fructose and glucose were found among selected trees (Table 3). Eight days after fruit removal and one week after application of foliar PK fertiliser significantly higher content of sorbitol, sucrose, and fructose were found in the leaves of trees without the fruits. Fertilisation affected the content of glucose in the leaves, which was higher in non-fertilised plants in comparison to PK-treated plants. The analysis of sugars performed 1 month after fruit picking (end of October) revealed the increase of all analysed sugars except glucose when compared to the second measurement (8 days after fruit picking). The increase was the most prominent in sucrose. Meanwhile the glucose content remained the same or even slightly decreased. At the third sampling effects of fertilisation or fruit removal on sucrose, fructose and glucose were no longer observed. The sorbitol content however, was significantly higher in leaves of PK fertilised trees, irrespective of the fruit presence.

The investigated carbohydrates in the bark were the same as those in the leaves. At the first two samplings, there were no significant differences in the content of investigated sugars among the treatments. At the third sampling a significant interaction between fertilisation and picking-treatment was observed in sorbitol, glucose and fructose, but not in sucrose. In all cases bark of PK-sprayed trees with fruits had the lowest content of analysed sugars. It was significantly lower than in CON-F treatment in glucose and fructose contents and lower than in from PK-E in sorbitol content.

P and K content in the leaves

The phosphorus content at the first sampling was low to medium and showed no significant differences among treatments (Table 4). There was no difference in leaf phosphorus concentration found one week (2nd sampling) and also one month (3rd sampling) after PK application. A clear decrease in P was observed when 2nd and 3rd samplings were compared. Potassium content in leaves showed a deficit in that nutrient. According to soil analysis the amount of potassium was slightly in deficit (169 ppm) but still in the normal range. Potassium content of the leaves increased from the first to second sampling in all treatments. From the second to third samplings there was a strong decrease in leaf potassium content in the treatment CON-F, while in other treatments there was little change or even an increase (PK-F).

Discussion

Measurements of photosynthesis showed high photosynthetic activity (A_{350}) and photosynthetic capacity (A_{2000}) of apple trees in the late season. High autumn

Table 3. The content of carbohydrates in the leaves and bark of apple 'Golden Delicious'. CON-F=non-fertilised trees with crop, CON-E=non-fertilised picked trees, PK-F=PK-fertilised trees with crop, PK-E=PK-fertilised picked trees. Samples were taken 2 days prior (1) and 7(2), 30 (3) after PK spraying. Means and standard errors are presented, two-way ANOVA, N=4.
Kohlenhydratgehalte in Blättern und Rinde der Apfelsorte 'Golden Delicious'. CON-F=nicht gedüngte Bäume mit Behang, CON-E=nicht gedüngte geerntete Bäume, PK-F=PK-gedüngte Bäume mit Behang, PK-E=PK-gedüngte geerntete Bäume. Ergebnisse und Standardfehler sind dargestellt in two-way ANOVA, N=4.

Leaf Carbohyd.	**date**	**Leaf carbohydrates (g/kg of dry weight)**				**factors**		
		CON-F	**CON-E**	**PK-F**	**PK-E**	**crop**	**spray**	**c x s**
Sucrose	1	4.26±0.26	4.06±0.45	3.56±0.25	3.63±0.12	NS	NS	NS
	2	3.22±0.29	4.36±0.72	2.23±0.11	3.69±0.46	*	NS	NS
	3	5.94±0.53	5.45±0.7	4.99±0.3	5.31±0.69	NS	NS	NS
Sorbitol	1	4.85±0.21	5.77±0.42	5.32±0.31	5.40±0.26	NS	NS	NS
	2	4.47±0.40	5.55±0.39	4.23±0.32	5.90±0.48	*	NS	NS
	3	5.83±0.48	6.09±0.47	7.08±0.38	7.04±0.26	NS	*	NS
Fructose	1	0.91±0.09	1.00±0.07	1.03±0.08	0.9±0.09	NS	NS	NS
	2	0.84±0.10	1.01±0.15	0.62±0.09	0.92±0.09	*	NS	NS
	3	1.73±0.19	1.71±0.39	1.48±0.23	1.25±0.16	NS	NS	NS
Glucose	1	4.38±0.15	4.51±0.44	4.21±0.17	3.85±0.25	NS	NS	NS
	2	4.69±0.21	5.16±0.21	4.21±0.26	3.88±0.12	NS	*	NS
	3	4.19±0.22	4.58±0.05	4.28±0.30	4.19±0.12	NS	NS	NS
Bark carbohyd.	**date**	**Bark carbohydrates (g/kg of dry weight)**				**factors**		
		CON-F	**CON-E**	**PK-F**	**PK-E**	**crop**	**spray**	**c x s**
Sucrose	1	0.29±0.04	0.27±0.04	0.29±0.07	0.18±0.03	NS	NS	NS
	2	0.24±0.03	0.38±0.13	0.19±0.02	0.27±0.04	NS	NS	NS
	3	0.55±0.11	0.46±0.11	0.37±0.05	0.48±0.10	NS	NS	NS
Sorbitol	1	1.37±0.25	1.74±0.18	1.43±0.15	1.32±0.08	NS	NS	NS
	2	1.31±0.16	1.58±0.29	1.15±0.13	1.89±0.35	NS	NS	NS
	3	1.78±0.14	1.69±0.05	1.37±0.13	2.03±0.32	NS	NS	*
Fructose	1	0.40±0.10	0.47±0.13	0.38±0.05	0.31±0.03	NS	NS	NS
	2	0.37±0.06	0.43±0.09	0.28±0.02	0.41±0.05	NS	NS	NS
	3	0.63±0.08	0.51±0.04	0.33±0.04	0.47±0.06	NS	*	*
Glucose	1	0.39±0.10	0.46±0.13	0.37±0.05	0.31±0.03	NS	NS	NS
	2	0.35±0.06	0.42±0.09	0.27±0.03	0.41±0.06	NS	NS	NS
	3	0.60±0.08	0.49±0.04	0.31±0.04	0.46±0.06	NS	*	*

Table 4. The content of phosphorus and potassium in the leaves of apple 'Golden Delicious'. CON-F=non-fertilised trees with crop, CON-E=non-fertilised picked trees, PK-F=PK-fertilised trees with crop, PK-E=PK-fertilised picked trees. Samples were taken 2 days prior (1) and 7(2), 30 (3) after PK spraying. Means and standard errors are presented.
Phosphor- und Kaliumgehalte in Blättern der Apfelsorte 'Golden Delicious'.CON-F=nicht gedüngte Bäume mit Behang, CON-E=nicht gedüngte geerntete Bäume, PK-F=PK-gedüngte Bäume mit Behang, PK-E=PK-gedüngte geerntete Bäume. Ergebnisse und Standardfehler sind dargestellt in two-way ANOVA, N=4.

	date	**Content in leaves (% of dry weight)**			
		CON-F	**CON-E**	**PK-F**	**PK-E**
Phosphorus	1	0.154±0.009	0.145±0.010	0.151±0.007	0.150±0.007
	2	0.149±0.013	0.170±0.015	0.156±0.001	0.172±0.010
	3	0.119±0.005	0.152±0.020	0.137±0.006	0.133±0.005
Potassium	1	0.350±0.022	0.345±0.030	0.434±0.020	0.556±0.069
	2	0.392±0.032	0.411±0.037	0.502±0.026	0.640±0.009
	3	0.244±0.019	0.394±0.070	0.509±0.077	0.680±0.019

photosynthetic rates were measured in some other studies as well (TERHOEVEN-URSELMANS and BLANKE 1999, TARTACHNYK and BLANKE 2001). TARTACHNYK and BLANKE (2001) reported that apple trees maintained a high photosynthetic rate after the harvest, i.e. 10-12 µmol CO_2 m^{-2} s^{-1} until the first frost. The authors concluded that apple photosynthesis in the autumn is primarily limited by the environmental factors such as

frost, decreasing light and temperature, shorter days etc. Natural senescence of leaves was the major cause for the decline in 'Golden Delicious' photosynthesis, greater than the effect of harvesting of fruits (TERHOEVEN-URSELMANS and BLANKE 1999).

In our experiment photosynthesis measured at 350 ppm CO_2 ranged between 10.89–16.32 µmol CO_2 m^{-2} s^{-1} in October. In this period significant ($p<0.05$) influences of harvest treatment (3rd measurement), fertilisation (4th measurement) or significant interaction (3rd and 5th measurements) were observed. In all tree measurements leaf photosynthesis of picked PK-sprayed tress was the lowest and that of PK fertilised un-picked trees the highest. A decrease in photosynthetic activity in defruited trees is in agreement with other research dealing with the sink regulation of photosynthesis in crop trees. In our case, no such effect was observed early after fruit removal, that is two days after picking but was present later. It is known that sink regulation of photosynthesis may function as a short term or long term feedback control (PAUL and FOYER 2001), hence a long term regulation which includes metabolic (C, N), hormonal signals is probably also involved in the observed response. Also in the research of GUCCI et al. (1994) no effects of defruiting were noticed during the first 8 h after fruit removal but they were present later. In our case a decline in photosynthesis was the highest 7 days after the fruit removal but only when the trees were sprayed with PK. This suggests that sink/source balance connected to nutritional status could significantly influence the photosynthetic performance of the apple. Foliar analyses, however, show no differences in P and K contents which could have been connected to the observed photosynthetic response.

A clear seasonal decrease in photosynthetic capacity (A_{2000}) can be seen in all four treatments. Although the weather conditions in October 2000 were good (only four days with minimum temperature below 5 °C, no frost, data not shown) the onset of the events connected to senescence can be seen from decline in A_{2000}. The same trend could be observed when following the seasonal leaf phosphorus levels. The general decline in photosynthesis was not so clearly observable in A_{350} measurements. Presumably the changes of photosynthetic apparatus, which appeared during the end of the season (early senescence), were not the limiting factors for the photosynthesis in the given environmental conditions (autumn).

Regarding transpiration, a significant interaction between the crop and fertiliser was found in the 3rd measurement only. The lowest transpiration rate was measured in the PK fertilised/picked trees. In other measurements ANOVA revealed no significant effects of treatments on the transpiration. High transpiration rates indicate that stomatal function is not the limiting factor for photosynthesis. Differences observed in water use efficiency for which crop (2nd and 3rd measurements) and both crop and fertilisation were significant components in the two-way ANOVA (4th measurement) are hence more the result of changes in photosynthetic CO_2 assimilation.

The involvement of mineral nutrients in sink regulation of photosynthesis is relatively well explained (PAUL and FOYER 2001) and has been studied for nitrogen and phosphorus (PAUL and STITT 1993, PAUL and DRISCOLL 1997, PIETERS et al. 2001). According to our study, however, no direct relations between leaf P and K contents and photosynthetic performance can be obtained. The analysis of phosphorus and potassium showed that the foliar application of both nutrients did not result in higher leaf P and K concentrations. Previous studies performed on 'Golden Delicious' showed that leaf content of nitrogen and potassium decreased slowly after the harvest, whereas calcium and magnesium content appeared hardly affected (TERHOEVEN-URSELMANS and BLANKE 1999). TARTACHNYK and BLANKE (2001) reported that five weeks after harvest leaf potassium content declined by 8-11 %, nitrogen by 30 % and phosphorus by 40 %. When 2nd and 3rd sampling are compared a decrease in leaf phosphorus content can be observed in our study, too. The same was not true for potassium where a decrease was observed only in non-fertilised non-picked trees. This may lead us to the assumption that ripe fruits present a sink for potassium, however, no significant effect of crop was proved. A thorough study of plant nutrient status would help to evaluate both the effectiveness of foliar fertilisation and nutrient sink relations.

The fact that nutrients in the late season do not generally present a limiting factor for apple leaf photosynthesis (TERHOEVEN-URSELMANS and BLANKE 1999) is confirmed by our study as well. Although the leaf potassium was very low in all measurements both photosynthesis measured at 350 ppm CO_2 and photosynthetic capacity were high.

In the absence of fruits, sucrose and sorbitol, both major transport sugars in *Malus,* accumulated in the leaves, as it was shown by measurements 8 days after defruiting. This is in accordance with other studies on apple (BLANKE 1997) and also with research on other fruit trees (NII 1997). In addition, higher fructose levels were measured in the leaves of picked trees in comparison with the leaves of non-picked trees. That was not the case in the study by BLANKE (1997). Glucose content does not seem to have been affected by crop load, but it was affected by spraying with PK. PK spraying increased the content of leaf sorbitol (measured one month after application of fertiliser). This could be important for the dormancy and further development of the tree (FRIEDRICH and FISCHER 2000); however, the whole carbohydrate budget should be considered, if developmental effect had to be addressed. It is interesting that the sorbitol content was higher in the bark of PK-fertilised trees but only in those without the crop. Those trees had the lowest photosynthesis among all four treatments. On the contrary trees with the lowest bark sorbitol had high photosynthetic rate. Obviously, a translocation pattern of carbohydrates in picked trees still differs from the one in non-picked trees despite the very late season. This can, however, not be seen from the leaf carbohydrates only. When ripeness of fruit (non-picked treatment) exceeded, the fructose, sucrose and sorbitol contents in the leaves were again high with no difference between the trees. Presumably the observed results of leaf and bark carbohydrates at the end of October are due to a lower sink strength of overripe apples in comparison to ripe fruits (beginning October).

The other effect of spraying was seen in the contents of glucose and fructose. The bark content of both

monosaccharides decreased 1 month after the application of fertiliser irrespective of the presence of crop. It is known that especially phosphorus plays a very important role in carbohydrate metabolism (MARSCHNER 1995), hence, direct effects of nutrients on carbohydrate biochemistry are not to be excluded.

It can be concluded that the photosynthetic activity of apple tree and carbohydrate translocation in the late season can be affected by the treatments such as fruit picking and foliar P and K fertilisation. Although no direct evidence of the correlation between foliar P and K content and measured parameters was provided it is to assume that nutritional status can strongly influence sink regulation of photosynthetic carbon assimilation in apple.

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