

Estimating the photosynthetic contribution of developing peach (*Prunus persica*) fruits to their growth and maintenance carbohydrate requirements

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CO₂ exchange rates (CO₂ evolution) of late-maturing cv. Cal Red peaches, exposed to different photon flux densities, were simulated from 24 days after flowering (DAF) until harvest by using light and temperature response curves measured on attached fruits in the field at biweekly intervals. The daily patterns of dark respiration rates per unit dry weight indicated their dependence on temperatures. Fruit CO₂ exchange rates in light were also affected by photosynthetic photon flux densities. Daily photosynthetic rates per unit dry weight and per fruit were significantly lower in shaded fruits receiving 7% of the full daily sunlight compared to fruits exposed to 35% sunlight. However, the difference in photosynthetic rates in peach fruits receiving 21 and 35% of total daily sunlight was small. Within the last 4 weeks before harvest, weekly carbohydrate requirements for the production of dry matter rose rapidly in cv. Cal Red peaches and were related to high carbohydrate accumulations, especially of sucrose, in the peach mesocarp. Weekly photosynthetic contribution of late-maturing cv. Cal Red peaches to these carbohydrate accumulations increased up to 115 DAF. A decline in photosynthetic contributions between 115 DAF and harvest was related to decreasing photosynthetic activities in association with declining chlorophyll contents. Photosynthesis of late-maturing cv. Cal Red peaches provided 3–9% of the weekly fruit carbohydrate requirements early in the season and 8–15% in the midseason depending on fruit exposure to light. Photosynthesis of mature fruits contributed 3–5% of the total fruit carbohydrate requirements. Since fruit photosynthetic rates approach saturation at a photosynthetic photon flux density of about 600 $\mu\text{mol m}^{-2} \text{s}^{-1}$, the difference in weekly photosynthetic contributions was small between exposed and partially exposed (35 and 21% sunlight, respectively) peach fruits. However, a shaded fruit (7% sunlight) supplied significantly less of its weekly carbohydrate requirements through photosynthesis compared to exposed fruits. During the growing period of 24 DAF until harvest, dry matter accumulation of late-maturing cv. Cal Red peaches accounted for 78% of the total carbohydrate requirements and 22% was used in respiration. Fruit photosynthesis of shaded peach fruit, partially exposed fruit and exposed fruit (receiving 7, 21 and 35% of full sunlight over the day, respectively) contributed 5, 8 and 9%, respectively, of the total growth and maintenance carbohydrate requirements during the growing season.

Key words – Carbohydrate budget, fruit photosynthesis, computer modeling, growth respiration, maintenance respiration.

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Introduction

The growth of reproductive organs depends on the uptake of mineral nutrients, water and carbon from the parent plant (Bazzaz et al. 1979). Assimilates are supplied by leaf photosynthesis and tree carbohydrate reserves. Very early in the season, when the leaf canopy is not fully developed, leaves act as sinks themselves and fruit growth seems to be partly supplied by tree carbohydrate reserves (Hansen 1971, Hansen and Grausland 1973, Jackson and Coombe 1966, Kellier and Loesch 1989, Martin et al. 1964). Considerable amounts of leaf assimilates are imported into apple, peach, apricot and cherry fruits during their growing period (Hansen 1967, Kappes 1985, Kriedemann 1968). As much as 90% of labelled carbon, assimilated by the leaves, has been reported to be translocated to apple fruits in the midseason (Hansen 1967).

Several studies indicate that flowers, fruits and legume pods are photosynthetically active (Bean et al. 1963, Clijsters 1969, Crookston et al. 1974, Flinn et al. 1977, Hansen 1971, Lenz and Noga 1982). Reproductive organs are therefore apparently able to contribute a fraction of their growth carbohydrate requirements through photosynthesis within their tissues. Bazzaz et al. (1979) estimated that in several temperate deciduous trees between 2.3 and 64.5% of the total carbon budget required for the production of mature seeds can be supplied by photosynthesis of flowers and fruits. Sambo et al. (1977) found that soybean pods can supply 4% of their final dry weight by photosynthesis. Kappes (1985) and Birkhold et al. (1992) estimated that photosynthesis of cherry and blueberry fruits contributes about 11 and 15%, respectively, to the total fruit growth carbohydrate requirements.

Most estimates of fruit photosynthetic contribution to carbon budgets have been based on CO₂ exchange measurements on detached fruits or fruits on excised shoots under laboratory conditions without taking into account the daily pattern of ambient temperature and fruit exposure to light in the field. DeJong and Walton (1989) and Walton and DeJong (1990) estimated the carbohydrate requirements of peach fruit and kiwifruit growth and respiration based on CO₂ exchange measurements in the field. However, they did not consider the fruit photosynthetic contribution in their calculations of the fruit carbohydrate budget.

Previous CO₂ exchange measurements, conducted in the field on attached fruits, indicated that peach fruits respond to light and temperature (Pavel and DeJong 1993a). In the present study, seasonal light and temperature response curves measured at biweekly intervals were used to develop a computer model to estimate photosynthesis over a range of temperature and light conditions. The gas exchange of representative shaded, partially exposed and exposed peach fruits was simulated with the model under actual temperature conditions in the field from 24 days after flowering (DAF)

until harvest. The resultant CO₂ exchange data were used to estimate the photosynthetic contribution of developing peach fruits to their growth carbohydrate requirements. The assumption was made that environmental factors, such as mineral nutrients and water supply, were nonlimiting.

Materials and methods

Plants

The study was conducted at the University of California's Kearney Agricultural Center, Parlier, on trees of a late-maturing peach cultivar [*Prunus persica* (L.) Batsch cv. Cal Red grown on Nemaguard rootstock] during the 1989 and 1990 growing seasons. The 6- and 7-year-old trees, respectively, were trained and planted to a high density-central leader system (2.0 × 4.0 m). Cultural practices, such as fertilization, pruning, thinning and irrigation, were conducted as in a commercial orchard.

Simulation model

CO₂ exchange (CO₂ evolution) of attached peach fruits was measured in the field in response to temperature [15 (early in the season), 20, 25, 30 and 35°C] and photosynthetic photon flux density (PPFD; 0, 150, 325, 600 and 1200 μmol photons m⁻² s⁻¹) from 24 DAF until harvest in biweekly intervals as described previously (Pavel and DeJong 1993a). These data were used to develop a computer model simulating the photosynthetic contribution of developing peach fruits to their growth and maintenance carbohydrate requirements under actual field conditions. At each measurement date and for each temperature level an equation for fruit gas exchange rates per unit dry weight in response to light (L) was calculated via regression:

$$y = e^{a+\beta L-\gamma L^2+\delta L^3} \quad (1)$$

Fruit CO₂ exchange rates per unit dry weight in response to temperature (T) at the various photon flux densities were calculated by regression analysis of the coefficients (α, β, γ, δ) of equation (1):

$$y_{\alpha,\beta,\gamma,\delta} = e^{a+bT+cT^2} \quad (2)$$

Equation (2) was integrated into equation (1) by replacing the coefficients α, β, γ, δ with equation (2) to calculate fruit CO₂ exchange in response to light and temperature:

$$y = e^{(e^{a+bT+cT^2})} + (e^{d+eT+fT^2}) L - (e^{h+iT+jT^2}) L^2 + (e^{k+lT+mT^2}) L^3 \quad (3)$$

The coefficients (a–d, f–m) of equation (3) calculated for each measurement date were interpolated to simulate the fruit CO₂ exchange for each day during the growing season. Mean peach fruit CO₂ exchange rates per unit dry weight in light and dark were simulated with the computer model in 15-min intervals for every day from 24 DAF until harvest using ambient air temperatures and photon flux densities that specific fruits were exposed to in the field.

Characterization of the environment of representative fruits

Mean hourly ambient air temperatures were monitored at a CIMIS (California Irrigation Management Information System) weather station located at the Kearney Agricultural Center in Parlier. The hourly air temperatures were interpolated to 15-min intervals assuming that a temperature increase or decrease within an hour was linear. Previous research, comparing actual fruit temperatures of peach and kiwifruit with ambient air temperatures, indicated that the diurnal pattern of fruit temperature is very similar to ambient air temperatures but lags slightly behind (T. M. DeJong and E. F. Walton, personal communications).

The daily exposure of peach fruits to photosynthetic photon flux densities was measured with light sensors attached to the fruits and the data were collected at 15-min intervals with a datalogger (Model CR 21, Campbell Scientific Inc., Logan, UT, USA). The light exposure of 36 different fruits was measured every second week during the growing season. The fruits were distributed radially on the east, west, south and north sides of the trees and vertically at the bottom, middle and top of the trees. Some fruits were on the periphery and some more towards the inside of the canopy. Fruit location relative to the site of the tree and height in the tree affected the time during the day when the fruits were exposed to light, but there was no clear effect on accumulated daily PPFD. However, fruits located on the periphery of the tree were clearly exposed to more accumulated PPFD over the day than those deeper in the canopy. Since the light sensors did not remain continuously at the same fruits over the entire growing season, the daily PPFD accumulations measured at these fruits every other week were quite variable. The effect of tree canopy development on fruit exposure to light could, therefore, not be clearly evaluated. A separate study indicated that, when the light sensors remained at the same fruit site for two consecutive days, the daily light patterns were nearly identical for both days. Because it was impossible to represent all the possible fruit light exposure patterns in the tree, the patterns of three fruits on one specific day during the growing season were selected as representatives to simulate daily gas exchange rates with the computer model. The light exposure pattern of a shaded (receiving 7% of the full sunlight over the day), partially exposed (21% full sunlight) and exposed fruit (35% full sunlight) were

used. The percentage values were calculated by taking the total sunlight accumulation of these fruits in relation to the total accumulated full sunlight over the day. Seasonal simulated fruit CO₂ exchange rates in light and photosynthetic rates were corrected for each day by solar radiation data monitored at the CIMIS weather station.

Fruit photosynthetic rates per unit dry weight were calculated by the difference of CO₂ exchange rates in light and dark. Fruit CO₂ exchange rates in light and dark and photosynthetic rates per unit dry weight were summed for each day. Daily CO₂ exchange rates per fruit were calculated by multiplication with fruit dry weight data (Pavel and DeJong 1993b). Since fruit dry matter accumulation was measured at weekly intervals, the data were interpolated by absolute growth rates to determine fruit dry weight accumulation per day.

Calculation of seasonal peach fruit growth and maintenance carbohydrate requirements, respiratory losses and fruit photosynthetic contribution

Fruit dry weight data of the late-maturing cv. Cal Red peach, collected during the 1988 growing season (Pavel and DeJong 1993b), were converted to carbohydrate equivalents. The carbon content of the fruit samples was determined by pyrolysis (Microanalytical Laboratory, Department of Chemistry, University of California, Berkeley, CA, USA). The carbon content per unit dry weight, ranging between 42.7 and 45.2% during the growing period, was then converted to carbohydrate equivalents by multiplying by 2.5.

Incremental fruit growth carbohydrate requirements were calculated on a weekly basis by subtracting the previous week's dry matter carbohydrate equivalents from those of the current week. Daily dark respiration and photosynthetic rates per fruit ($\text{mmol CO}_2 \text{ fruit}^{-1} \text{ day}^{-1}$) were converted to $\text{g CO}_2 \text{ fruit}^{-1} \text{ day}^{-1}$ and then multiplied by 0.68 to convert them to carbohydrate equivalents. Weekly respiratory losses and photosynthetic rates were calculated by summing the daily dark respiration and photosynthetic rates per fruit. Total seasonal carbohydrate requirements for fruit growth and respiration, and the fruit photosynthetic contribution were calculated from fruit dry matter carbohydrate equivalents at harvest (based on a mean carbon content per unit dry weight of 43.1%) and summing daily dark respiration and photosynthetic rates per fruit.

Results

Simulation of seasonal fruit gas exchange of late-maturing cv. Cal Red peaches

Peach fruit CO₂ exchange rates per unit dry weight were simulated in response to temperature and light over the season using the computer model. Temperature and light response curves of simulated fruit gas exchange

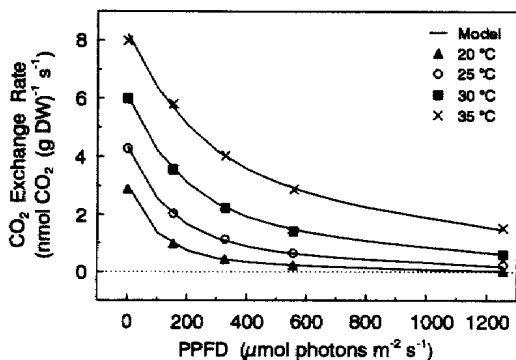


Fig. 1. Simulated and measured (mean of 3–4 measurements) fruit CO_2 exchange (CO_2 evolution) rates per unit dry weight of late-maturing cv. Cal Red peaches in response to temperature and PPFD at 82 DAF.

rates followed a pattern similar to those of measured CO_2 exchange rates (Fig. 1).

The daily pattern of peach fruit dark respiration rates per unit dry weight clearly indicated their dependence on temperature. Fruit CO_2 exchange rates in light were affected by photosynthetic photon flux densities in addition to temperature over the day (Fig. 2). CO_2 exchange rates per unit dry weight in light followed a pattern opposite to that of fruit exposure to photon flux densities.

Daily fruit CO_2 exchange rates per unit dry weight were simulated over the entire season for a shaded (receiving 7% of full sunlight over the day), partially

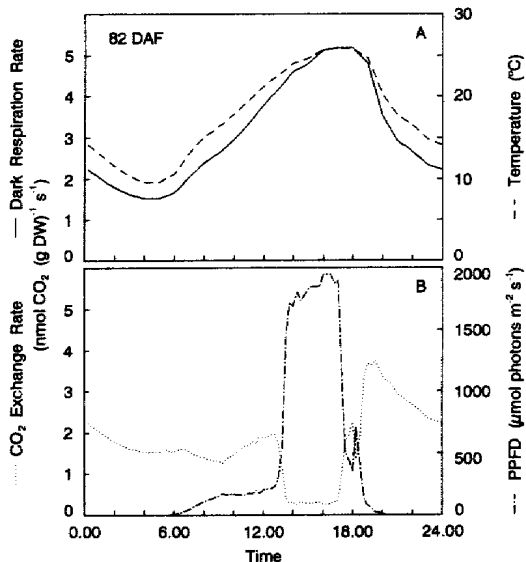


Fig. 2. Daily patterns of simulated dark respiration (A) and CO_2 exchange (CO_2 evolution) rates (B) per unit dry weight of late-maturing cv. Cal Red peach fruits in response to temperature and PPFD at 82 DAF.

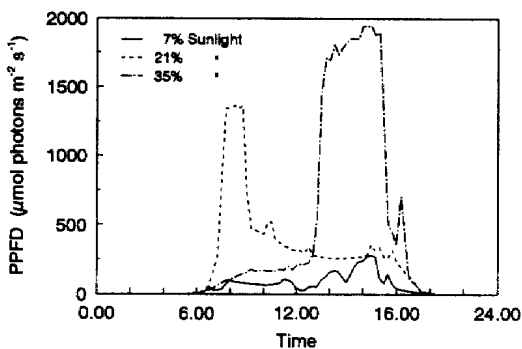


Fig. 3. Daily patterns of PPFDs of representative shaded, partially exposed and exposed (7, 21 and 35% of total daily sunlight, respectively) cv. Cal Red peach fruits.

exposed (21% sunlight) and an exposed fruit (35% sunlight). An example of the daily pattern of light exposure for specific fruits is represented in Fig. 3.

Over the day, CO_2 exchange rates in light and calculated photosynthetic rates per unit dry weight were higher in exposed and partially exposed peach fruits than in shaded fruits (Fig. 4). Differences in CO_2 exchange and photosynthetic rates of fruits at different light exposures also occurred in mature fruits, although fruit gas exchange rates decreased over the growing season. Fruit photosynthetic rates followed a pattern similar to that of the fruit exposure to light (Fig. 3).

Daily CO_2 exchange rates per unit dry weight in light and dark decreased over the growing season (Fig. 5). Seasonal calculated photosynthetic rates per unit dry weight of exposed and partially exposed (35 and 21% sunlight) peach fruits were higher than in shaded fruits (7% sunlight). However, the differences in photosynthetic and CO_2 exchange rates per unit dry weight and per fruit in light were small between exposed and partially exposed fruits (Figs 5, 6). Daily CO_2 exchange rates per fruit in light and dark and calculated photosynthetic rates increased over the season (Fig. 6). Shaded fruits (7% sunlight) had significantly lower photosynthetic rates per fruit than those of more exposed (21 and 35% sunlight) fruits.

Photosynthetic contribution of peach fruits to their growth carbohydrate requirements

Weekly incremental fruit dry matter carbohydrate equivalents increased slightly between 24 and 115 DAF and then rapidly in maturing fruits (Fig. 7). Respiratory losses per fruit increased initially and then remained relatively constant over the season with a slight increase towards harvest.

The photosynthetic contribution of peach fruits to their growth carbohydrate requirements was expressed as percentage of incremental fruit dry matter carbohydrate equivalents and respiratory losses per fruit on a weekly basis. Weekly photosynthetic contributions of

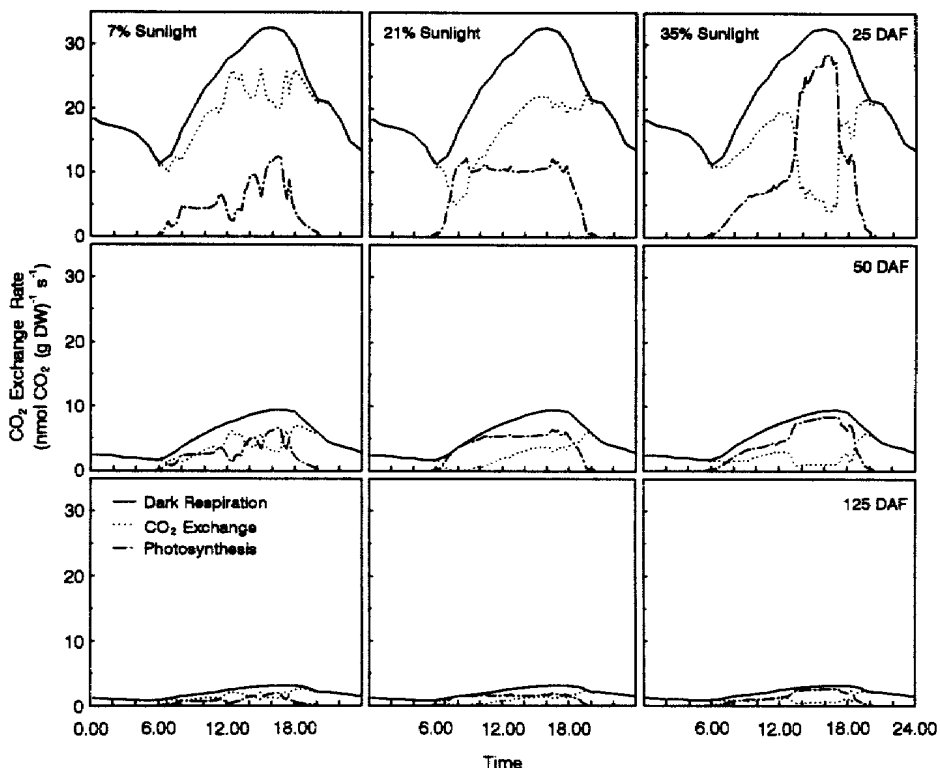


Fig. 4. Daily patterns of simulated dark respiration rates, CO₂ exchange rates in light, and calculated photosynthetic rates per unit dry weight of representative shaded, partially exposed and exposed (7, 21 and 35% of total daily sunlight, respectively) cv. Cal Red peach fruits at 25, 50 and 125 DAF of the 1989 growing season.

exposed, partially exposed and shaded fruit increased up to 115 DAF and then decreased in mature fruits (Fig. 8). The decrease of the photosynthetic contribution in mature fruits, between 115 DAF and harvest, coincided with the rapid increase in fruit dry matter carbohydrate equivalents (Fig. 7). In comparison to shaded fruits (7% sunlight), the differences in weekly photosynthetic contributions were small between exposed (35% sunlight) and partially exposed (21% sunlight) fruits. The photosynthetic contribution of shaded fruits to total fruit carbohydrate requirements was significantly less than that of exposed fruits. Peach fruits contributed about 3–9% early in the season, 8–15% in midseason and 3–5% at maturity, to their growth carbohydrate requirements depending on the exposure to light.

A carbohydrate budget was calculated for late-maturing cv. Cal Red peaches to estimate fruit carbon utilization efficiency and the contribution of fruit photosynthesis to fruit growth and maintenance carbohydrate requirements (Tab. 1). Seventy-eight percent of the total seasonal carbohydrate costs were used for dry matter and 22% for respiration to grow a peach fruit with a final dry weight of 27.3 g. Fruit photosynthesis contributed 5% to fruit growth carbohydrate requirements of a

shaded fruit (7% sunlight). The photosynthetic contribution of a partially exposed (21% sunlight) and an exposed (35% sunlight) peach fruit accounted for 8 and 9% of the carbohydrate requirements, respectively.

Discussion

CO₂ exchange rates per unit dry weight (CO₂ evolution) of late-maturing cv. Cal Red peach have been simulated for fruits of differing light exposures from 24 DAF until harvest by using light and temperature response curves measured in the field on attached fruits at biweekly intervals. Over the day, dark respiration rates per unit dry weight of peach fruits were primarily affected by temperature, whereas CO₂ exchange rates in light were influenced by PPFDs in addition to temperature. Under field conditions, fruit light exposures ranged from 35% of full sunlight calculated over the entire day in the most exposed sites to 7% in the most shaded areas. Daily photosynthetic rates per unit dry weight were higher in exposed peach fruits, receiving 21 and 35%, respectively, of full sunlight over the day, than in shaded fruits (7% sunlight). Peach fruits responded to light and temperature over the entire growing season. However, fruit

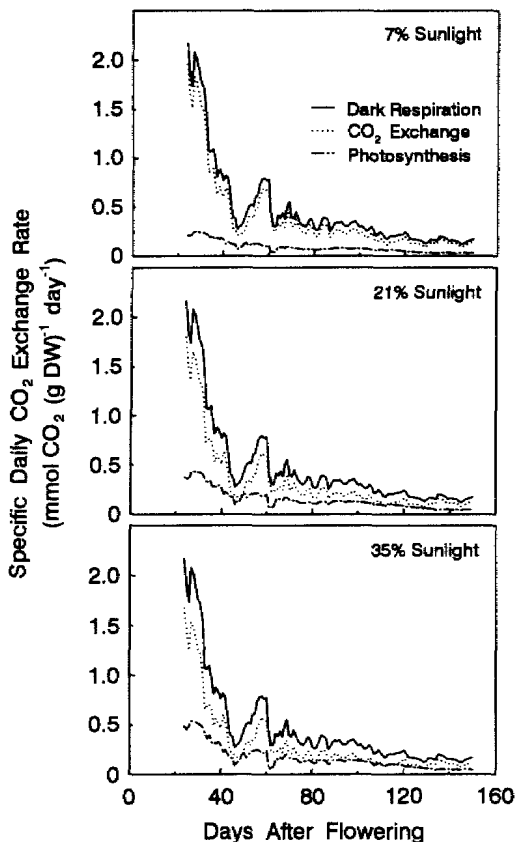


Fig. 5. Specific daily dark respiration rates, CO₂ exchange rates in light and calculated photosynthetic rates per unit dry weight of representative shaded, partially exposed and exposed (7, 21 and 35% sunlight, respectively) cv. Cal Red peach fruits during the 1989 growing season.

gas exchange rates in light and dark and photosynthetic rates per unit dry weight decreased over the growing period as reported previously in peach (DeJong et al. 1987, Pavel and DeJong 1993a) and in apple (Clijsters 1969, Jones 1981) and grape berry (Koch and Alleweldt 1978).

Daily dark respiration rates per unit dry weight declined and on a per fruit basis increased throughout the growing season in a manner similar to that reported by DeJong and Walton (1989) for early- and late-maturing peach cultivars. Within the first 4 weeks after flowering, specific dark respiration rates per unit dry weight increase in peach fruits and then decline until harvest (DeJong et al. 1987). The seasonal pattern of daily CO₂ exchange rates per unit dry weight and per fruit indicated the influence of warmer and cooler weather periods (data not shown) on peach fruit gas exchange as reported by DeJong and Walton (1989).

Weekly carbohydrate requirements for fruit growth

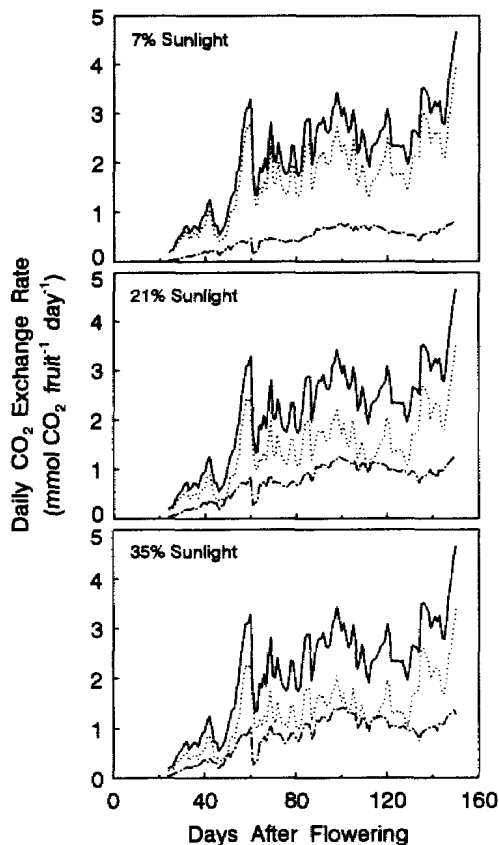


Fig. 6. Daily dark respiration rates (—), CO₂ exchange rates in light (.....) and calculated photosynthetic rates (-----) per fruit of representative shaded, partially exposed and exposed (7, 21 and 35% sunlight, respectively) cv. Cal Red peach fruits during the 1989 growing season.

of late-maturing cv. Cal Red peaches were relatively constant in midseason after an initial rise early in the

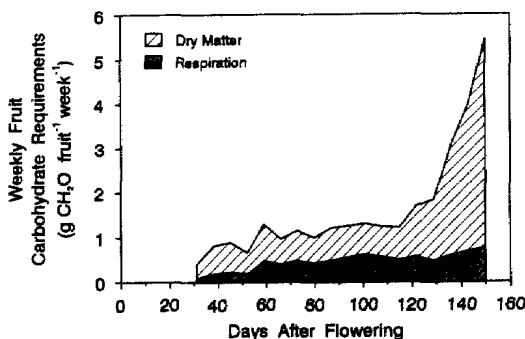


Fig. 7. Weekly carbohydrate requirements per fruit for dry matter production and respiration in late-maturing cv. Cal Red peaches during the 1989 growing season.

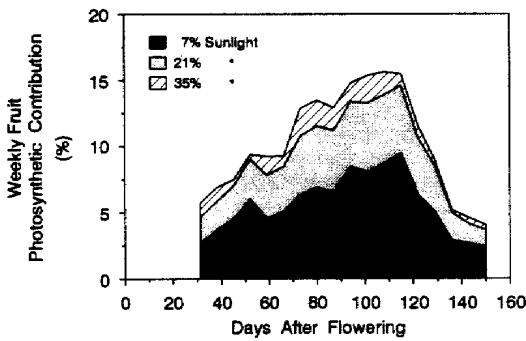


Fig. 8. Weekly photosynthetic contribution of representative shaded, partially exposed and exposed (7, 21 and 35% sunlight, respectively) cv. Cal Red peach fruits to their growth carbohydrate requirements during the 1989 growing season.

growing season. Within the last 4 weeks before harvest, the demand for carbohydrates increased very rapidly. High amounts of sucrose are accumulated in the peach mesocarp during this growth period as reported by Chapman and Horvat (1990), Moriguchi et al. (1990) and Pavel and DeJong (1993b). Weekly respiratory losses of peach fruits, quantified as dark respiration, increased initially and then remained constant over the season. In mature fruits, weekly carbohydrate requirements used for respiration increased slightly indicating higher metabolic rates in these fruits, coinciding with high accumulations of dry matter carbohydrate equivalents.

Weekly photosynthetic contributions of late-maturing cv. Cal Red peaches to their growth carbohydrate requirements followed a pattern similar to that of their photosynthetic activity (Pavel and DeJong 1993a). With increasing fruit dry matter the photosynthetic contribution of young fruits increased up to 115 DAF. In maturing peach fruits, 115 DAF until harvest, the decrease in photosynthetic contribution seems to be related to the color change in association with declining chlorophyll contents as reported in apple fruits by Clijsters (1969), Jones (1981) and Knee (1972). Since fruit photosynthetic rates approach saturation at a PPFD of about 600 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ (Pavel and DeJong 1993a), the difference in weekly photosynthetic contributions was small between exposed and partially exposed (35 and 21% sunlight, respectively) peach fruits. The photosynthetic contribution of late-maturing cv. Cal Red peaches was calculated on the basis of simulated CO_2 exchange rates by using mean ambient air temperatures. Therefore, the effect of radiant heating, leading to increasing CO_2 exchange rates in light, especially in exposed peach fruits, was not considered by the simulation, and calculated photosynthetic rates may have been slightly underestimated. Thorpe (1974) found that surface temperatures of apple fruits exposed to light are higher than ambient air temperatures.

Since it was impossible to model the light exposure of

all fruits in the canopy, three fruits exposed to 7, 21 or 35% of the total daily light were used for the simulation model as representatives of other fruits on the tree. Using these three representative fruits the model indicated that peach fruits supplied about 3–9% early in the season, 8–15% in midseason and 3–5% towards maturity to their weekly carbohydrate requirements by photosynthesis. Olliker et al. (1978) estimated that the photosynthetic contribution by the bean pod accounts for 2.5–3.5% of the daily weight increment of the pod within the first 2 weeks of growth. Thereafter its contribution decreases rapidly. Kappes (1985) estimated that cherry fruits provide 19.4% in stage I of the double-sigmoid growth curve and 29.7% and 1.5% in stage II and III, respectively. However, his estimates were made under the assumption that cherry fruits were exposed to full sunlight ($1000 \mu\text{mol photons m}^{-2} \text{s}^{-1}$) over a 16-h period at constant day and night temperatures (25 and 15°C, respectively). Our fruit exposure data indicated that even the most exposed fruits received only 35% of the total daily sunlight.

The estimates that 78% of the total seasonal carbohydrate requirements could be attributed to dry matter production and 22% to respiration are very close to those estimated by DeJong and Walton (1989) for another late-maturing peach cultivar and for kiwifruits (Walton and DeJong 1990) (79.5 and 20.5%, respectively). Penning de Vries et al. (1983) estimated that, on average, 20% of the carbohydrate budget is needed for respiration in various kinds of seeds, fruits and storage organs. However, Kappes (1985) estimated that 69.1% of the total seasonal costs are required for dry matter production and 30.9% for respiration in cherry fruits.

The total photosynthetic contribution of late-maturing cv. Cal Red peaches to their carbohydrate budget depended on the fruit's exposure to light. A shaded fruit (7% sunlight) was estimated to contribute 5% to its total seasonal carbohydrate requirements. The photosynthetic contribution of partially exposed (21% sunlight) and exposed (35% sunlight) fruit accounted for 8 and 9%, respectively. These estimates of photosynthetic contribution in peach fruits are lower than the

Tab. 1. Carbohydrate budget of late-maturing cv. Cal Red peaches during the 1989 growing season. The data are based on mean dry weights of 27.3 g.

	$\text{g CH}_2\text{O fruit}^{-1}$ season ⁻¹	%
CH₂O requirements		
Dry matter	29.4	78
Respiration	8.2	22
Total	37.6	100
Fruit photosynthetic contribution		
Shaded (7% sunlight)	1.8	5
Partially exposed (21% sunlight)	2.9	8
Exposed (35% sunlight)	3.2	9

values Kappes (1985) calculated for cherry fruits (11.2%), exposed to full sunlight over a 16-h period, and for blueberries (15%; Birkhold et al. 1992). In comparison to tree fruits, soybean pods, exposed to 88.6 W m⁻² over a 14-h photoperiod per day, contribute only 4% to the total pod dry weight (Sambo et al. 1977).

The results of the present research indicate that, based on the estimated carbon budget for fruit growth of the late-maturing cv. Cal Red peach cultivar, 78% of the total carbohydrate requirements were used for dry matter production and 22% were attributed to respiration. Under actual field conditions, peach fruits can contribute a part of their total growth carbohydrate requirements by fruit photosynthesis. Depending on the fruit exposure to light this contribution amounts to 5–9%.

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