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Seasonal CO_2 exchange patterns of developing peach (*Prunus persica*) fruits in response to temperature, light and CO_2 concentration

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CO_2 exchange rates per unit dry weight, measured in the field on attached fruits of the late-maturing Cal Red peach cultivar, at 1 200 µmol photons $m^{-2} s^{-1}$ and in dark, and photosynthetic rates, calculated by the difference between the rates of CO_2 evolution in light and dark, declined over the growing season. Calculated photosynthetic rates per fruit increased over the season with increasing fruit dry matter, but declined in maturing fruits apparently coinciding with the loss of chlorophyll. Slight net fruit photosynthetic rates ranging from 0.087 ± 0.06 to 0.003 ± 0.05 nmol CO_2 (g dry weight)$^{-1}$ s^{-1} were measured in midseason under optimal temperature (15 and 20°C) and light (1 200 µmol photons $m^{-2} s^{-1}$) conditions. Calculated fruit photosynthetic rates per unit dry weight increased with increasing temperatures and photon flux densities during fruit development. Dark respiration rates per unit dry weight doubled within a temperature interval of 10°C; the mean seasonal Q_{10} value was 2.03 between 20 and 30°C. The highest photosynthetic rates were measured at 35°C throughout the growing season. Since dark respiration rates increased at high temperatures to a greater extent than CO_2 exchange rates in light, fruit photosynthesis was apparently stimulated by high internal CO_2 concentrations via CO_2 refixation. At 15°C, fruit photosynthetic rates tended to be saturated at about 600 µmol photons $m^{-2} s^{-1}$. Young peach fruits responded to increasing ambient CO_2 concentrations with decreasing net CO_2 exchange rates in light, but more mature fruits did not respond to increases in ambient CO_2. Fruit CO_2 exchange rates in the dark remained fairly constant, apparently uninfluenced by ambient CO_2 concentrations during the entire growing season. Calculated fruit photosynthetic rates clearly revealed the difference in CO_2 response of young and mature peach fruits. Photosynthetic rates of younger peach fruits apparently approached saturation at 370 µl CO_2 l^{-1}. In CO_2-free air, fruit photosynthesis was dependent on CO_2 refixation since CO_2 uptake by the fruits from the external atmosphere was not possible. The difference in photosynthetic rates between fruits in CO_2-free air and 370 µl CO_2 l^{-1} indicated that young peach fruits were apparently able to take up CO_2 from the external atmosphere. CO_2 uptake by peach fruits contributed between 28 and 16% to the fruit photosynthetic rate early in the season, whereas photosynthesis in maturing fruits was supplied entirely by CO_2 refixation.

Key words – Fruit CO_2 exchange, fruit CO_2 refixation, fruit CO_2 uptake.

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Introduction

Although leaves are the main sources of photosynthate production, there is evidence that reproductive organs, such as flowers, tree fruits and legume pods, are photosynthetically active. They can, to a small extent, contribute to their own carbon budget. Hansen (1970, 1971), Kriedemann (1968a) and Moreshet and Green

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(1980) showed that flowers and fruits of apples, apricots and oranges are able to fix carbon when exposed to labelled CO_2 and light. If fruits were incapable of photosynthesis, their exposure to light would not change CO_2 evolution in comparison to evolution from fruits in the dark. CO_2 exchange rates of illuminated apple and orange fruits and legume pods are lower than in those exposed to dark, indicating that they fix CO_2 in the light. However, the dark CO_2 evolution is not fully compensated by the light fixation of CO_2 in most fruits or pods (Andrews and Svec 1975, Clijsters 1969, Flinn et al. 1977).

Phan (1970) found that not only the peel of preclimacteric apple fruits but also the inner fruit tissues are photosynthetically active. The apple peel contains chlorophyll *a* and *b* and both photosynthetic pigment systems function (Downs et al. 1965). Over the season the chlorophyll concentration of the apple and soybean pod epidermis decreases, whereas carotenoid and anthocyanin concentrations increase with ripening of apple fruits (Jones 1981, Knee 1972, Quebedeaux and Chollet 1975). The epidermis of several fruits and legume pods contains functional stomata, although the stomatal density per unit surface area is much less than that of leaves (Andrews and Svec 1975, Atkins et al. 1977, Blanke 1986, Crookston et al. 1974, Ishida et al. 1990). The shape and size of apple, quince, and tomato fruit stomata are similar to those of C_3 leaves (Blanke 1986). During fruit ontogenesis, stomatal density decreases with expanding surface area; in midseason, stomata of apple fruits are transformed into lenticels in contrast to those of leaves (Blanke 1987).

Fruit gas exchange rates in the light, and dark respiration rates per unit dry or fresh weight or surface area decrease over the season in apples, peaches, grape and kiwifruit berries (DeJong et al. 1987, Geisler and Radler 1963, Jones 1981, Walton and DeJong 1990). Photosynthetic rates of apples and grape berries, calculated by the difference between CO_2 evolution in the dark and that in light, follow the same seasonal pattern (Clijsters 1969, Koch and Alleweldt 1978, Lenz and Noga 1982). Bean et al. (1963), Clijsters (1969), Jones (1981) and Moreshet and Green (1980) found that the chlorophyll concentration of apple and citrus peel is positively correlated with the photosynthetic rate or $^{14}CO_2$ uptake. Slight net photosynthetic rates, i.e. CO_2 exchange rates in light exceeding those in dark, have been measured in pea pods (Flinn et al. 1977) and under specific conditions in apple fruits (Noga and Lenz 1982). In comparison to other fruits, relatively high net photosynthetic rates occur in young, green blueberries (Birkhold et al. 1992).

Several experiments have been conducted to study the fruit gas exchange response to environmental factors. Photosynthetic rates of apple, cherry and citrus fruits increased with increasing photosynthetic photon flux densities, temperatures and CO_2 concentrations (Bean et al. 1963, Clijsters 1969, Kappes 1985, Moreshet and Green 1980, Noga and Lenz 1982). CO_2 exchange of apple fruits has been reported to be insensitive to changing relative humidity (Noga and Lenz 1982). Jones (1981) described the seasonal trend of CO_2 exchange in apple fruits exposed to light and dark, but fruit gas exchange rates were measured at only one photosynthetic photon flux density (about 1 200 µmol photons m^{-2} s^{-1}). Most of the studies of fruit gas exchange responses to environmental factors have been conducted on detached fruits at selected times during fruit development but not in consistent time intervals over the growing season. DeJong et al. (1987) studied the seasonal dark respiration patterns of early- and late-maturing peach cultivars in the field, but CO_2 exchange responses of developing peach fruits to light, temperature and CO_2 concentration have not been reported. The following experiments were designed to study the seasonal CO_2 exchange pattern of attached peach fruits in response to temperature, photon flux density and CO_2 concentration in the field during fruit development. In a subsequent study, the data presented in this paper will be used to develop a simulation model of seasonal fruit CO_2 exchange and to estimate the importance of fruit photosynthesis to the carbon economy of peach fruit growth.

Materials and methods

Plants

The study was conducted at the University of California's Kearney Agricultural Center, Parlier, on 6-year-old 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 trees 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.

Fruit gas exchange measurements

CO_2 exchange of attached peach fruits was measured in response to different temperatures, photon flux densities and CO_2 concentrations in the field from about three weeks after flowering until harvest using a mobile, gas analysis laboratory. Individual fruits were enclosed in a cylindrical, temperature-controlled, well-stirred cuvette similar to that described by DeJong (1982). Early in the season, 3–4 fruits on a defoliated shoot (leaves and shoot tips were removed prior to the measurement) were enclosed in the cuvette. As the fruits grew, one fruit was measured and the cuvette volume was increased by using a cuvette cover of a greater depth. Fruit and cuvette temperatures were controlled by circulating water from a temperature-controlled water bath (Lauda RC3, Brinkmann Instruments Inc., Westbury, NY, USA) to a heat exchange plate on the bottom

of the cuvette. Fruit temperature was measured to the nearest 0.1°C using three type E (chromel-constantan) thermocouples (0.02 mm wire) appressed to the shaded, lower fruit surface and a digital thermometer (Model 2190A, Fluke Manufacturing Co. Inc., Everett, WA, USA). Temperature differences between fruit interior and fruit surface were neglected, since Walton and De-Jong (1990) found that on average, temperatures of partially shaded fruits, exposed to dark, were within 1.6°C of ambient air temperatures in kiwifruits.

Gas exchange measurements were made with an open system apparatus similar to that described by Augustine et al. (1976). CO_2 concentrations were measured with a differential infrared gas analyzer (Model 225 MK III, ADC Ltd., Hoddesdon, UK). The infrared gas analyzer was calibrated before each set of measurements with mixed gas of a known CO_2 concentration (350 µl CO_2 l^{-1}) supplied from a cylinder (Matheson Science, Inc.). Ambient air from 6 m above the ground was passed through the system by a pump. Ambient CO_2 concentrations, entering the assimilation cuvette, were 368 ± 0.5 µl CO_2 l^{-1}. Flow rates were controlled and measured with an electronic mass flow controller (Model FC 260, Tylan Inc., Carson, CA, USA).

Measurements of fruit gas exchange in response to temperature were made at 15 (early in the season), 20, 25, 30 and 35°C at biweekly intervals. Since it was difficult to maintain temperatures below 20°C inside the cuvette without condensation, measurements were taken at 15°C only early in the season. Three or four fruits were measured during each set of measurements. At each temperature, the CO_2 evolution by fruits was measured in response to various photosynthetic photon flux densities (PPFD) of ~1 200, 600, 325, 150 and 0 µmol photons m^{-2} s^{-1}. The different PPFDs were attained by covering the cuvette with layers of white cheesecloth or a dark-colored, opaque canvas. PPFD was measured with a quantum meter (Model LI-185 B, Li-Cor, Omaha, NE, USA) and a quantum sensor (Model LI-190 SB, Li-Cor). Approximately 30–60 min were required to establish a constant temperature/CO_2 exchange equilibrium prior to each measurement.

Measurements of fruit gas exchange in response to various CO_2 concentrations (20, 100, 230, 370 and 880 µl CO_2 l^{-1} in the assimilation cuvette) were conducted at monthly intervals by using gas mixtures of known CO_2 concentrations (Matheson Science, Inc.) from cylinders.

Fruit CO_2 exchange rates were calculated from measurements of CO_2 flux and fruit temperatures according to Von Caemmerer and Farquhar (1981). CO_2 exchange rates were calculated on a dry weight or per fruit basis. Fruit photosynthetic rates were determined by taking the difference between CO_2 evolution in the light and dark. Immediately after a set of measurements, the fruit was harvested and dried at 75°C; the dry weight was then determined.

Results

Seasonal CO_2 exchange patterns of peach fruits

Fruit CO_2 exchange rates per unit dry weight in light (1 200 µmol photons m^{-2} s^{-1}) and in dark decreased over the season. Since fruit gas exchange rates (CO_2 evolution) followed the same seasonal pattern at different temperatures, the pattern at 25°C was chosen as a representative example (Fig. 1A). However, fruit CO_2 exchange rates increased with rising temperatures as described below (temperature response curves). The first data point represented only one set of measurements. Fruit gas exchange rates exhibited a similar pattern in the 1989 and 1990 growing seasons. Slightly positive net photosynthetic rates ranging from 0.087 ± 0.06 to 0.003 ± 0.05 nmol CO_2 (g dry weight)$^{-1}$ s^{-1} were measured in midseason, between 104 and 115 days after flowering (DAF), at 20 and 25°C and at a PPFD of 1 200 µmol photons m^{-2} s^{-1}. Since CO_2 exchange rates were quite similar for the 1989 and 1990 growing seasons, the data were pooled; CO_2 exchange rates per fruit in light and dark and photosynthetic rates were calculated for the entire growing season. Dark respiration rates per fruit increased rapidly early in the season (24–55 DAF) and remained relatively constant at midseason (55–125

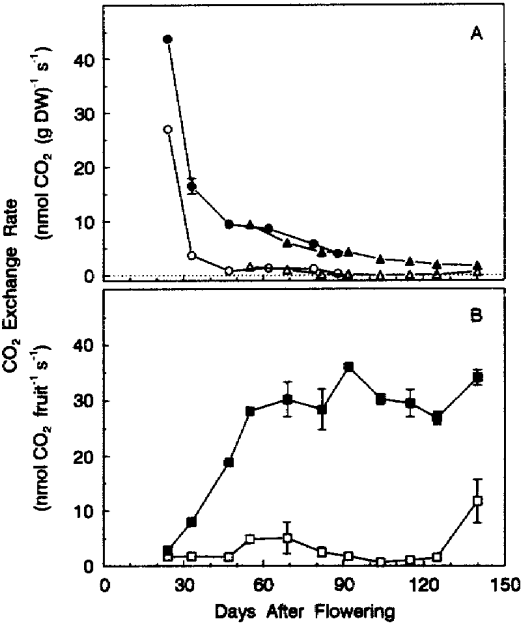

Fig. 1. Fruit CO_2 exchange rates per unit dry weight (A) and per fruit (B) of late-maturing cv. Cal Red peaches at 25°C and at 1 200 (open symbols) and 0 (closed symbols) µmol photons m^{-2} s^{-1} (PPFD) during the 1989 (△, ▲) 1990 (○, ●) and 1989/90 (□, ■; data were pooled for both years in Fig. 1B) growing seasons (mean ± SE of 3–4 measurements except for the data points at 24 DAF; SE bars are visible when larger than the symbols depicting data points).

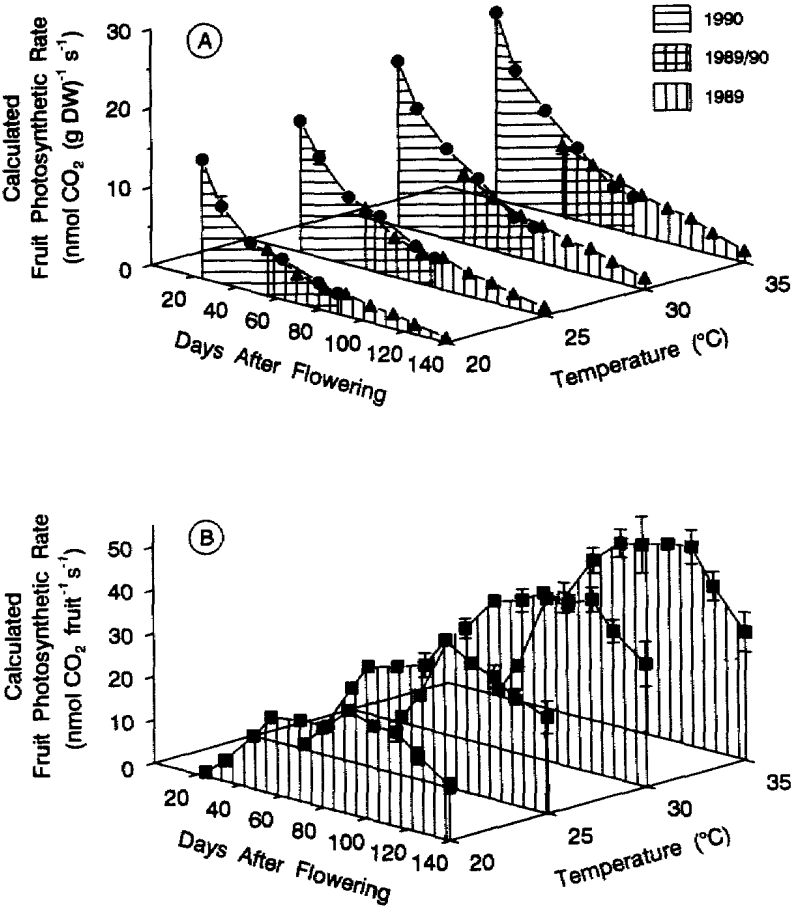

Fig. 2. Calculated fruit photosynthetic rates (difference between CO_2 evolution at 1200 µmol photons m^{-2} s^{-1} and in dark) per unit dry weight (A) and per fruit (B) of late-maturing cv. Cal Red peaches at 20, 25, 30 and 35°C during the 1989 and 1990 growing seasons (mean ± SE of 3–4 measurements; SE bars are visible when larger than the symbols depicting data points).

DAF), while CO_2 exchange rates per fruit in light continued to be low during that time (Fig. 1B). CO_2 exchange rates in light and dark increased in mature fruits.

Fruit photosynthetic rates per unit dry weight, calculated by subtraction of CO_2 exchange rates at 1200 µmol photons m^{-2} s^{-1} from dark respiration rates, declined over the season at the different temperatures (Fig. 2A). Calculated photosynthetic rates per fruit increased between 24 and 69 DAF, remained fairly constant between 69 and 115 DAF, and then declined in maturing fruits (Fig. 2B). Calculated photosynthetic rates per unit dry weight and per fruit increased with rising temperatures.

Seasonal fruit CO_2 exchange responses to temperature, light and CO_2 concentration

Fruit CO_2 exchange rates per unit dry weight in the light and dark increased as temperatures increased from 15 to 35°C, but the response decreased over the season both in light and dark (Fig. 3). The highest CO_2 exchange rates in light and dark were measured at 35°C. Dark respiration rates doubled between temperature intervals of 10°C. The seasonal mean Q_{10} value, calculated for the interval between 20 and 30°C, was 2.03 ± 0.05.

Fruit CO_2 exchange rates per unit dry weight decreased with increasing PPFD during development (Fig. 4). At any given PPFD, fruit CO_2 exchange rates were generally greater at higher temperatures than at lower temperatures.

Calculated fruit photosynthetic rates increased with increasing light flux densities during the entire fruit growing period (Fig. 5). At 15°C, young peach fruits showed no significant response in their photosynthetic rates to PPFDs above 600 µmol photons m^{-2} s^{-1}. However, at higher temperatures (25 and 35°C) calculated fruit photosynthetic rates continued to increase between 600 and 1200 µmol photons m^{-2} s^{-1}.

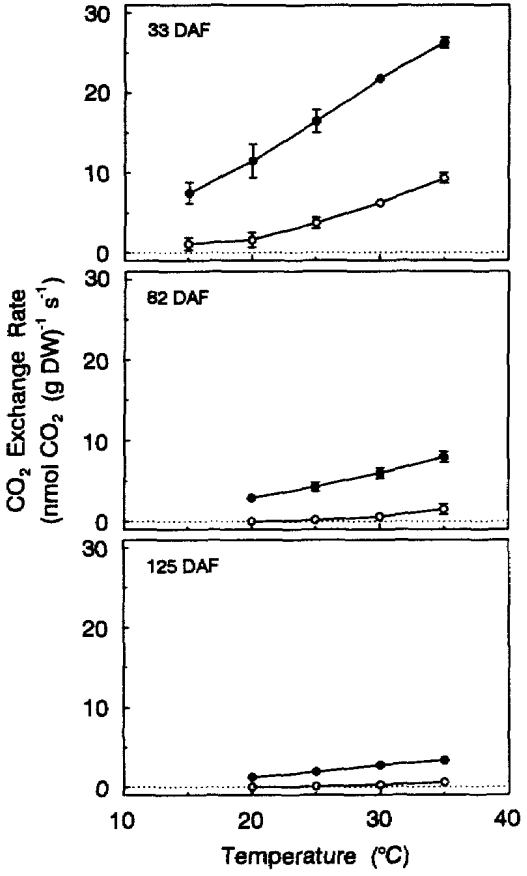

Fig. 3. Fruit CO_2 exchange rates per unit dry weight of late-maturing cv. Cal Red peaches in response to temperature at 1 200 (○) and 0 (●) μmol photons m^{-2} s^{-1} (PPFD) and at 33, 82 and 125 DAF (mean ± SE of 3–4 measurements; SE bars are visible when larger than the symbols depicting data points).

Immature peach fruits responded to increasing ambient CO_2 concentrations with decreasing CO_2 exchange rates per unit dry weight in light (1 200 μmol photons m^{-2} s^{-1}), but no change in CO_2 exchange rates was found in more mature fruits from 131 DAF until harvest (Fig. 6). Fruits exposed to dark showed no response in their respiration rates to changing CO_2 concentrations.

Calculated fruit photosynthetic rates indicated even more clearly that young fruits responded to increasing CO_2 concentrations with increasing photosynthetic rates (Fig. 7). In mature fruits, however, photosynthetic rates remained nearly constant even when CO_2 concentrations were increased. Photosynthetic rates of young fruits (40 DAF) approached saturation at ambient CO_2 concentrations of 370 μl CO_2 l^{-1}.

In nearly CO_2-free air (20 μl CO_2 l^{-1}) fruit photosynthetic rates appeared to be supplied by internal CO_2 concentrations (CO_2 refixation), since no significant CO_2 uptake from the external atmosphere could occur. Considering that at 370 μl CO_2 l^{-1} the fruit photosynthetic response curve was saturated and that in nearly CO_2-free air (20 μl CO_2 l^{-1}) no CO_2 uptake from the external atmosphere took place, then the increase of photosynthetic rates between these two CO_2 concentrations was apparently provided from the CO_2 uptake by the fruit from the external atmosphere. The CO_2 uptake by developing peach fruits contributed 28, 19 and 16% of the photosynthetic rate per unit dry weight at 40, 65 and 87 DAF, and CO_2 refixation accounted for 72, 81 and 84%, respectively (Fig. 8). However in more mature fruits (131 DAF until harvest), fruit photosynthetic rates were solely supplied by CO_2 refixation and there was no net CO_2 uptake from the external atmosphere by the fruit.

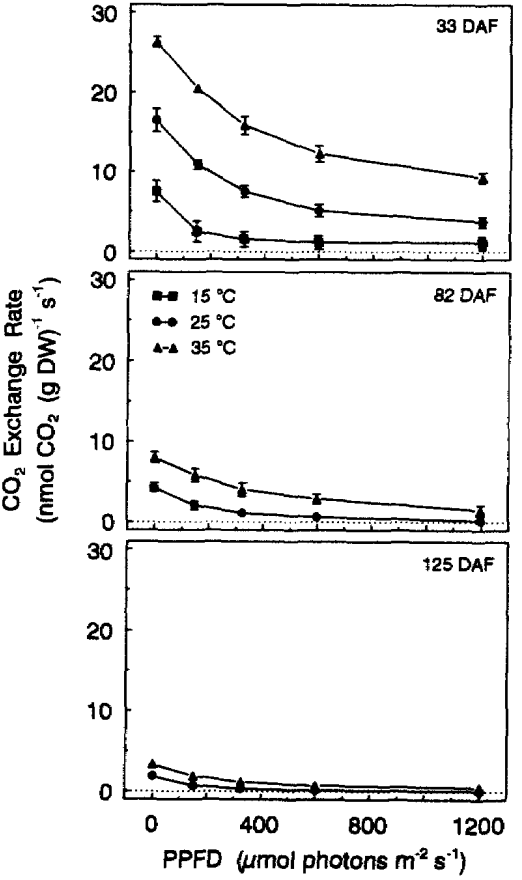

Fig. 4. Fruit CO_2 exchange rates per unit dry weight of late-maturing cv. Cal Red peaches in response to light at 15 (early in the season), 25 and 35°C and at 33, 82 and 125 DAF (mean ± SE of 3–4 measurements; SE bars are visible when larger than the symbols depicting data points).

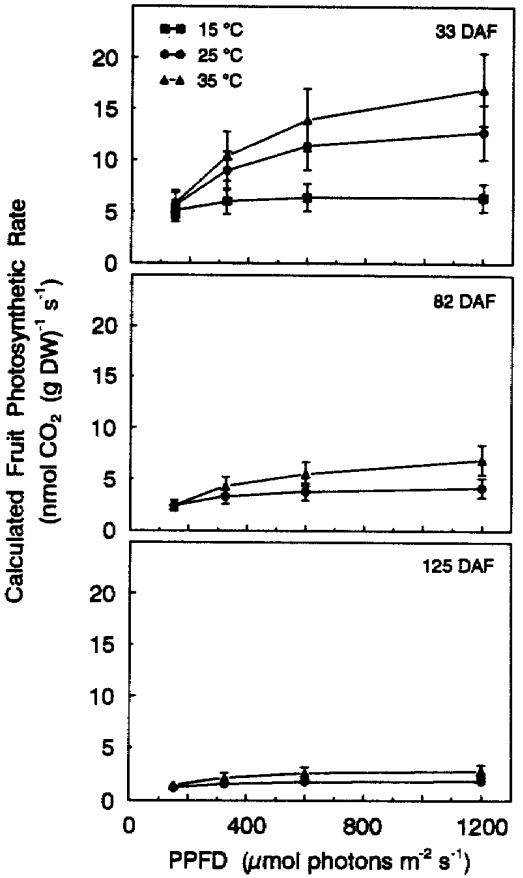

Fig. 5. Fruit photosynthetic rates per unit dry weight of late-maturing cv. Cal Red peaches, calculated from data in Fig. 4, in response to light at 15 (early in the season), 25 and 35°C and at 33, 82 and 125 DAF (mean ± SE of 3–4 measurements; SE bars are visible when larger than the symbols depicting data points).

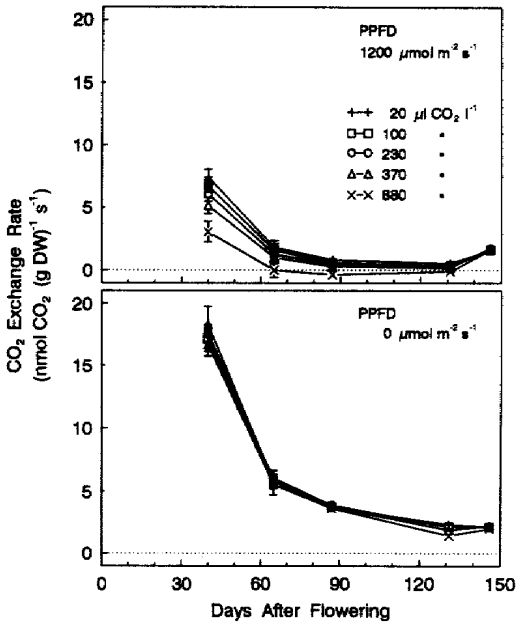

Fig. 6. Fruit CO_2 exchange rates per unit dry weight of late-maturing cv. Cal Red peaches in response to CO_2 concentration at 25°C and at 1200 and 0 μmol photons $m^{-2} s^{-1}$ (PPFD) during the growing season (mean ± SE of 3–4 measurements; SE bars are visible when larger than the symbols depicting data points).

Discussion

Dark respiration rates per unit dry weight of the late-maturing Cal Red peach cultivar declined over the season as described by DeJong et al. (1987) and as shown for several other fruits (Geisler and Radler 1963, Jones 1981, Walton and DeJong 1990). The seasonal patterns of peach fruit gas exchange were quite similar in both 1989 and 1990. The CO_2 production of peach fruits exposed to light was generally reduced in comparison to that in dark as was found in apple (Clijsters 1969) and grape (Koch and Alleweldt 1978). Fruit gas exchange rates in light (1200 μmol photons $m^{-2} s^{-1}$) and calculated photosynthetic rates per unit dry weight followed a pattern similar to that reported for apple by Jones (1981) and Lenz and Noga (1982) and for grape by Koch and Alleweldt (1978). Slight net fruit photosynthetic rates were measured at midseason under optimal temperature (20 and 25°C) and light (1200 μmol photons $m^{-2} s^{-1}$) conditions as has been reported for apple fruits and pea pods (Flinn et al. 1977, Noga and Lenz 1982). In comparison to peach and apple, relatively high net

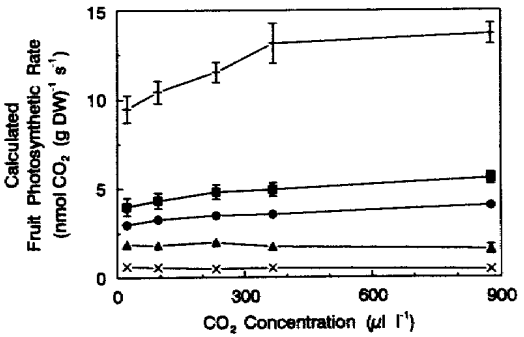

Fig. 7. Fruit photosynthetic rates per unit dry weight of late-maturing cv. Cal Red peaches, calculated from data in Fig. 6, in response to CO_2 concentration at 25°C and at 40 (+), 65 (■), 87 (●), 131 (▲) and 146 (×) DAF (mean ± SE of 3–4 measurements; SE bars are visible when larger than the symbols depicting data points).

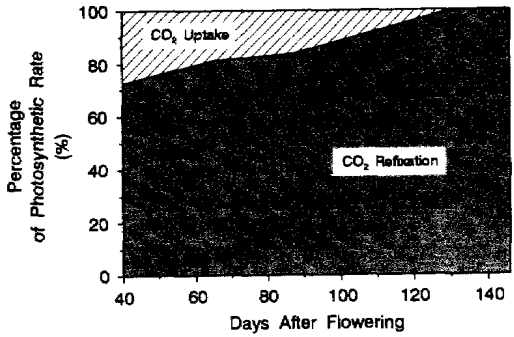

Fig. 8. CO_2 uptake and CO_2 refixation as a percentage of calculated fruit photosynthetic rates during the growing season calculated from data in Fig. 7.

photosynthetic rates occur in young, green blueberries (Birkhold et al. 1992).

The pattern of dark respiration rates per fruit early in the season (24–55 DAF) and in mature fruits (125 DAF until harvest) was similar to that of fruit dry matter accumulation (Pavel and DeJong 1993). The rapid increase of dark respiration rates may be related to high metabolic activities in young and mature fruits. CO_2 exchange rates per fruit at 1 200 μmol photons m^{-2} s^{-1}, however, remained consistently low up to 125 DAF but then increased rapidly in mature fruits, coinciding with high dry matter accumulation (DeJong et al. 1987). Calculated photosynthetic rates per fruit increased with increasing fruit dry matter until fruit began to mature. The decline of fruit photosynthetic rates about 4 weeks before harvest appeared to be related to the changes in fruit color. Carotenoid and anthocyanin concentrations of the peel increase in ripening apple fruits, whereas the chlorophyll concentration continuously decreases (Knee 1972).

Peach fruits responded to increasing temperatures with increasing CO_2 exchange rates in light and in dark during their development, although fruit CO_2 exchange rates decreased over the season. A similar temperature response has been found in apple, cherry and citrus fruits (Bean et al. 1963, Jones 1981, Kappes 1985, Noga and Lenz 1982). The mean seasonal Q_{10} value of 2.03 ± 0.05 was slightly higher than that reported by DeJong et al. (1987). The continuously increasing rates of calculated fruit photosynthesis rates up to 35°C are in contrast to assimilation rates of peach and grape vine leaves that have a temperature optimum between 25 and 32°C (Crews et al. 1975, Kriedemann 1968b). High temperatures increased dark respiration rates to a greater extent than CO_2 exchange rates in light. It appears that high temperatures increase dark respiration rates and, therefore, internal CO_2 concentrations of peach fruits, and this may stimulate fruit photosynthesis via CO_2 refixation. Flinn et al. (1977) found that, at night, internal CO_2 concentrations of pea pods are primarily influenced by temperature and fruit age, whereas during the day they are also affected by the radiant flux intercepted by the fruit.

CO_2 exchange rates of developing peach fruits decreased and calculated photosynthetic rates increased in response to increasing photon flux densities as reported for apples, cherries and citrus fruits (Bean et al. 1963, Clijsters 1969, Kappes 1985, Moreshet and Green 1980, Noga and Lenz 1982). At 35°C, calculated fruit photosynthetic rates continued to increase as light increased from 600 to 1 200 μmol photons m^{-2} s^{-1}. In comparison to peach fruits, net assimilation rates of peach, cherry, plum and apricot leaves approach light saturation between 400 and 700 μmol photons m^{-2} s^{-1} (Crews et al. 1975, DeJong 1983). At 15°C, there was only a slight increase of calculated fruit photosynthetic rates between 600 and 1 200 μmol photons m^{-2} s^{-1}, indicating that low temperatures may limit the photosynthetic response of peach fruits to light.

Peach fruits exposed to light responded to changes in ambient CO_2 concentrations between 40 and 131 DAF, but maturing fruits did not respond. CO_2 exchange rates of illuminated fruits decreased with increasing ambient CO_2 concentrations in a trend similar to that reported in apple (Noga and Lenz 1982) and pea pods (Hole 1977). No significant gas exchange response to CO_2 occurred in developing peach fruits exposed to dark as was reported for pea pods by Hole (1977). Calculated fruit photosynthetic rates increased with increasing ambient CO_2 concentration between 40 and 131 DAF in a manner similar to that reported for apples by Noga and Lenz (1982) and for cherries by Kappes (1985). However, maturing fruits showed no response to CO_2 and apparently did not take up CO_2 from the external atmosphere because of high internal CO_2 concentrations as has been reported for several fruits and legume pods (Burg and Burg 1965, Flinn et al. 1977, Henze 1969). Photosynthetic rates of younger fruits appeared to approach saturation at 370 μl CO_2 l^{-1}. Peach fruits showed responses to CO_2 similar to those reported for C_3 leaves (DeJong 1983, Hellmuth 1971) and as suggested by Kappes (1985) for cherry fruits and by Noga and Lenz (1982) for apple fruits. In CO_2-free air, fruit photosynthesis seemed to be supported entirely by CO_2 refixation, since no net CO_2 uptake from the external atmosphere occurred. The difference in photosynthetic rates between CO_2-free air and 370 μl CO_2 l^{-1} indicates that young peach fruits were apparently able to take up CO_2 from the external atmosphere as reported for citrus, apricot and apple fruits (Hansen 1971, Kriedemann 1968a, Moreshet and Green 1980).

Several researchers suggest that the CO_2 metabolism of fruits and legume pods exhibit similarities to those of C_4 and/or Crassulacean Acid Metabolism (CAM) plants. High activities of phosphoenolpyruvate carboxylase and carboxykinase have been found in reproductive tissues (Atkins et al. 1977, Blanke et al. 1988, Edwards

and Walker 1983, Farineau and Laval-Martin 1977, Willmer and Johnston 1976), but there is little evidence that those enzyme activities are related to photosynthesis in fruit tissues. Kriedemann (1968c) found no evidence for CAM in grape berries, and the photosynthetic metabolism in sour cherry apparently indicates C_3 characteristics (Kappes 1985). CO_2 exchange responses of developing peach fruits to temperature, light and CO_2 did not rule out C_4-type photosynthesis in peach fruits, but the CO_2 response curves are more similar to that expected for C_3 photosynthesis.

The present research points out that peach fruits respond to temperature and light over the growing season as analyzed by fruit CO_2 exchange rates. Young peach fruits responded to ambient CO_2 concentrations and were apparently able to take up CO_2 from the external atmosphere. As the season progressed, the CO_2 uptake from the external atmosphere by the fruit decreased and the majority of calculated fruit photosynthetic rates was apparently supplied by CO_2 refixation.

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