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Fruiting Effects on Diurnal Changes in Sorbitol and Starch Contents in Peach Leaves

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Summary

Using potted peach (*Prunus persica* Batsch.) trees at the fruit maturation stage, fruiting effects on sorbitol and starch contents in leaves from day to night as well as before and after fruit removal were examined. Sorbitol content per unit fresh weight in leaves before fruit removal increased significantly during the day; it decreased at night. Within one day after fruit removal, sorbitol increased to a level greater than that before fruit removal, whereas the decrease at night did not differ significantly between before and after fruit removal. The diurnal changes in starch content of the leaves exhibited a similar pattern to those of sorbitol before fruit removal. Likewise, within one day after fruit removal, starch content increased during the day to a higher level but the decrease at night was smaller compared to the level before fruit removal.

Key Words: *Prunus persica* Batsch, peach leaves, sorbitol, starch, fruit removal.

Introduction

The effects of fruiting on the anatomical and physiological features of leaves have been well characterized in fruit trees (Flore and Layne, 1996). Changes in leaf physiology are particularly conspicuous at the sugar-accumulation stage of fruit development when fruits serve as a major sink. During the fruit maturation stage, carbohydrates are typically transported via mass-flow from the leaves to fruit tissues so that the concentrations of solute, nonstructural carbohydrates in the leaves are influenced by the fruit removal. Gucci et al. (1991a, b) found that harvest of mature fruit from sweet-cherry trees (*Prunus avium* L.) resulted in a significant decrease in leaf photosynthesis and a 51% increase in leaf starch within 24 hr, but that the levels of chlorophyll, fructose, glucose, sorbitol and sucrose in leaves were unaffected by defruiting. Contrarily, in peach trees one day after the removal of fruits, the increase in sorbitol paralleled the accumulation of starch (Nii, 1997). This accumulation of starch and sorbitol in leaves after the removal of fruit is attributed to the decrease in sink demand.

Layne and Flore (1993) reported that the concentrations of starch, sucrose and sorbitol in sour cherry remaining leaves were altered within 24 hr of partial defoliation and that the diurnal decline in photosynthetic rate in partially defoliated plants was associated with increase of sucrose and sorbitol in leaves. Studies on the export of sorbitol and sucrose from mature peach leaves, by simulation of carbon fluxes, revealed that these carbohydrates were translocated via the phloem from peach leaves at near maximum rate after 2 hr of illumination (Moing et al., 1992, 1994).

Nonstructural carbohydrate levels in leaves change in response to the demand by sink organs. Accordingly, we studied the diurnal changes in carbohydrate partitioning and, in particular, the accumulation of sorbitol in the cytosol and starch in the chloroplasts before and after fruit removal. The role of leaves during the sugar-accumulation stage of fruit development because no data exist on the diurnal fluctuation in the translocation on sorbitol from leaves to peach fruits during the fruit-maturation stage, especially, in relation to the effect of the number of fruits per tree. Although sorbitol and starch contents of peach leaves were formed to increase one day after fruit removal (Nii, 1997), their diurnal levels following fruit removal were not examined. Furthermore, determination of sorbitol amounts translocated diurnally from leaves to fruits would also contribute to our understanding of leaf physiology.

In the present experiments, we examined the diurnal changes in the contents of nonstructural carbohydrates in peach leaves, focusing on sorbitol and starch, before and after complete removal of fruits and the crop load. The diurnal differences in sorbitol and starch contents of leaves was used to estimate the amount of sorbitol translocated from leaves to fruits.

Materials and Methods

Experiment I (1996)

Eighteen 10-year-old, own-rooted peach trees (*Prunus persica* Batsch. cv. Hakuto) were transplanted into 50-l black pots. Experiments were started at the end of May, 1996, at the fruit-enlargement stage, by thinning the crop to 10, 15, and 20 fruits per tree. Each treatment group included six trees with an average of

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541 ± 49 (mean ± s.d.) leaves at the beginning of the experiment. During the experiment, new lateral shoots which emerged continuously were not removed. No new lateral shoots and leaves emerged from the end of June to the leaf-sampling time because this is the stage of fruit maximum development.

Five leaves, at the fifth to seventh nodal positions during the first cycle of shoot elongation, were harvested at each sampling time. Leaves were harvested at 8:30 a.m. 2 hr after sunrise and 6 p.m. (just before sunset) on July 11th and 12th, and at 8:30 a.m. on July 13th and 19th and on August 9th. Leaves, harvested within 10 minutes, were put in a vinyl bag and the bags placed in an ice box and immediately brought to the laboratory. Sorbitol was determined by high-pressure liquid chromatography (Nii, 1997).

All fruits were removed in the morning of July 12th, just after leaf harvest one week before normal fruit harvest. Fruits from individual trees were weighed and the soluble solids contents in the juice determined with a hand refractometer.

Experiment II (1997)

At the completion of Exp. I (1996), the trees were grouped with 12 unused trees and grown under the same management. During the second year, 12 peach trees were selected and their crop thinned to 15 or 25 fruits per tree. Experiments were started on July 6th. All fruits were removed during the fruit-maturation stage; in the morning of July 15th (removal I) just after leaf sampling and on July 16th (removal II). Each treatment group included 3 trees with 699 ± 61 (mean ± s.d.) leaves per tree in mid-May. During the experiment, new lateral shoots which emerged continuously were removed. The crop size of individual trees and the soluble solids of fruits determined as above. Leaf samples were collected at 6:30 a.m. and at 6 p.m. as in Exp. I.

Seven leaves were harvested between July 14th and 17th of which 3 were analysed for sorbitol content; the remaining 4 leaves were prepared for starch analyses by boiling the ethanol-insoluble residue with water. After cooling, the mixture was incubated with 2% glucoamylase at 55 ℃ for 1 hr. The mixture was then filtered through filter paper (no. 6, Toyo Roshi Kaisha, Ltd) and an aliquot of the filtrate was analyzed with the anthrone reagent.

The weather remained fine between July 11th and July 13th in 1996, but unsettled between July 13th and July 17th in 1997 (Fig. 1).

Results and Discussion

In 1996 experiment, total fruit weight per tree was lowest on the 10-fruit trees; both fruit weight and the soluble solids content increased with decreases in the number of fruit per tree (Table 1).

The amount of sorbitol per unit fresh weight in leaves changed diurnally (Fig. 2). Before fruit removal, the leaf sorbitol content in the morning was low but increased during the day. For the following six days, the sorbitol content fluctuated cyclically at a similar level; the

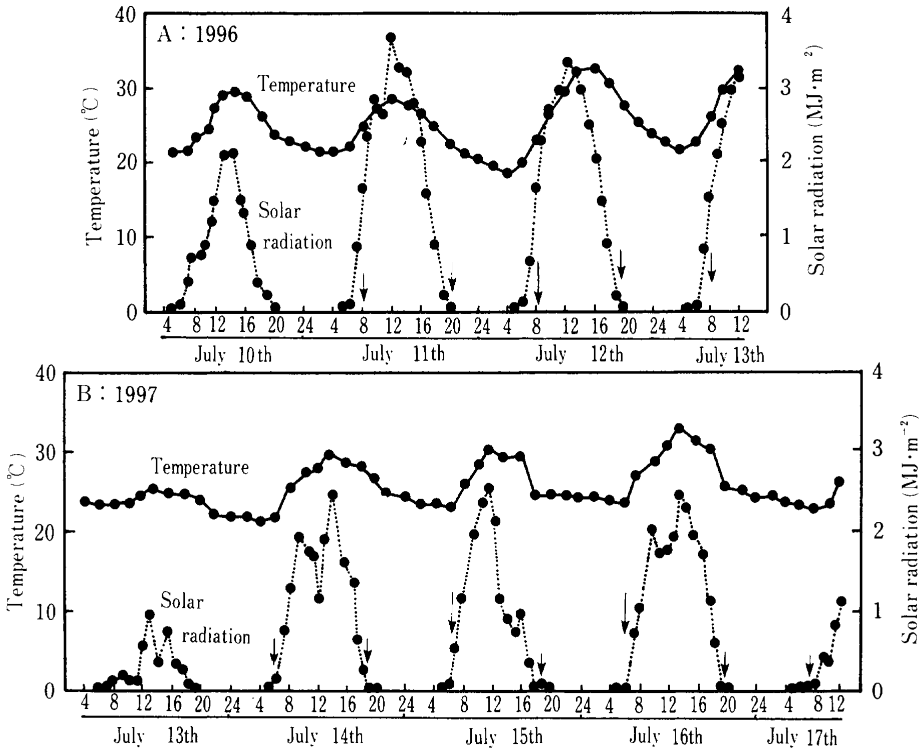

Fig. 1. Changes in air temperature and solar radiation between July 11th and 13th in 1996 (A) and between July 13th and 17th in 1997 (B). Small arrows show leaf-sampling times and the large arrows show the leaf- and fruit-sampling times.

Table 1. Fresh weight and soluble solids contents of fruit from trees with different crop loads.

Number of fruits per tree	Total fruit weight per tree (kg)	Fruit weight (g)	Soluble solids (%)
	Experiment in 1996		
10 (8.6)[z]	0.92a[y]	108.1b	15.3b
15 (13.8)	1.48b	107.7b	12.1a
20 (19.0)	1.65b	90.5a	11.2a
	Experiment in 1997		
15 (14.0)	1.47a	168.4b	10.8b
25 (22.0)	2.25b	127.8a	8.7a

[z] Actual average numbers of fruits per tree at harvest are given in parenthesis.
[y] Mean separation by Duncan's multiple range test (p=0.01) within the column.
Values are means of the results from six trees in each case.

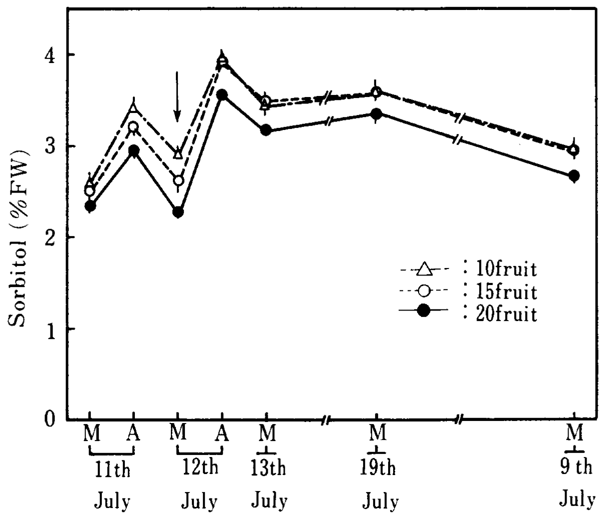

Fig. 2. Effects of fruit removal (arrow) on the sorbitol content of peach leaves (1996 experiment). Vertical bars represent the S.E. of the mean of results from six replicates. M, 8:30 a.m.; A, 6 p.m.

magnitute of the cycle decreased gradually thereafter (Fig. 2). The accumulation of sorbitol by day increased markedly after than before fruit removal (Table 2). On the other hand, nocturnal decrease of the sorbitol content was greater before than after fruit removal. The maximum sorbitol content during the day before fruit removal did not differ significantly among the thinning plots, whereas sorbitol content the day after fruit removal was higher with increased crop load. The crop load had no effect on sorbitol content at night before and after fruit removal. Sucrose content of leaves did not change markedly either before or after removal of fruit (data not shown) (Nii, 1997).

Based on sorbitol contents in the morning and the afternoon, the amount of sorbitol translocated from leaves to fruits (Table 2) during the day was 2.9 ± 0.7 (mean ± s.e.) mg per 1 g leaf fresh weight in 10-fruit trees, 6.0 ± 0.6 mg in 15-fruit trees, and 6.8 ± 0.3 mg in 20-fruit trees. By contrast, the amount of sorbitol translocated into fruits at night was 2.2 ± 1.0 mg per 1 g

Table 2. Diurnal changes in leaf sorbitol content at fruit maturation stage in peach trees (n=6) in 1996.

Number of fruits per tree	Daytime			Nighttime		
	A (before fruit removal)	B (after fruit removal)	B–A	C (before fruit removal)	D (after fruit removal)	C–D
	Sorbitol (mg/g leaf fresh weight, mean ± s.e.)					
10	7.83 ± 1.26a[z]	10.75 ± 0.62a	2.92 ± 0.66a	5.65 ± 1.28a	4.93 ± 0.40a	0.72 ± 0.83a
15	7.13 ± 0.57a	13.10 ± 0.73b	5.97 ± 0.60b	6.26 ± 0.95a	4.08 ± 0.22a	2.18 ± 1.04a
20	6.20 ± 1.34a	12.98 ± 1.08b	6.78 ± 0.29b	6.83 ± 1.94a	3.83 ± 0.88a	3.00 ± 0.24a

A: Subtraction of the value at 8:30 a.m. on July 11th from the value at 6 p.m. on the same day. Amount of sorbitol in leaves accumulated before fruit removal during the daytime.
B: Subtraction of the value at 8:30 a.m. on July 12th from the value at 6 p.m. on the same day. Amount of sorbitol in leaves accumulated after fruit removal during the daytime.
B–A: Estimated approximate amount of sorbitol changed in the leaves before and after removal of fruit during the daytime.
C: Subtraction of the value at 8:30 a.m. on July 12th from the value at 6 p.m. on July 11th. Amount of sorbitol in leaves decreased before fruit removal during the night.
D: Subtraction of the value at 8:30 a.m. on July 13th from the value at 6 p.m. on July 12th. Amount of sorbitol in leaves decreased after fruit removal during the night.
C–D: Estimated approximate amount of sorbitol changed in the leaves before and after removal of fruit during the night.
[z] Values separation by Duncan's multiple range test (p=0.01) within the column.

leaf fresh weight in 15-fruit trees and 3.0 ± 0.2 mg in 20-fruits tree. In 10-fruit trees, the amount of sorbitol translocated into fruits was much smaller at night. This showed that more sorbitol was translocated from leaves to fruits during the day than at night.

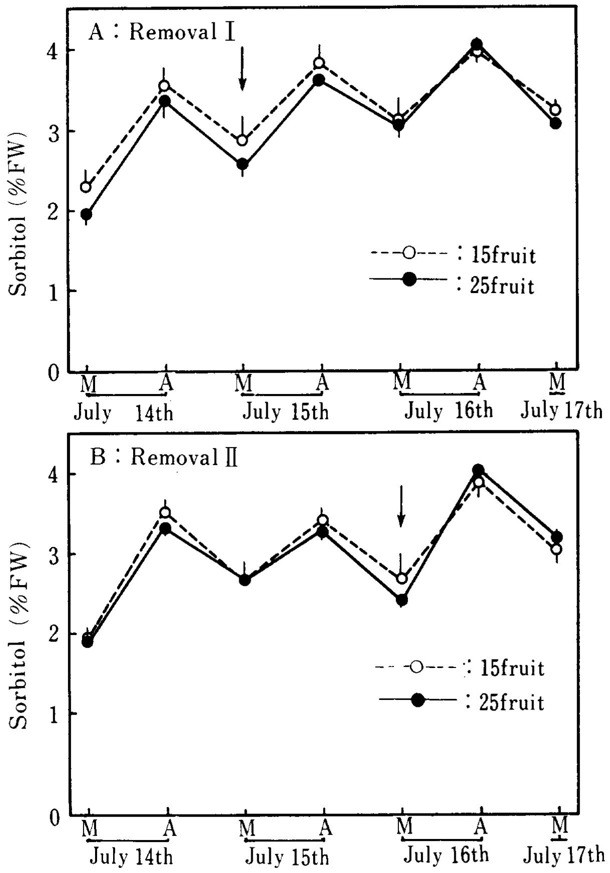

Fig. 3. Effects of fruit removal (arrow) on the sorbitol content of peach leaves (1997 experiment). A, Removal I; B, Removal II. Vertical bars represent the S.E. of the mean of results from three replicates. M, 6:30 a.m.; A, 6 p.m.

During 1997, the weather was unsettled on many days (Fig. 1), particularly on July 13th, 2 days before fruit removal in removal I, when it rained. Sorbitol content in the leaves was low at 6:30 a.m. on July 14th (Fig. 3), presumably because the rate of photosynthesis was low on July 13th, whereas translocation of photoassimilates from leaves was unaffected. Consequently, the accumulation of these sugar in the leaves was higher during the day on July 14th. The sorbitol content in the leaves during the day after fruit removal on July 15th (removal I) did not increase significantly, compared with the increase during the day on July 14th (Fig. 3A). In contrast to removal I, when the fruits were removed on July 16th (removal II), sorbitol accumulated markedly during the day after fruit removal (Fig. 3B). These results indicate that nonstructural carbohydrate content in the leaves depends largely on the weather. The diurnal changes in sorbitol content of the leaves in Removal II exhibited a similar pattern to those in Experiment I (Table 3).

Leaves for determination of sorbitol in the morning were harvested at 8:30 a.m., 2 hr after dawn, in Experiment I. Moing et al. (1992, 1994) reported that the rate of photosynthesis in mature peach leaves peaked approximately 4 hr after the onset of the photoperiod, with light from sodium-vapor lamps that gave 200 μmol photons m^{-2} sec^{-1} in the 400-700 nm range. In their simulation, during the first part of the photoperiod, the sorbitol content increased from 35 to 64 mmol cm^{-2} of leaf area. After 2 hr of illumination, the sorbitol was exported at near maximum value. By contrast, starch content of leaves increased linearly during the photoperiod after a lag period of a few hours (Moing et al., 1994). Therefore, in 1997, sorbitol which accumulated

Table 3. Diurnal changes in leaf sorbitol content at fruit maturation stage in peach trees (n=3) of removal II in 1997.

Number of fruits per tree	Daytime			Nighttime		
	A (before fruit removal)	B (after fruit removal)	B-A	C (before fruit removal)	D (after fruit removal)	C-D
	Sorbitol (mg/g leaf fresh weight)					
15	7.6 ± 1.20a[z]	11.7 ± 2.32a	4.1 ± 1.92a	7.3 ± 2.21a	8.6 ± 0.49a	-1.3 ± 1.95a
25	6.1 ± 1.07a	16.3 ± 0.32b	10.2 ± 1.33b	8.7 ± 0.72a	9.0 ± 0.99a	-0.3 ± 1.49a

A: Subtraction of the value at 6:30 a.m. on July 15th from the value at 6 p.m. on the same day. Amount of sorbitol in leaves accumulated before fruit removal during the daytime.

B: Subtraction of the value at 6:30 a.m. on July 16th from the value at 6 p.m. on the same day. Amount of sorbitol in leaves accumulated after fruit removal during the daytime.

B-A: Estimated approximate amount of sorbitol changed in the leaves before and after removal of fruit during the daytime.

C: Subtraction of the value at 6:30 a.m. on July 16th from the value at 6 p.m. on July 15th. Amount of sorbitol in leaves decreased before fruit removal during the night.

D: Subtraction of the value at 6:30 a.m. on July 17th from the value at 6 p.m. on July 16th. Amount of sorbitol in leaves decreased after fruit removal during the night.

C-D: Estimated approximate amount of sorbitol changed in the leaves before and after removal of fruit during the night.

[z] Values separation by Duncan's multiple range test (p=0.01) within the column.

Table 4. Diurnal changes in leaf sorbitol and starch contents between fruiting and nonfruiting peach trees (n=3) in 1997.

Treatment	Sorbitol (mg/g leaf fresh weight)		Starch (mg/g leaf dry weight)	
	Daytime A	Nighttime B	Daytime A	Nighttime B
	15-fruit trees			
Nonfruiting[z]	9.17 ± 0.79a[y]	9.17 ± 0.89a	37.6 ± 3.4a	12.0 ± 7.5a
Fruiting	7.60 ± 1.20a	7.27 ± 2.21a	33.2 ± 3.1a	24.1 ± 1.6b
	25-fruit trees			
Nonfruiting[z]	10.80 ± 2.13b	6.13 ± 2.18a	40.9 ± 5.12a	12.3 ± 5.0a
Fruiting	6.08 ± 1.07a	8.70 ± 0.72a	38.7 ± 1.60a	34.6 ± 4.7b

A: Subtraction of the value at 6:30 a.m. on July 15th from the value at 6 p.m. on the same day. Amount of sorbitol or starch in leaves accumulated during the daytime.
B: Subtraction of the value at 6:30 a.m. on July 16th from the value at 6 p.m. on July 15th. Amount of sorbitol or starch in leaves decreased during the night.
[z] All fruits were completely removed at 6:30 a.m. on July 15th.
[y] Values separation by Duncan's multiple range test (p=0.01) within the column.

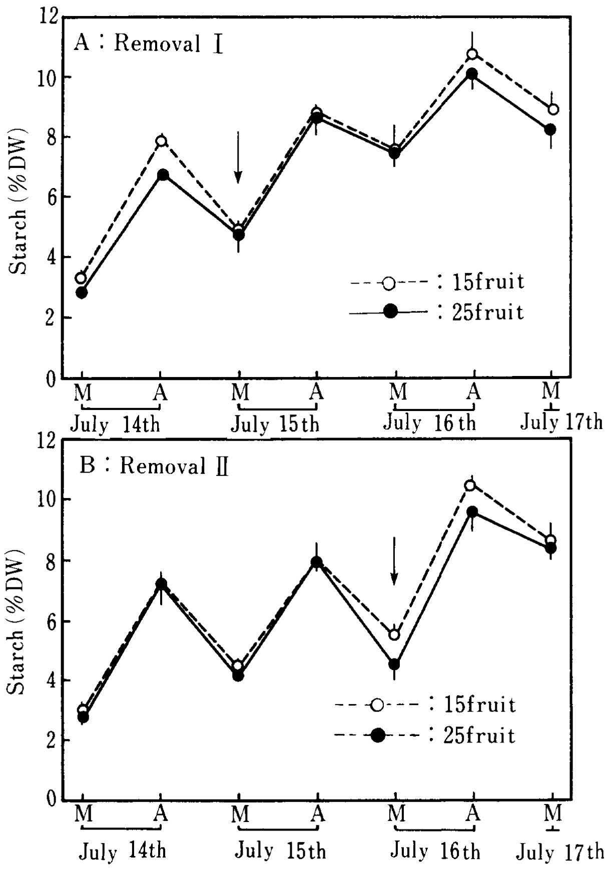

Fig. 4. Effects of fruit removal (arrow) on the starch content of peach leaves (1997 experiment). A, Removal I; B, Removal II. Vertical bars represent the S.E. of the mean of results from three replicates. M, 6:30 a.m.; A, 6 p.m.

in peach were measured before 8:30 a.m., whereas sorbitol and starch were determined at 6:30 a.m. and 6 p.m..

In the present calculation, one question can be raised with respect to the determination of the amount of sorbitol translocated from leaves to fruits. There have been reports that the rate of photosynthesis decreases within 24 hr after the removal of fruits (Gucci et al.,1991a, b). Consequently, the rate of photosynthesis in leaves on the day of fruit removal was presumably lower than in the leaves on intact, bearing trees. The amount of sorbitol translocated from leaves to fruits was assumed to be the amount of sorbitol translocated to the shoots and roots from the leaves was the same one day before and after fruit removal, even though interconversion of sorbitol, starch and other sugars in the leaves were not examined.

The diurnal sorbitol content in the leaves between fruiting and non-fruiting trees and among trees with different crop loads changed (Table 4). It was increased by defruiting, particularly on the 25-fruit trees, it was significantly higher by day in non-bearing trees than that in fruiting trees. There was no significant difference in sorbitol content reduction at night on trees with or without fruit.

There were differences in leaf starch content between day and night before and after fruit harvest (Fig. 4). The leaf starch content usually was low in the morning and increased during the day. Hence, the pattern of changes in starch content was similar to that of changes in sorbitol content. The increase on the day of fruit removal was higher and the decrease during the following night was smaller than the changes before removal of fruit (Fig. 4B). This pattern of changes in starch content was clear at removal II. The increase in starch content during the day was not significantly different with the crop load before and after removal of fruit. The decrease in starch content at night before removal of fruit increased with the crop load, whereas the decrease in starch content at night after removal of fruit was significantly lower (Table 5). When the demand by a sink for photosynthates is reduced, the excess is accumulated as starch in the leaves. Starch accumulated continuously in

Table 5. Diurnal changes in leaf starch content at fruit maturation stage in peach trees (n=3) of removal II in 1997.

Number of fruits per tree	Daytime		Nighttime	
	A (before fruit removal)	B (after fruit removal)	C (before fruit removal)	D (after fruit removal)
	Starch (mg/g leaf dry weight)			
15	33.3 ± 5.37a[z]	51.4 ± 1.65a	24.1 ± 2.80a	14.9 ± 2.55b
25	38.7 ± 0.87a	50.9 ± 5.92a	34.6 ± 2.73b	10.7 ± 3.18a

A: Subtraction of the value at 6:30 a.m. on July 15th from the value at 6 p.m. on the same day. Amount of starch in leaves accumulated before fruit removal during the daytime.

B: Subtraction of the value at 6:30 a.m. on July 16th from the value at 6 p.m. on the same day. Amount of starch in leaves accumulated after fruit removal during the daytime.

C: Subtraction of the value at 6:30 a.m. on July 16th from the value at 6 p.m. on July 15th. Amount of starch in leaves decreased before fruit removal during the night.

D: Subtraction of the value at 6:30 a.m. on July 17th from the value at 6 p.m. on July 16th. Amount of starch in leaves decreased after fruit removal during the night.

[z] Values separation by Duncan's multiple range test (p=0.01) within the column.

leaves by fruit removal (Fig. 4A) (Nii, 1997).

The leaf starch content during the day was greater in defruited than on bearing trees, but the difference was not significantly different (Table 4). However, leaf starch content at night was significantly smaller in the leaves on defruited than that on fruiting trees.

In conclusion, diurnal changes in sorbitol and starch levels in peach leaves became apparent in that it increased during the day and decreased at night. One day after fruit removal, the increase in sorbitol content during the day was greater, and the decrease at night was smaller than prior to fruit removal. The amount of sorbitol translocated from leaves to fruits increased with the crop load on the trees; it was higher during the day than at night. This knowledge on the diurnal changes in leaf carbohydrate content offers another evidence on the sink-source relationship in fruit trees.

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モモ樹における葉内ソルビトールならびにデンプン含量の日変化に及ぼす着果の影響

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摘　要

鉢植えのモモ樹を用いて，果実成熟期における果実収穫前後の葉内炭水化物含量，とくにソルビトールとデンプン含量の日変化に及ぼす着果の影響を調査した．果実収穫前では，生体重当たりの葉内ソルビトール含量は昼間増加し，夜間減少した．果実収穫当日の昼間における増加程度は，果実収穫前と比べて高かった．これに対して，夜間におけるソルビトール含量の低下は，果実収穫前後で有意な差はなかった．果実収穫前の乾物重当たり葉内デンプン含量の日変化もソルビトールと同様な傾向がみられた．果実収穫当日の昼間におけるデンプンの増加量は果実収穫前と比べて有意な差はみられなかったが，夜間における低下の程度は明らかに小さかった．