CARBOHYDRATE PRODUCTION, BALANCE AND TRANSLOCATION IN LEAVES, SHOOTS AND FRUITS OF 'MONTMORENCY' SOUR CHERRY

By

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ABSTRACT

CARBOHYDRATE PRODUCTION, BALANCE AND TRANSLOCATION IN LEAVES, SHOOTS AND FRUITS OF 'MONTMORENCY' SOUR CHERRY

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Carbohydrate production, export and use were studied for different organs of sour cherry (Prunus cerasus L. 'Montmorency'). Gross carbohydrate ($^{14}CO_2$) export started between 27.2 and 77.6% of full leaf expansion. The 10th leaf developing started export later than the 7th leaf, suggesting that higher carbohydrate availability during leaf expansion delays export initiation. In support of this, gross export started earlier (44.4 - 52.4% full expansion) after source leaf removal, than in the control (77.6%). Translocation was primarily vertical (following orthostichies). Most leaves of fruiting shoots exported bidirectionally to the apex and fruits, only leaves closest to fruits exported exclusively to fruits during rapid cell division (Stage I) and rapid cell expansion (Stage III).

Net export, determined from carbohydrate balance models started at 17 and 51% expansion for the 7th and terminal leaf, and at 26.5% of shoot elongation. Cumulative carbohydrate production of the 7th and terminal leaves during the first 9 and 11 days after emergence, exceeded carbohydrate accumulated at final size, 464.2 and 148.9 mg.

A fruit carbohydrate balance was developed to determine contributions by fruit photosynthesis and fruit respiration, and to identify periods of greatest carbohydrate import. Fruit photosynthesis contributed 11.2% of total carbohydrates accumulated and respired. Fruit photosynthetic contribution was high during stage I (19.4%) and the subsequent embryo developmentstage (II) (29.7%) and negligible during stage III (1.5%). Respiratory consumption was 30.9% overall, with 32.7, 70.9 and 19.9% during stages I, II and III, respectively. Carbohydrate imports were highest (16.54 and 35.14 mg day^{-1}) during mid stages I and III.

Fruit photosynthesis during development was characterized under different environmental conditions. Gross photosynthesis and chlorophyll content per fruit increased to a maximum during stage II and decreased thereafter. Light saturation was at 1000 μmol $m^{-2}s^{-1}$ and CO_2 saturation at 400 cm^3m^{-3}. Gross photosynthesis approached a maximum at 40°C. Since dark respiration increased exponentially over the same temperature range, net photosynthesis reached a maximum at 18°C. Photorespiration was not detected. Dark CO_2 fixation was 10% of light CO_2 fixation during stages I and II, and 100% during stage III.

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Guidance Committee:

The journal paper format was chosen for this thesis in accordance with departmental and university regulations. The thesis is divided into four sections. Sections one, two and three are intended for publication in The Journal of the American Society for Horticultural Science and section four is intended for publication in Photosynthetica. Appendix A is intended for publication in Acta Horticulturae.

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INTRODUCTION

A major goal in horticulture is the improvement of crop yield. To accomplish this goal one must understand the limitations to yield. Yield is the product of net photosynthetic production and the harvest index, which is an efficiency factor representing the proportion of assimilates partitioned to the harvested plant parts. Yield can theoretically be limited by either, net photosynthetic production or harvest index.

Net photosynthetic production appears to limit yield in sour cherry only in the rare case of a leaf-to-fruit ratio below 1.5 or 2 (Flore and Sams, 1985). Thus, assimilate partitioning (which determines the harvest index) plays the key role in sour cherry fruit production.

The partitioning process starts at the source leaf where assimilates are either used by the leaf (accumulation, respiration) or exported (phloem loading). Phloem unloading in various organs further determines partitioning and seems to be controlled by the carbohydrate demand of the sinks connected to the particular phloem strand.

Source-sink relationships can be summarized in a translation of a statement by Walter Eschrich (1984), which could apply as well to sour cherries: "It is not because a lot of sugar migrates along the sieve tubes that potatoes grow, but because potatoes grow, a lot of sugar migrates along the sieve tubes". Thus, fruit number, growth rate and duration of the growth period, rather than carbohydrate production, seem

to control carbohydrate allocation in the fruit crop. However, carbohydrate availability during early reproductive development might affect fruit number, since an adequate carbohydrate supply is associated with high fruit set in sweet cherry (Feucht et al., 1972) and grape (Sartorius, 1926).

Carbohydrates imported by sour cherry fruits are incorporated into fruit dry matter or used for respiration to supply energy for transport and synthesis. Respiration leads to a loss of carbohydrates sometimes regarded as wasteful. Besides the carbohydrates supplied by the transport system, fruits use carbohydrates produced by their own photosynthetic activity.

A better understanding of yield formation requires a better knowledge of carbohydrate partitioning in the leaf, export from the leaf and import, production and use by the fruit. Thus the major objectives of this study were to investigate a) the initiation and regulation of carbohydrate export from leaves and shoots, b) the carbohydrate need, import, production and use by the fruits, and c) the factors affecting fruit photosynthesis.

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Section I

The Influence of Phyllotaxy and Stage of Leaf and Fruit Development on the Initiation and Direction of Gross Carbohydrate Export from Sour Cherry (*Prunus cerasus* L. 'Montmorency') Leaves

Abstract. The influence of phyllotaxy and stage of leaf and fruit development on the initiation and direction of carbohydrate (CH_2O) export from sour cherry leaves was investigated during 2 different seasons. One-year-old sour cherry trees on Mahaleb rootstock were pruned to a single shoot, the 7th and 10th leaf (from the base) were pulsed with $^{14}CO_2$, and labelled carbon products were located after 24 hr using autoradiography. In 1983 gross export (E_G) from the 7th and 10th leaf was initiated when the area of the 7th leaf reached 8.5 cm^2 (27.2% expansion) and when that of the 10th leaf reached 13.8 to 20.8 cm^2 (48.0 - 72.3% expansion), respectively. E_G was generally initiated later in 1985 than in 1983, for the 7th leaf later than 26.3 cm^2 (47.5% expansion) and for the 10th leaf at 36.3 cm^2 (77.6% expansion). Leaf size was greater at full expansion in 1985 than in 1983. We suggest that after a leaf has developed the potential for phloem loading, the onset of CH_2O export is a function of the CH_2O availability in the plant at the time of leaf expansion. To test the effect of CH_2O availability on the initiation of E_G, in 1985 all leaves older than the 10th leaf were removed at the beginning of its development. On defoliated shoots the 10th leaf (53.8±16.1 cm^2 full expansion) started export between 23.9 and 28.2 cm^2 (44.4 - 52.4% expansion), whereas control leaves on non-defoliated shoots started export at 36.3 cm^2 (77.6% expansion). Translocation paths followed closely the orthostichy of the exporting leaf. Fruit effects on the direction of translocation were studied in 2-year-old trees. During stages I and III of fruit development leaves closest to the base showed basipetal translocation only. All leaves

during stage II and leaves distal to the the midpoint of the shoot during stages I and III showed bidirectional translocation to the shoot apex and the fruits.

Leaf ontogeny in relation to CH_2O utilization usually passes through 3 phases: i. a phase when the leaf imports CH_2O, ii. a phase when both import and export occur simultaneously and, iii. a phase when only export takes place (8). The transition between source and sink is accompanied and may be caused by morphological and physiological changes (2,3,10). Leaves might not accept messages from sinks demanding assimilates until a certain degree of maturity is reached (17). Sugar beet leaves start gross carbohydrate export (E_G) (phase ii) at 35% of the final laminar length (3), while soybean and squash begin gross export at 30% and 35% of full expansion, respectively (15,16). The onset of E_G from grape leaves occurs at 30% (7) or 50% (4) of leaf expansion. Simultaneous export and import of CH_2O has been observed in soybean (15), squash (18), grape (7) and sugar beet (3). The start of gross export is therefore a first step in leaf development towards autotrophy. Total autotrophy cannot be reached until export exceeds import, i. e. the onset of net export (E_N).

The direction of translocation is coupled to a leaf's orthostichy, as demonstrated in peach (11), apple (8), willow (5) and cottonwood (9). This phenomenon is known as autonomy of orthostichies (8). Sink-source relationships can also affect the direction of translocation and create distinct zones for acropetal and basipetal translocation. The removal of the basal leaves in apple causes translocation from apical leaves to the

roots (13). Grape fruits become strong sinks during their development and attract photosynthates from an increasing number of leaves (7,14). Grape leaves close to the apex translocate acropetally, leaves close to the base translocate basipetally, and only a few intermediate leaves translocate bidirectionally (4,7).

The objectives of this study were: a) to determine when E_G by leaves at different positions on the shoot is initiated, b) to determine the effect of orthostichies on the pattern of translocation within the shoot, c) to determine if distinct zones for acropetal and basipetal translocation exist in sour cherry and, d) to test whether CH_2O supply affects the initiation of E_G.

Materials and Methods

Plant material fo r studying the start of gross export: One-year-old 'Montmorency' sour cherry trees on Mahaleb rootstock were obtained from Hilltop Orchards and Nurseries, Hartford, MI, potted in the spring of 1983 and 1985 in 7.5 liter containers using a mixture of peat, sand and field loam (3:2:5,v:v:v), and pruned to a single bud. During the study only 1 shoot was permitted to grow. Trees were grown outside at the Horticulture Research Center in East Lansing, MI. Water, fertilizer (20% N, 20% P_2O_5, 20% K_2O) and pesticides (Captan, Guthion, Kelthane) were applied as necessary.

Trees were placed in a completely randomized design. Twenty trees were used as a control to measure leaf expansion. Fourty trees were used for the labelling treatment, 20 of them to label the 7th leaf from the shoot base and the remaining 20 to label the 10th leaf. The study was

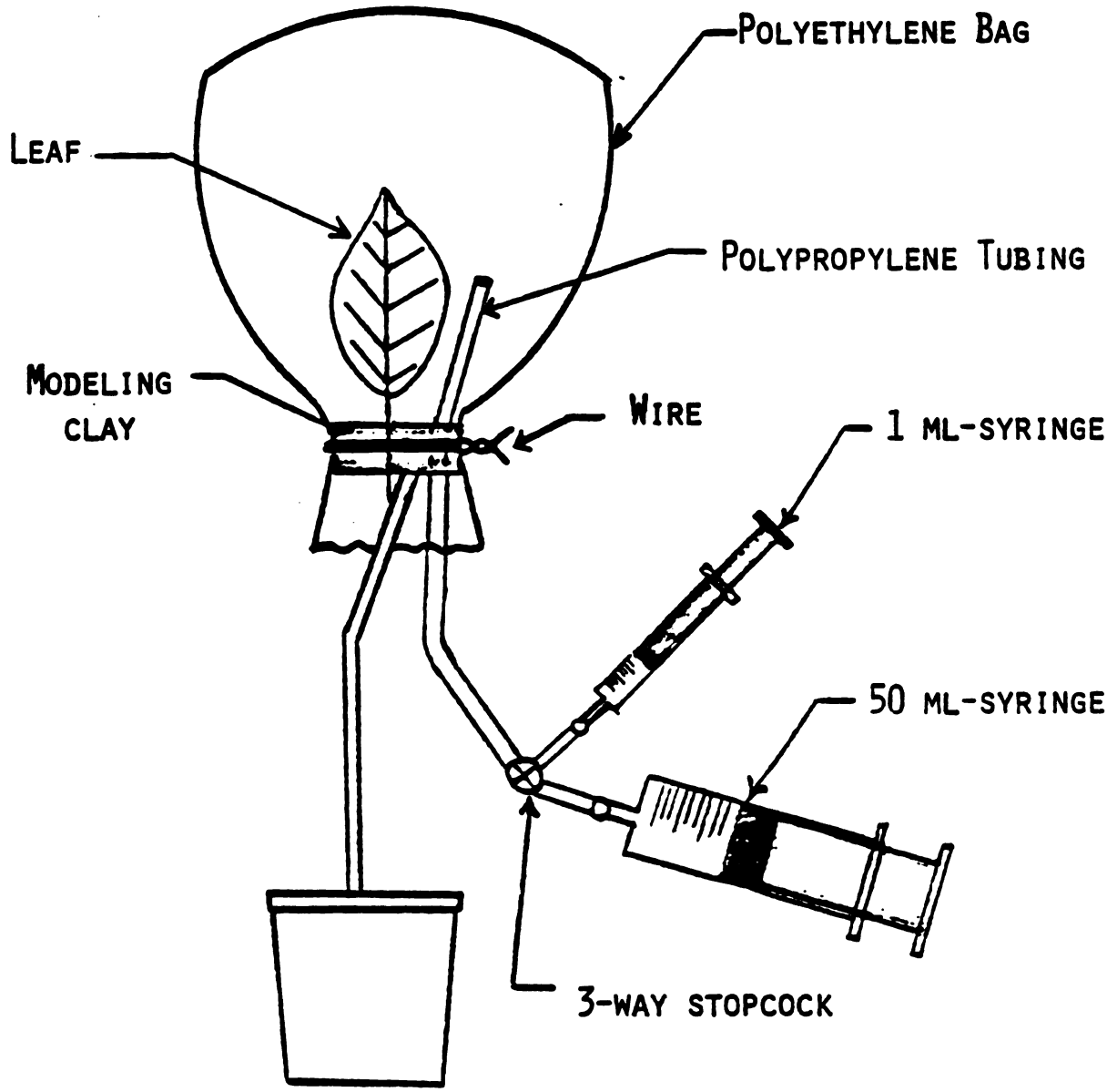
repeated a 2nd season, with 40 additional trees which were defoliated below the 10th leaf at the beginning of its development. Twenty defoliated trees were used to determine the initiation of export from the 10th leaf and 20 were used to determine leaf area at full expansion.

Plant material for studying fruit effects on the direction of translocation: Some of the trees potted in 1983 were transferred to 12-liter containers in the spring of 1984. The flowers (lateral on 1-year-old wood) were hand-pollinated with 'Montmorency' pollen. Nine fruiting plants were selected at random, and extension shoots with fruits in close proximity to them were used for the experiments.

^{14}C-labelling: One leaf per plant was selected and exposed to $^{14}CO_2$ using the method of Quinlan (12) modified as follows (Fig. 1). The leaf was enclosed in a polyethylene bag containing about 1 liter of ambient air. The bag was sealed around the petiole using modelling clay. A 30 cm plastic tube leading from the interior of the bag to a disposable three-way stopcock was connected to a 1 ml and a 50 ml syringe. An aliquot of a stock solution of ^{14}C-sodium bicarbonate (47.1 mCi/mmol) obtained from New England Nuclear (Boston, MA) was diluted to contain 10 μCi/ml, and 0.5 ml (5 μCi) were transferred to the 50 ml syringe. The 1 ml syringe was filled with 5N sulfuric acid. While the valve was open between the two syringes the acid was transferred to the bicarbonate to release the $^{14}CO_2$. Then the connection between the large syringe and the bag was opened by turning the valve, and the plunger was moved back and forth several times to mix the acid with the bicarbonate and to mix the releasead $^{14}CO_2$ with the air in the bag. The bag was kept in position

Figure 1. ^{14}C-pulsing apparatus (schematic drawing).

Figure 1.


POLYETHYLENE BAG
LEAF
POLYPROPYLENE TUBING
MODELING CLAY
WIRE
1 ML-SYRINGE
50 ML-SYRINGE
3-WAY STOPCOCK

for 30 min, after which $^{14}CO_2$ uptake was almost complete (97.4%) (Table 1). Area (A) of the treated leaves was calculated from length (L) and width (W) using the following regression equation:

$$A = L * W * 0.65 \quad r^2 = 0.998 \quad n = 73$$

Determination of transport patterns: Twenty-four hr after pulsing the shoot was sampled, mounted on paper and dried for 3 days at 105°C in a forced draft oven. The dry samples were placed in contact with X-Omat AR film (Eastman Kodak Co., Rochester, NY) for 3 days using Kodak exposure holders and then developed according to manufacturer guidelines.

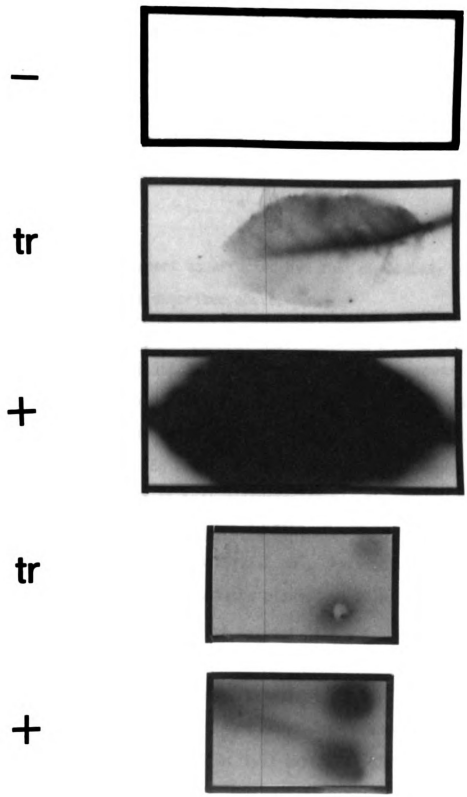
Autoradiographs were used to examine whether radioactivity occurred in non-treated leaves or fruits. To determine levels of detection by autoradiography, samples were combusted using a Biological Oxidizer - OX400 (R. J. Harvey Instument Corporation, Hillsdale, NJ). The combustion products were trapped in Carbon-14-Cocktail (R. J. Harvey Instrument Company, Hillsdale, NJ) and the radioactivity counted in a liquid scintillation counter (1211 Rackbeta, LKB-Wallac, Turku, Finland). Corrections were made for combustion, trapping and counting efficiency, and data were calculated as disintegrations per minute (dpm). Levels of visual detection by autoradiography are shown in Table 2 and Figure 2.

Table 1. $^{14}CO_2$ uptake by the seventh leaf of 'Montmorency' sour cherry during pulsing

Time (min)	Residual Activity		Activity (absorbed)	
	μCi	%	μCi	%
1	0.62±0.33	12.4	4.38	87.6
2	0.79±0.39	15.8	4.21	84.2
5	0.49±0.05	9.8	4.51	90.2
10	0.38±0.08	7.6	4.62	92.4
30	0.13±0.03	2.6	4.87	97.4

Figure 2. Levels of detection by autoradiography in leaf and fruit tissue, as presented in Table 2, no (-), trace (tr) and high (+) activity.

Figure 2.



A 2/5 phyllotaxy configuration was determined according to the method of Allard (1). The angular distances from orthostichy a for orthostichies a-f are therefore (6):

Orthostichy a	0^o
b	144^o
c	-72^o
d	72^o
e	-144^o
f	0^o

The direction of export as affected by the phyllotaxy was then determined by the methods described above.

Results

Start of gross carbohydrate export in 1983: At full expansion the sizes of the 7th and 10th leaf were 31.2±15.0 cm^2 and 28.8±10.2 cm^2, respectively. E_G from the 7th leaf was initiated at 8.5 cm^2 or 27.2% of full expansion (Table 3). E_G from the 10th leaf started between 13.8 and 20.8 cm^2 or 48.0 and 72.3% of full expansion (Table 4).

Start of gross carbohydrate export in 1985: The final size of the 7th and 10th leaf was 55.6±13.5 and 46.8±12.2 cm^2, respectively. The final size of the 10th leaf of the defoliated plants was 53.8±16.1 cm^2.

E_G from the 7th leaf was initiated between 26.3 and 55.0 cm^2, or 47.5 and 98.9% of full expansion (Table 5). E_G from the 10th leaf started at 36.3 cm^2 or 77.6% of full expansion (Table 6).

E_G from the 10th leaf of defoliated shoots started between 23.9 and 28.2 cm^2 or between 44.4 and 52.4% of full expansion (Table 7).

Table 2. Levels of visual detection by autoradiography after 3 d exposure of autoradiography film to oven dried samples. Sampling of shoots after 30 min exposure of a leaf to $^{14}CO_2$ (5μCi) and 24 hr translocation.

		Activity		
	Pulsed leaf	High (+)	Trace (tr)	No (-)
Leaf (dpm cm-1)	165802±30434	77978± 20710	1339± 1256	84± 61
Pedicel[z] (dpm)	-	33608± 21236	2636± 2387	344± 275
Fruit[z] (dpm)	-	460307±272687	18599±19271	2290±1463

[z]Fruits were lateral on 1-year-old wood proximal to the treated leaf on the current seasons growth

Table 3. Gross carbohydrate[z] export from the 7th leaf of 'Montmorency' sour cherry during expansion in 1983 (31.2±15.0 cm^2 final size)

Leaf area		Export
cm^2	% of Final size of control	
7.3	23.4	tr
8.5	27.2	+
8.6	27.5	+
8.8	28.2	+
12.0	38.4	+
12.6	40.4	+
14.2	45.5	+
14.3	45.8	+
14.8	47.4	+
15.0	48.0	+
16.7	53.5	+
18.1	57.9	+
18.3	58.6	+
18.5	59.3	+
19.0	60.9	+
19.5	62.5	+
20.3	65.0	+
23.5	75.3	+
25.1	80.4	+
36.1	115.6	+

[z] Pulsed with 5 μCi of $^{14}CO_2$ for 30 min, and ^{14}C distribution determined 24 hr after pulsing.

Table 4. Gross carbohydrate[z] export from the 10th leaf of 'Montmorency' sour cherry during expansion in 1983 (28.8±10.2 cm^2 final size)

Leaf area		Export
cm^2	% of final size of control	
1.7	5.9	tr
3.7	12.9	-
3.7	12.9	-
4.3	14.9	tr
6.3	21.9	-
8.1	28.2	tr
9.1	31.6	-
10.3	35.8	-
13.8	48.0	+
15.1	52.5	+
16.0	55.6	-
16.9	58.8	-
20.8	72.3	+
24.7	85.9	+
26.4	91.8	+
28.7	99.8	+
31.1	108.1	+
33.8	117.5	+

[z]Pulsed with 5 μCi of $^{14}CO_2$ for 30 min, and ^{14}C distribution determined 24 hr after pulsing

Table 5. Gross carbohydrate[z] export from the 7th leaf of 'Montmorency' sour cherry during expansion in 1985 (55.6±13.5 cm^2 final size)

Leaf area		Export
cm^2	% final size of control	
3.3	5.9	-
6.3	11.3	-
7.0	12.6	-
7.8	14.0	-
8.5	15.3	-
8.8	15.8	-
10.5	18.9	-
11.2	20.1	-
12.2	21.9	-
17.8	32.0	-
20.0	36.0	-
26.3	47.5	-
55.0	98.9	+

[z]Pulsed with 5 μCi of $^{14}CO_2$ for 30 min, and ^{14}C distribution determined 24 hr after pulsing.

Table 6. Gross carbohydrate[z] export from the 10th leaf of 'Montmorency' sour cherry during expansion (1985)(46.8±12.2 cm^2 final size)

Leaf area		Export
cm^2	% final size of control	
5.2	11.1	-
10.6	22.6	-
12.4	26.5	-
14.3	30.5	-
19.4	41.5	-
26.9	57.5	-
36.3	77.6	+
36.4	77.8	+
37.4	79.9	+
38.1	81.4	+
48.6	103.8	+
55.7	119.0	+

[z]Pulsed with 5 μCi of $^{14}CO_2$ for 30 min, and ^{14}C distribution determined 24 hr after pulsing.

Table 7. Gross carbohydrate[y] export from the 10th leaf of defoliated[z] 'Montmorency' sour cherry during expansion (1985)(53.8±16.1 cm^2 final size).

Leaf area		Export
cm^2	% final size of control	
3.4	6.3	-
4.9	9.1	-
9.5	17.7	tr
10.5	19.5	-
11.0	20.4	tr
14.3	26.6	-
20.9	38.8	tr
23.9	44.4	+
24.0	44.6	+
24.5	45.5	-
26.8	49.8	+
27.2	50.6	-
28.2	52.4	+
33.7	62.6	+
44.2	82.2	+
46.4	86.2	+
48.3	89.8	+
72.4	134.6	+

[y]Pulsed with 5 μCi of $^{14}CO_2$ for 30 min, and ^{14}C distribution determined 24 hr after pulsing.

[z] Shoots were defoliated below the 10th leaf at the beginning of its expansion.

Effects of phyllotaxy on direction of translocation: Translocation followed closely the 2/5 phyllotaxy for the distal leaves near the pulsed leaf, but not for the less developed apical leaves (Fig. 3 and 4). The 7th and 8th and the 7th and 11th leaf obviously do not share translocation paths (Fig. 3). Angular distances between the 7th and 8th and the 7th and 11th leaf are 144° (Fig. 3). Part of the 9th leaf shares translocation paths with the 7th leaf, the angular distance between them is 72° (Fig. 3). The 10th leaf is also at an angular distance of 72° and the 12th leaf is at an angular distance of 0° to the 7th leaf (same orthostichy) (Fig. 3). Both the 10th and 12th leaf seemed to share the same translocation paths with the 7th leaf (Fig. 3 and 4b-d). Leaves distal to the 12th leaf imported from the 7th leaf regardless of their orthostichies. There was no translocation to leaves proximal to the pulsed leaf. Translocation out of the shoot was not determined.

Fruit effects on direction of translocation: During stage I of fruit development leaves close to the apex (Fig. 5a), midpoint (Fig. 5b) or base (Fig. 5c) of fruiting shoots were pulsed. Apical and center leaves exported bidirectionally to apex and fruits. From the basal leaf no export could be detected. Export could have occurred to fruits or vegetative growth proximal to the examined shoot, however this was not examined. During stage II of fruit development leaves close to the apex (Fig. 5d), midpoint (Fig. 5e) and base (Fig. 5f) were again pulsed. In all cases bidirectional export to the shoot apex and fruits was detected. During stage III of fruit development leaves close to the apex (Fig. 5g) and the midpoint (Fig. 5h) exported bidirectionally. The leaf

Figure 3. Pattern of carbohydrate export developed from autoradiographs from the 7th leaf of non-fruiting 'Montmorency' sour cherry. Each field represents a leaf; leaves are numbered in sequence from shoot base to apex. Leaves of common orthostichies are shown in the same angle (schematic drawing).

Figure 3.

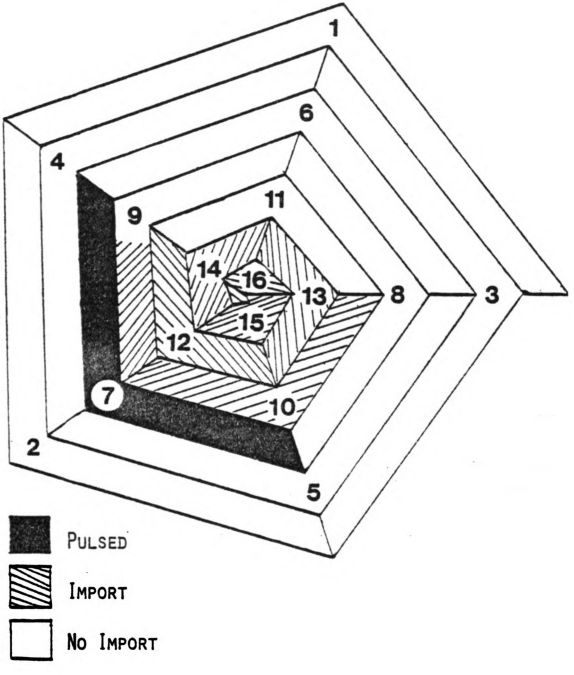
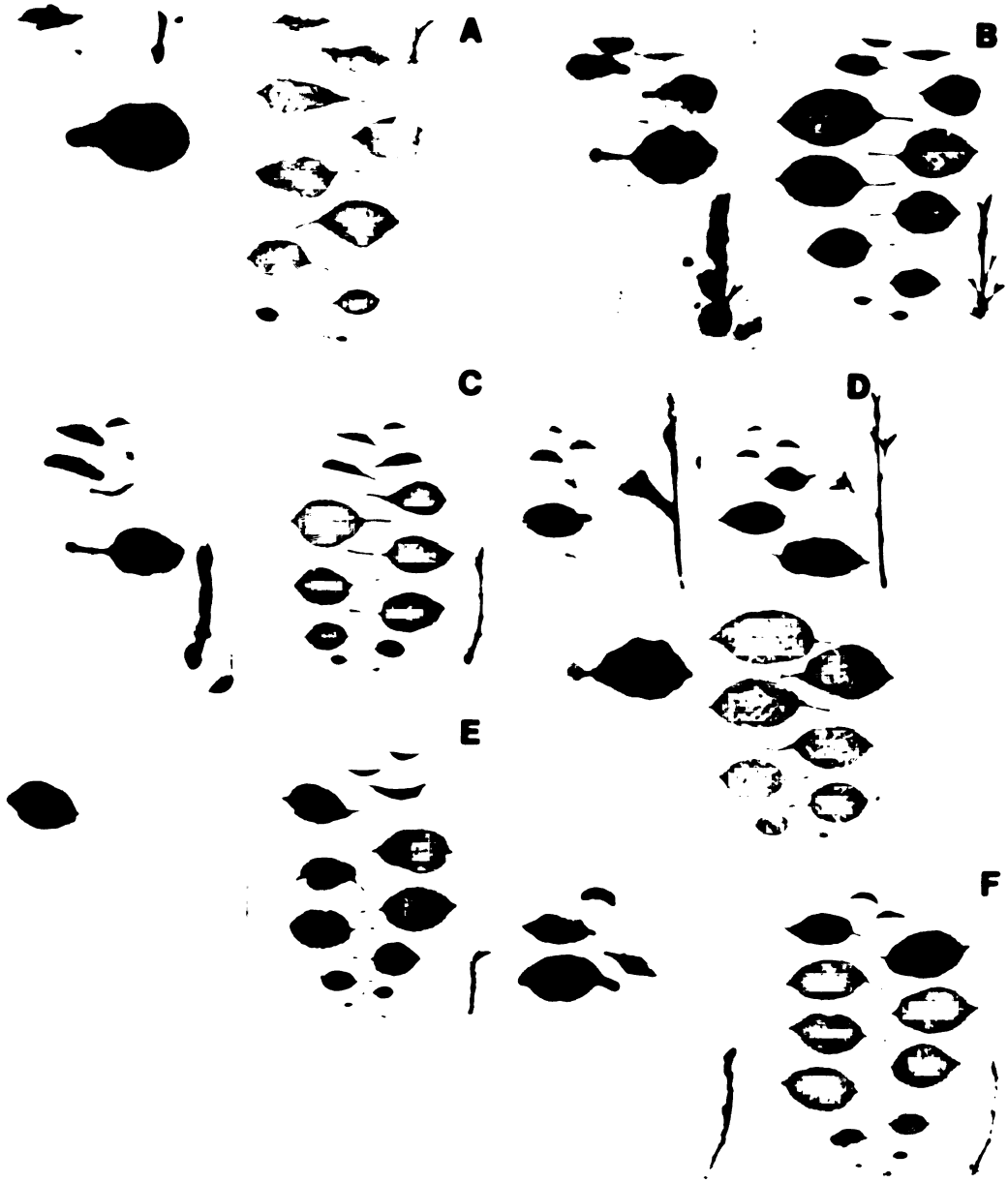


Figure 4. Autoradiographs (left) and corresponding shoots (right) showing the pattern of ^{14}C-carbohydrate export from the 7th (a-d) and 10th (e-f) leaf of non-fruiting 'Montmorency' sour cherry during shoot elongation.

a. Shortly after onset of export. Exporting to part of the 9th leaf, to the 10th leaf and the shoot apex. Traces can be detected in the proximal leaves.
b. Exporting to part of the 9th leaf, to the 10th, 12th and the shoot apex, and traces only to the 11th leaf. Traces are also detected in petioles of other leaves.
c. Exporting to the 10th, 12th, 13th leaf and the apex, and traces to the 9th and 11th leaf, and proximal petioles.
d. Exporting to the 10th, 12th, 13th, 14th leaf, the apex and its axial shoot, and traces to the 9th and 11th leaf.
e. Before initiation of export.
f. Exporting to part of the 11th leaf, to the 12th, 14th and the shoot apex. Traces are detected in the 13th leaf and proximal leaves and petioles.

Figure 4.



close to the base (Fig. 5i) exported basipetally to the fruit only. Translocation between leaves seemed to follow phyllotaxy, as was demonstrated for non-fruiting shoots (Fig. 3 and 4). Leaf to fruit translocation also seemed to follow distinct phloem connections (Fig. 5), since activity could not be detected in all fruits. However whether translocation followed the phyllotaxy could not be determined since orthostichies are hard to follow across the demarcation between current and last year's growth.

Discussion

The use of autoradiography was inadequate to determine the exact degree of leaf expansion for the initiation of E_G. Variability in final leaf size and initiation of export between plants and years was very high, so that generally over a range of absolute leaf sizes some leaves exported while others did not. In 1983 E_G started for the 7th leaf at 27.2% (Table 3) and for the 10th leaf between 48.0 and 72.3% of full expansion (Table 4). In 1985 E_G started later, the 7th leaf started E_G after 47.5% (Table 5) and the 10th leaf at 77.6% of full expansion (Table 6). In the 1985 season, later initiation of E_G was accompanied by a greater final leaf area. Differences in growth between seasons might have been caused by different temperatures and light intensities, which could also explain differences reported for grape, which started E_G at 50% of full expansion in California (4), but only at 30% in Switzerland (7). The 7th leaf of sour cherry develops rapidly, expanding from 25 to 75% expansion in 6 days (data not shown); therefore differences between seasons in leaf age at initiation of E_G were small in relation to time.

Figure 5. Autoradiographs (left) and corresponding shoots (right) showing the pattern of ^{14}C-carbohydrate export from leaves of fruiting 'Montmorency' sour cherry shoots during fruit and shoot development. The pulsed leaf is marked with an arrow. a-c. Stage I of shoot development. d-f. Stage II of fruit development. g-i. Stage III of fruit development.

Figure 5.

Small increases in leaf growth rate due to nutrition or temperatures, or decreases in photosynthetic rate due to light conditions may cause a delay in the initiation of E_G.

To the best of our knowledge the onset of E_G as a function of leaf position on the shoot has never been studied. Our results from both seasons (Table 3 - 6) indicate that leaves developing later in the season started E_G at a greater absolute leaf area and % of full leaf expansion. During the expansion of the 10th leaf more carbohydrates are available to the plant, because more expanded leaves are present and acting as sources. We propose that the initiation of CH_2O export from a leaf capable of phloem loading is a function of CH_2O availability in the total plant. To test this, CH_2O supply to the plant was decreased by defoliation prior to development of the 10th leaf. The 10th leaf of the control shoots started E_G at 77.6% of full expansion, as compared to defoliated shoots which, in support of the proposal, started considerably earlier between 44.4 and 52.4%. The mechanism involved in regulation of the initiation of E_G by CH_2O availability is not known.

Our study demonstrates that translocation in sour cherry, as in peach (11), apple, willow (5) and cottonwood (9) is limited to the leaf orthostichy. Leaves with angular distances of 144^o used separate translocation paths, with the exception of the tenth leaf in which the entire blade was usually labelled when the seventh leaf was pulsed. This could have been caused by radial transport in the phloem. Leaves with angular distances of 72^o shared some of their translocation paths. The

leaves closest to the apex did not have differentiated phloem connections with respect to their phyllotaxy and were therefore uniformly labelled.

Carbohydrate translocation from leaves to fruits probably also followed the orthostichies, as is the case in peach (11). This is difficult to determine if the translocation occurs between tissues of different years. Sour cherry, with separate leaf and fruit buds, is not well suited for translocation studies along orthostichies between leaves and fruits. In 2-year-old apple seedlings translocation followed a spiral pattern (6) because the sieve tubes are arranged helically (8).

Generally during stage II of fruit growth all leaves supplied new expanding leaves and fruits at the same time by bidirectional translocation. However, during stages I and III of fruit development the leaves closest to the fruits exported basipetally only. This differs from grape (7), where leaves close to the apex show acropetal translocation, some of the leaves distal to the fruit clusters show basipetal translocation and those in a small transition zone shows both. The rapid stages of fruit development (I and III) in sour cherry seemed to attract translocated carbohydrates most strongly and caused the development of a distinct zone of basipetal translocation. During grape fruit set (4) and veraison (7,14) translocation becomes markedly directed toward the clusters.

The present study demonstrates that both initiation and direction of E_G in sour cherry are regulated by CH_2O supply and demand. Gross export is limited within the autonomous orthostichies.

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Section II

Estimation of Net Carbohydrate Export from Sour Cherry (*Prunus cerasus* L. 'Montmorency') Leaves and Shoots

Abstract. The initiation of net carbohydrate export from leaves and shoots of 'Montmorency' sour cherry trees on Mahaleb rootstock was estimated using carbohydrate (CH_2O) balance modeling for determination of the empirical models. Using 1-year-old trees pruned to a single shoot, expansion of the 7th (from the base), and the terminal leaf, and shoot elongation were measured from bud break until terminal bud set. Comparable trees were used to measure daily CO_2 gas exchange of leaves and whole shoots as a function of their development. After destructive harvest, CH_2O contents of the 7th and the terminal leaves and whole shoots were determined. Mathematical models were fitted to leaf area and shoot extension as a function of CH_2O content, leaf and shoot CH_2O content as a function of time and to respiration and net and gross photosynthesis as a function of leaf and shoot CH_2O content. The 7th leaf and the terminal leaf started net export approximately at 17 and 51% expansion, respectively, which coincides with the onset of gross export. The whole shoot started exporting at 27% elongation.

Initial leaf expansion and shoot elongation in deciduous trees occurs at the expense of reserves stored during the previous season until the shoot's daily net photosynthetic rate (DP_N), equals the CH_2O accumulation rate. Leaf expansion and shoot elongation require import of CH_2O from either reserves or from exporting leaves until the CH_2O fixation rate exceeds utilization. This marks the beginning of net CH_2O export and the point when a leaf or shoot becomes autonomous with respect to its CH_2O supply. At this time a leaf or shoot is able to support other vegetative and reproductive growth and replenish CH_2O reserves in the tree. Fruits and leaves develop concurrently early in the season and compete for CH_2O from reserves or exporting leaves.

Gross export (E_G) refers to detectable movement of CH_2O out of the source leaf or shoot, while net export (E_N) occurs when CH_2O export exceeds import of CH_2O and DP_N exceeds CH_2O accumulation rate. Kappes and Flore (11) demonstrated that E_G for sour cherry began between 27.2 and 98.9% of full leaf expansion depending on the leaf position and the growing season (11). Kappes and Flore (11) hypothesized that the initiation of CH_2O export was regulated by supply from earlier expanded leaves and demand by the terminal growth or by other sinks within the plant. A hypothesis concerning source-sink effects on rate , rather than the initiation of, CH_2O export was reported for tomato, where Khan and Sagar (12) demonstrated that a decrease of source strength by leaf removal or an increase of sink strength by growth regulator application to fruits accelerated ^{14}C-export from leaves.

Various methods have been used to determine when E_N begins in deciduous fruit crops. Apple leaves were reported to start E_N at 5% of full expansion (21). Apple shoots start E_N 19 days after bud break, when shoots are 4 cm long (8% elongation), and 10 leaves are unfolded (10). Relative leaf expansion values for the start of E_N in grape have not been reported, however, Martinez de Toda (15) reported that E_N occurred after plastochron index 10. This is much later than suggested by Koblet's (13) data, which might be a result of the method used.

Few studies on E_N in woody perennials have been reported (10,15,21). Budgeting techniques using punched leaf disks have been used with annuals having large leaves (7,8,20); however most fruit tree leaves are too small to excise disks at an early stage without affecting leaf physiology, thus limiting the general use of this technique. An alternative method applicable to fruit trees (10,21) is the use of CH_2O balance modeling (daily CH_2O fixation vs accumulation). Using this method, Hopkinson (8) showed that cucumber leaves started to export between 17 and 25% expansion, while Turgeon and Webb (20) found that pumpkin leaves started to export at about 45% expansion.

The objectives of this study were to a) define when E_N occurs for leaves and shoots of sour cherry, and b) determine if the magnitude or the initiation of E_N is influenced by leaf position on the shoot during development.

Materials and Methods

Plant material. One-year-old 'Montmorency' sour cherry trees on Mahaleb rootstock (Hilltop Orchards and Nurseries, Hartford, MI), were potted in 9-liter containers using a mixture of sandy loam and peat (3:1,v:v). A single shoot was allowed to develop, creating a simple uniform system to study the source-sink relationship. Trees were grown outdoors at the Horticulture Research Center, East Lansing, MI. Water, fertilizer (20% N, 20% P_2O_5, 20% K_2O), and pesticides (Captan, Guthion, Kelthane) were used as necessary. Treatments were assigned in a completely randomized design. Ten trees were used for the measurement of leaf expansion and shoot elongation, 56 for whole shoot photosynthesis, 24 for the photosynthesis of the 7th leaf and 20 for the photosynthesis of the terminal leaf. Photosynthesis was followed by a destructive analysis for CH_2O content which was expressed as a function of leaf area and shoot length.

Curve fitting: Relationships between variables were determined by curve fitting with PLOTIT (2), a program designed for the fitting of linear and nonlinear regression models, as well as the graphic display of data. Models were chosen on the basis of the residual sums of squares, the coefficient of determination (r^2), and the visual fit of the regression lines in relation to the observed data.

Measurement of CO_2-fixation: Gas exchange was measured in an open system, as described by Sams and Flore (18). Photosynthesis of leaves and small shoots was measured in a leaf chamber (18), that of larger shoots in a 40-liter polyethylene bag attached to a large chamber where temperature, light and incoming water vapor pressure were controlled.

Unless otherwise stated standard conditions were as follows: photosynthetic photon flux density (PPFD), 1000 μmol $m^{-2}sec^{-1}$; 16 hr light, 8 hr darkness; day and night temperature, 25° and 15°C, respectively. The dew point of the air entering the chamber was held at 5°C, resulting in vapor pressure deficits of approximately 2.5 and 1.5 kPa during the light and the dark periods, respectively, for the leaf chamber, and 1.5 and 0.5 kPa for the large chamber. Photosynthesis (light period) and respiration (dark period) were determined at 2 hr intervals over a 24-hr period. The first measurement in the dark was taken at 25°C, to estimate respiration during the light period. Daily net photosynthesis (DP_N), daily dark respiration (DR_D) and, by addition, daily gross photosynthesis (DP_G) were calculated for the 24-hr period. DP_N, DP_G, and DR_D (mg CH_2O $leaf^{-1}$ day^{-1}) or (mg CH_2O $shoot^{-1}$ day^{-1}) were correlated with leaf or shoot size during leaf expansion or shoot elongation.

Definitions: DP_N = net photosynthesis (day) - dark respiration (night)

DR_D = dark respiration (day) + dark respiration (night)

$DP_G = DP_N + DR_D$

Measurement of carbohydrate accumulation: Areas (A) of the 7th and terminal leaves were estimated from length (L) and width (W) using equation 1 (11).

$$A=L*W*0.65 \qquad \text{(Eq.1)}$$

Leaf area and shoot length of control plants were determined every 2nd day during leaf expansion and shoot elongation. Length of shoots and area of leaves used in gas exchange determination were measured. Then shoots and leaves were dried in a forced-draft oven (105°C) for 3 days and ashed for 6 hr (500°C) in a muffle furnace. Weight loss during ashing was used as an estimate of the total CH_2O content. Dry ashing was used because dry weight alone (10) does not account for the mineral content, and wet ashing (7) limits sample size. Mineral contents (%) of the 7th and terminal leaves increased slightly with increasing dry weight (DW) (g) following equations 2 and 3, respectively, while shoot mineral content decreased with increasing DW (Eq. 4).

$Y = 5.232 + 3.306E\text{-}3 * DW$ (Eq.2) $r^2=0.287$

$Y = 4.111 + 3.747E\text{-}3 * DW$ (Eq.3) $r^2=0.037$

$Y = 6.927 - 1.636E\text{-}4 * DW + 3.217E\text{-}9 * DW^2$ (Eq.4) $r^2=0.628$

The relationship between CH_2O content and leaf area or shoot length was determined and the resulting regression equations were used to estimate CH_2O content during growth. Nonlinear regression models were fitted for CH_2O accumulation vs time, after the beginning of leaf emergence and bud break, and the difference between CH_2O of $day_{(n+0.5)}$ and $day_{(n-0.5)}$ was used as an estimate of the CH_2O accumulation rate of day_n.

Estimation of the onset of export: Net CH_2O export from a shoot or a leaf equals the DP_N minus the CH_2O accumulation rate. Negative net export values represent net import. The point of transition from net import to net export was determined by comparison of daily values for DP_N and the CH_2O accumulation rate.

Results

Seventh leaf: Leaf area and leaf CH_2O were linearly related (Fig. 1), indicating a constant specific leaf weight (SLW) during expansion. Carbohydrate accumulation data best fit Weibull's model (9) (Eq. 5 and 6, Fig. 2). Carbohydrate content increased mainly during the first 15 days and then remained constant. The accumulation rate reached a maximum of 38.4 mg/day at day 7. The coefficients for the model equation of leaf CH_2O accumulation (in mg CH_2O) and the difference equation (in mg CH_2O day^{-1}) as determined by nonlinear regression analysis are as follows:

$$B(1)=464.212$$

$$B(2)=0.236$$

$$B(3)=0.0849$$

$$B(4)=2.401$$

$$Y = B(1) * (1 - e^{(-(B(2) + B(3) * X)^{B(4)})}) \qquad \text{(Eq.5)}$$

$$YD = Y_{(X+0.5)} - Y_{(X-0.5)} \qquad \text{(Eq.6)}$$

Where:

Y = Leaf or shoot CH_2O in mg

YD = Leaf or shoot CH_2O accumulation rate in mg day^{-1}

X = Progressive days from leaf emergence or start of shoot elongation

Estimated area at full expansion of the 7th leaf equaled 63.2 cm^2, compared to the mean of the control plants used in the study, 64.3 ± 16.8 cm^2. The DP_N, DP_G and DR_D of the 7th leaf in units of CH_2O $leaf^{-1}$ day^{-1} were linearly related to leaf CH_2O content (mg CH_2O $leaf^{-1}$) (Eq. 7, Table 1, Fig. 3).

Figure 1. Relationship between leaf area and carbohydrate content of the 7th leaf of 'Montmorency' sour cherry during leaf expansion, observations (circles) and fitted curve (line).

Figure 1.

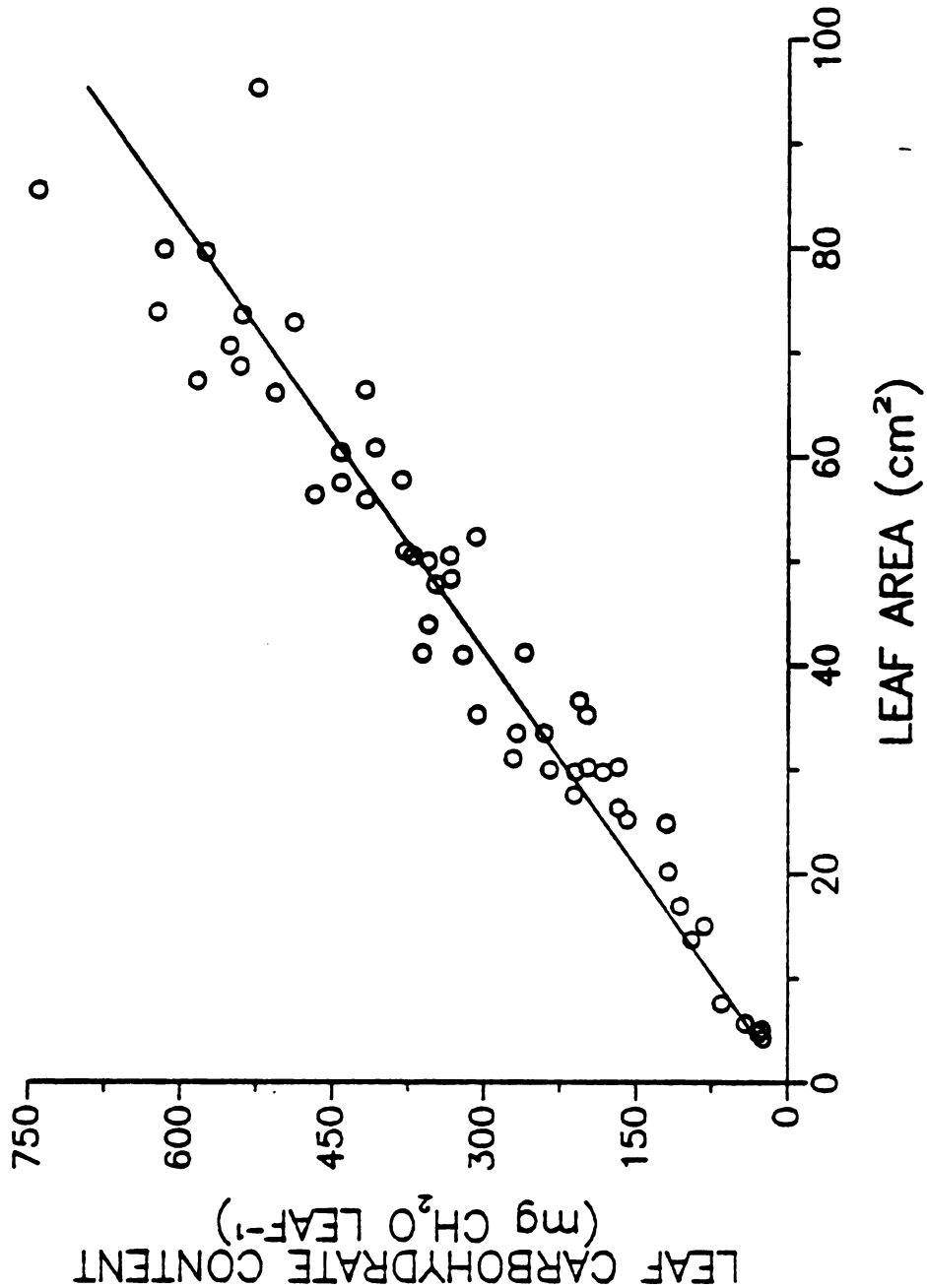

LEAF CARBOHYDRATE CONTENT
(mg CH2O LEAF-1)
750
600
450
300
150
0
0
20
40
60
80
100
LEAF AREA (cm2)

Figure 2. Carbohydrate accumulation by the 7th leaf of 'Montmorency' sour cherry, starting at leaf emergence, observations (circles), fitted curve (solid line) and carbohydrate accumulation rate (broken line).

Figure 2.

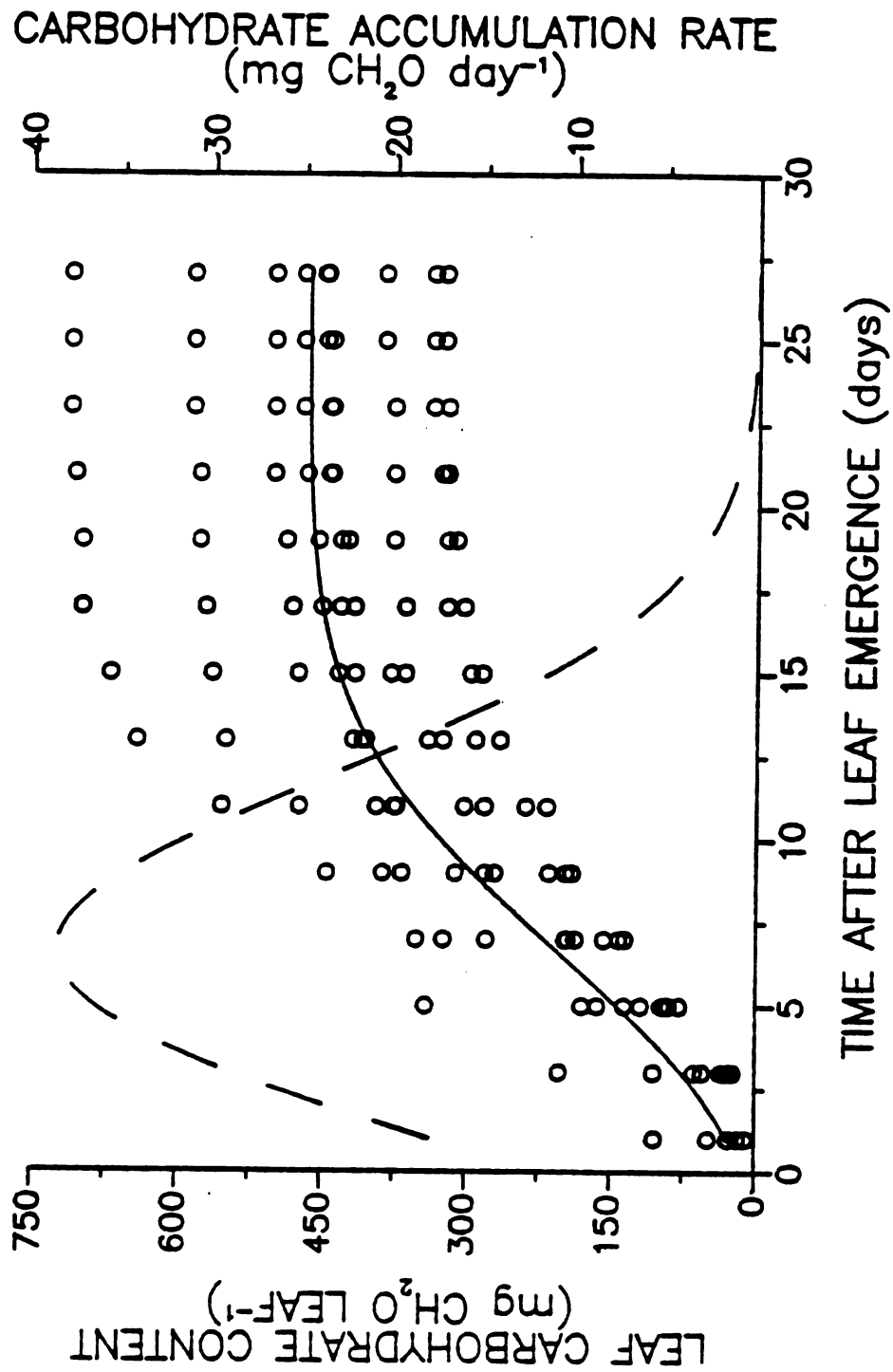

CARBOHYDRATE ACCUMULATION RATE
(mg CH_2O day^{-1})
40
30
20
10
0
5
10
15
20
25
30
TIME AFTER LEAF EMERGENCE (days)
LEAF CARBOHYDRATE CONTENT
(mg CH_2O $LEAF^{-1}$)
750
600
450
300
150
0

Figure 3. Daily gross photosynthesis (DP_G) (A), daily net photosynthesis (DP_N) (B), and daily dark respiration (DR_D) (C) of the 7th leaf of 'Montmorency' sour cherry, observations (circles) and fitted curves (lines) at different leaf sizes during leaf expansion.

Figure 3

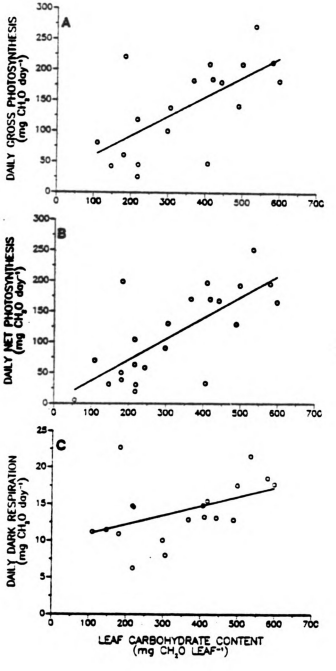

A
DAILY GROSS PHOTOSYNTHESIS (mg CH2O day-1)
B
DAILY NET PHOTOSYNTHESIS (mg CH2O day-1)
C
DAILY DARK RESPIRATION (mg CH2O day-1)
LEAF CARBOHYDRATE CONTENT (mg CH2O LEAF-1)

Table 1. Correlation coefficients (B(1) - B(4)) and coefficients of determination (r^2) of the regression equations for daily net photosynthesis (DP_N), daily gross photosynthesis (DP_G) and daily dark respiration (DR_D) for the 7th and terminal leaf and shoots of 'Montmorency' sour cherry during growth.

	B(1)	B(2)	B(3)	B(4)	r^2
Seventh leaf					
DP_N	3.064	0.340			0.540
DP_G	28.568	0.319			0.440
DR_D	9.716	0.0125			0.207
Terminal leaf					
DP_N	-7.348	0.235			0.936
DP_G	-3.484	0.258			0.946
DR_D	3.919	0.0234			0.309
Shoot					
DP_N	21.977	0.172	-.331E-5		0.907
DP_G	58.853	0.207	-.406E-5		0.911
DR_D	34.308	0.0457	-.176E-5	0.249E-10	0.772

$$Y = B(1) + B(2) * X \qquad \text{(Eq.7)}$$

E_N from the 7th leaf was initiated after 3 days, when 76.9 mg of CH_2O were accumulated (leaf area = 10.6 cm^2 and 17% full expansion) (Table 2). Five days after leaf emergence the cumulative CH_2O balance (Table 2) was positive, indicating that the leaf had fixed more CH_2O than it had consumed to that date. Daily E_N reached a maximum of 161 mg CH_2O per day by day 24, while total CH_2O exported exceeded 3000 mg by day 29 (Table 2).

Terminal Leaf. Leaf area and total leaf CH_2O were linearly related (Fig. 4). The CH_2O accumulation data of the terminal leaf best fit the sigmoid Gompertz model (1,9) (Eq. 8 and 9, Fig. 5). At day 2 CH_2O accumulation rate reached a maximum of almost 10 mg , which equaled 25.5% of the maximum rate estimated for the 7th leaf. Model equation coefficients for the terminal leaf are as follows:

$$B(1)=156.471$$

$$B(2)=1.515$$

$$B(3)=0.171$$

$$Y = B(1) * e^{(-B(2) * e^{(-B(3) * X)})} \qquad \text{(Eq.8)}$$

$$YD = Y_{(X+0.5)} - Y_{(X-0.5)} \qquad \text{(Eq.9)}$$

With definitions for Y, YD and X identical to those used in equations 5 and 6.

Estimated terminal leaf area at full expansion was 18.1 cm^2, while the mean for the control plants in the study was 18.0$\pm$5.7 cm^2. DP_N, DP_G, and DR_D (CH_2O $leaf^{-1}$ day^{-1}) were linearly related to the leaf CH_2O (mg CH_2O $leaf^{-1}$) (Eq. 7,Table 1, Fig. 6). Linear regression coefficients and r^2

Table 2. Thirty day simulated carbohydrate balance for the 7th leaf of 'Montmorency' sour cherry from the beginning of leaf emergence until full expansion.

Progressive days	CH_2O accumulation rate	Cumulative CH_2O	DPN rate	Cumulative DP_N	Daily export	Cumulative export
	$mgCH_2O$ day^{-1}	$mgCH_2O$	$mgCH_2O$ day^{-1}	$mgCH_2O$	$mgCH_2O$ day^{-1}	$mgCH_2O$
1	18.0	29.3	13.0	13.0	-5.0	-16.3
2	23.8	50.3	20.2	33.2	-3.7	-17.1
3	29.1	76.9	29.2	62.4	0.1	-14.5
4	33.4	108.2	39.9	102.3	6.4	-6.0
5	36.5	143.4	51.8	154.1	15.3	10.7
6	38.2	180.9	64.6	218.7	26.4	37.7
7	38.4	219.4	77.7	296.3	39.3	76.9
8	37.2	257.4	90.6	386.9	53.4	129.5
9	34.8	293.5	102.8	489.7	68.1	196.3
10	31.4	326.7	114.1	603.9	82.7	277.2
11	27.4	356.1	124.2	728.0	96.7	371.9
12	23.2	381.5	132.8	860.8	109.6	479.3
13	19.0	402.5	139.9	1000.7	121.0	598.2
14	15.0	419.4	145.7	1146.4	130.7	726.9
15	11.5	432.6	150.2	1296.5	138.7	863.9
16	8.5	442.6	153.5	1450.1	145.0	1007.5
17	6.1	449.8	156.0	1605.1	149.9	1156.3
18	4.2	454.9	157.7	1763.8	153.5	1308.9
19	2.8	458.4	158.9	1922.7	156.1	1464.3
20	1.8	460.7	159.7	2082.4	157.9	1621.7
21	1.2	462.1	160.2	2242.6	159.0	1780.4
22	0.7	463.0	160.5	2403.1	159.8	1940.0
23	0.4	463.6	160.7	2563.7	160.3	2100.2
24	0.2	463.9	160.8	2724.5	160.5	2260.6
25	0.1	464.0	160.8	2885.3	160.7	2421.3
26	0.1	464.1	160.9	3046.2	160.8	2582.1
27	0.0	464.2	160.9	3207.1	160.8	2742.9
28	0.0	464.2	160.9	3368.0	160.9	2903.8
29	0.0	464.2	160.9	3528.9	160.9	3064.7
30	0.0	464.2	160.9	3689.8	160.9	3225.6

Figure 4. Relationship between leaf area and carbohydrate content of the terminal leaf of 'Montmorency' sour cherry, observations (circles) and fitted curve (line) during leaf expansion.

Figure 4.

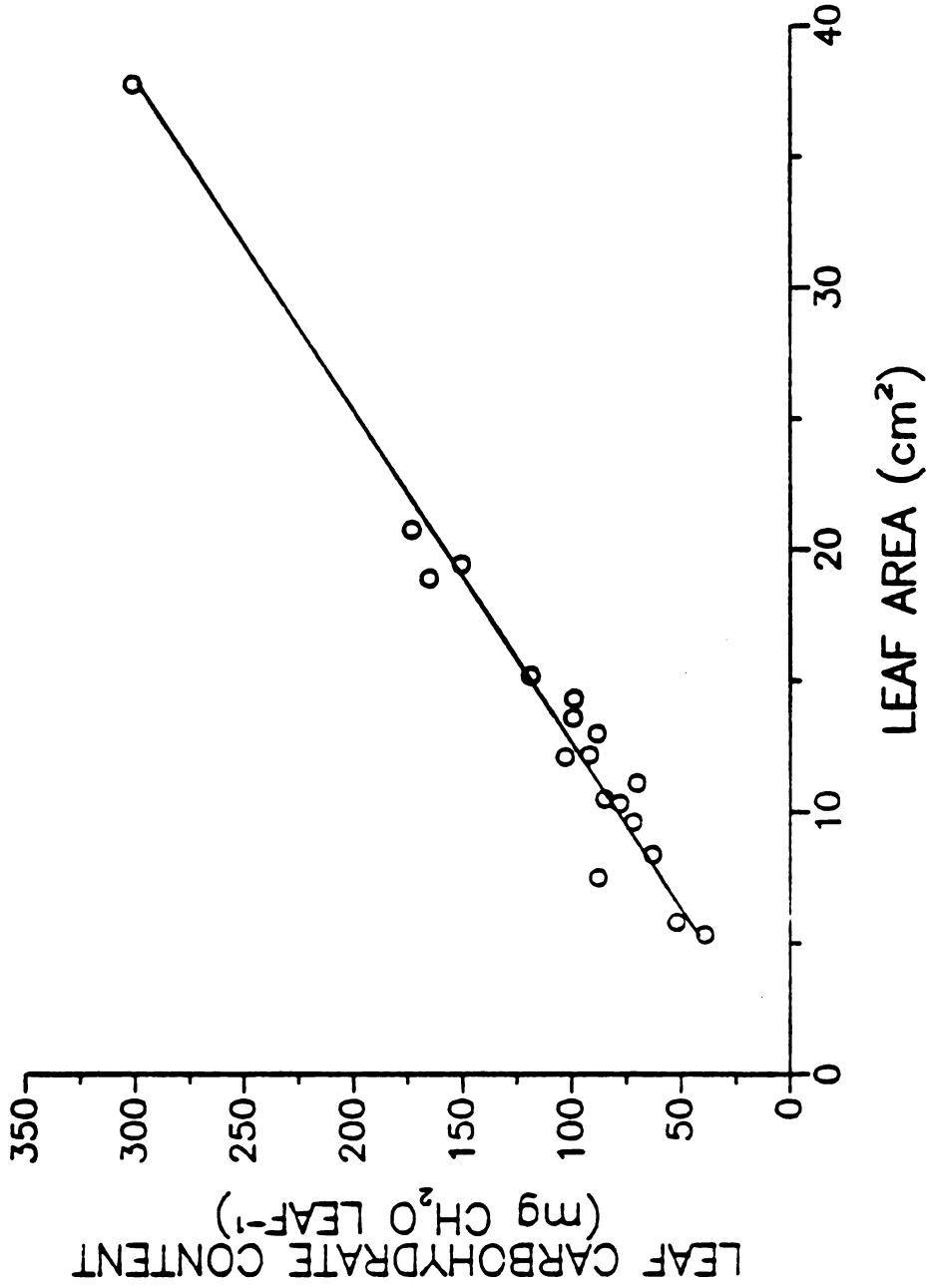
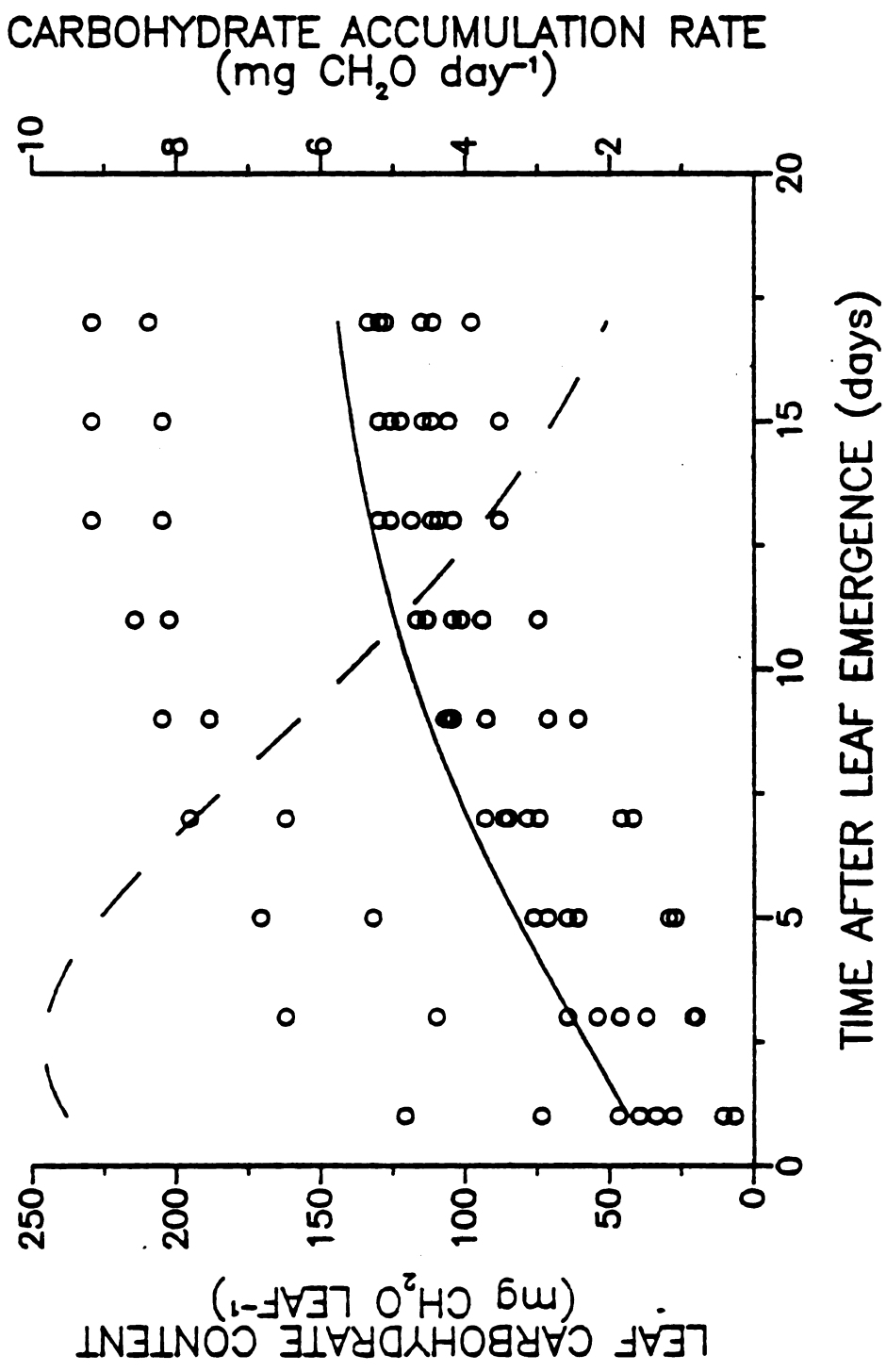

LEAF CARBOHYDRATE CONTENT
(mg CH2O LEAF-1)
350
300
250
200
150
100
50
0
0
10
20
30
40
LEAF AREA (cm2)

Figure 5. Carbohydrate accumulation of the terminal leaf of 'Montmorency' sour cherry during leaf expansion, observations (circles), fitted curve (solid line) and carbohydrate accumulation rate (broken line).

Figure 5.


CARBOHYDRATE ACCUMULATION RATE
(mg CH_2O day^{-1})
10
8
6
4
2
0
5
10
15
20
TIME AFTER LEAF EMERGENCE (days)
LEAF CARBOHYDRATE CONTENT
(mg CH_2O $LEAF^{-1}$)
250
200
150
100
50
0

are shown in Table 1. The terminal leaf initiated E_N (Table 3) after accumulating 72.9 mg of CH_2O (leaf area = 9.2 cm^2, 51% expansion).

Cumulative CH_2O export (Table 3) became positive after 10 days of growth. Maximum daily E_N of the expanding terminal leaf was slightly over 25 mg, 16.4% of the maximum E_N of the seventh leaf. Carbohydrate accumulation, photosynthesis and export by the 7th leaf and the terminal leaf are compared in Table 4.

Shoot. Shoot CH_2O content as a function of shoot length was best described by a second order equation (Fig. 7). Total shoot CH_2O accumulation best fit the sigmoid Weibull's model (Eq. 5 and 6, Fig. 8). The CH_2O accumulation rate reached a maximum of more than 700 mg day^{-1} by day 33. Model equation coefficients for the shoot are as follows:

B(1)=19424.785

B(2)=0.0902

B(3)=0.02524

B(4)=3.815

DP_N and DP_G of the whole shoot in units of CH_2O $shoot^{-1}$ day^{-1} were best related to the shoot CH_2O content (mg CH_2O $shoot^{-1}$) with a 2nd order equation (Eq. 10, Table 1, Fig. 9). DR_D showed a 3rd order relation to the shoot CH_2O content (Eq. 11, Fig. 9, Table 1).

$$Y = B(1) + B(2) * X + B(3) * X^2 \qquad \text{(Eq.10)}$$

$$Y = B(1) + B(2) * X + B(3) * X^2 * B(4) * X^3 \qquad \text{(Eq.11)}$$

Figure 6. Daily gross photosynthesis (DP_G) (A), daily net photosynthesis (DP_N) (B), and daily dark respiration (DR_D) (C) of the terminal leaf of 'Montmorency sour cherry, observations (circles) and predicted curves (line) at different leaf sizes during leaf expansion.

Figure 6

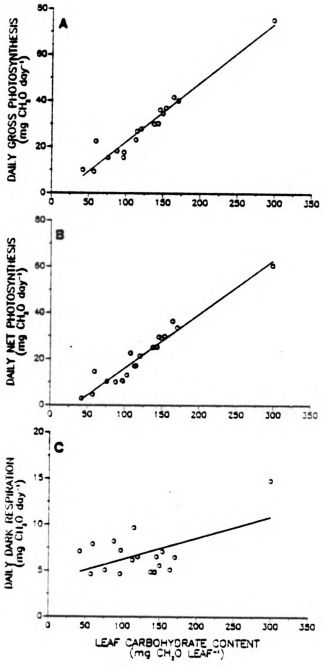

A
B
C
DAILY GROSS PHOTOSYNTHESIS (mg CH2O day-1)
DAILY NET PHOTOSYNTHESIS (mg CH2O day-1)
DAILY DARK RESPIRATION (mg CH2O day-1)
LEAF CARBOHYDRATE CONTENT (mg CH2O LEAF-1)
0
50
100
150
200
250
300
350
20
40
60
80
5
10
15

Table 3. Twenty day simulated carbohydrate balance for the terminal leaf of 'Montmorency' sour cherry from the beginning of leaf emergence until full expansion

Progressive days	CH_2O accumulation rate	Cumulative CH_2O	DP_N rate	Cumulative DP_N	Daily export	Cumulative export
	$mgCH_2O\ day^{-1}$	$mgCH_2O$	$mgCH_2O\ day^{-1}$	mgCH2O	$mgCH_2O\ day^{-1}$	$mgCH_2O$
1	9.5	43.6	2.9	2.9	-6.6	-40.7
2	9.8	53.3	5.2	8.1	-4.6	-45.2
3	9.8	63.2	7.5	15.6	-2.3	-47.6
4	9.5	72.9	9.8	25.4	0.3	-47.5
5	9.0	82.2	12.0	37.3	2.9	-44.8
6	8.4	90.9	14.0	51.3	5.6	-39.6
7	7.7	99.0	15.9	67.3	8.2	-31.8
8	7.0	106.4	17.7	84.9	10.6	-21.5
9	6.3	113.0	19.2	104.1	12.9	-8.9
10	5.6	119.0	20.6	124.7	15.0	5.8
11	4.9	124.2	21.8	146.6	16.9	22.4
12	4.3	128.8	22.9	169.5	18.6	40.7
13	3.7	132.8	23.9	193.4	20.1	60.6
14	3.2	136.3	24.7	218.0	21.5	81.8
15	2.8	139.3	25.4	243.4	22.6	104.1
16	2.4	141.8	26.0	269.4	23.6	127.6
17	2.0	144.0	26.5	295.9	24.5	151.9
18	1.7	145.9	26.9	322.8	25.2	176.9
19	1.5	147.5	27.3	350.2	25.8	202.6
20	1.3	148.9	27.6	377.8	26.4	228.9

Table 4. Comparison of 7th leaf and terminal leaf and the whole shoot of 'Montmorency' sour cherry.

Parameter	7th	Terminal	Shoot
Area (cm^2), Length (mm) (Full Size)	62.3	18.1	603
Area (cm^2), Length (mm) (Start of export)	10.6	9.2	160
CH_2O content (mg) (Full size)	464	149	19.4
CH_2O content (mg) (Start of export)	76.9	72.9	1531
Expansion (%) (Start of export)	17	51	27
CH_2O accumulation (%) (Start of export)	17	49	7.9
Days after emergence (Start of export)	3	4	17
Net photosynthesis ($mg\ day^{-1}$) (Start of export)	29.2	9.8	277.5
Export maximum ($mg\ day^{-1}$)	161	27	2.1
Net photosynthesis (Maximum)	(same as export maximum)		

Net export of the whole shoot started after it had accumulated 1531 mg of CH_2O (shoot length = 160 mm, 26.5% of full extension) (Table 5). The estimated cumulative photosynthesis always exceeded CH_2O accumulation, which likely results from an overestimation of DP_N at the beginning of shoot development. Modeling does not allow us to estimate these relatively small changes in the CH_2O balance in the initial phase of shoot development accurately enough to calculate when the balance becomes positive. However, whole shoot E_N began at day 15, and reached a maximum rate of more than 2100 mg day^{-1} after 61 days (shoot length = 600 mm) with approximately 21 to 22 leaves.

Discussion

Methods involving heat girdling of the petiole or measuring leaf CH_2O accumulation using leaf disks to determine E_N from developing leaves are not adequate for sour cherry leaves. Heat girdling has been used in grape (15), although its disadvantages include the potential damage to the leaf, the inhibition of the movement of non-carbohydrate substances to and from the leaf and the difficulty in estimating import and export quantitatively. The removal of leaf disks can also physically affect photosynthesis and export. These problems were avoided by developing empirical models for leaf and shoot CH_2O accumulation and CO_2 gas exchange in sour cherry. The models of Weibull (9) and Gompertz (1,9) gave the best fit for leaf and shoot CH_2O accumulation in sour cherry and were used to estimate the onset of CH_2O export. These models have also been reported for other sigmoid growth phenomena (1,9).

Figure 7. Relationship between length and carbohydrate content of the whole shoot of 'Montmorency' sour cherry during leaf expansion, observations (circles), fitted curve) (line).

Figure 7.

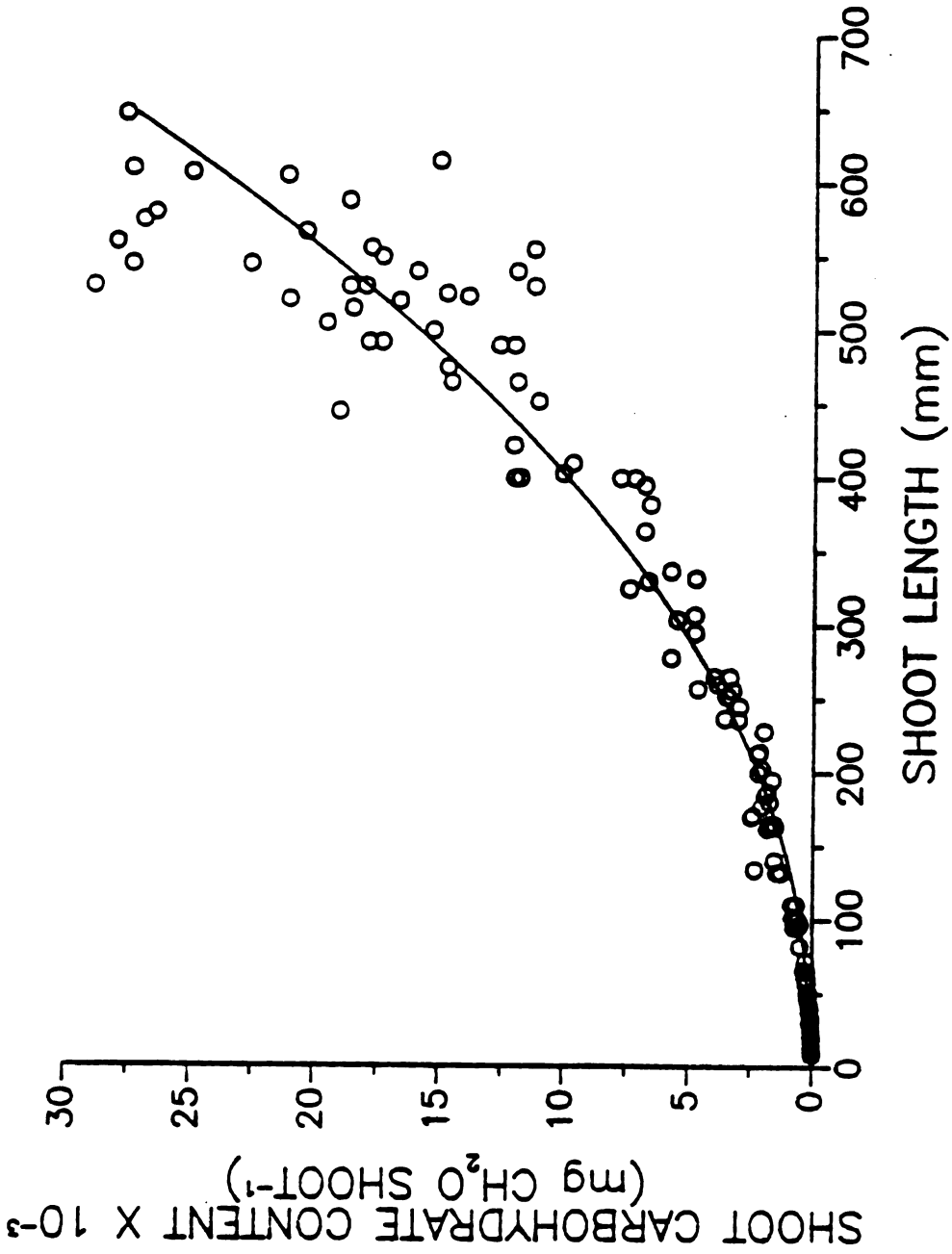

SHOOT CARBOHYDRATE CONTENT X 10-3
(mg CH2O SHOOT-1)
0
5
10
15
20
25
30
0
100
200
300
400
500
600
700
SHOOT LENGTH (mm)

Figure 8. Carbohydrate accumulation of the whole shoot of 'Montmorency' sour cherry during shoot elongation, observations (circles), fitted curve (solid line) and carbohydrate accumulation rate (broken line).

Figure 8.

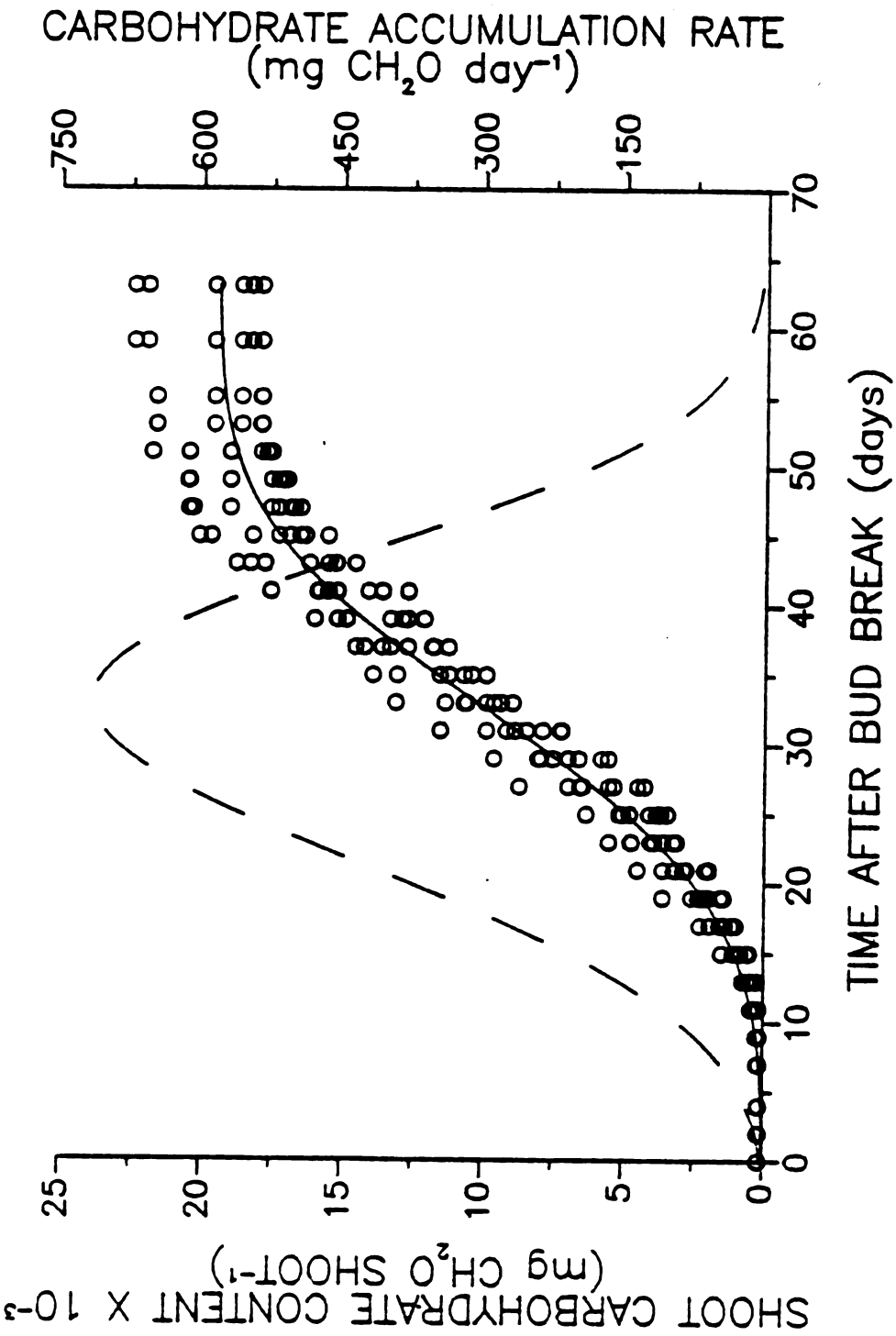

CARBOHYDRATE ACCUMULATION RATE
(mg CH_2O day^{-1})
750
600
450
300
150
70
60
50
40
30
20
10
0
TIME AFTER BUD BREAK (days)
SHOOT CARBOHYDRATE CONTENT X 10^{-3}
(mg CH_2O $SHOOT^{-1}$)
25
20
15
10
5
0

Figure 9. Daily gross photosynthesis (DP_G) (A), daily net photosynthesis (DP_N) (B), and daily dark respiration (DR_D) (C) of the whole shoot of 'Montmorency' sour cherry, observations (circles) and fitted curves (lines) at different shoot sizes during shoot elongation.

Figure 9.

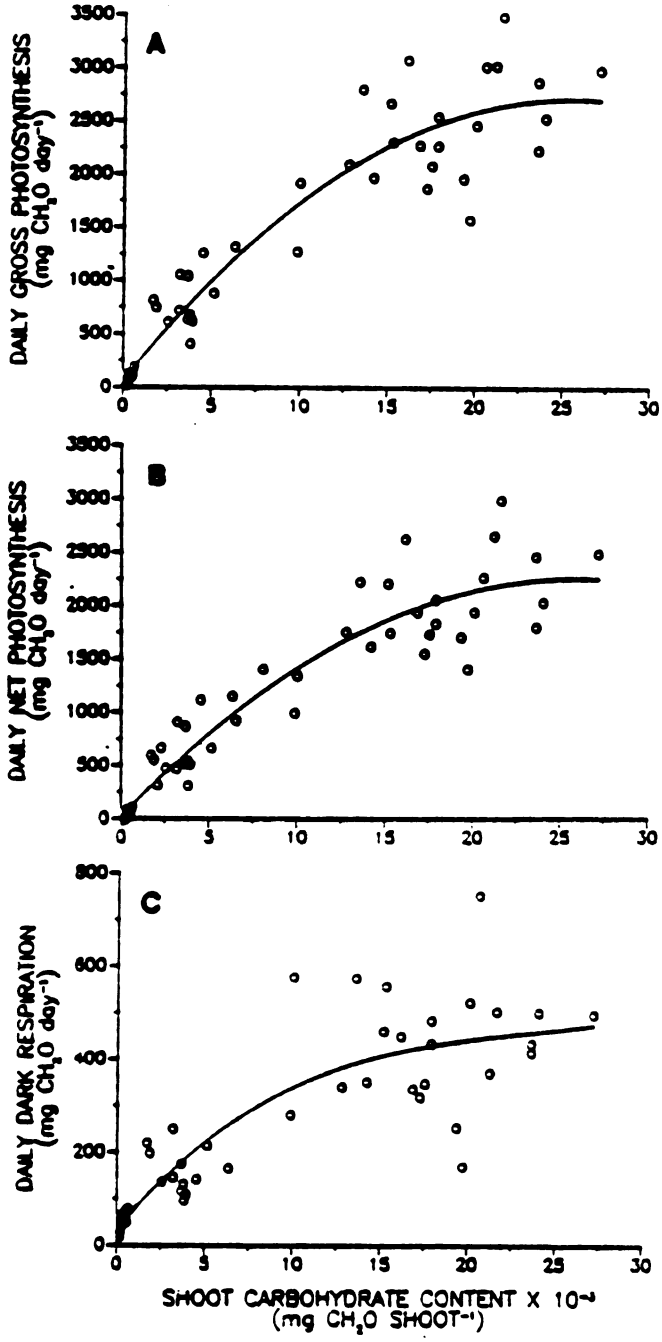

A
B
C
DAILY GROSS PHOTOSYNTHESIS (mg CH_2O day^{-1})
DAILY NET PHOTOSYNTHESIS (mg CH_2O day^{-1})
DAILY DARK RESPIRATION (mg CH_2O day^{-1})
SHOOT CARBOHYDRATE CONTENT X 10^{-3} (mg CH_2O $SHOOT^{-1}$)

Table 5. Sixty-five day simulated carbohydrate balance for the whole shoot of 'Montmorency' sour cherry from bud break until full expansion.

Progressive days	CH_2O accumulation rate	Cumulative CH_2O	DP_N rate	Cumulative DP_N	Daily export	Cumulative export
	mg CH_2O day^{-1}	mg CH_2O	mg CH_2O day^{-1}	mg CH_2O	mg CH_2O day^{-1}	mg CH_2O
1	4.3	5.1	22.9	22.9	18.5	17.7
2	7.5	10.9	23.9	46.7	16.3	35.8
3	12.0	20.5	25.5	72.2	13.5	51.7
4	17.8	35.2	28.0	100.2	10.3	65.2
5	25.2	56.5	31.7	131.9	6.5	73.5
6	34.2	85.9	36.7	168.7	2.5	82.7
7	45.2	125.4	43.5	212.2	-1.7	86.7
8	58.1	176.8	52.3	264.4	-5.8	87.6
9	73.1	242.1	63.4	327.9	-9.7	85.7
10	90.3	323.5	77.3	405.1	-13.0	81.6
11	109.7	423.2	94.2	499.3	-15.5	76.1
12	131.3	543.4	114.5	613.8	-16.9	70.4
13	155.3	686.5	138.5	752.3	-16.8	65.9
14	181.5	854.6	166.5	918.8	-14.9	64.3
15	209.8	1049.9	198.9	1117.8	-10.9	67.8
16	240.2	1274.7	235.8	1353.6	-4.3	78.9
17	272.4	1530.8	277.5	1631.1	5.1	100.3
18	306.3	1820.0	324.0	1955.2	17.7	135.2
19	341.6	2143.8	375.5	2330.7	33.9	186.9
20	377.8	2503.4	431.8	2762.5	54.0	259.1
21	414.8	2899.6	492.9	3255.3	78.1	353.7
22	451.9	3333.0	558.5	3813.8	106.6	480.9
23	488.6	3803.2	628.3	4442.1	139.6	638.8
24	524.6	4310.0	701.8	5143.9	177.2	833.9
25	559.1	4862.0	778.6	5922.5	219.5	1070.4
26	591.6	5427.7	858.0	6780.5	266.4	1352.3
27	621.3	6034.6	939.4	7719.9	317.9	1688.3
28	648.1	6669.8	1021.9	8741.8	373.8	2072.0
29	670.9	7329.8	1104.9	9846.7	433.9	2516.8
30	689.4	8010.6	1187.4	11034.1	498.0	3023.5
31	703.1	8707.4	1268.7	12302.8	565.6	3595.4
32	711.5	9415.4	1348.0	13650.8	636.5	4235.4
33	714.4	10129.0	1424.6	15075.3	710.2	4946.4
34	711.5	10842.7	1497.8	16573.1	786.2	5732.4
35	703.0	11550.7	1567.1	18140.2	864.1	6596.5
36	688.7	12247.2	1632.0	19772.2	943.4	7539.9
37	668.8	12926.6	1692.3	21464.5	1023.4	8563.4
38	643.9	13583.9	1747.6	23212.1	1103.7	9667.1
39	614.3	14213.2	1798.0	25010.2	1183.7	10850.8
40	580.5	14811.1	1843.4	26853.4	1262.8	12113.6
41	543.4	15373.4	1883.9	28737.4	1340.5	13454.1
42	503.7	15897.2	1919.8	30657.1	1416.1	14870.3
43	462.1	16380.3	1951.3	32608.4	1489.2	16359.5
44	419.5	16821.2	1978.7	34587.1	1559.1	17918.6
45	376.3	17219.4	2002.3	36589.5	1625.4	19544.0
46	334.1	17573.1	2022.5	38611.8	1687.7	21231.7
47	294.3	17889.3	2039.5	40651.5	1745.6	22977.3
48	257.2	18169.7	2054.1	42705.6	1799.9	24777.3
49	218.9	18400.4	2066.2	44771.7	1847.1	26571.4
50	183.4	18602.1	2076.2	46847.9	1890.3	28248.8
51	155.0	18771.9	2084.4	48932.2	1929.4	30160.4
52	127.9	18912.9	2091.0	51023.2	1963.1	32110.4
53	104.1	19028.5	2096.4	53119.6	1992.2	34091.1
54	83.6	19122.0	2100.7	55220.3	2017.0	36096.3
55	66.2	19196.5	2104.0	57324.3	2037.8	38127.8
56	51.6	19255.1	2106.6	59431.0	2055.0	40175.9
57	39.7	19300.4	2108.7	61539.6	2069.3	42239.2
58	30.0	19335.0	2110.2	63649.8	2080.2	44314.8
59	22.3	19360.9	2111.3	65761.1	2089.0	46400.2
60	16.4	19380.1	2112.2	67873.3	2095.8	48493.2
61	11.8	19394.0	2112.8	69986.0	2101.0	50592.0
62	8.3	19403.9	2113.2	72099.2	2104.9	52695.3
63	5.8	19410.9	2113.5	74212.7	2107.7	54801.8
64	4.0	19415.7	2113.7	76326.4	2109.7	56910.7
65	2.7	19418.9	2113.9	78440.3	2111.2	59021.3

DP_N, DP_G, and DR_D were linearly related to leaf area and CH_2O content (Fig. 3 and 6), resulting in approximately constant rates when expressed on an area basis. In contrast, Sams and Flore (18) reported that P_N in developing sour cherry leaves first increased, then and remained constant thereafter. The proposed model for DP_N, however, should not be extrapolated to the period after full leaf expansion for several reasons. First, different source-sink relationships could influence DP_N. Fruiting trees reportedly have higher photosynthetic rates than non-fruiting trees (14), although this relationship has not been consistent for sour cherry (19). Second, linearity might be lost within a tree canopy, where the light intensity decreases during leaf expansion. Third, leaf P_N decreases during senescence (18).

The correlation of DP_N, DP_G, and DR_D with leaf CH_2O content was much closer for the terminal leaf than for the 7th leaf. This was probably due to greater uniformity of source-sink relationships during expansion of the terminal leaves. The slopes of the regression lines for DP_N and DP_G represented by the parameter B(2) were greater for the 7th leaf than for the terminal leaf. This indicates greater rates of photosynthesis for the 7th leaf than for the terminal leaf (Table 4), not only because of its greater size but also in terms of unit leaf area. A reduced leaf size is generally observed before terminal bud set, although the reasons for this are not known. The reduction in P_N per unit leaf area is probably due to intrinsic differences in photosynthetic capacity. A reduction of P_N due to feedback inhibition is not likely, since no marked diurnal rate changes were observed (data not shown). The DP_N and DP_G of the whole shoot were related to the shoot CH_2O content by a 2nd

order equation. The slope decreased with shoot CH_2O accumulation. The shoot's leaf area was probably proportional to the CH_2O content, as is the case in apple (10). This supports the hypothesis that distal leaves have lower photosynthetic rates per unit area. DR_D showed 3rd order relations to the shoot CH_2O content, following a similar pattern as DP_N and DP_G (Fig. 9).

The models for CH_2O accumulation and DP_N indicated that the onset of E_N occurred at approximately 17% and 51% of full expansion, and 27% of full elongation, for the 7th and terminal leaves and the shoot, respectively (Table 4). In an earlier study with sour cherry we reported (11) that E_G from the 7th leaf starts between 27.2% and 98.9% expansion and from the tenth leaf between 48.0% and 77.6% expansion. Net CH_2O export did not start later than E_G, indicating that CH_2O import stops close to the time when export starts. These findings are in contrast to those reported for grape, in which import and export occur simultaneously for leaves between 30% and 50% expansion (13). Our results for the onset of E_N from leaves are similar to those reported for herbaceous plants (8,20). We found, however, that in terms of degree of leaf expansion, E_N for sour cherry leaves started much later than reported for apple leaves (21). It is difficult to compare results of export initiation, since neither time after emergence, nor absolute or percent expansion are closely linked to the mechanism involved (11). Apple shoots were 4 cm long and had 10 unfolded leaves when E_N began (10), while sour cherry shoots were 16 cm long and had an almost fully expanded seventh leaf. The apple shoots had used 831 mg of CH_2O for

accumulation and respiration (10), while the cherry shoots had accumulated 1531 mg, not accounting for respiration. This indicates that the sour cherry shoots started export at a greater size, even though leaf number was similar. The differences observed betweeen sour cherry and apple could have resulted from different growing conditions.

The earlier start of E_N from the 7th leaf, as compared to the terminal leaf, supports the hypothesis of Kappes and Flore (11) that CH_2O supply and demand regulate the time of onset of export. Net export for the 7th and terminal leaf occurred at approximately the same absolute size (10.6 and 9.2 cm^2) (Table 4), although the percentage of full expansion was much greater for the terminal leaf (51%) than for the 7th leaf (17%). Reaching a certain absolute leaf size, however, does not seem to trigger export (11).

Leaves begin making a positive contribution to the CH_2O balance of the plant after a short period of expansion. The overall CH_2O balance became positive after 5 days in the 7th leaf (Table 2) and after 10 days in the terminal leaf (Table 4). After this time leaves stopped being net consumers of CH_2O produced by the rest of the plant. The whole shoot started to export 17 days after bud break, at 27% of full elongation, 7.9% CH_2O accumulation and when the 7th leaf was almost fully expanded. The plants studied did not bore fruits, thus demand for CH_2O came from the shoot, root growth, growth of the trunk and replenishment of CH_2O reserves. We speculate that replenishment of reserves was a strong sink, since export from the shoot started at a time when shoot CH_2O accumulation rates were still increasing.

This study demonstrates that leaves start E_N soon after initiation of their expansion. Shortly after E_N starts leaves have produced more CH_2O than they use for development and become net sources of CH_2O for the plant. Shoot cumulative E_N remains close to 0 indicating that the shoot does not use much of the reserves, although E_N takes 17 days to start. Even the terminal leaf, which develops latest in the season when growth has slowed down, produces more CH_2O than needed for its development. Near the end of leaf or shoot expansion, cumulative DP_N exceeds the cumulative CH_2O several fold.

The models in this study were developed for non-fruiting plants, trained to 1 shoot, which is a much simpler system than a bearing fruit tree. Fruits could cause an earlier initiation of export from leaves and shoots if sour cherry fruits have the first priority for CH_2O, as has been speculated for other plants (5,6). The shoots in our experiment exported, according to our model (Table 6), a maximum of more than 2g of CH_2O per day, which is equivalent to the CH_2O accumulated by 3 mature fruits in 57 days.

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Section III

Sour Cherry Fruit Carbohydrate Balance during Development, from Empirical Models of Carbohydrate Accumulation, Net Photosynthesis, Gross Photosynthesis, and Dark Respiration

Abstract. A fruit carbohydate (CH_2O) balance was developed from models derived from measurements of CH_2O accumulation and CO_2 gas exchange from shortly after full bloom to maturity. Daily gross photosynthesis (DP_G) never compensated for daily dark respiration (DR_D) under the conditions tested. DP_G increased during stage I of fruit development and decreased thereafter as fruit chlorophyll decreased and anthocyanin increased. DP_G as a percentage of DR_D decreased during the entire period. Fruit gross photosynthesis accounted for 11.2% of the total CH_2O utilized during development of the fruit, while 88.8% had to be imported. Fruit gross photosynthesis contributed 19.4%, 29.7% and 1.5% of the CH_2O used during stages I, II and III of fruit development, respectively. Of the total CH_2O used, 30.9% was used for dark respiration and 69.1% was incorporated into fruit dry matter. The share of CH_2O used by the fruit for dark respiration was 32.7%, 70.9% and 19.9% during stages I, II, and III of development, respectively. Sour cherry fruit photosynthesis contributes a significant portion of the CH_2O used for fruit growth and dark respiration. The major part of this contribution is made during stages I and II of fruit development when the leaf area of the tree is still small. Use of CH_2O for dark respiration is high during the lag phase (stage II), probably due to synthesis of lignin and lipids, during pit hardening and embryo development. Dark respiration is intermediate during cell division (stage I) and low during cell expansion (stage III).

The influence of fruit photosynthesis on subsequent fruit size and fruit set is not well documented. Fruit photosynthesis, however, appears to contribute to, and perhaps limit yield in grape (9, 10, 13, 17) and apple (3, 16). During bud break and immediately thereafter vegetative and reproductive buds compete for the CH_2O reserves stored within the plant, leaves and shoots become net exporters. For sour cherry the minimum leaf to fruit ratio for maximum fruit size has been estimated to be 1.5 to 2 (35-50 cm^2 $fruit^{-1}$), which in practice is usually exceeded (19,8). Thus fruit photosynthesis may make a significant CH_2O contribution early in the season during fruit set and cell division when competition for CH_2O is high, or later in the season in cases of excessive fruit load (less than 1.5 leaves per fruit) or severe defoliation.

Most of the work related to fruit photosynthesis has focused on the effects of environmental factors (16, 9). Noga and Lenz (16) observed that evolution of CO_2 from apple fruits was much greater in the dark than in the light and suggested that this may alter the net photosynthetic balance of the plant. CH_2O fixed by grape berries is assumed to be of minor importance in the CH_2O balance of the fruit, even though in some cultivars it compensates for most of the fruit respiration (9, 10, 17). Koch and Alleweldt (13), however, concluded that fruit photosynthesis is an important factor for growth, especially of the young grape berry. A survey (1) focusing on the contribution of fruit photosynthesis to the CH_2O balance of the reproductive organs in several species showed that the contribution ranged from 2.3% in Quercus macrocarpa to 64.5% in Acer platanoides. In the closest relative

of sour cherry studied, Prunus serotina, the fruit contributed 19.2% of the CH_2O used for its development. Similar CH_2O balance calculations are needed to estimate more precisely the fruit photosynthetic contribution of commercially produced fruits.

The main objectives of this study were to determine a) the share of CH_2O supplied by fruit photosynthesis in sour cherry, b) the share of CH_2O used by dark respiration during the different stages of fruit development, c) the share of CH_2O import required and the change of import rates during fruit development.

Materials and Methods

Plant material: Branches with an average to high fruit load (2-6 leaves/fruit) were randomly selected from the outer edge of all quadrants of the tree, approximately 2 m from the ground, in a 12-year-old sour cherry ('Montmorency' on Mahaleb) orchard at the Horticulture Research Center, East Lansing, MI. Branches were cut, immediately immersed in water and transported to the laboratory. Bases were then recut under water to eliminate air from the vascular system and branches were used for CO_2 gas exchange determination. Previous studies (20) indicated that this procedure gives results equal to that of attached branches for leaf gas exchange characteristics, if the precautions of Lakso (15) are considered.

Curve fitting: Mathematical relationships between variables were determined by curve fitting with PLOTIT (5). Models were chosen on the basis of the residual sums of squares, the coefficient of determination and the visual fit of the regression lines in relation to the observed data.

Measurement of CO_2 gas exchange: Fruit gas exchange was measured with an open system as previously described by Sams and Flore (19). Photosynthesis and dark respiration were determined at 4-day intervals from full bloom until maturity, using 4 attached fruits per assimilation chamber, replicated with 4 different shoots and 4 chambers. Standard assimilation chamber conditions were: photosynthetic photon flux density, 1000 μmol m^{-2} sec^{-1}, 16 hr light, 8 hr darkness, day and night temperature, 25° and 15°C, respectively. The dew point of the air entering the chamber was kept at 5°C, resulting in vapor pressure deficits of approximately 2.5 and 1.5 kPa during the light and the dark periods, respectively. The fruits were kept in the chamber for 24 hr while photosynthesis (light period) and dark respiration (dark period) were determined at 2-hr intervals. The first measurement in the dark was taken at 25° to estimate respiration during the light period. Daily net photosynthetis (DP_N), daily gross photosynthesis (DP_G) and daily dark respiration (DR_D) were calculated in terms of mg CH_2O $fruit^{-1}$ day^{-1}.

Definitions: DP_N = net photosynthesis (day) - dark respiration night

DR_D = dark respiration (day) + dark respiration night

$DP_G = DP_N - DR_D$

Fruit DP_N, DP_G and DR_D were correlated with fruit CH_2O content. Using these regression equations and the CH_2O accumulation equation, data were calculated for the photosynthetic parameters as a function of time over 57 days of fruit development. Cumulative DP_G and DR_D were calculated from fitted equations at different times of fruit development and for the entire period of fruit growth.

Measurement of carbohydrate accumulation: Fruit growth was estimated from observations made on 20 fruits which were selected randomly and tagged 5 days after full bloom. Suture diameter (S) and length (L) were measured using calipers (precision = 0.1 mm) at 2-day intervals at 10 a.m. Fruit volume (V) was estimated (Eq. 1) assuming that the fruit is a sphere whose diameter equals the mean of suture diameter and length (22).

$$V = 4/3 * Pi * ((S + L) * 0.5 * 0.5)^3 \qquad \text{(Eq.1)}$$

Fruits (n = 16) were sampled at random from the same trees used for photosynthesis and CH_2O accumulation studies at 4-day intervals during fruit development. Fruit volume was estimated and composite samples were dried in a forced draft oven for 3 days and ashed at 650 ^oC for 7 hr in a muffle furnace. The weight loss per fruit during ashing was used as an estimate of fruit CH_2O content (12). Relative mineral content decreased during fruit development following a quadratic curve (Eq. 2).

$$Y = 6.341 - 1.176E\text{-}2 * DW + 8.312E\text{-}6 * DW^2 \qquad \text{(Eq.2)}$$

$$r^2=0.771$$

The regression between total fruit CH_2O content and fruit volume was used to convert fruit volume increase to CH_2O accumulation.

Because of the large variation in final fruit sizes, the CH_2O accumulation data were normalized by dividing all data by the final CH_2O content of the respective fruit. The normalized data were then multiplied by the mean of the final fruit CH_2O content. The values obtained were correlated with time to obtain a CH_2O accumulation curve. The final value of this curve was used as an estimate of the total CH_2O accumulated during the entire period of fruit growth. Daily differences from this curvve were used as an estimate for the rate of CH_2O accumulation.

Stages of development were defined according to Tukey (22), stage I being the first period of rapid growth (days 1-22 after full bloom), stage II the lag phase (days 23-35 after full bloom) and stage III the second period of rapid growth (days 36-57 after full bloom).

Results

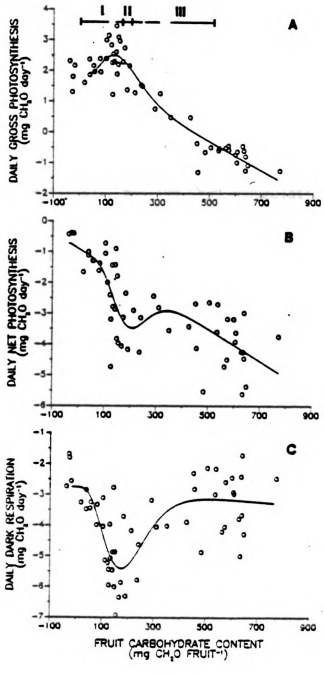
Fruit DP_G (Fig. 1A) increased with fruit CH_2O content during stage I. DP_G peaked during stage II and decreased as the fruits lost chlorophyll (data not shown) and turned red.

Fruit DP_N (Fig. 1B) was negative during the entire course of fruit development. It decreased as the fruit CH_2O content increased, reached temporary minimum during stage II, then increased slightly and decreased further during stage III.

Fruit DR_D (Fig. 1C) increased with the fruit CH_2O content during stage I, peaked during stage II, then decreased to its original level during stage III.

Figure 1. CO_2 gas exchange of fruits as a function of fruit carbohydrate content during development of 'Montmorency' sour cherry fruit, observations (circles) and fitted curves (lines). A. Daily gross photosynthesis, B. Daily net photosynthesis and C. Daily dark respiration.

Figure 1.


I
II
III
A
DAILY GROSS PHOTOSYNTHESIS
(mg CH2O day-1)
B
DAILY NET PHOTOSYNTHESIS
(mg CH2O day-1)
C
DAILY DARK RESPIRATION
(mg CH2O day-1)
FRUIT CARBOHYDRATE CONTENT
(mg CH2O FRUIT-1)

DP_N, DP_G, and DR_D as a function of fruit CH_2O could be simulated best using a multiplicative exponential model to which a linear part was added (Eq. 3, Table 1).

$$Y=B(1)+B(2)*X+B(3)*(X^{B(4)})*e^{(B(5)*X)} \qquad \text{(Eq.3)}$$

Where: $Y=DP_N$, DP_G or DR_D (mg CH_2O day^{-1})

X=cumulative fruit CH_2O (mg CH_2O)

Fruit CH_2O accumulation (Fig. 2) followed the double sigmoid pattern of sour cherry fruit growth (22), and the CH_2O accumulation curve could best be modeled using a general logistic equation with a saddle (11) (Eq. 4, Table 1). The resulting curve for the growth rate (Eq. 5, Table 1) exhibits peaks during stages I and III and a minimum during stage II.

$$Y=B(1)/(1+e^{(B(2)+B(3)*X+B(4)*X*X+B(4)*B(4)*X*X*X/(3*B(3)))}) \qquad \text{(Eq.4)}$$

$$YD = Y_{(X+0.5)} - Y_{(X-0.5)} \qquad \text{(Eq.5)}$$

Where: Y = cumulative fruit CH_2O (mg CH_2O)

X = time after full bloom (days)

YD = daily CH_2O accumulation at day X

The simulated cumulative CH_2O balance for the fruit (Table 2) indicates that 30.9% of the CH_2O was utilized for dark respiration, while 69.1% was incorporated into the fruit. The fruit imported most of the CH_2O it used from external sources (i.e., leaves or reserves). However, a significant share of the CH_2O was fixed by the fruit itself. Under the given conditions, fruit gross photosynthesis accounted for

Table 1. Regression coefficients for 'Montmorency' sour cherry fruit daily net photosynthesis (DP_N), daily gross photosynthesis (DP_G) and daily dark respiration (DR_D) as a function of carbohydrate content, and of carbohydrate accumulation (CH_2O) as a function of time,during fruit growth

	DP_N	DP_G	R_D	CH_2O
B(1)	-0.897	2.007	-2.757	513.9
B(2)	-0.522E-2	-0.467E-2	-0.679E-3	9.354
B(3)	-0.680E-17	0.152E-7	-0.411E-8	-0.947
B(4)	9.375	4.525	4.872	0.345E-1
B(5)	-0.486E-1	-0.302E-1	-0.281E-1	--
r^2	0.624	0.908	0.551	0.929

Figure 2. Relationship between time after full bloom and carbohydrate accumulation of 'Montmorency' sour cherry fruit during development, observations (circles), fitted curve (solid line), carbohydrate accumulation rate (broken line).

Figure 2.

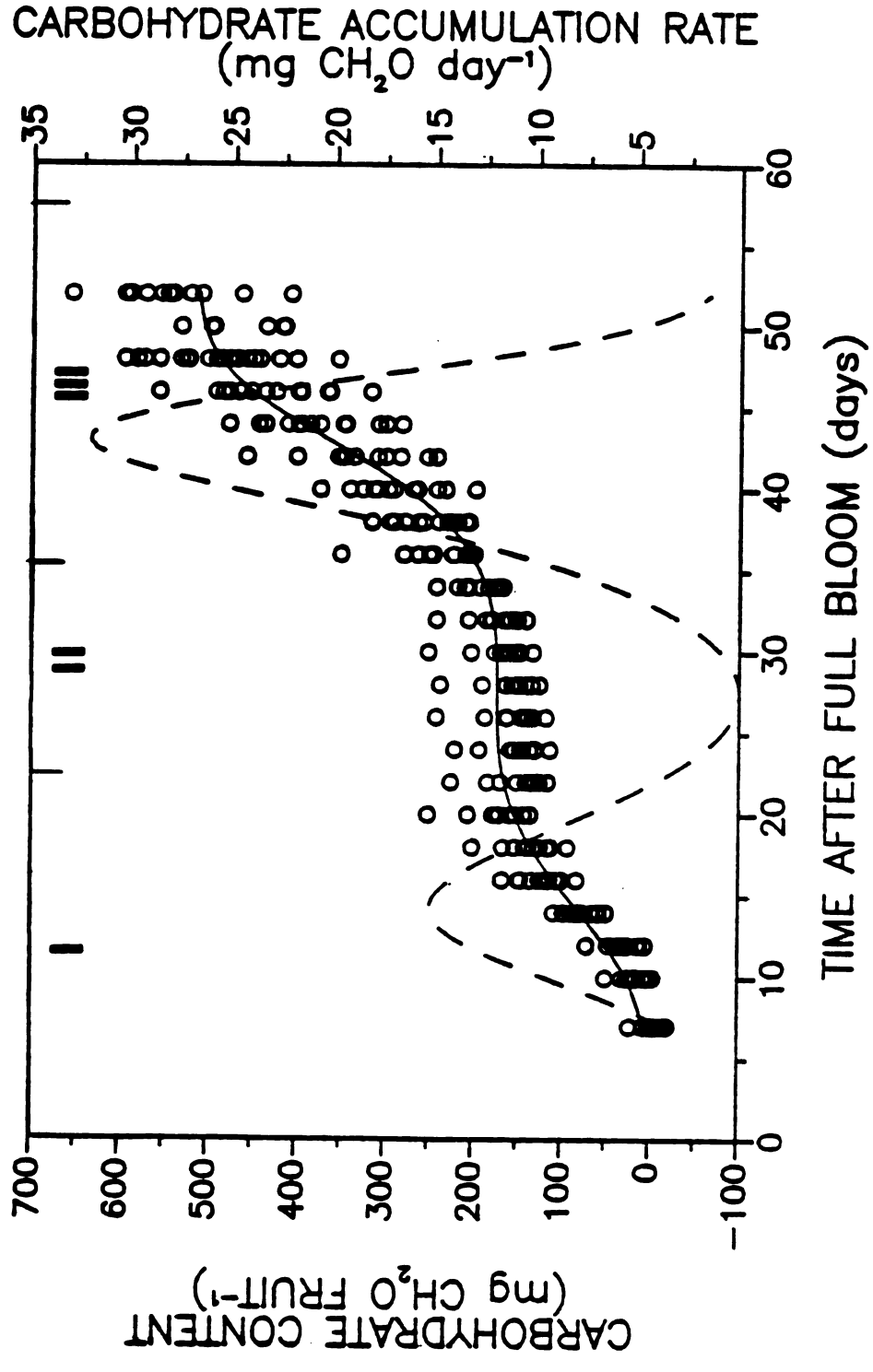

CARBOHYDRATE ACCUMULATION RATE
(mg CH2O day-1)
35
30
25
20
15
10
5
60
50
40
30
20
10
0
TIME AFTER FULL BLOOM (days)
700
600
500
400
300
200
100
0
-100
CARBOHYDRATE CONTENT
(mg CH2O FRUIT-1)
III
II
I

Table 2. Simulated carbohydrate balance (mg CH_2O, % of total CH_2O in parentheses) of 'Montmorency' sour cherry fruits during their development [z]

		Stage I (Day 1-22)	Stage II (Day 23-35)	Stage III (Day 36-57)	Total (Day 1-57)
CH_2O accumulated	(A)	164.1 (67.3)	28.9 (29.1)	320.9 (80.1)	513.9 (69.1)
CH_2O respired	(B)	79.9 (32.7)	70.4 (70.9)	79.8 (19.9)	230.0 (30.9)
Total CH_2O required	(A+B)	244.0 (100)	99.3 (100)	400.7 (100)	743.9 (100)
CH_2O produced	(C)	47.3 (19.4)	29.5 (29.7)	6.2 (1.5)	83.0 (11.2)
CH_2O imported	(A+B-C)	196.7 (80.6)	69.8 (70.3)	394.5 (98.5)	660.9 (88.8)

[z] Derived from empirical models as described in Materials and Methods.

11.2% of the total CH_2O, which was 36.1% of fruit dark respiration (Table 2). The percentage of CH_2O contributed by fruit gross photosynthesis was highest during stage II of fruit development (29.7%) and lowest during stage III (1.5%)(Table 2). The percentage of CH_2O used by dark respiration was also highest during stage II (70.9%) and lowest during stage III (19.9%)(Table 2). The gross photosynthesis as a percentage of dark respiration (Table 3) decreased markedly during the course of fruit growth.

Throughout the period of its development, the fruit remained a net importer of CH_2O (Table 4), since the DP_G never exceeded the CH_2O accumulation rate. The period of greatest CH_2O import (Table 4) coincided with the two peaks for growth rate (Fig. 2), 14-15 and 43 days after full bloom.

Discussion

The importance of fruit photosynthesis for the CH_2O production of a tree becomes evident only if a fruit CH_2O balance is calculated. Under the given conditions sour cherry fruits produced a substantial share (11.2%) of their CH_2O needs. Sour cherry fruit photosynthetic contribution to its CH_2O balance is relatively low when compared to most species surveyed by Bazzaz and coworkers (1). One must consider that the sour cherry CH_2O balance was obtained at high light intensities which are only found early in the season, at the canopy surface or after severe defoliation. However, since the highest percentage contribution

Table 3. Time course of daily gross photosynthesis (DP_G) as a percentage of daily respiration (DR_D)(experimental data)

Days after full bloom	DP_G/DR_D %	sd
4	86.4	9.5
8	61.1	8.3
12	63.1	7.3
16	69.8	5.5
20	55.9	8.2
24	41.8	4.8
28	34.3	10.7
32	31.4	4.3
36	19.3	9.3
40	-25.8	18.3
44	-12.3	0.6
48	-25.4	3.9
52	-23.1	2.2
56	-53.3	19.7

Table 4. Simulated carbohydrate import (mg CH_2O day^{-1}) of 'Montmorency' sour cherry fruits during development from full bloom to maturity.

Stage I		Stage II		Stage III	
Day	Import	Day	Import	Day	Import
1	1.00	23	6.00	36	14.77
2	1.11	24	4.92	37	17.83
3	1.33	25	4.10	38	21.22
4	1.71	26	3.55	39	24.82
5	2.34	27	3.28	40	28.42
6	3.29	28	3.29	41	31.69
7	4.62	29	3.60	42	34.13
8	6.34	30	4.20	43	35.14
9	8.40	31	5.10	44	34.25
10	10.62	32	6.32	45	31.34
11	12.78	33	7.88	46	26.84
12	14.61	34	9.80	47	21.56
13	15.90	35	12.09	48	16.41
14	16.54			49	12.05
15	16.54			50	8.77
16	15.97			51	6.54
17	14.94			52	5.16
18	13.59			53	4.36
19	12.02			54	3.94
20	10.39			55	3.74
21	8.78			56	3.65
22	7.30			57	3.61

by fruit photosynthesis, 19.4 and 29.7%, occurred during stages I and II, respectively, when the light intensity in the canopy is still high (7), this balance seems realistic.

The importance of fruit photosynthesis for yield will depend on the changing CH_2O supply and demand during the season. Our results suggest, in agreement with the findings of Koch and Alleweldt for grape (13), that fruit photosynthesis is highest and most important early in the season. At this time carbohydrate demand is high due to the first peak of fruit growth, which competes with early vegetative growth for CH_2O. At this time CH_2O supply is limiting because of the small leaf area (5, 12). Fruit set is determined between bloom and 'June drop' (Stage I and II). If the CH_2O supply limits fruit persistence on the tree, which has been suggested, but never conclusively demonstrated (22, 7), then the photosynthetic contribution of the fruit should be important. Light intensity in the canopy is high at that time, for there is little shading by leaves. Fruit photosynthesis may be important to supplement leaf photosynthesis in the case of large fruit load (leaf to fruit ratio below 1.5) or defoliation. However, later in the season leaf photosynthesis becomes more important, light intensity and fruit photosynthetic capacity are low and fruit photosynthesis loses its importance.

The decrease of DP_N during fruit development could be caused by several factors. There is evidence that fruit photosynthesis is subject to feedback inhibition by leaf photosyntates (14). However, chlorophyll loss seems to be the main cause for the decrease in fruit photosynthesis

in sour cherry, as suggested for several other species (2, 3, 9). DP_G compensation for DR_D decreased steadily from full bloom to maturity (Table 3) due to decreasing fruit photosynthesis.

Import maxima of 16.54 and 35.14 mg CH_2O day^{-1} occurred 14-15 and 43 days after full bloom, respectively. If during the second maximum a leaf area of 35 to 50 cm^2 $fruit^{-1}$ is required for fruit growth, export to the fruit must be approximately 0.7 to 1.0 mg CH_2O cm^{-2} day^{-1}. A maximum rate of CH_2O export of 1.5 to 2.5 mg cm^{-2} day^{-1} can be calculated from previously reported estimates (12), which is more than twice the rate required for fruit growth and leaves sufficient CH_2O for vegetative growth.

Dark respiration required 30.9% of all CH_2O used during fruit development. However, the share used by dark respiration changed throughout fruit development, being 32.7, 70.9 and 19.9% during stages I, II and III respectively. The levels of dark respiration were, according to the expected energy requirement for the different stages, high for lignin and lipid synthesis during pit hardening and embryo development (Stage II), intermediate during cell division (Stage I) and low during cell expansion with accumulation of sugars, sugar alcohols and organic acids.

The present study demonstrates that fruits are not only sinks for CH_2O, but are capable of contributing significantly to yield by means of their photosynthetic activity.

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Section IV

Photosynthesis and Respiration of Sour Cherry (*Prunus cerasus* L. 'Montmorency') Fruits during Development, as influenced by the Environment

ABSTRACT

Gross photosynthesis (P_G), net photosynthesis (P_N) and dark respiration R_D rates of 'Montmorency' sour cherry fruits during development were investigated. P_G was closely related to the chlorophyll content of the fruit and reached a maximum rate during stage II of fruit growth. R_D rate per unit fruit volume also reached its maximum during stage II, indicating a high respiratory need for energy and biosynthesis. Light saturation was reached at 1000 μmoles m^{-2} s^{-1}. P_G approached a maximum at 40°C. R_D increased exponentially with temperature. As a result, P_N reached its maximum at 18°C. P_N rates increased with increasing CO_2, reaching saturation at 400 cm^3 m^{-3}. A postillumination CO_2 burst could not be detected. R_D increased with increasing O_2 levels and P_N decreased as a result of increased R_D. P_G was not affected by the O_2 concentration. The data suggest that sour cherry fruits do not have an apparent photorespiration.

Abreviations: P_G, gross photosynthesis; P_N, net photosynthesis; R_D, dark respiration; R_L, photorespiration; g'_s, stomatal conductance to CO_2; c_a, ambient CO_2 concentration; c_i, internal CO_2 concentration; PPFD, photosynthetic photon flux density; VPD, vapor pressure deficit; LSD, least significant difference.

Photosynthesis by fruits of sour cherry (Kappes and Flore 1985a) and from other species (Clijsters 1969 and 1975, Frieden 1984, Jones 1981, Noga and Lenz 1982a) contributes to the fruits' carbon balance. Kappes and Flore (1985a) demonstrated that the sour cherry fruit's overall contribution to its carbon balance amounted to 11%, while the contribution during stages I and II (according to Tukey's (1934) description of fruit development) was 47.3 and 29.5%, respectively (Kappes and Flore 1985a).

R_D of sour cherry fruits has been reported (Pollack et al. 1961, Blanpied 1972). However, no reports are known concerning sour cherry fruit photosynthesis or how the fruit's CO_2 gas exchange is affected by different environmental factors, or on the effect of O_2 concentration on P_N, P_G or R_D in fruit tissues. The objective of this study was to investigate the influence of developmental stage and environmental factors on sour cherry fruit P_G, P_N, R_D and R_L.

MATERIALS AND METHODS

Unless otherwise stated all experiments were conducted with fruit on excised branches from 12-year-old sour cherry ('Montmorency' on Mahaleb rootstock) trees growing at the Horticulture Research Center in East Lansing, Michigan. Branches (50 cm in length) were excised around 07:00 h, the cut ends submerged in water, and transported to the laboratory, where the bases were recut under water. Four adjacent fruits were placed in each of 4 assimilation chambers, while remaining attached to the branch (see Sams and Flore 1982 for details concerning assimilation chamber design and environmental control). Gas exchange rates were expressed per fruit, per unit surface area or per unit fruit volume.

Fruit chlorophyll content was determined at 6-day intervals, using the method of Moran (1982). Chlorophyll was extracted from intact fruits using 10 to 600 mg fruit fresh weight cm^{-3} N,N-dimethylformamide as chlorophyll concentration in fruits decreased from full bloom to maturity.

Fruit surface area and volume were estimated from fruit diameters (Tukey 1934). P_G was calculated from P_N and R_D, assuming that R_D was the same in the light as in the dark. This assumption is conventional and holds for tissues with high metabolic need for respiration, even though R_D can be affected by light (Graham 1980). Seasonal changes in P_G, P_N and R_D were determined by measurements at 4-day intervals from full bloom to maturity. Standard conditions, unless otherwise stated, were: temperature, 25°C, PPFD, 1000 or 0 $\mu mol\ m^{-2}\ s^{-1}$ for the light and dark treatment, respectively, and leaf to air VPD, approximately 2kPa.

Fruit stomata were observed by scanning electron microscopy in the Michigan State University Center for Electron Optics. Fruit surface sections (6 - 8 mm diameter) were fixed in buffered glutaraldehyde (5%, 1 h), rinsed in sodium phosphate buffer (0.1M, pH 1, 15 min) and dehydrated in a graded series of aqueous ethanol (25%, 50%, 75%, 95%, 100%, 15 min each). Samples were critical point dried, transferred to specimen stubs and coated with a film of evaporated gold. Samples were viewed at 15 kV, from a 90° angle to the surface, at 360-fold magnification.

The effects of PPFD on P_N were determined during mid stage I, 9 days after full bloom. PPFD was reduced during the experiment from 2000 to 0 μmol m^{-2} s^{-1}. Fruits were kept in ambient air adjusted for a VPD of 2.3kPa.

Temperature effects on P_G, P_N and R_D were examined during mid to late stage I, 15 days after full bloom, and during early stage III, 41 days after full bloom. The fruit temperature was increased from 10 to 40°C in increments of 5°, while the VPD increased from 0.3 to 6 kPa. At the beginning of stage III, R_D was measured only at the highest and the lowest temperature and was found to be equal to P_N.

Fruit photosynthesis response to increasing c_a was measured in late stage I, 19 days after full bloom. R_D was determined at a c_a of 50 cm^3 m^{-3}, assuming that R_D was not affected by c_a.

The effect of O_2 concentration on P_G, P_N and R_D of fruits (plants described above) was examined in late stage I (15 days after full bloom) and in early stage II (19 days after full bloom) and for young fully expanded 7th leaves on 1-year-old sour cherry ('Montmorency' on Mahaleb) trees obtained from Hilltop Orchards and Nurseries, Hartford, Michigan, potted in spring in 9-liter containers. The air supplied to the chambers consisted of a mixture of N_2, O_2, CO_2 and water vapor to give a c_a of 350 cm^3 m^{-3}, a VPD of 2.0$\pm$0.2 kPa for the fruits and 1.3$\pm$0.2 for the leaves. Increasing (stage I fruits and leaves) and decreasing (stage II fruits) O_2 concentrations between 1.5 and 70% used were measured using an oxygen analyzer (Model 0260, Beckman Instruments, Inc., Irvine, CA).

$^{14}CO_2$ uptake in the light and dark fruits and leaves of 3-year-old sour cherry trees ('Montmorency' on Mahaleb, in 15-liter containers) was determined by exposing the leaf or fruit to $^{14}CO_2$ (185,000 Bq) as described previously (Kappes and Flore 1985b). Plant material was sampled after 30 min exposure, immersed in liquid nitrogen and transported frozen to the laboratory. Samples were combusted using a Biological Oxidizer - OX400 (R. J. Harvey Instrument Corporation, Hillsdale, New Jersey). The combustion products were trapped in Carbon-14-Cocktail (R. J. Harvey Instrument Corporation, Hillsdale, NJ) and the radioactivity counted in a liquid scintillation counter (1211 Rackbeta, LKB-Wallac, Turku, Finland). Corrections were made for combustion, trapping and counting efficiency, and data were calculated as dpm.

The occurrence of a post illumination CO_2 burst in sour cherry fruits was examined using smaller chambers (2.5 * 1.0 * 1.7 cm, L * W * H) to reduce the dead time to approximately 1 min. The infrared gas analyzer response was monitored using a strip chart recorder. Fruits were kept at light saturation, 25°C, 340 cm^3 m^{-3} CO_2 and 66% O_2.

RESULTS

Seasonal changes: The total chlorophyll content per fruit increased during the first twenty days after full bloom (stage I), from 5 ug $fruit^{-1}$ to a maximum of 30 ug $fruit^{-1}$, then decreased to 0 (Figure 1a). Total chlorophyll per unit surface area (Figure 1a) and per unit fresh weight (data not shown) decreased continuously starting from 130 mg m^{-2} and 200 mg kg^{-1} fresh weight at full bloom to 0 at maturity. Fruit

surface and volume increased following a double sigmoid curve (Figure 1b), as first described by Tukey (1934). The chlorophyll a/b ratio during stage I was 3.22±0.82.

P_G per fruit followed a pattern similar to that of total chlorophyll, increasing during stage I and then decreasing (Figure 2a). P_G per unit fruit surface area increased slightly during stage I and then decreased (Figure 2b). R_D per fruit remained constant during fruit development, with the exception of a marked increase during stage II (Figure 2a). R_D per unit fruit volume decreased during fruit development, with the exception of a transient rise during stage II (Figure 2c).

Stomata remained intact throughout fruit development (Figure 3), whether they remained functional cannot be judged from the visual appearance. Stomatal conductance to CO_2 decreased during the course of fruit development. g'_s was lower in the dark than in the light (Figure 4).

PPFD: During stage I of fruit development P_N increased with increasing PPFD until saturation at approximately 1000 μmoles m^{-2} s^{-1} (Figure 5). At light saturation P_G did not compensate for R_D.

Temperature: P_N during stage I followed a curve with a maximum at approximately 18°C (Figure 6a, Equation 1), which is the sum of an exponential saturation curve for P_G (Figure 6a, Equation 2) and an exponential curve for R_D (Figure 6a, Equation 3). At the beginning of stage III P_N was equal to R_D, and P_G was 0. Dark respiration followed an exponential curve (Figure 6b, Equation 4).

Figure 1. A. Total chlorophyll per fruit (open circles) and per unit fruit surface area (closed circles) during 'Montmorency' sour cherry fruit development. B. Surface area (open circles) and volume (closed circles) of 'Montmorency' sour cherry fruit during development. Vertical bars indicate standard error of the mean.

Figure 1

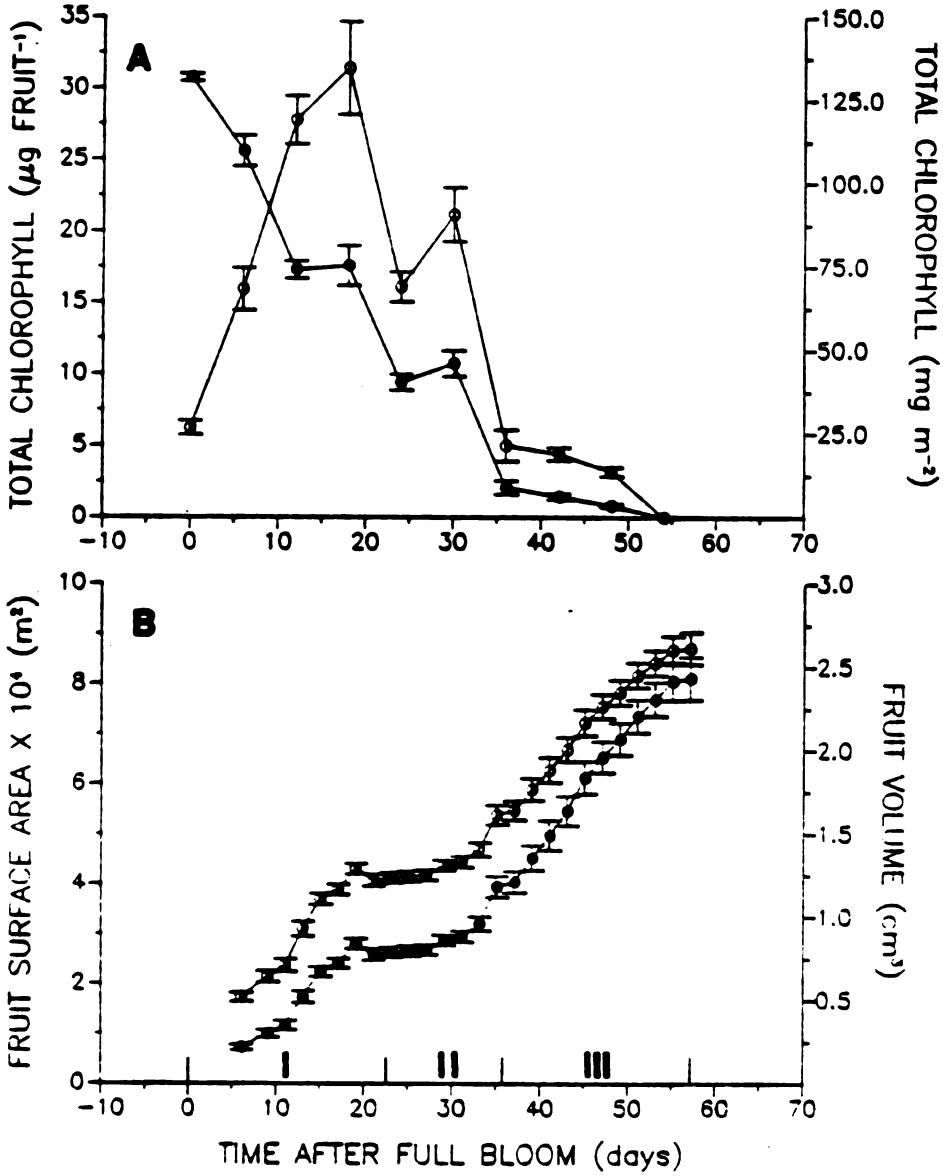

A
B
TOTAL CHLOROPHYLL (µg FRUIT⁻¹)
TOTAL CHLOROPHYLL (mg m⁻²)
FRUIT SURFACE AREA X 10⁴ (m²)
FRUIT VOLUME (cm³)
TIME AFTER FULL BLOOM (days)
I
II
III

Figure 2. Fruit gross photosynthesis (P_G)(open circles) and dark respiration (R_D) rates (closed circles) per fruit (A), per unit surface area (B) and per unit volume (C) of 'Montmorency' sour cherry fruit during development. Vertical bars indicate standard errors of the mean.

Figure 2

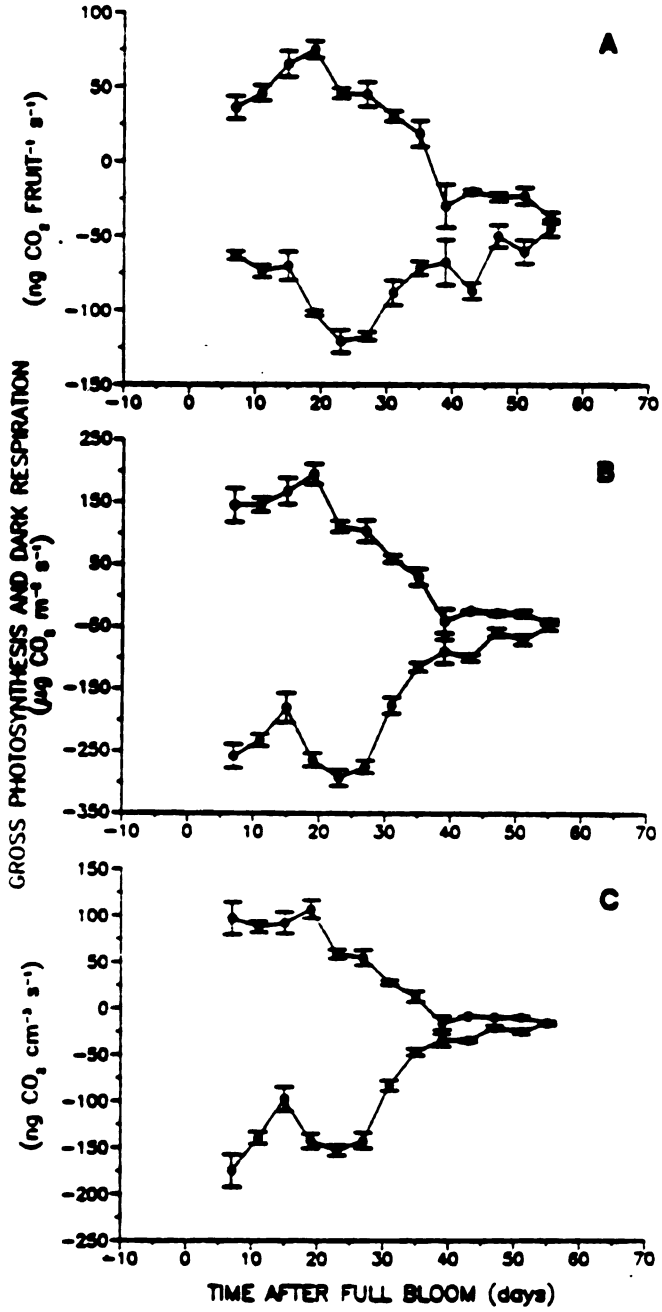

A
B
C
GROSS PHOTOSYNTHESIS AND DARK RESPIRATION
(ng CO2 FRUIT-1 s-1)
(μg CO2 m-2 s-1)
(ng CO2 cm-2 s-1)
TIME AFTER FULL BLOOM (days)

Figure 2. Fruit gross photosynthesis (P_G) (open circles) and dark respiration (R_D) rates (closed circles) per fruit (A), per unit surface area (B) and per unit volume (C) of 'Montmorency' sour cherry fruit during development. Vertical bars indicate standard errors of the mean.

Figure 2

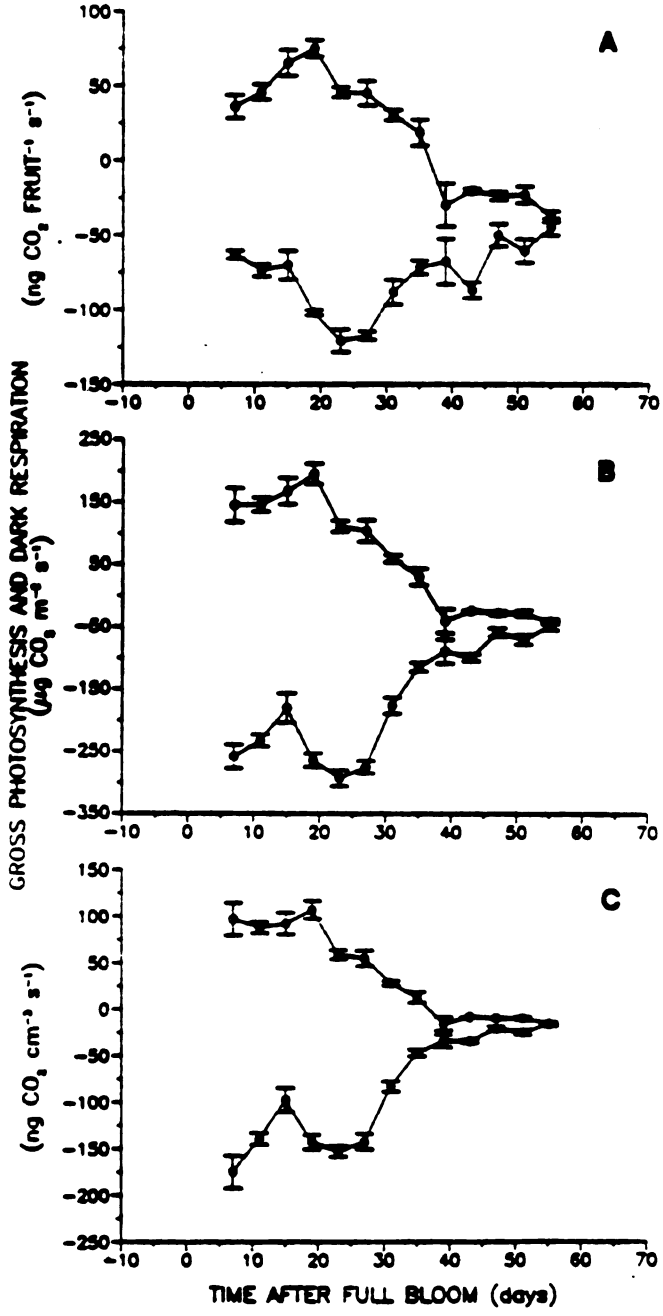
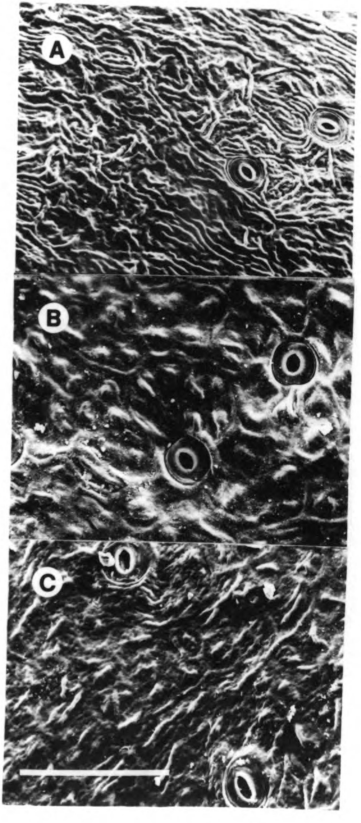

A
B
C
GROSS PHOTOSYNTHESIS AND DARK RESPIRATION
(ng CO2 FRUIT-1 s-1)
(μg CO2 m-2 s-1)
(ng CO2 cm-2 s-1)
TIME AFTER FULL BLOOM (days)

Figure 3. Scanning electron micrograph of fruit surface of 'Montmorency' sour cherry during stages I (a), II (b) and III (c) of fruit development illustrating size and shape of stomata.

Figure 3.



Literature Cited

1.Lenz, F. 1979. Sink-source relationships in fruit trees. Pp. 141-153. In: T. K. Scott (ed.). Plant regulation and world agriculture. Plenum Press, New York.

2.Neales, T. F. and L. D. Incoll. 1968. The control of leaf photosynthesis rate by the level of assimilate concentration in the leaf: A review of the hypothesis. Bot. Rev. 34:107-125.

3.Sams, C. E. and J. E. Flore. 1982. The influence of age, position and environmental variables on net photosynthetic rate of sour cherry leaves. J. Amer. Soc. Hort. Sci. 107:339-344.

Figure 1.

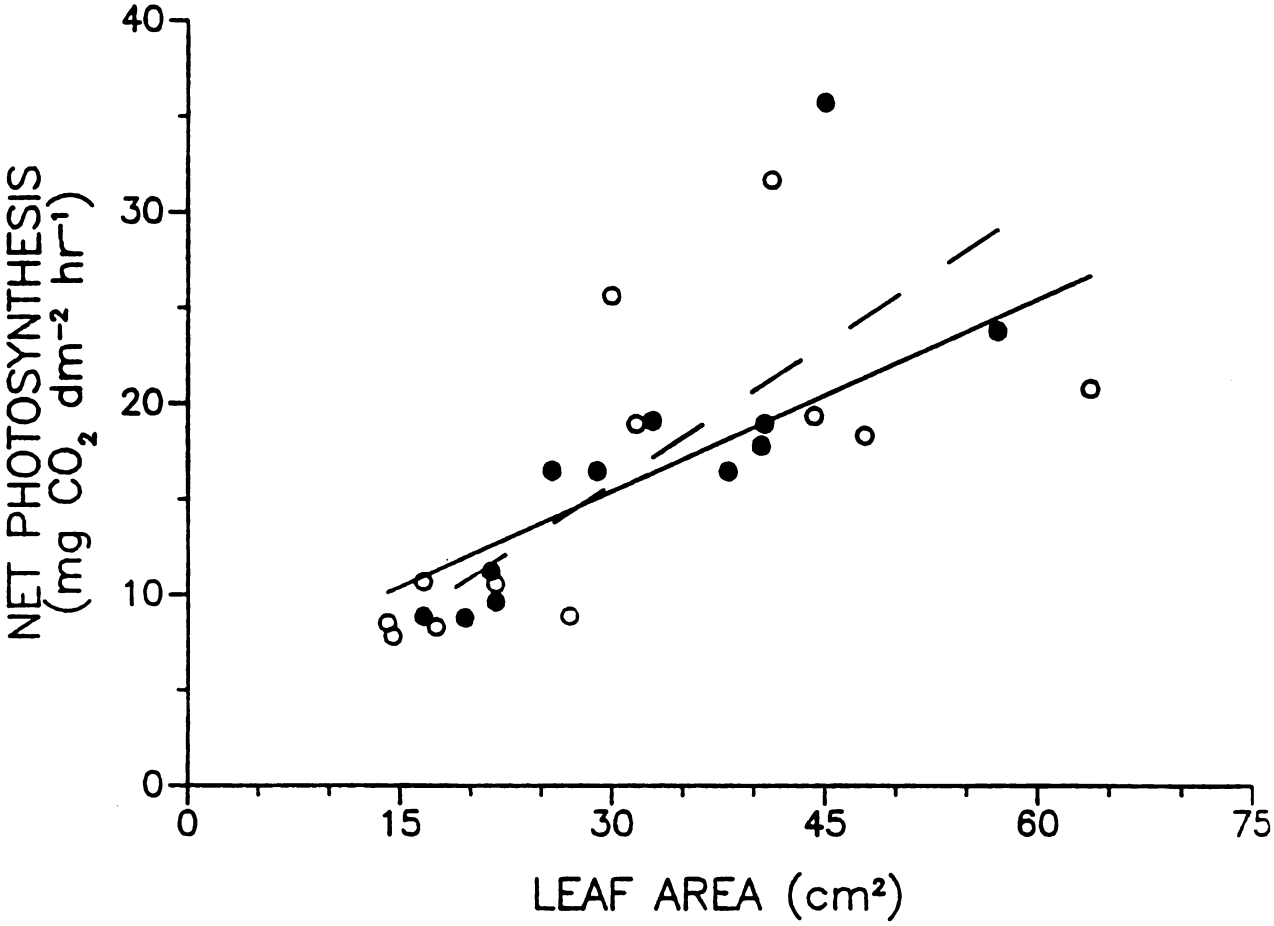

NET PHOTOSYNTHESIS
(mg CO_2 dm^{-2} hr^{-1})
40
30
20
10
0
0
15
30
45
60
75
LEAF AREA (cm^2)

Figure 1. Comparison of rates of net photosynthesis of the tenth leaf of defoliated (closed circles, broken lines) and control (open circles, solid lines) 'Montmorency' sour cherry during development, observations and regression lines.

Table 1. Rate of net photosynthesis (P_N)(mg CO2 dm^{-2} h^{-1}) and stomatal conductance (g'_s)(cm s^{-1}) of the tenth leaf (just fully expanded). At the beginning of the 10th leaf's expansion proximal leaves were removed, as compared to the non-defoliated control. Measurements were taken outside with a portable photosynthesis unit.

	P_N			g's		
Treatment	10:00 hr	15:00 hr	Mean	10:00 hr	15:00 hr	Mean
Control	17.5	5.4	11.5	0.129	0.077	0.103
Defoliated	16.7	12.3	14.5	0.103	0.118	0.111
Mean	17.1	8.8	13.0	0.116	0.098	0.107

	LSD (5%)	
Treatment	P_N	g's
Time	4.95	0.0602
Defoliation	4.95	0.0602
Time*Defol.	7.00	0.0850

at 10:00 and 15:00 hr, respectively, full sunlight, ambient CO_2 concentration, 363±2 cm^3m^{-3}, and vapor pressure deficit, 1.9±0.1 and 3.0±0.2 kPa at 10:00 and 15:00 hr, respectively.

Net photosynthesis rates of partially defoliated and control plants, measured in the laboratory, increased at a similar rate during leaf expansion (Figure 1). A t-test did not reveal significant differences in slopes of the regression lines.

Net photosynthesis rates of fully expanded leaves, measured outside, showed statistical differences at the level of interaction between defoliation treatment and time of the day (Table 1). Net photosynthesis rate decreased significantly during the day in leaves of control plants, but not in leaves of partially defoliated plants. The decrease in P_N was parallel to a small, but statistically nonsignificant, decrease in stomatal conductance to CO_2 (g'_s).

The results indicate that leaves from defoliated and control plants were not intrinsically different with respect to their photosynthetic capacity; however, control plants were subject to feedback inhibition in contrast to the partially defoliated plants. Short term P_N measurements in the laboratory show intrinsic maximum rates only, not affected by feedback inhibition. It can be assumed that feedback inhibition can only be observed after the whole plant has been carrying on photosynthesis for an extended period of time. Under laboratory conditions, working with single leaf assimilation chambers, where the rest of the plant is under low light conditions, the single leaf will usually have maximum P_N for the given environment.

Sink-source relationships affect net photosynthetic rates (P_N) of fruit trees (Lenz, 1979) and other plants (Neales and Incoll, 1968). The objective of this study was to determine intrinsic differences between and effects of feedback inhibition on P_N in partially defoliated and intact plants.

Plant material: One-year-old sour cherry trees ('Montmorency' on Mahaleb) (Hilltop Orchards and Nurseries, Hartford, MI) were potted in 7.5 liter containers, using a mixture of peat, sand and field loam (3:2:5,v:v:v) and pruned to a single bud. During the study 1 single shoot was permitted to develop. Trees were grown outside at the Horticulture Research Center, East Lansing, MI. Water, fertilizer (20% N, 20% P, 20% K) and pesticides (Captan, Guthion, Kelthane) were used as necessary. Trees were placed in a random design, and at the beginning of emergence of the 10th leaf from the base, half of the trees was defoliated below the 10th leaf. Photosynthesis of the 10th leaf of defoliated and control plants was measured.

Photosynthesis measurements: Photosynthesis of the 10th leaf was measured during leaf development, as described by Sams and Flore (1982). Conditions were: temperature, 24.9±1.0°C, photosynthetic photon flux density, 1000 μmol $m^{-2}s^{-1}$, ambient CO_2 concentration, 328±14 cm^3m^{-3}, and vapor pressure deficit, 1.6±0.5 kPa.

Photosynthesis was measured in the field using a portable chamber and gas analyzer (Analytical Development Co. Ltd., Hoddesdon, England) at 10:00 and 15:00 hr. Conditons were: temperature, 21.3±0.5°C and 29.0±0°C

Appendix D

Comparison of Photosynthesis Measurements under Field and Laboratory Conditions

Figure 2.

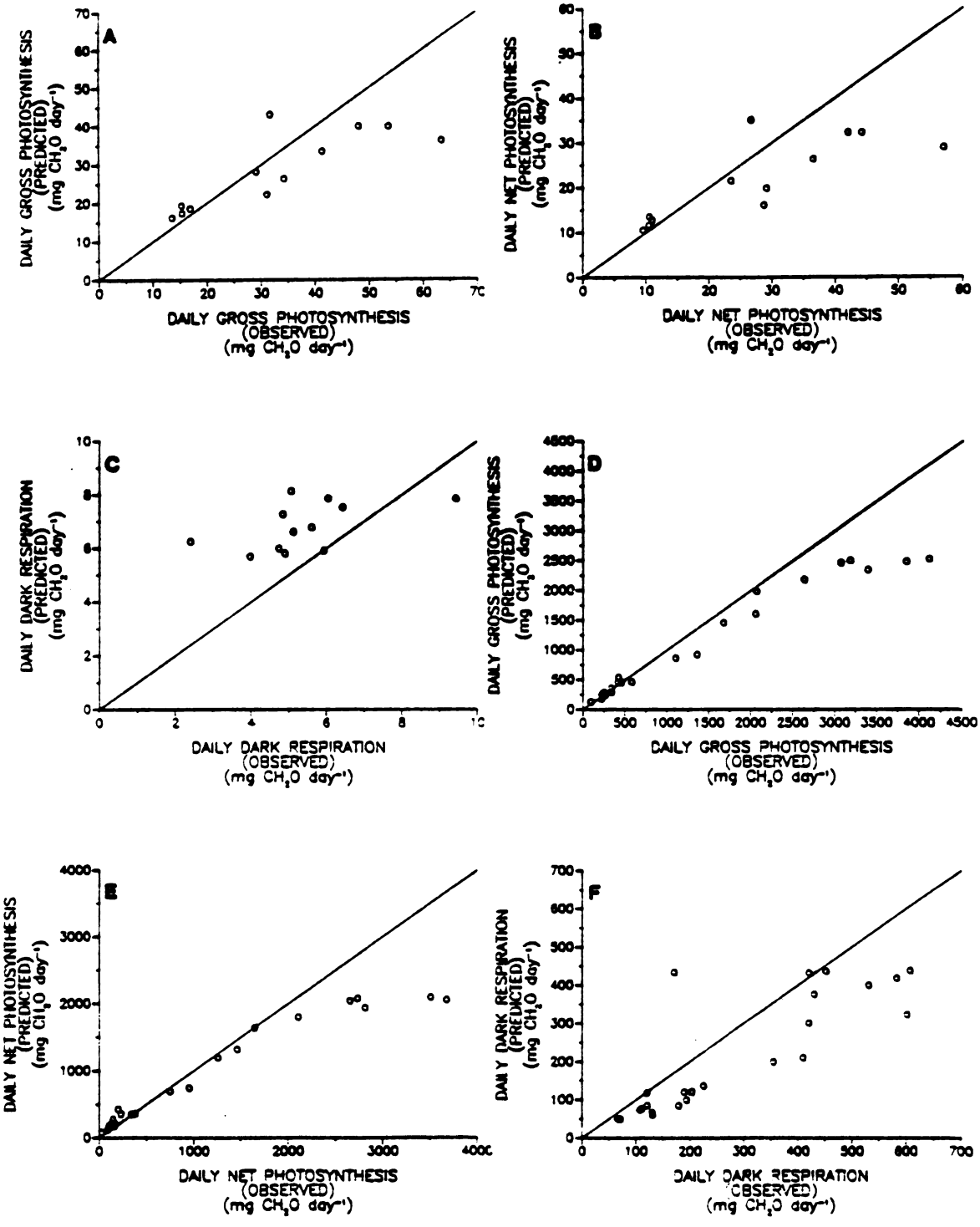

A
DAILY GROSS PHOTOSYNTHESIS (PREDICTED) (mg CH_2O day^{-1})
DAILY GROSS PHOTOSYNTHESIS (OBSERVED) (mg CH_2O day^{-1})
B
DAILY NET PHOTOSYNTHESIS (PREDICTED) (mg CH_2O day^{-1})
DAILY NET PHOTOSYNTHESIS (OBSERVED) (mg CH_2O day^{-1})
C
DAILY DARK RESPIRATION (PREDICTED) (mg CH_2O day^{-1})
DAILY DARK RESPIRATION (OBSERVED) (mg CH_2O day^{-1})
D
DAILY GROSS PHOTOSYNTHESIS (PREDICTED) (mg CH_2O day^{-1})
DAILY GROSS PHOTOSYNTHESIS (OBSERVED) (mg CH_2O day^{-1})
E
DAILY NET PHOTOSYNTHESIS (PREDICTED) (mg CH_2O day^{-1})
DAILY NET PHOTOSYNTHESIS (OBSERVED) (mg CH_2O day^{-1})
F
DAILY DARK RESPIRATION (PREDICTED) (mg CH_2O day^{-1})
DAILY DARK RESPIRATION (OBSERVED) (mg CH_2O day^{-1})

Figure 2. Comparison of predicted and experimental data for:
A.Daily net photosynthesis of the terminal leaf
B.Daily gross photosynthesis of the terminal leaf
C.Daily dark respiration of the terminal leaf
D.Daily net photosynthesis of the whole shoot
E.Daily gross photosynthesis of the whole shoot
F.Daily dark respiration of the whole shoot

Figure 1.

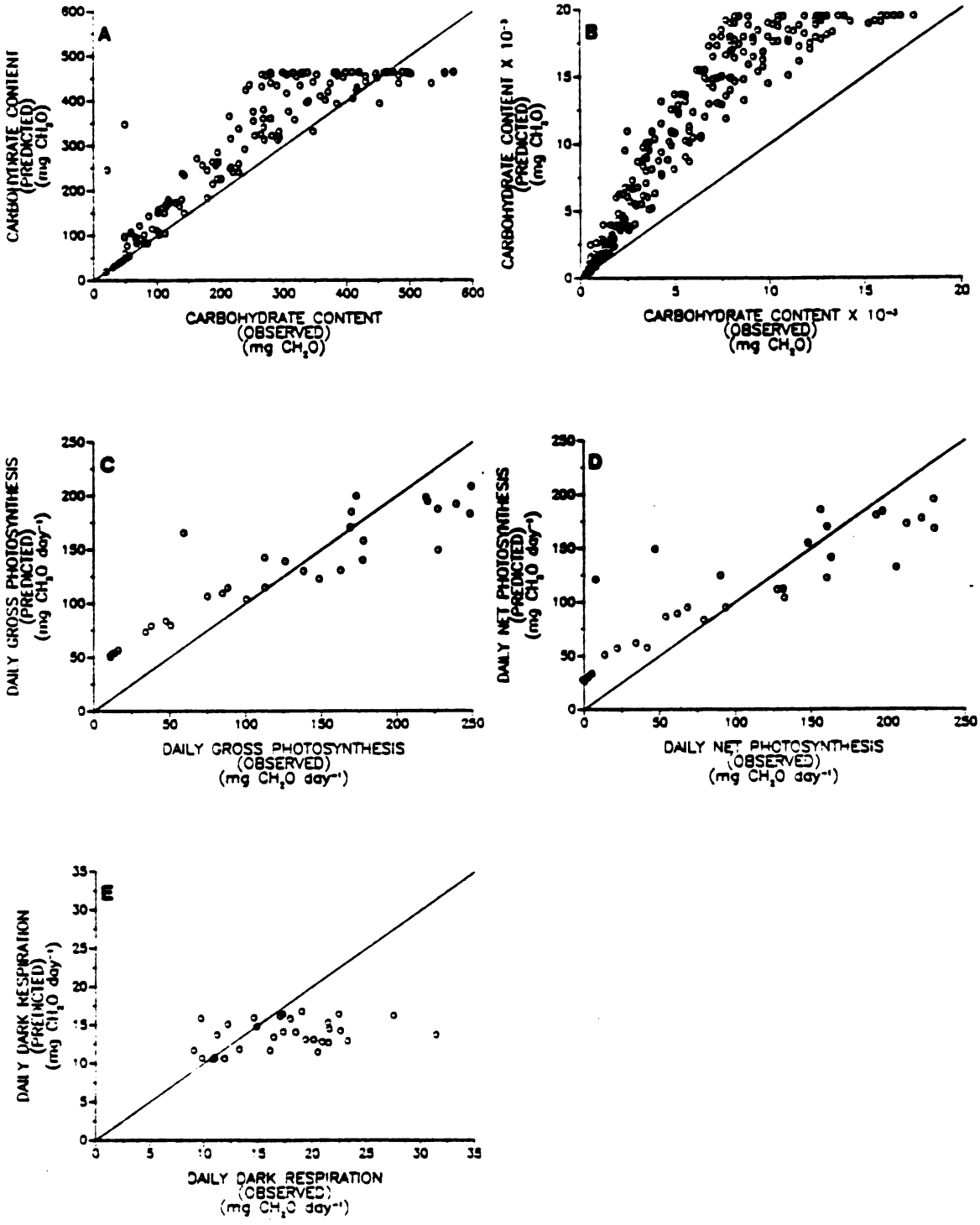

A
CARBOHYDRATE CONTENT (PREDICTED) (mg CH2O)
CARBOHYDRATE CONTENT (OBSERVED) (mg CH2O)
B
CARBOHYDRATE CONTENT X 10⁻³ (PREDICTED) (mg CH2O)
CARBOHYDRATE CONTENT X 10⁻³ (OBSERVED) (mg CH2O)
C
DAILY GROSS PHOTOSYNTHESIS (PREDICTED) (mg CH2O day⁻¹)
DAILY GROSS PHOTOSYNTHESIS (OBSERVED) (mg CH2O day⁻¹)
D
DAILY NET PHOTOSYNTHESIS (PREDICTED) (mg CH2O day⁻¹)
DAILY NET PHOTOSYNTHESIS (OBSERVED) (mg CH2O day⁻¹)
E
DAILY DARK RESPIRATION (PREDICTED) (mg CH2O day⁻¹)
DAILY DARK RESPIRATION (OBSERVED) (mg CH2O day⁻¹)

Figure 1. Comparison of predicted and experimental data for:
A.Carbohydate accumulation of the seventh leaf
B.Carbohydrate accumulation of the whole shoot
C.Daily net photosynthesis of the seventh leaf
D.Daily gross photosynthesis of the seventh leaf
E.Daily dark respiration of the seventh leaf

Table 1. Chi^2 values calculated from predicted and observed data sets of daily gross photosynthesis (DP_G), daily net photosynthesis (DP_N), daily dark respiration (DR_D) and cumulative carbohydrate content (CH_2O) of seventh and terminal leaves and shoots of 'Montmorency' sour cherry during development.

	DP_G		DP_N		DR_D		CH_2O	
	n	Chi^2	n	Chi^2	n	Chi^2	n	Chi^2
Seventh Leaf	32	449	32	539	32	86.9	167	3311
Terminal Leaf	12	39.1	12	56.3	12	6.67[z]	-	-
Shoot	24	3200	24	3550	24	1495	305	788653

[z] Significant at the 5% level

Models for leaf and shoot gross photosynthesis, net photosynthesis, respiration and carbohydrate accumulation, presented earlier were designed to be descriptive, rather than predictive. The validity of descriptive models is indicated by the r^2 of the model equations. In order to test the usefulness of the models as a predictive tool, validity of model equations (1984) was tested using experimental data from the following (1985) growth season. Predicted and experimental data sets were compared using the Chi^2 test. None of the model equations, except the one for dark respiration of the terminal leaf, was able to predict the experimental data (Table 1).

Model equations overestimated carbohydrate accumulation rates for the 7th leaf (Figure 1A) and the whole shoot (Figure 1B). Seventh leaf daily gross photosynthesis (DP_G) (Figure 1C), daily net photosynthesis (P_N) (Figure 1D) and daily dark respiration (DR_D)(Figure 1E) were overestimated for lower rates (smaller leaves) and underestimated for higher rates (larger leaves). Terminal leaf DP_G (Figure 1A) and DP_N (Figure 2B) were predicted closely for lower rates (small leaves) but underestimated for higher rates (larger leaves). Terminal leaf DR_D (Figure 2C) was mostly overestimated. Shoot DP_G (Figure 2D) and DP_N (Figure 2E) were predicted closely for the lower rates, but underestimated for the higher range. Shoot DR_D (Figure 2F) was mostly overestimated.

From the results of the Chi^2 test and the graphs of predicted vs. experimental data it can be concluded that the models cannot be used as a predictive tool.

Appendix C

Validation of Leaf and Shoot Carbohydrate Balance Models

```
22120 FOR PERIOD = START TO FINISH
22130 FRUITCH2O = B1/(1+EXP(B2+B3*PERIOD + B4*PERIOD^2 +B4 2*PERIOD^3/(3*B3)))
22140 FRUITPNET = C1 + C2*FRUITCH2O +C3*(FRUITCH2O C4) * EXP(C5*FRUITCH2O)
22150 FRUITPN = FRUITPN + FRUITPNET
22160 PERIOD1 = PERIOD - .5
22170 PERIOD2 = PERIOD + .5
22180 FRUITCH2O1 = B1/(1+EXP(B2+B3*PERIOD1 + B4*PERIOD1^2 +B4^2*PERIOD1^3/(3*B3)))
22190 FRUITCH2O2 = B1/(1+EXP(B2+B3*PERIOD2 + B4*PERIOD2^2 +B4^2*PERIOD2^3/(3*B3)))
22200 FRUITDIFF = FRUITCH2O2 - FRUITCH2O1
22210 CH2ODIFF = CH2ODIFF + FRUITDIFF
22220 NEXT PERIOD
22230 FRUITEXPORT = FRUITPN - CH2ODIFF
22240 PRINT
22250 PRINT "FOR THE PERIOD FROM " START " TO " FINISH " DAYS AFTER FULL BLOOM,"
22260 PRINT
22270 PRINT "          CARBOHYDRATE EXPORT WAS:"
22280 PRINT
22290 PRINT "(NEGATIVE VALUES FOR EXPORT SIGNIFY IMPORT)"
22300 PRINT
22310 PRINT USING "##########.# mg";FRUITEXPORT
22320 PRINT
22330 INPUT "DO YOU WANT TO CONTINUE, Y(es) OR N(o)"; CONTINUE$
22340 IF CONTINUE$ = "N" THEN 25000
22350 IF CONTINUE$ = "Y" THEN 5600 ELSE 5570
25000 END
```

```
20600 PRINT "       mg CH2O       mg CH2O       mg CH2O"
20610 PRINT "      PER FRUIT     PER FRUIT     PER FRUIT"
20620 PRINT
20630 PRINT USING "############.#";FRUITPN,FRUITPG,FRUITRD
20640 PRINT
20650 PRINT
20660 INPUT "DO YOU WANT TO CONTINUE, Y(es) OR N(o)"; CONTINUE$
20670 IF CONTINUE$ = "N" THEN 25000
20680 IF CONTINUE$ = "Y" THEN 5600 ELSE 5570
20690 GOTO 25000
21000 REM FRUIT CH2O ACCUMULATION
21010 B1=513.9001
21020 B2=9.354
21030 B3=-.947
21040 B4 =.0345
21050 PRINT "          DAYS        AVG  FRUIT        CH2O          CH2O"
21060 PRINT "                       DIAMETER      CUMULATIVE   ACCUMULATION RATE"
21070 PRINT "                          mm             mg          mg/day"
21080 FOR PERIOD = START TO FINISH
21090 PERIOD1 = PERIOD - .5
21100 PERIOD2 = PERIOD + .5
21110 FRUITCH2O = B1/(1+EXP(B2+B3*PERIOD + B4*PERIOD^2 +B4^2*PERIOD^3/(3*B3)))
21120 FRUITCH2O1 = B1/(1+EXP(B2+B3*PERIOD1 + B4*PERIOD1^2 +B4^2*PERIOD1^3/(3*B3)))
21130 FRUITCH2O2 = B1/(1+EXP(B2+B3*PERIOD2 + B4*PERIOD2^2 +B4^2*PERIOD2^3/(3*B3)))
21140 FRUITDIFF = FRUITCH2O2 - FRUITCH2O1
21150 SQ=.943589454#^2 - 4*5.098E-05*(-FRUITCH2O)
21160 FRUITDW = (-.943589454# + SQR(SQ))/(2*5.098E-05)
21170 FRUITVOL =(FRUITDW + 62.238)/275.773
21180 FRUITDIA =((FRUITVOL/4 *3/3.1415927#) (1/3))*20
21190 PRINT
21200 PRINT USING "##############.#";PERIOD,FRUITDIA,FRUITCH2O,FRUITDIFF
21210 PRINT
21220 NEXT PERIOD
21230 PRINT
21240 PRINT
21250 INPUT "DO YOU WANT TO CONTINUE, Y(es) OR N(o)"; CONTINUE$
21260 IF CONTINUE$ = "N" THEN 25000
21270 IF CONTINUE$ = "Y" THEN 5600 ELSE 5570
21280 GOTO 25000
22000 REM FRUIT CH2O EXPORT
22010 B1=513.9001
22020 B2=9.354
22030 B3=-.947
22040 B4 =.0345
22050 C1 = -.897
22060 C2 = -.00522
22070 C3 = -6.8E-18
22080 C4 = 9.375
22090 C5 = -.0486
22100 FRUITPN = 0
22110 CH2ODIFF=0
```

```
20100 PRINT "STAGE   I: DAY  1 - 22"
20110 PRINT "STAGE  II: DAY 23 - 35"
20120 PRINT "STAGE III: DAY 36 - 57"
20130 PRINT
20140 INPUT "STARTING DAY! DAYS AFTER FULL BLOOM (1-57)";START
20150 PRINT
20160 INPUT "FINISH AFTER DAY! DAYS AFTER FULL BLOOM (1-57)";FINISH
20170 PRINT
20180 INPUT "DO YOU WANT TO CALCULATE CARBOHYDRATE F(ixation), A(ccumulation) OR
      E(xport)"; SUBMODULE$
20190 IF SUBMODULE$="F" THEN 20220
20200 IF SUBMODULE$="A" THEN 21000
20210 IF SUBMODULE$="E" THEN 22000
20220 REM FRUIT CH2O FIXATION
20230 B1=513.9001
20240 B2=9.354
20250 B3=-.947
20260 B4 =.0345
20270 C1 = -.897
20280 C2 = -.00522
20290 C3 = -6.8E-18
20300 C4 = 9.375
20310 C5 = -.0486
20320 D1 = 2.007
20330 D2 = -.00467
20340 D3 = 1.52E-08
20350 D4 = 4.525
20360 D5 = -.0302
20370 E1 = -2.757
20380 E2 = -.000679
20390 E3 = -4.11E-09
20400 E4 = 4.872
20410 E5 = -.0281
20420 FRUITPN = 0
20430 FRUITPG = 0
20440 FRUITRD = 0
20450 FOR PERIOD = START TO FINISH
20460 FRUITCH2O = B1/(1+EXP(B2+B3*PERIOD + B4*PERIOD 2 +B4 2*PERIOD 3/(3*B3)))
20470 FRUITPNET = C1 + C2*FRUITCH2O +C3*(FRUITCH2O^C4) * EXP(C5*FRUITCH2O)
20480 FRUITPN = FRUITPN + FRUITPNET
20490 FRUITPGRO = D1 + D2*FRUITCH2O +D3*(FRUITCH2O^D4) * EXP(D5*FRUITCH2O)
20500 FRUITPG = FRUITPG + FRUITPGRO
20510 FRUITRESP = E1 + E2*FRUITCH2O +E3*(FRUITCH2O^E4) * EXP(E5*FRUITCH2O)
20520 FRUITRD = FRUITRD + FRUITRESP
20530 NEXT PERIOD
20540 PRINT
20550 PRINT "FOR THE PERIOD FROM " START " TO " FINISH " DAYS AFTER FULL BLOOM,"
20560 PRINT
20570 PRINT "               GAS EXCHANGE WAS:"
20580 PRINT
20590 PRINT "         PNET        PGROSS        RESP"
```

```
16210 PRINT
16220 NEXT PERIOD
16230 PRINT
16240 PRINT
16250 INPUT "DO YOU WANT TO CONTINUE, Y(es) OR N(o)"; CONTINUE$
16260 IF CONTINUE$ = "N" THEN 25000
16270 IF CONTINUE$ = "Y" THEN 5600 ELSE 5570
16280 GOTO 25000
17000 REM SHOOT CH2O EXPORT
17010 B1=19424.785#
17020 B2=.0902
17030 B3=.02524
17040 B4=3.815
17050 C1 = 21.977
17060 C2 = .172
17070 C3 = -3.31E-06
17080 SHOOTPN = 0
17090 CH2ODIFF=0
17100 FOR PERIOD = START TO FINISH
17110 SHOOTCH2O = B1 * (1-EXP(-(B2+B3*PERIOD)^B4))
17120 SHOOTPNET = C1 + C2*SHOOTCH2O +C3*SHOOTCH2O^2
17130 SHOOTPN = SHOOTPN + SHOOTPNET
17140 SHOOTCH2O1 = B1 * (1-EXP(-(B2+B3*(PERIOD-.5))^B4))
17150 SHOOTCH2O2 = B1 * (1-EXP(-(B2+B3*(PERIOD+.5))^B4))
17160 SHOOTDIFF = SHOOTCH2O2 - SHOOTCH2O1
17170 CH2ODIFF = CH2ODIFF + SHOOTDIFF
17180 NEXT PERIOD
17190 SHOOTEXPORT = SHOOTPN - CH2ODIFF
17200 PRINT
17210 PRINT "FOR THE PERIOD FROM " START " TO " FINISH " DAYS AFTER BUD BREAK,"
17220 PRINT
17230 PRINT "          CARBOHYDRATE EXPORT WAS:"
17240 PRINT
17250 PRINT "(NEGATIVE VALUES FOR EXPORT SIGNIFY IMPORT)"
17260 PRINT
17270 PRINT USING "##########.# mg";SHOOTEXPORT
17280 PRINT
17290 INPUT "DO YOU WANT TO CONTINUE, Y(es) OR N(o)"; CONTINUE$
17300 IF CONTINUE$ = "N" THEN 25000
17310 IF CONTINUE$ = "Y" THEN 5600 ELSE 5570
17320 GOTO 25000
20000 REM FRUIT MODULE
20010 REM
20020 REM FFFFFFFF   RRRRRR    UU     UU  IIII  TTTTTTTTTT
20030 REM FF         RR    R   UU     UU   II       TT
20040 REM FF         RR     R  UU     UU   II       TT
20050 REM FFFFFFFF   RRRRRRR   UU     UU   II       TT
20060 REM FF         RR   R    UU     UU   II       TT
20070 REM FF         RR    R   UU     UU   II       TT
20080 REM FF         RR     R    UUUUU    IIII      TT
20090 REM
```

```
15320 E4 = 2.49E-11
15330 SHOOTPN = 0
15340 SHOOTPG = 0
15350 SHOOTRD = 0
15360 FOR PERIOD = START TO FINISH
15370 SHOOTCH2O = B1 * (1-EXP(-(B2+B3*PERIOD)^B4))
15380 SHOOTPNET = C1 + C2*SHOOTCH2O + C3*SHOOTCH2O^2
15390 SHOOTPN = SHOOTPN + SHOOTPNET
15400 SHOOTPGRO = D1 + D2*SHOOTCH2O + D3*SHOOTCH2O^2
15410 SHOOTPG = SHOOTPG + SHOOTPGRO
15420 SHOOTRESP = E1 + E2*SHOOTCH2O + E3*SHOOTCH2O^2 + E4*SHOOTCH2O^3
15430 SHOOTRD = SHOOTRD + SHOOTRESP
15440 NEXT PERIOD
15450 PRINT
15460 PRINT "FOR THE PERIOD FROM " START " TO " FINISH " DAYS AFTER BEGINNING OF BUD
      BREAK,"
15470 PRINT
15480 PRINT "               GAS EXCHANGE WAS:"
15490 PRINT
15500 PRINT "          PNET          PGROSS          RESP"
15510 PRINT "        mg CH2O       mg CH2O       mg CH2O"
15520 PRINT "       PER SHOOT     PER SHOOT     PER SHOOT"
15530 PRINT
15540 PRINT USING "############.#";SHOOTPN,SHOOTPG,SHOOTRD
15550 PRINT
15560 PRINT
15570 INPUT "DO YOU WANT TO CONTINUE, Y(es) OR N(o)"; CONTINUE$
15580 IF CONTINUE$ = "N" THEN 25000
15590 IF CONTINUE$ = "Y" THEN 5600 ELSE 5570
15600 GOTO 25000
16000 REM SHOOT CH2O ACCUMULATION
16010 B1=19424.785#
16020 B2=.0902
16030 B3=.02524
16040 B4=3.815
16050 C1=555!
16060 C2=.2247
16070 C3=.0267
16080 C4=2.789
16090 PRINT
16100 PRINT "           DAYS          SHOOTLENGTH        CH2O            CH2O"
16110 PRINT "                                          CUMULATIVE   ACCUMULATION RATE"
16120 PRINT "                                 mm          mg             mg/day"
16130 FOR PERIOD = START TO FINISH
16140 SHOOTCH2O = B1 * (1-EXP(-(B2+B3*PERIOD)^B4))
16150 SHOOTCH2O1 = B1 * (1-EXP(-(B2+B3*(PERIOD-.5))^B4))
16160 SHOOTCH2O2 = B1 * (1-EXP(-(B2+B3*(PERIOD+.5))^B4))
16170 SHOOTDIFF = SHOOTCH2O2 - SHOOTCH2O1
16180 SHOOTLENGTH = C1 * (1-EXP(-(C2+C3*PERIOD)^C4))
16190 PRINT
16200 PRINT USING "############.#";PERIOD,SHOOTLENGTH,SHOOTCH2O,SHOOTDIFF
```

```
12140 TOPLEAFDIFF = TOPLEAFCH202 - TOPLEAFCH201
12150 CH2ODIFF = CH2ODIFF + TOPLEAFDIFF
12160 NEXT PERIOD
12170 TOPLEAFEXPORT = TOPLEAFPN - CH2ODIFF
12180 PRINT
12190 PRINT "FOR THE PERIOD FROM " START " TO " FINISH " DAYS AFTER BEGINNING OF LEAF
      EXPANSION,"
12200 PRINT
12210 PRINT "          CARBOHYDRATE EXPORT WAS:"
12220 PRINT
12230 PRINT "(NEGATIVE VALUES FOR EXPORT SIGNIFY IMPORT)"
12240 PRINT
12250 PRINT USING "##########.# mg";TOPLEAFEXPORT
12260 PRINT
12270 INPUT "DO YOU WANT TO CONTINUE, Y(es) OR N(o)"; CONTINUE$
12280 IF CONTINUE$ = "N" THEN 25000
12290 IF CONTINUE$ = "Y" THEN 5600 ELSE 5570
12300 GOTO 25000
15000 REM SHOOT MODULE
15010 REM
15020 REM  SSSSSS    H     H     000        000      TTTTTTT
15030 REM S      S   H     H    0   0      0   0        T
15040 REM S          H     H   00   00    00   00       T
15050 REM  SSSSSS    HHHHHHH  00     00  00     00      T
15060 REM        S   H     H   00   00    00   00       T
15070 REM S      S   H     H    0   0      0   0        T
15080 REM  SSSSSS    H     H     000        000         T
15090 REM
15100 INPUT "STARTING DAY! DAYS AFTER BUD BREAK (1-65)";START
15110 PRINT
15120 INPUT "FINISH AFTER DAY! DAYS AFTER BUD BREAK (1-65)";FINISH
15130 PRINT
15140 INPUT "DO YOU WANT TO CALCULATE CARBOHYDRATE F(ixation), A(ccumulation) OR
      E(xport)"; SUBMODULE$
15150 IF SUBMODULE$="F" THEN 15180
15160 IF SUBMODULE$="A" THEN 16000
15170 IF SUBMODULE$="E" THEN 17000
15180 REM SHOOT CH2O FIXATION
15190 B1=19424.785#
15200 B2=.0902
15210 B3=.02524
15220 B4=3.815
15230 C1 = 21.977
15240 C2 = .172
15250 C3 = -3.31E-06
15260 D1 = 58.853
15270 D2 = .207
15280 D3 = -4.06E-06
15290 E1 = 34.308
15300 E2 = .0457
15310 E3 = -1.76E-06
```

```
10330 PRINT
10340 PRINT "                GAS EXCHANGE WAS:"
10350 PRINT
10360 PRINT "          PNET          PGROSS          RESP"
10370 PRINT "        mg CH2O        mg CH2O        mg CH2O"
10380 PRINT "        PER LEAF       PER LEAF       PER LEAF"
10390 PRINT
10400 PRINT USING "############.#";TOPLEAFPN,TOPLEAFPG,TOPLEAFRD
10410 PRINT
10420 PRINT
10430 INPUT "DO YOU WANT TO CONTINUE, Y(es) OR N(o)"; CONTINUE$
10440 IF CONTINUE$ = "N" THEN 25000
10450 IF CONTINUE$ = "Y" THEN 5600 ELSE 5570
11000 REM TERMINAL LEAF CH2O ACCUMULATION
11010 B1=156.471
11020 B2=1.515
11030 B3=.171
11040 PRINT
11050 PRINT "           DAYS          LEAFAREA          CH2O              CH2O"
11060 PRINT "                                          CUMULATIVE    ACCUMULATION RATE"
11070 PRINT "                            cm2             mg              mg/day"
11080 FOR PERIOD = START TO FINISH
11090 TOPLEAFCH2O = B1 * EXP(-B2 * EXP(-B3*PERIOD))
11100 TOPLEAFCH2O1 = B1 * EXP(-B2 * EXP(-B3*(PERIOD-.5)))
11110 TOPLEAFCH2O2 = B1 * EXP(-B2 * EXP(-B3*(PERIOD+.5)))
11120 TOPLEAFDIFF = TOPLEAFCH2O2 - TOPLEAFCH2O1
11130 TOPLEAFAREA = TOPLEAFCH2O/7.91
11140 PRINT
11150 PRINT USING "############.#";PERIOD,TOPLEAFAREA,TOPLEAFCH2O,TOPLEAFDIFF
11160 PRINT
11170 NEXT PERIOD
11180 PRINT
11190 PRINT
11200 INPUT "DO YOU WANT TO CONTINUE, Y(es) OR N(o)"; CONTINUE$
11210 IF CONTINUE$ = "N" THEN 25000
11220 IF CONTINUE$ = "Y" THEN 5600 ELSE 5570
11230 GOTO 25000
12000 REM TERMINAL LEAF CH2O EXPORT
12010 B1=156.471
12020 B2=1.515
12030 B3=.171
12040 C1 = -7.348
12050 C2 = .235
12060 TOPLEAFPN = 0
12070 CH2ODIFF=0
12080 FOR PERIOD = START TO FINISH
12090 TOPLEAFCH2O = B1 * EXP(-B2 * EXP(-B3*PERIOD))
12100 TOPLEAFPNET = C1 + C2*TOPLEAFCH2O
12110 TOPLEAFPN = TOPLEAFPN + TOPLEAFPNET
12120 TOPLEAFCH2O1 = B1 * EXP(-B2 * EXP(-B3*(PERIOD-.5)))
12130 TOPLEAFCH2O2 = B1 * EXP(-B2 * EXP(-B3*(PERIOD+.5)))
```

```
7170 NEXT PERIOD
7180 SEVENLEAFEXPORT = SEVENLEAFPN - CH2ODIFF
7190 PRINT
7200 PRINT "FOR THE PERIOD FROM " START " TO " FINISH " DAYS AFTER BEGINNING OF LEAF
     EXPANSION,"
7210 PRINT
7220 PRINT "          CARBOHYDRATE EXPORT WAS:"
7230 PRINT
7240 PRINT "(NEGATIVE VALUES FOR EXPORT SIGNIFY IMPORT)"
7250 PRINT
7260 PRINT USING "##########.# mg";SEVENLEAFEXPORT
7270 PRINT
7280 INPUT "DO YOU WANT TO CONTINUE, Y(es) OR N(o)"; CONTINUE$
7290 IF CONTINUE$ = "N" THEN 25000
7300 IF CONTINUE$ = "Y" THEN 5600 ELSE 5570
7310 GOTO 25000
10000 REM TERMINAL LEAF MODULE
10010 INPUT "STARTING DAY! DAYS AFTER BEGINNING OF LEAF EXPANSION (1-20)";START
10020 PRINT
10030 INPUT "FINISH AFTER DAY! DAYS AFTER BEGINNING OF LEAF EXPANSION (1-20)";FINISH
10040 PRINT
10050 INPUT "DO YOU WANT TO CALCULATE CARBOHYDRATE F(ixation), A(ccumulation) OR
      E(xport)"; SUBMODULE$
10060 IF SUBMODULE$="F" THEN 10090
10070 IF SUBMODULE$="A" THEN 11000
10080 IF SUBMODULE$="E" THEN 12000
10090 REM TERMINAL LEAF CH2O FIXATION
10100 B1=156.471
10110 B2=1.515
10120 B3=.171
10130 C1 = -7.348
10140 C2 = .235
10150 D1 = -3.484
10160 D2 = .258
10170 E1 = 3.919
10180 E2 = .0234
10190 TOPLEAFPN = 0
10200 TOPLEAFPG = 0
10210 TOPLEAFRD = 0
10220 FOR PERIOD = START TO FINISH
10230 TOPLEAFCH2O = B1 * EXP(-B2 * EXP(-B3*PERIOD))
10240 TOPLEAFPNET = C1 + C2*TOPLEAFCH2O
10250 TOPLEAFPN = TOPLEAFPN + TOPLEAFPNET
10260 TOPLEAFPGRO = D1 + D2*TOPLEAFCH2O
10270 TOPLEAFPG = TOPLEAFPG + TOPLEAFPGRO
10280 TOPLEAFRESP = E1 + E2*TOPLEAFCH2O
10290 TOPLEAFRD = TOPLEAFRD + TOPLEAFRESP
10300 NEXT PERIOD
10310 PRINT
10320 PRINT "FOR THE PERIOD FROM " START " TO " FINISH " DAYS AFTER BEGINNING OF LEAF
      EXPANSION,"
```

```
5550 PRINT
5560 PRINT
5570 INPUT "DO YOU WANT TO CONTINUE, Y(es) OR N(o)"; CONTINUE$
5580 IF CONTINUE$ = "N" THEN 25000
5590 IF CONTINUE$ = "Y" THEN 5600 ELSE 5570
5600 PRINT
5610 INPUT "YOU WANT TO CONTINUE WITH L(eaves), S(hoots), OR F(ruits)"; ORGAN$
5620 GOTO 1380
5630 GOTO 25000
6000 REM SEVENTH LEAF CH2O ACCUMULATION
6010 B1=464.212
6020 B2=.236
6030 B3=.0849
6040 B4=2.401
6050 PRINT
6060 PRINT "          DAYS        LEAFAREA          CH2O            CH2O"
6070 PRINT "                                    CUMULATIVE   ACCUMULATION RATE"
6080 PRINT "                        cm2             mg             mg/day"
6090 FOR PERIOD = START TO FINISH
6100 SEVENLEAFCH2O = B1 * (1-EXP(-(B2+B3*PERIOD)^B4))
6110 SEVENLEAFCH2O1 = B1 * (1-EXP(-(B2+B3*(PERIOD-.5))^B4))
6120 SEVENLEAFCH2O2 = B1 * (1-EXP(-(B2+B3*(PERIOD+.5))^B4))
6130 SEVENLEAFDIFF = SEVENLEAFCH2O2 - SEVENLEAFCH2O1
6140 SEVENLEAFAREA = SEVENLEAFCH2O/7.27
6150 PRINT
6160 PRINT USING "##############.#";PERIOD,SEVENLEAFAREA,SEVENLEAFCH2O,SEVENLEAFDIFF
6170 PRINT
6180 NEXT PERIOD
6190 PRINT
6200 PRINT
6210 INPUT "DO YOU WANT TO CONTINUE, Y(es) OR N(o)"; CONTINUE$
6220 IF CONTINUE$ = "N" THEN 25000
6230 IF CONTINUE$ = "Y" THEN 5600 ELSE 5570
6240 GOTO 25000
7000 REM SEVENTH LEAF CH2O EXPORT
7010 B1=464.212
7020 B2=.236
7030 B3=.0849
7040 B4=2.401
7050 C1 = 3.064
7060 C2 = .34
7070 SEVENLEAFPN = 0
7080 CH2ODIFF=0
7090 FOR PERIOD = START TO FINISH
7100 SEVENLEAFCH2O = B1 * (1-EXP(-(B2+B3*PERIOD)^B4))
7110 SEVENLEAFPNET = C1 + C2*SEVENLEAFCH2O
7120 SEVENLEAFPN = SEVENLEAFPN + SEVENLEAFPNET
7130 SEVENLEAFCH2O1 = B1 * (1-EXP(-(B2+B3*(PERIOD-.5))^B4))
7140 SEVENLEAFCH2O2 = B1 * (1-EXP(-(B2+B3*(PERIOD+.5))^B4))
7150 SEVENLEAFDIFF = SEVENLEAFCH2O2 - SEVENLEAFCH2O1
7160 CH2ODIFF = CH2ODIFF + SEVENLEAFDIFF
```

```
5060 REM  L           EEEEEEE     AAAAAAA   FFFFFFF
5070 REM  L           E           A     A   F
5080 REM  L           E           A     A   F
5090 REM  L           EEEEEEE     AAAAAAA   FFFFFFF
5100 REM  L           E           A     A   F
5110 REM  L           E           A     A   F
5120 REM  LLLLLLLL    EEEEEEE     A     A   F
5130 REM
5140 INPUT "STARTING DAY! DAYS AFTER BEGINNING OF LEAF EXPANSION (1-30)";START
5150 PRINT
5160 INPUT "FINISH AFTER DAY! DAYS AFTER BEGINNING OF LEAF EXPANSION (1-30)";FINISH
5170 PRINT
5180 INPUT "DO YOU WANT TO CALCULATE CARBOHYDRATE F(ixation), A(ccumulation) OR
     E(xport)"; SUBMODULE$
5190 IF SUBMODULE$="F" THEN 5220
5200 IF SUBMODULE$="A" THEN 6000
5210 IF SUBMODULE$="E" THEN 7000
5220 REM SEVENTH LEAF CH2O FIXATION
5230 B1=464.212
5240 B2=.236
5250 B3=.0849
5260 B4=2.401
5270 C1 = 3.064
5280 C2 = .34
5290 D1 = 28.568
5300 D2 = .319
5310 E1 = 9.715999
5320 E2 = .0125
5330 SEVENLEAFPN = 0
5340 SEVENLEAFPG = 0
5350 SEVENLEAFRD = 0
5360 FOR PERIOD = START TO FINISH
5370 SEVENLEAFCH2O = B1 * (1-EXP(-(B2+B3*PERIOD)^B4))
5380 SEVENLEAFPNET = C1 + C2*SEVENLEAFCH2O
5390 SEVENLEAFPN = SEVENLEAFPN + SEVENLEAFPNET
5400 SEVENLEAFPGRO = D1 + D2*SEVENLEAFCH2O
5410 SEVENLEAFPG = SEVENLEAFPG + SEVENLEAFPGRO
5420 SEVENLEAFRESP = E1 + E2*SEVENLEAFCH2O
5430 SEVENLEAFRD = SEVENLEAFRD + SEVENLEAFRESP
5440 NEXT PERIOD
5450 PRINT
5460 PRINT "FOR THE PERIOD FROM " START " TO " FINISH " DAYS AFTER BEGINNING OF LEAF
     EXPANSION,"
5470 PRINT
5480 PRINT "                GAS EXCHANGE WAS:"
5490 PRINT
5500 PRINT "          PNET          PGROSS          RESP"
5510 PRINT "        mg CH2O       mg CH2O       mg CH2O"
5520 PRINT "        PER LEAF      PER LEAF      PER LEAF"
5530 PRINT
5540 PRINT USING "############.#";SEVENLEAFPN,SEVENLEAFPG,SEVENLEAFRD
```

```
1000 REM ************************************************************************
1010 REM        CCCCCC  HH      HH  EEEEEEEEE  RRRRRRR   RRRRRRR    YY         YY
1020 REM      CC        HH      HH  EE         RR     R  RR     R    YY       YY
1030 REM    CC          HH      HH  EE         RR      R RR      R    YY     YY
1040 REM   CC           HH      HH  EE         RR     R  RR     R      YY  YY
1050 REM   CC           HHHHHHHHHH  EEEEEEEEE  RRRRRRR   RRRRRRR        YYYY
1060 REM   CC           HH      HH  EE         RR  R     RR  R           YY
1070 REM    CC          HH      HH  EE         RR   R    RR   R          YY
1080 REM     CC         HH      HH  EE         RR    R   RR    R         YY
1090 REM       CCCCCC   HH      HH  EEEEEEEEE  RR     R  RR     R        YY
1100 REM
1110 REM                   CCCCCC  AAAAAAAAAA  RRRRRRR   BBBBBBB
1120 REM                 CC        AA      AA  RR     R  BB     B
1130 REM               CC          AA      AA  RR      R BB      B
1140 REM             CC            AA      AA  RR     R  BB     B
1150 REM             CC            AAAAAAAAAA  RRRRRRR   BBBBBBB
1160 REM             CC            AA      AA  RR  R     BB     B
1170 REM              CC           AA      AA  RR   R    BB      B
1180 REM               CC          AA      AA  RR    R   BB     B
1190 REM                 CCCCCC    AA      AA  RR     R  BBBBBBB
1200 REM ************************************************************************
1210 REM PROGRAM TO SIMULATE CARBOHYDRATE PRODUCTION AND USE IN
1220 REM DEVELOPING LEAVES, SHOOTS AND FRUITS OF
1230 REM 'MONTMORENCY' SOUR CHERRY (PRUNUS CERASUS L.)
1240 REM DRIVER MODULE
1250 REM
1260 REM   DDDDD      RRRRRR        III  V           V  EEEEEEE  RRRRRRR
1270 REM   D   DD     R     R        I    V         V   E        R      R
1280 REM   D     DD   R      R       I     V       V    E        R      R
1290 REM   D     DD   RRRRRRR        I      V     V     EEEEEEE  RRRRRRR
1300 REM   D     DD   R    R         I       V   V      E        R    R
1310 REM   D   DD     R     R        I        V V       E        R     R
1320 REM   DDDDD      R      R      III        V        EEEEEEE  R      R
1330 REM
1340 PRINT "THIS IS 'CHERRYCARB' A BASIC PROGRAM TO SIMULATE CARBOHYDRATE PRODUCTION
     AND USE "
1350 PRINT "OF DEVELOPING LEAVES, SHOOTS AND FRUITS IN 'MONTMORENCY' SOUR CHERRY"
1360 PRINT
1370 INPUT "DO YOU WANT TO CALCULATE CARBOHYDRATE DATA FOR L(eaves), S(hoots) or
     F(ruits)";ORGAN$
1380 PRINT
1390 IF ORGAN$="L" THEN 5000
1400 IF ORGAN$="S" THEN 15000
1410 IF ORGAN$="F" THEN 20000 ELSE 1370
5000 INPUT "FOR WHICH LEAF? S(eventh) or T(erminal)";VATLEAF$
5010 PRINT
5020 IF VATLEAF$="T" THEN 10000
5030 IF VATLEAF$="S" THEN 5040 ELSE 5000
5040 REM SEVENTH LEAF MODULE
5050 REM
```

Appendix B

CHERRYCARB: A BASIC Carbohydrate Balance Model Program for 'Montmorency' Sour Cherry Leaves Shoots and Fruits during Development

Fruit respiration accounts for 30.9% of the carbohydrates used by the fruit (Table 1). The percentage of carbohydrates used by respiration is much higher (70.9%) during stage II (pit hardening, embryo development; Tukey, 1934), when the requirements are high for lignin and lipid biosynthesis. The requirements for respiration are lower during stage III, when cells expand and less biosynthetic activity is expected.

References

Kappes, E.M. 1985. Carbohydrate production, balance, and translocation in leaves, shoots and fruits of 'Montmorency' sour cherry. Ph.D. Thesis, Michigan State University, East Lansing, Michigan.

Kappes, E.M. and Flore, J.A. 1984. Assimilate export from 'Montmorency' sour cherry (Prunus cerasus L.) leaves. HortScience 19:583-584. Abstract # 464.

Kappes, E.M. and Flore, J.A. 1985. The relationship between fruit growth, and fruit photosynthesis, fruit respiration and carbohydrate accumulation for 'Montmorency' sour cherry. HortScience 20:568. Abstract # 334.

Tukey, H. B. 1934. Growth of the embryo, seed and pericarp of the sour cherry (Prunus cerasus) in relation to season of fruit ripening. Proc. Amer. Soc. Hort. Sci. 31:125-144.

Table 1 - Carbohydrate balance (mg CH_2O, % of total CH_2O in parenthesis) of 'Montmorency'sour cherry fruits during their development.

		STAGE I (DAY 1-22)	STAGE II (DAY 23-35)	STAGE III (DAY 36-57)	TOTAL (DAY 1-57)
CH_2O ACCUMULATED	(A)	164.1 (67.3)	28.9 (29.1)	320.9 (80.1)	513.9 (69.1)
CH_2O RESPIRED	(B)	79.9 (32.7)	70.4 (70.9)	79.8 (19.9)	230.0 (30.9)
TOTAL CH_2O REQUIRED	(A+B)	244.0 (100)	99.3 (100)	400.7 (100)	743.9 (100)
CH_2O PRODUCED	(C)	47.3 (19.4)	29.5 (29.7)	6.2 (1.5)	83.0 (11.2)
CH_2O IMPORTED	(A+B-C)	196.7 (80.6)	69.8 (70.3)	394.5 (98.5)	660.9 (88.8)

After 9 days the cumulative net photosyntnesis exceeds the final leaf carbohydrate content of 464.2 mg. At that time the leaf's total carbohydrate balance becomes positive. After 30 days the leaf is fully expanded. By then its cumulative net photosynthesis equals 3690 mg CH_2O, which equals its 8-fold CH_2O content.

3.2 Terminal leaf

The terminal leaf starts net export at day 4 and its overall balance becomes positive at day 11, when the net photosynthesis reaches the final leaf CH_2O content of 148.9 mg. Full expansion is reached after 20 days. By the time the terminal leaf is fully expanded its cumulative net photosynthesis amounts to 378 mg or its 2.5-fold CH_2O content.

3.3 Shoot

The whole shoot starts net export at day 17 after bud break. Its overall balance becomes positive at day 36, when the cumulative net photosynthesis exceeds the 19.4 g of final shoot CH_2O content. After 65 days when the shoot reaches its full length the cumulative net photosynthesis equals 78.4 g or the 4-fold shoot CH_2O content.

3.4 Fruit

Fruit photosynthesis contributes a significant share (11.2%) to the fruits carbohydrate balance (Table 1). This contribution is highest (29.7%), during stage II, when the fruit's gross photosynthesis rate is at its maximum and fruit carbohydrate accumulation reaches a minimum (Table 1). It is lowest during stage III (1.5%), when the fruit looses its chlorophyll.

2.3 Shoot

CH_2O = 219.9 - 4.27 * LENGTH + 0.0710 * LENGTH^2

CH_2O = 19424.785 * (1 - EXP(-(0.0902 + 0.02524*DAY) 3.815))

PNET = 21.977 + 0.172 * CH_2O - 0.331E-5 * CH_2O^2

PGROSS = 28.853 + 0.207 * CH_2O - 0.406E-5 * CH_2O^2

RESP = 34.308+0.0457*CH_2O-0.176E-5*CH_2O^2+0.249E-10*CH_2O^3

2.4 Fruit

DW = -62.238 + 275.773 * 4/3 * PI * (MEANDIAMETER/2)^3

CH_2O = 0.937DW + 0.118E-3 * DW^2 - 0.831E-7 * DW^3

CH_2O = 513.9/(1 + EXP(9.354 -0.947 * DAY + 0.0345 *
DAY^2+ 0.0345^2 * DAY^3/(3 * (-0.947))))

PNET = -0.897 - 0.522E-2 * DAY - 0.680E-17 *
DAY^9.375 * EXP(-0.0486 * DAY)

PGROS = 2.007 - 0.467E-2 * DAY + 0.152E-7 *
DAY^4.525 * EXP(-0.0302 * DAY)

RESP = -2.757 -0.679E-3 * DAY - 0.411E-8 *
DAY^4.872 * EXP(-0.0281 * DAY)

2.5 General

CH_2O ACCUMULATION $RATE_{DAY}$ = $CH_2O_{DAY+0.5}$ - $CH_2O_{DAY-0.5}$

EXPORT = PNET - CH_2O ACCUMULATION RATE

3. Predictions

3.1 Seventh leaf

Using the model equations it can be calculated, that positive export for the seventh leaf occurs for the first time at day 3. This signifies the beginning of net export.

fixation and loss by photosynthesis and respiration. Carbohydrate content measurements are destructive. To obttain a time course of carbohydrate accumulation, it is therefore necessary to correlate carbohydrate content to a parameter which can be measured non-destructively. This correlation is the first model needed. Further models are necessary if the photosynthesis, respiration and carbohydrate accumulation are to be predicted for a representative sample, rather than destructively for one single plant.

Model equations for carbohydrate accumulation (CH_2O), gross (PGROSS) and net photosynthesis (PNET) and respiration (RESP) were derived earlier (Kappes and Flore 1984; 1985; Kappes 1985).

2. Equations

2.1 Seventh leaf (from the base)

CH_2O = 7.27 * AREA

CH_2O = 464.212 * (1 - EXP(-(0.236 + 0.0849*DAY)^2.401))

PNET = 3.064 + 0.340 * CH_2O

PGROSS = 28.568 + 0.319 * CH_2O

RESP = 9.716 + 0.0125 * CH_2O

2.2 Terminal leaf

CH_2O = 7.91 * AREA

CH_2O = 156.471 * (EXP(-(1.515 * EXP(-0.171 * DAY))

PNET = -7.348 + 0.235 * CH_2O

PGROSS = -3.484 + 0.258 * CH_2O

RESP = 3.919 + 0.0234 * CH_2O

19.9%. The increased need for respiration during stage II is thought to be caused by lignification and lipid synthesis during pit hardening and embryo development.

1. Introduction

A program in BASICA was written to calculate values for the carbohydrate balance of leaves, shoots and fruits of 'Montmorency' sour cherry. The objective was to use the carbohydrate balances:

- to determine the start of net carbohydrate export from leaves and shoots (Kappes and Flore, 1984; Kappes, 1985).
- to estimate the overall carbohydrate economy of leaves and shoots (Kappes and Flore, 1984; Kappes, 1985).
- to evaluate the contribution of fruit photosynthesis to the fruit's carbohydrate need (Kappes and Flore, 1985; Kappes, 1985).
- to estimate the portion of carbohydrates used by respiration during the different stages of fruit development (Kappes and Flore, 1985; Kappes 1985).
- to calculate the carbohydrate fluxes into and out of leaves, shoots and fruits during the development of these organs (Kappes and Flore, 1984; 1985; Kappes, 1985).

Modeling is essential to generate an accurate carbohydrate balance for plant organs (Kappes and Flore, 1984). Information is needed on carbohydrate accumulation by the organ, and on the rates of carbohydrate

Abstract

Photosynthesis and respiration were measured and modeled for leaves, whole shoots and fruits of sour cherry during leaf area expansion, shoot elongation and fruit growth respectively. At the same time with a comparable set of plants, leaf, shoot and fruit growth were measured and correlated to carbohydrate (CH_2O) contents. Leaf, shoot and fruit carbohydrate accumulation was modeled.

These models were combined in a BASIC computer program to estimate carbohydrate fixation, accumulation, import and export for the various organs at different times and time periods during their development.

Assuming photosynthesis and growth rates measured in 1984, it could be estimated that carbohydrate net export started after 3, 4, and 17 days for the seventh and, the terminal leaf, and the shoot respectively, at a leaf size of 10.6 and 9.2cm^2 and a shoot length of 16cm. While the absolute size at the start of net export was similar, the percentage of full expansion was 17 and 51 for the seventh and the terminal leaf respectively. The onset of export seems to depend on the leaf position. It was also estimated that fruits produced 11.2% of their required carbohydrate. During stages I, II, and III of fruit development fruits produced 19.4, 29.7 and 1.5% of the carbohydrate used during the respective period. This shows the importance of fruit photosynthesis during its early development when leaf area is still small. Respiration was estimated to use 30.9% of the total carbohydrates required. During stages I, II, and III the share of respiration was 32.7, 70.9, and

Appendix A

Carbohydrate Balance Models for 'Montmorency' Sour Cherry Leaves, Shoots and Fruits During Development

After descriptive empirical models for leaf, shoot and fruit carbohydrate balances for a constant set of environmental conditions were developed in this study, the next step should be to develop a mechanistic, predictive model, integrating the other parts of the tree (roots, trunk) and the interactions between them.

Fruit photosynthesis research should focus on differences between fruits and leaves, i.e. the effects of the different internal atmosphere and the different metabolic features. To test for the existence of photorespiration, a pulse chase experiment testing for the occurrence metabolites of the glycolate pathway could be done. The existence of C_4 or CAM pathways in cherry fruit could be determined studying carbon isotope discrimination patterns in fruits which have been disconnected from leaf carbohydrate supply (girdling, defoliation) for an extended period of time. Isolation from leaf carbohydrate supply is necessary to avoid refixation of respired leaf carbohydrates.

CO_2 fixation and lack of photorespiration do not necessarily mean that fruits have C_4 or CAM photosynthesis, since dark fixation seems to be limited to malate production for dark respiration use or for storage.

Further research is necessary on the initiation of net export. To exclude yearly differences plants should be grown in a controlled environment. It is unlikely that photosynthesis of a single leaf in an assimilation chamber (laboratory conditions) becomes feedback inhibited, since the rest of the plant is under low light and photosynthesizes below its capacity. A realisitic diurnal course of photosynthesis can be observed only when all plant parts under equal environmental conditions. Measuring photosynthesis under less ideal conditions might have led to an overestimation of daily net and gross photosynthetis, and export in the present study of net export.

To investigate mechanisms behind the initiation of carbohydrate export, a study is needed, where source-sink relationships are widely varied, e.g. by changing source activity of complementary sources by defoliation or feeding of translocatable carbohydrates and changing sink activity by heating and cooling or adding artificial sinks (aphids) to see whether carbohydrate supply and demand consistently affect the initiation of export. A further study is needed to determine the upper and lower limits of leaf expansion for export initiation.

Fruit carbohydrate balance was established to determine the periods of greatest need for import and whether the fruit's own photosynthetic contribution was significant for fruit growth. Fruit carbohydrate import paralelled fruit growth rate, with maxima in mid stage I and mid stage III, and a minimum in stage II. Fruit photosynthesis contributed significantly to the fruit's carbohydrate balance, especially during stages I and II. During this period competition for carbohydrates was high due to high carbohydrate demand by developing leaves and fruits, and it is possible that fruit photosynthesis might have limited yield. Fruit photosynthesis would be especially important if carbohydrate availability influences fruit set.

Environmental effects on fruit photosynthesis were studied because of the importance of fruit photosynthetic carbohydrate production. In general, fruit response to environmental changes was similar to that of leaves. Main differences found were due to the difference in surface-volume ratio and the resulting negative net photosynthesis rates and high internal CO_2 concentration. Fruits were found to fix CO_2 in the dark, even though during stages I and II dark fixation was only one tenth of light fixation. The existence of dark fixation leads to an underestimation of dark respiration and gross photosynthesis during gas exchange measurements, since part of the CO_2 respired in the dark is immediately refixed. Fruit photosynthesis was insensitive to O_2, indicating that there was no apparent photorespiration. Presence of dark

SUMMARY AND CONCLUSIONS

Carbohydrate production and distribution in the plant determines fruit yield. Thus the present study was designed to characterize some processes involved in the carbohydrate production, translocation and utilization in sour cherry.

The initiation of carbohydarte export from leaves and shoots was investigated to determine at what stage of development leaves and shoots are able to supply carbohydrates to the rest of the plant. Gross export coincided with net export of carbohydrates, although differences between seasons made it impossible to establish this with certainty. The differences between years could probably be attributed to the effects of solar radiation and temperature on growth and photosynthetic rates. Net export was initiated during the first week of leaf emergence, and after 5-10 days of development leaves had an overall positive carbohydrate balance. None of the leaves studied accumulated more carbohydrates than it produced during its growth. Export was subject to feedback inhibition. Leaves closer to the apex, which developed when carbohydrate availability was higher compared to more basal leaves exported less and initiated export later in their development. Export initiation from developing leaves could be advanced by removing active source leaves, supporting the hypothesis that carbohydrate availability regulates the initiation of export.

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Photosynthetic CO_2 fixation by sour cherry fruits is important for the fruit's carbohydrate balance (Kappes and Flore 1985a). In this study we demonstrated some of the limitations to fruit photosynthesis resulting from both physiology and environment.

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The lack of R_L and a report that some fruits are rich in enzymes commonly linked to CAM and C_4 metabolism (Blanke 1985) suggest that there may also be a light independent mechanism for CO_2 fixation. In our investigation we demonstrated dark CO_2 fixation in sour cherry fruits (Table 3). During stages I and II the rate was about 10% of the fixation in the light. This is similar to the percentage in leaves and is probably due to malate synthesis for use in R_D (Lance and Rustin 1984). During stage III, where there is essentially no photosynthesis, dark fixation and light fixation were equal and appeared to be higher than during the earlier stages. Higher rates of dark CO_2 fixation during stage III could be expected since malate synthesis requires CO_2 fixation (Lance and Rustin 1984). Malic acid, the major organic acid in sour cherry fruits, is accumulated during stage III with a maximum near maturity (Das et al. 1965). Dark fixation could be demonstrated earlier in apple peel (Clijsters 1975). Blanke (1985) suggested that apple fruit photosynthetic metabolism is intermediate between CAM, C_4 and C_3. We found no evidence for other than C_3 characteristics in sour cherry fruits.

Our investigations have shown that fruit photosynthesis and leaf photosynthesis are similarly affected by environmental changes. However, structural differences between fruits and leaves, particularly the surface to volume ratio, are responsible for a different ratio between P_G and R_D and for a different internal atmosphere resulting in a a low CO_2 saturation point and lack of R_L.

Fruit P_G was O_2-insensitive (Table 2). O_2-insensitive photosynthesis has been documented in leaves of C_3 plants (Sharkey 1985) under saturating light and CO_2. In the reported cases (Sharkey 1985) a post-illumination CO_2 burst was detected, therefore R_L occurred. We did not detect a CO_2-burst, even at 66% O_2 (data not shown). Therefore sour cherry fruits in a c_a of 340 $cm^3\ m^{-3}$ do not have an appearent R_L. Tomato fruits, in contrast, were reported to have R_L, as indicated by their glycolic acid content (Bravdo et al. 1977). In tomato the ratio of ribulose bisphosphate oxygenase to ribulose bisphosphate carboxylase activity increased 300% during ripening, indicating that the ratio is not fixed (Bravdo et al. 1977). If sour cherry ribulose bisphosphate carboxylase/oxygenase has a low ratio of oxygenase to carboxylase activity as does green tomato, then this could explain the lack of R_L. Both a decrease of P_G with increasing O_2 and a post-illumination CO_2 burst were observed in cherry leaves (data not shown). Fruit P_N decreased significantly with increasing O_2 concentrations, but this could be attributed to increasing R_D. In fruits R_D was limited by O_2 even at 20% O_2, while in leaves R_D was limited at 1.5%, but not at 20% O_2 (Table 2). The limitation of R_D in fruits appears to reflect a lower conductance for gases in fruits than in leaves. The $k_m(O_2)$ of soybean ribulose bisphosphate oxygenase equals 690μM (Jordan and Ogren 1981), while the $k_m(O_2)$ of the terminal oxidase in R_D (cytochrome c oxidase) equals 0.1μM (Ikuma et al. 1964). This indicates that if R_D is limited by O_2 diffusion to the oxidation site, R_L must be limited significantly more due to its almost 7000 times lower affinity for O_2.

Q_{10} values decreased with increasing temperature (Table 1). Dark respiration Q_{10} values for the higher temperature ranges were higher during stage III than during stage I. A similar response was reported for grape (Koch and Alleweldt 1978). Apple fruit respiration Q_{10} however, decreased during fruit development (Jones 1981).

P_N increased with increasing c_a (Figure 7). CO_2-saturation was reached around 400 $cm^3\ m^{-3}$ while Sams and Flore (1982) reported that sour cherry leaf P_N increased even at 600 $cm^3\ m^{-3}$, which was the highest c_a in the study. A comparison of CO_2 saturation concentrations between leaves and fruits is difficult. c_i rather than c_a values should be compared since leaves with positive values of P_N have smaller c_i than c_a while in fruits with a negative P_N, c_i values are greater than c_a. Sour cherry fruits at the CO_2 saturation point (c_a = 400 $cm^3\ m^{-3}$) had a c_i of approximately 480 $cm^3\ m^{-3}$.

The increase in P_N with increasing c_a is commonly attributed to a decrease in R_L (Tolbert 1980) since the competitive substrate avalability of CO_2 and O_2 is the major factor determining the ratio between P_G and R_L. This did not seem to be the case for sour cherry fruits, since P_G was not affected by O_2 concentration. In the absence of high internal O_2 concentration the increase in P_N could be caused simply by the substrate (CO_2) availability for the ribulose bisphosphate carboxylase reaction. This could activate the ribulose bisphosphate carboxylase/oxygenase enzyme, i.e., an increase of k_m and $V_{max}(CO_2)$ (Tolbert 1984). This could explain the observed P_N increase in sour cherry fruit with increasing c_a.

those reported here. g'_s of sour cherry fruits was lower in the dark than in the light (Figure 4), as reported for apple (Noga and Lenz, 1982b). Fruit stomata, unlike leaf stomata, do not appear to optimize c_i. Since they open in the light, they allow respiratory CO_2 to escape and c_i to decrease when CO_2 could be fixed by photosynthesis.

Sour cherry fruit P_N increased with increasing PPFD (Figure 5), light saturation being reached at a PPFD of 1000 μmol m^{-2} s^{-1}. Apple fruit photosynthesis also increased with increasing light intensity (Noga and Lenz 1982a). 'Jonathan' fruits reached light saturation at 18 klx (about 250 μmol m^{-2} s^{-1}), 'Golden Delicious' at 25 klx (about 350 μmol m^{-2} s^{-1}), while in 'Cox's Orange' fruits net photosynthesis continued to increase at 35 klx (about 490 μmol m^{-2} s^{-1}).

Sour cherry fruit P_N reached a maximum at 18°C (Figure 6a). Apple P_N reached its maximum at 15°C (Noga and Lenz 1982a). A higher temperature optimum for P_N in sour cherry can be expected because of the higher P_G to R_D ratio which results from a higher surface-volume ratio (surface-weight ratio) in relation to apple. The surface-volume ratio also explains why under comparable conditions the optimum temperature for P_N in sour cherry leaves (Sams and Flore 1982) is approximately 10 degrees higher than in fruits. During stage I, P_G followed an exponential saturation curve without reaching saturation before 40°C (Figure 6a, Equation 1). During early stage III, P_G could no longer be detected (Figure 6b). During stages I (Equation 3) and III (Equation 4), R_D increased exponentially with increasing temperatures, as reported for apple (Jones 1981).

fruits (1.51 μg CO_2 mg^{-1} chlorophyll s^{-1}) than for leaves (0.99 μg CO_2 mg^{-1} chlorophyll s^{-1}). The high P_G per unit chlorophyll indicates that in fruits the light harvesting system limits photosynthesis.

R_D per fruit (Figure 2a) was relatively constant during fruit development with the exception of a marked increase during stage II. An initial increase in R_D per fruit followed by a decrease during ripening has been reported for sweet cherry (Ulrich, 1945) and grape (Koch and Alleweldt 1978, Frieden 1984). Fruit R_D per unit volume (Figure 2c) decreased during development but also exhibited a rise during stage II. This rise in R_D could be due to increased lignin and lipid biosynthesis during pit hardening and embryo development. Both lignin and lipid biosynthesis have high carbon dioxide production factors as compared to carbohydrate and organic acid biosynthesis (Penning de Vries et al. 1974). In sweet cherry (Ulrich 1945) and grape (Geisler and Radler 1976, Pandey and Farmahan 1977, Koch and Alleweldt 1978, Frieden 1984) a rise in fruit R_D when expressed on a unit fresh weight basis could not be detected during stage II. Earlier reported R_D studies of sour cherry fruits started at stage II and therefore do not permit a comparison for the entire development (Pollack et al. 1961, Blanpied 1972).

The g'_s of the sour cherry fruits decreased during the course of their development (Figure 4). This decrease in stomatal conductance can be attributed to the increase in surface area, since, according to Tukey and Young (1939), the number of stomata remains the same and stoma size increases much less than the surface area of epidermal cells. A similar decrease in surface conductance was observed in apple, although absolute conductance values reported (Jones 1981) were approximately one third

fruits in fixing CO_2 in the light, and dark fixation was quantitatively similar to light fixation,and although higher, not significantly greater than in the earlier stages of development.

Post illumination CO_2 burst: A post illumination CO_2 outburst was not observed in sour cherry fruits. Respiration reached a plateau rather than a transient maximum after darkening (data not shown).

DISCUSSION

Total chlorophyll content per unit fresh weight in sour cherry fruits (Figure 1a) was similar to that reported for 'Mueller-Thurgau' grape berries (Frieden 1984). Total chlorophyll per unit surface area (Figure 1a) was slightly lower than reported for 'Jonathan' (Clijsters 1969) or 'Golden Delicious' (Jones 1981) apple. The pattern of chlorophyll loss was similar to that in grape and apple. The chlorophyll a/b ratio of fruits was considerably higher than the ratio of 1.99 reported for 'Montmorency' sour cherry leaves (Sams 1980).

P_G (Figure 2a) closely paralled chlorophyll content (Figure 1a). Thus P_G per unit surface area (Figure 2b) rose initially until the end of stage I and then declined, as reported for grape (Frieden 1984), although the maximum P_G rate observed was 50% higher than for grape. Maximum P_G rate of sour cherry fruits was 196 ± 16 $\mu g\ m^{-2}\ s^{-1}$, as compared to 850 ± 175 $\mu g\ m^{-2}\ s^{-1}$ (Kappes and Flore, unpublished results) for P_G in the young fully expanded seventh leaf of vigorously growing sour cherry shoots. Fruit chlorophyll content (130 mg m^{-2}) was considerably lower than that reported for sour cherry leaves (860 mg m^{-2}) (Sams 1980). From this it can be calculated that P_G per unit chlorophyll is higher for

Table 3 - ^{14}Carbon dioxide fixation by 'Montmorency' sour cherry leaves and fruits, in full sunlight and in the dark, during exposure to 185,000 Bq.

Sample	Light	Dark	Dark as % of light
	(Bq fruit^{-1} or leaf^{-1})		
Fruits Stage I	782.1	86.9	11.1
Fruits Stage II	635.0	80.1	12.6
Fruits Stage III	205.8	223.1	108.4
Leaves	113114.3	11585.6	10.2

Least significant difference for the interaction of light and fruit growth stage:
$LSD_{5\%}$ = 149.4

Table 2 - Oxygen response of gross photosynthesis (P_G[z], net photosynthesis, and dark respiration (R_D) of 'Montmorency' sour cherry fruits and leaves

		Oxygen concentration			$LSD_{5\%}$
		1.5%	20.0%	70.0%	
Leaves	n=4	(mg CO_2 m^{-2} s^{-1})			
P_G		1.089	0.906	0.372	0.147
P_N		1.031	0.786	0.272	0.178
R_D		0.058	0.122	0.100	0.039
Fruits	n=8	(ng CO_2 $fruit^{-1}$ s^{-1})			
P_G		59.4	68.9	74.2	17.2
P_N		-3.9	-8.9	-35.8	15.0
R_D		63.3	77.8	110.0	13.9

[z] Light, 1000 umol $m^{-2}s^{-1}$; dark, 0 umol $m^{-2}s^{-1}$; temperature, 25°C; ambient CO_2, 350 cm^3 m^{-3}.

Figure 7.

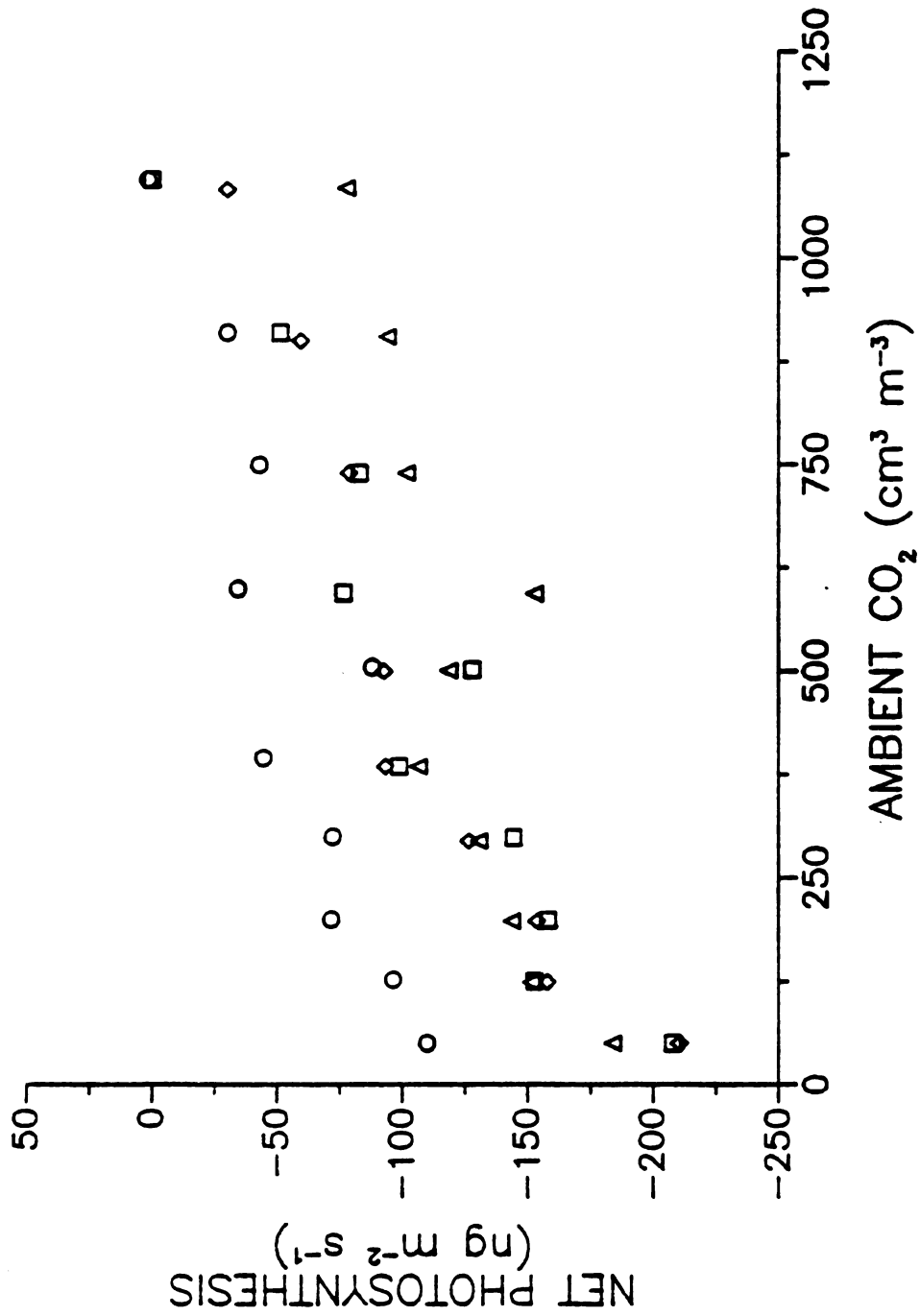
NET PHOTOSYNTHESIS
(ng m⁻² s⁻¹)
50
0
−50
−100
−150
−200
−250
0
250
500
750
1000
1250
AMBIENT CO_2 (cm^3 m^{-3})

Figure 7. Effect of external CO_2 concentrations (c_a) on net photosynthesis (P_N) of 'Montmorency' sour cherry fruits during Stage I. Different symbols on the graph represent different replications, and each replication is the average of 4 fruits.

Table 1 - Dark respiration Q_{10} of 'Montmorency' sour cherry fruit

Days after full bloom	Temperature range (°C)		
	10 - 20	20 - 30	30 - 40
15 (Stage I)	2.3	1.7	1.5
41 (Stage III)	2.0	1.9	1.8

P_N (ng fruit^{-1} s^{-1})= $P_G + R_D$ (Eq. 1)

P_G (ng fruit^{-1} s^{-1})= $189.533 * (1 - e^{(-0.0705 * t)}) - 76.466$

r^2=0.961 DF = 25 (Eq. 2)

R_D (ng fruit^{-1} s^{-1})= $- 116.309 * e^{(0.0227 * t)} + 117.650$

r^2= 0.943 DF = 25 (Eq. 3)

R_D (ng fruit^{-1} s^{-1})= $- 26.144 * e^{(0.0519 * t)} + 15.264$

r^2= 0.748 DF = 20 (Eq. 4)

Dark respiration Q_{10} values resulting from equations 3 (Stage I) and 4 (Stage III) decreased with increasing temperatures (Table 1). Values for stage I fruits were higher than for stage III fruits at 10 to 20°C, but lower at 20 to 30° and 30 to 40° (Table 1).

Carbon dioxide concentration: P_N increased with increasing c_a until saturation at approximately 400 cm^3 m^{-3} (Figure 7). CO_2-compensation point was not reached even at 1200 cm^3 m^{-3}.

Oxygen concentration: Leaf P_G and P_N decreased (Table 2) with an increase in ambient O_2 concentration from 1.5 to 20% and from 20 to 70%. Leaf R_D increased when O_2 concentration increased from 1.5 to 20%, but was no significantly affected by raising the concentration further to 70%. Fruit P_N did not drop significantly with increasing O_2 concentration from 1.5 to 20%, but decreased significantly at 70% O_2. Fruit R_D increased with increasing O_2 levels, but fruit P_G was not significantly affected (Table 2).

Dark ^{14}Carbon dioxide fixation: Under dark conditions leaves and both stage I and II fruits fixed approximately 10% of the $^{14}CO_2$ fixed in the light (Table 3). Stage III fruits were only 1/3 as effective as younger

Figure 6.

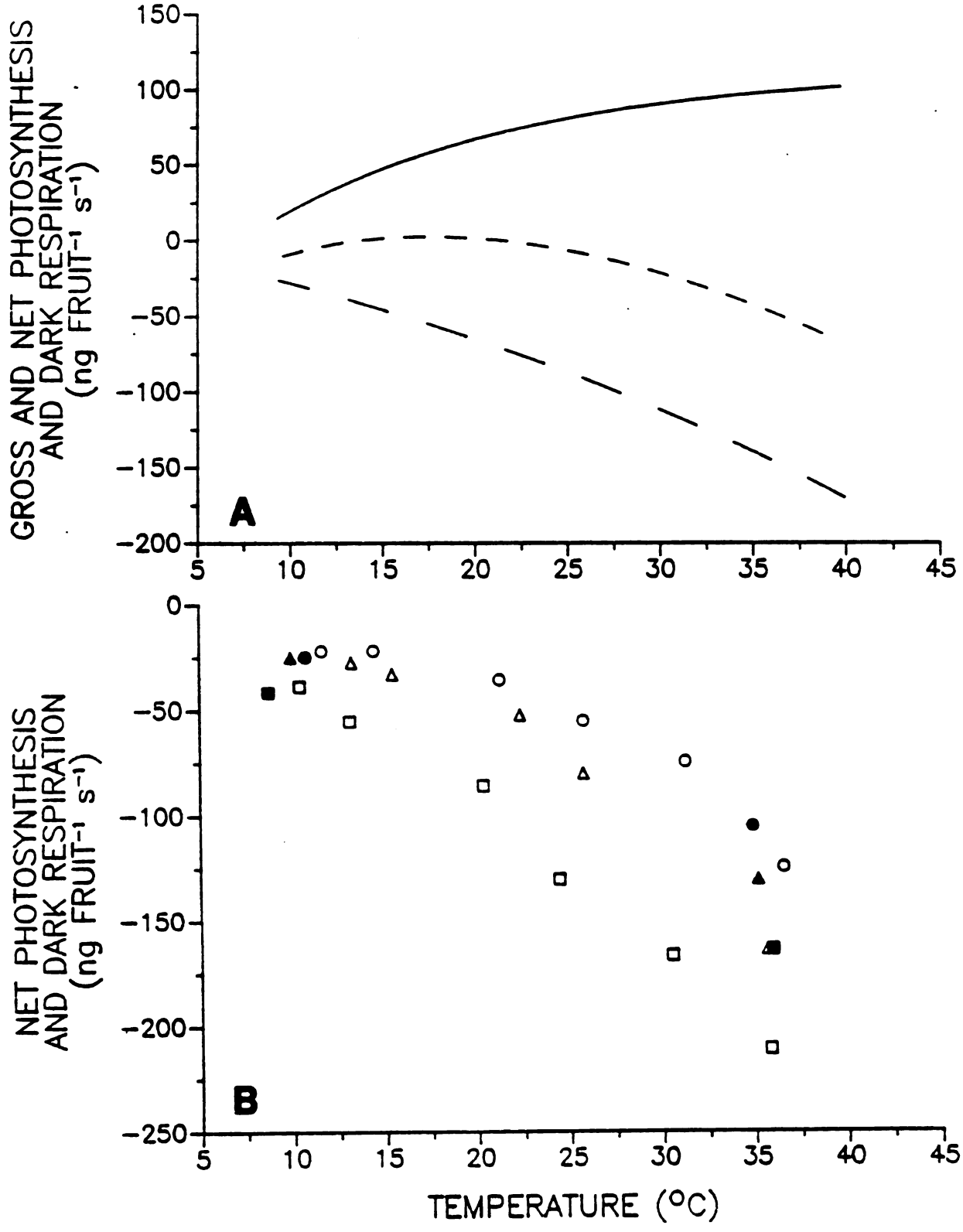
GROSS AND NET PHOTOSYNTHESIS AND DARK RESPIRATION (ng FRUIT⁻¹ s⁻¹)
150
100
50
0
-50
-100
-150
-200
A
5
10
15
20
25
30
35
40
45
NET PHOTOSYNTHESIS AND DARK RESPIRATION (ng FRUIT⁻¹ s⁻¹)
0
-50
-100
-150
-200
-250
B
TEMPERATURE (°C)

Figure 6. A. Mathematical functions for the effect of temperature on gross photosynthesis (P_G) (top line), net photosynthesis (P_N) (center line) and dark respiration (R_D) (bottom line) in stage I. B. Observed values for net photosynthesis (P_N) (open symbols) and dark respiration (P_D) (closed symbols) in stage III of 'Montmorency' sour cherry fruits, as affected by temperature. Different symbols on the graph represent different replications, and each replication is the average of 4 fruits.

Figure 5.

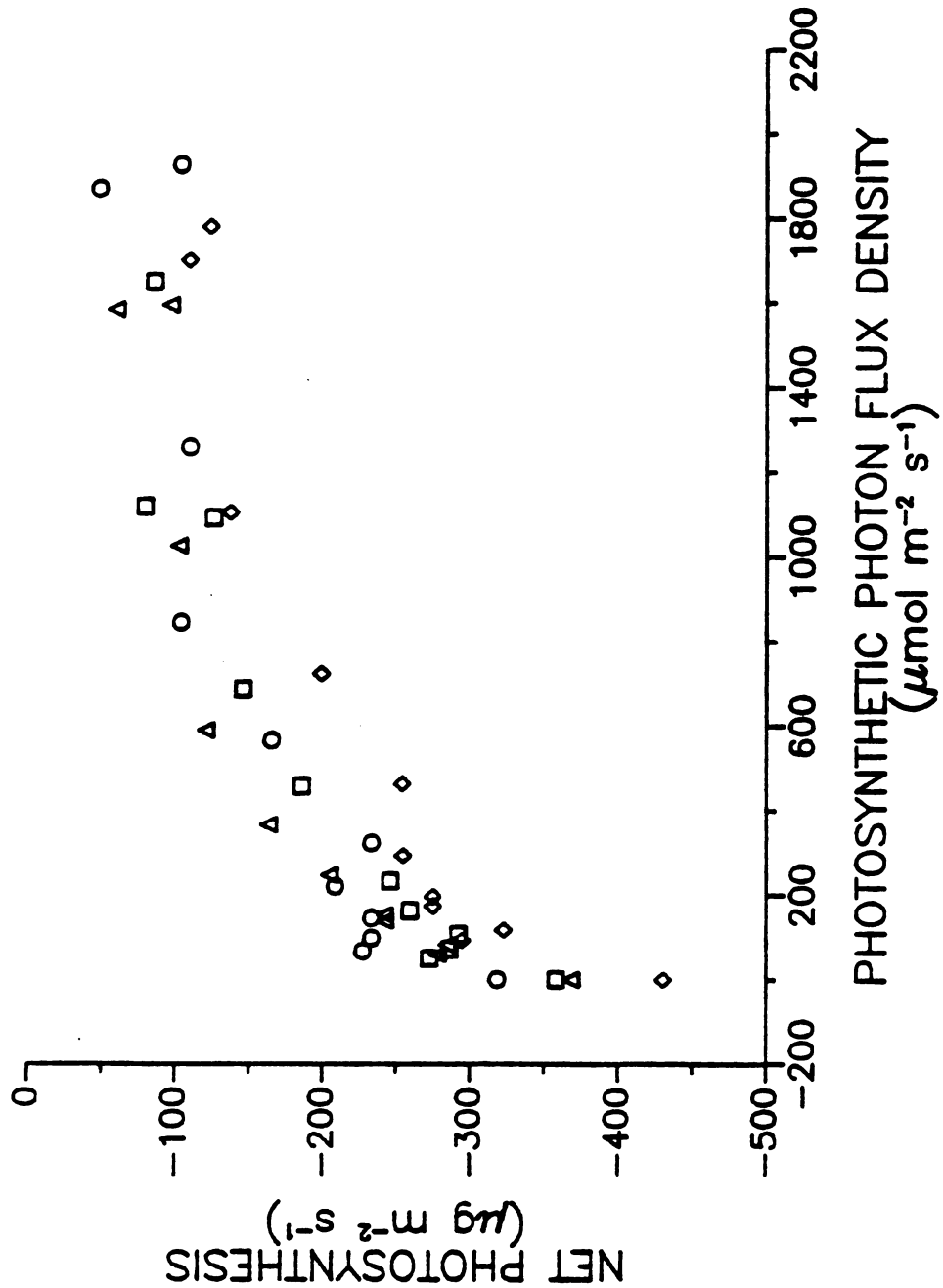
NET PHOTOSYNTHESIS
(μg m⁻² s⁻¹)
0
-100
-200
-300
-400
-500
-200
200
600
1000
1400
1800
2200
PHOTOSYNTHETIC PHOTON FLUX DENSITY
(μmol m⁻² s⁻¹)

Figure 5. Effect of photosynthetic photon flux density (PPDF) on net photosynthesis rate (P_N) of 'Montmorency' sour cherry fruits during Stage I. Different symbols on the graph represent different replications, and each replication is the average of 4 fruits.

Figure 4.

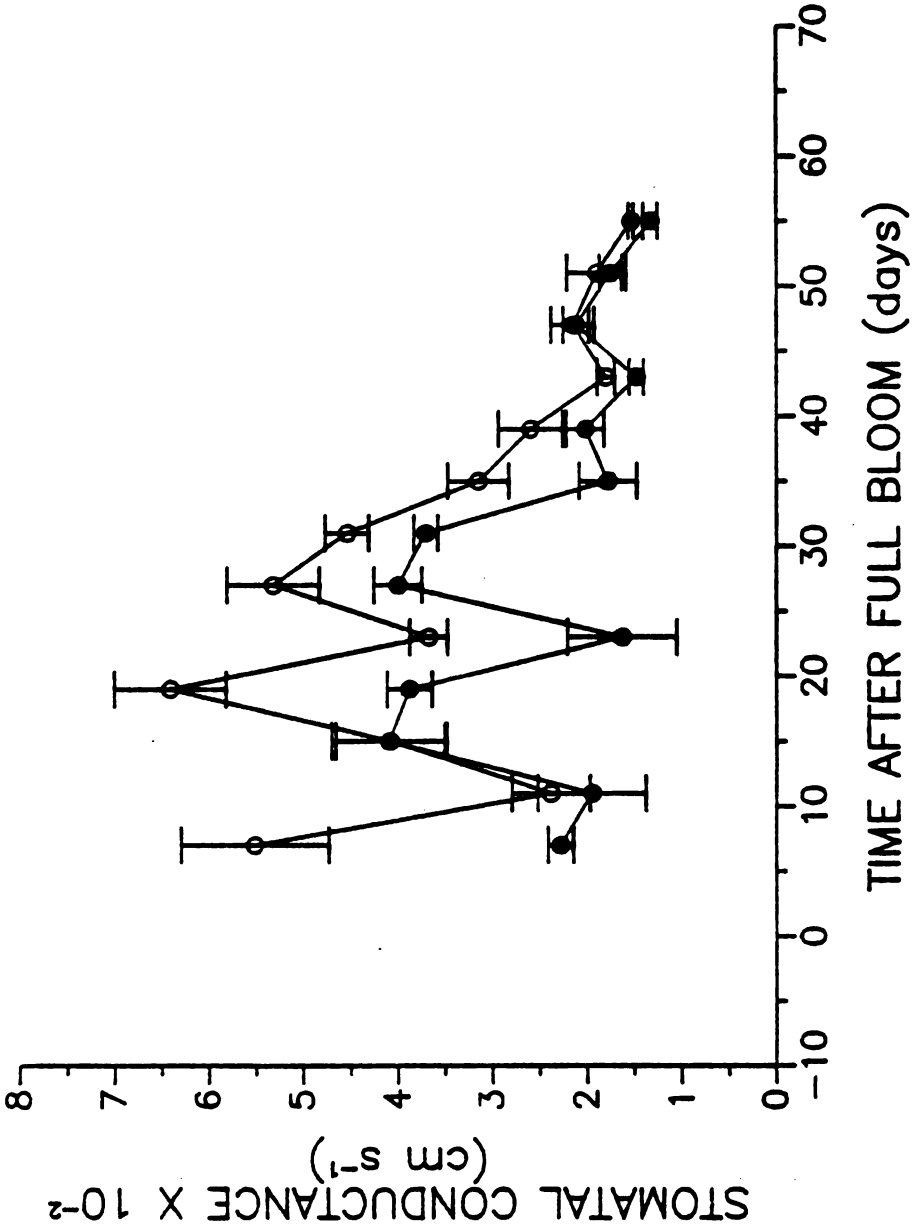
STOMATAL CONDUCTANCE X 10-2
(cm s-1)
0
1
2
3
4
5
6
7
8
-10
0
10
20
30
40
50
60
70
TIME AFTER FULL BLOOM (days)

Figure 4. Fruit stomatal conductance to CO_2 (g'_s) in the light (open circles) and in the dark (closed circles) of 'Montmorency' sour cherry fruit during development. Vertical bars indicate standard errors of the mean.