one-year-old stems (1.3 nmol $CO_2$ $g_{dw}^{-1}$ $s^{-1}$), and about 30 times greater than that of the trunk $R_{20}$ (0.1 nmol $CO_2$ $g_{dw}^{-1}$ $s^{-1}$). The $Q_{10}$s of leaves and stems were approximately 2 for a temperature increase between 20 and 30. The $Q_{10}$s above 30 were 2.03 for leaves but only 1.61 for stems. Leaves and

measurements near 12 and 35 °C were made on some dates. Most measurements were replicated 6–8 times.

Leaves or stems were enclosed in a cylindrical, temperature-controlled, stirred cuvette described by DeJong (1983) and DeJong et al. (1987). Because measurements were made during the day, the cuvette was covered with aluminum foil and opaque cloth. The temperature of the enclosed tissue was controlled to within 0.5 °C by circulating water from a temperature-controlled water bath through a heat exchange plate in the cuvette. Cuvette temperature was measured to the nearest 0.1 °C with type E (chromel-constantan) thermocouples and a digital thermocouple thermometer (Model 2190A, John Fluke Manufacturing Co., Inc., Everett, WA).

Gas exchange measurements were made after steady state had been maintained for at least 15 min. The $CO_2$ concentrations of the air exiting the cuvette and the reference air were measured with an infrared gas analyzer in differential mode (225 MK III, ADC Ltd., Hoddeson, Herts., UK). Flow rates were controlled and measured with electronic mass flow controllers (FC-26, Tylan Inc., Carson, CA).

Immediately after each set of measurements, the tissue was dried at 70 °C for 48 h. Respiration was expressed as a specific respiration rate (nmol $CO_2$ $g_{dw}^{-1}$ $s^{-1}$).

*Respiration measurements: trunks*

Trunk respiration rates were determined during the spring and fall of 1991 with the gas exchange apparatus. The cuvette was replaced by a two-piece Plexiglas box (23 × 23 × 10 cm) that was attached to the tree trunk approximately 30 cm above the soil line. The box was sealed to the trunk with wax (Master Plumber Bol-Wax #1, Cotter and Company, Chicago, IL), and covered with aluminum foil and opaque cloth.

Trunk respiration measurements were made when ambient temperatures were near 20 °C. Trunk temperature was determined from a shaded thermocouple taped to the trunk immediately below the box. Five replicate measurements were made in both the spring and fall.

The volume of the enclosed trunk section was converted to dry weight using the average density (0.54 mg $mm^{-3}$) of similar sections of trunk from five trees that were destructively harvested in the fall (see next section).

*Standing biomass*

The standing biomass of five fruited trees was determined. Fruit yield per tree was recorded at harvest in August 1991. Trunk circumference at 40 cm above the soil line was measured in March and October 1990 and October 1991.

In October 1991, the tree trunks were sawn through just above the ground line. An area 4 × 2 m around each tree was excavated by backhoe to a depth of 2 m. The soil was thoroughly sifted with shovels to remove all the roots. Tree biomass was separated into leaves, current-year stems, branches, trunk, stump, and roots. The branch classification included all stems one-year-old and older that were less than 10 mm in diameter. The trunk classification included the central leader and the larger one-year-old and older stems. Roots were severed as close to the stump as possible. After recording fresh weights for each organ type, subsamples were weighed, dried

to constant weight at 70 °C, and reweighed.

*Annual biomass increment*

The annual increments of current-year stems and leaves were determined directly from the standing biomass data; that of fruits was obtained from the weight of fruits harvested from the sample trees in August. The annual increment of the trunk was estimated by determining the percent increase in trunk cross-sectional area at 40 cm above the soil from October 1990 to October 1991. In the absence of other data, it was assumed that the same factor applied to the branches, stump, and roots.

*Data analysis*

Shoot, leaf and stem specific respiration data were standardized to 12, 20, 30, and 35 °C with data from the measurements near these temperatures and the temperature response determined for each organ. Organ, temperature, and time of year effects were tested with standard techniques of analysis of variance for unbalanced designs (SAS GLM procedure, SAS Institute, Inc., Cary, NC). Temperature effects were studied with a repeated measures design. Values of $Q_{10}$ were calculated by Van't Hoff's reaction rate/temperature rule (Larcher 1980):

$$Q_{10} = \exp\left[(\ln[\mathrm{resp}T_2] - \ln[\mathrm{resp}T_1])\left(\frac{10}{(T_2 - T_1)}\right)\right],$$

where resp$T_1$ and resp$T_2$ represent specific respiration rates at temperatures $T_1$ and $T_2$, respectively. Values of $Q_{10}$ for the temperature increase from 20–30 °C ($Q_{10,(20-30)}$) were calculated from respiration measurements near 20 and 30 °C. Values of $Q_{10,(30-40)}$s were calculated from respiration measurements near 30 and 35 °C, because of difficulty in maintaining tissue at 40 °C. Trunk specific respiration rates were standardized to 20 °C using the average $Q_{10,(20-30)}$ for stem respiration.

*Leaf, stem, and trunk daily (24 h) respiration*

The seasonal patterns of current-year stem, leaf, and trunk growth determined during 1990 and 1991 (Grossman 1993) and the end-of-season standing biomass data were used to estimate the standing biomass of each organ type on the dates in 1991 when respiration measurements were made. Daily temperature patterns were simulated for each sample period by averaging the minimum and maximum temperatures for one week in 1990 corresponding to the developmental stage at which respiration measurements were made in 1991. Developmental stage was determined with a degree-day index, which uses time and temperature to predict growth (Zalom et al. 1983, DeJong and Goudriaan 1989, Grossman 1993). Temperature data were obtained from the California Irrigation Management System (CIMIS) weather station located at the Kearney Agricultural Center. Daily temperature patterns were simulated with an algorithm that assumed a sinusoidal curve for day temperature, and an exponential decrease for night temperature (van Kraalingen and Rappoldt 1987).

Daily (24 h) specific respiration rates for each organ type were estimated at hourly

intervals from the temperature curves, the specific respiration rates determined for 20 and 30 °C, and the $Q_{10}$s. One-year-old stem specific respiration rates were used to estimate respiration by small branches less than 10 mm in diameter. Trunk specific respiration rates were used to estimate respiration by branches greater than 10 mm in diameter. Standing organ dry weight was multiplied by daily organ-specific respiration to obtain estimates of daily respiration by organ type.

## Results and discussion

### *Seasonal patterns of specific respiration rate at 20 °C*

The trees reached full bloom on March 6, 1991. Vegetative bud break began about one week after bloom (50 degree-days after bloom), and significant shoot extension was apparent by 5 weeks after bloom (200 degree-days) (Grossman 1993). Specific respiration rates at 20 °C ($R_{20}$) of young shoots declined from high rates early in the growing season to relatively constant rates by July (Figure 1). The highest $R_{20}$ recorded was that of young leaves and stems (shoots) during the early stages of shoot extension shortly after vegetative bud break (Figure 1). The current-year stem $R_{20}$ was significantly higher than that of leaves in May, but no differences were detected later in the season. The $R_{20}$s of one-year-old stems were always significantly lower than those of current-year stems and leaves. Trunk $R_{20}$s in the spring and fall were similar, and were much lower than the $R_{20}$s of the other organs.

Leaf and current-year stem $R_{20}$s were similar in magnitude to those reported for apple leaves and stems (Proctor et al. 1976) and mature leaves of tall fescue and cotton, but they were only 30–50% of the $R_{20}$s reported for mature leaves of alfalfa, barley, potato, and ryegrass (summarized in Amthor 1989). Peach leaves have a low specific leaf area, and are somewhat more xeromorphic than alfalfa, barley, potato, and ryegrass leaves (Grossman, unpublished data). This suggests that, on a unit weight basis, peach leaves have proportionately more inert structural material (e.g.,

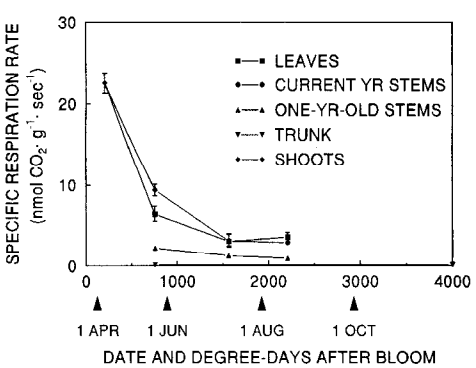


Figure 1. Seasonal patterns of specific respiration rates of leaves, current-year stems, one-year-old stems, and trunks of the mid-August maturing peach cultivar, Cal Red. Symbols represent the mean ± one standard error. The shoot respiration rate for April represents measurements on young leaves and stems shortly after vegetative bud break.

cell walls) than more mesophytic crop plants. Leaves with a greater proportion of inert material would likely have lower maintenance respiration requirements than mesophytic leaves, explaining the relatively low leaf $R_{20}$ found in this study.

The rate of decline of peach leaf and stem $R_{20}$ through the growing season was comparable to that of peach fruits (DeJong et al. 1987, Pavel and DeJong 1993), and qualitatively similar to that reported for apple (Butler and Landsberg 1981), *Pinus sylvestris* L. (Linder and Troeng 1980), *Nothofagus truncata*, and *Pinus radiata* D. Don (Benecke 1985).

The relative growth rates of leaves and stems declined from high rates in the early spring, following vegetative bud break, to lower rates later in the season (Grossman 1993). The high rate of growth respiration associated with a high relative growth rate explains the high $R_{20}$ recorded in the early spring (Thornley 1976, Amthor 1989). The more rapid decline of leaf $R_{20}$ compared to current-year stem $R_{20}$ probably resulted from a more rapid rate of tissue maturation in the leaves, and thus, a decrease in the rate of growth respiration. Because stems continued to increase in dry weight throughout the growing season, even after shoot extension had ceased (Grossman 1993), the observed stem respiration included growth respiration on all measurement dates.

Later in the season, leaf and current-year stem $R_{20}$s were not significantly different. At this time, leaves were not growing and the observed $R_{20}$ was due to maintenance respiration. However, current-year stems increased in dry weight and the observed $R_{20}$s were due to a combination of growth and maintenance respiration. Taken together, these data suggest that the maintenance respiration rate of leaves probably exceeded that of stems. The higher maintenance requirement of leaves may be due to the carbohydrate cost of maintaining the carbon fixation, compartmentation, and transport functions of the leaves.

The proportion of current-year stem $R_{20}$ due to growth probably remained constant throughout the growing season, because dry weight gain per unit stem length was nearly linear during the entire season (Grossman 1993). Linder and Troeng (1980) examined diameter increases rather than dry weight gains in *Pinus sylvestris* stems and found that the maximum respiration rate occurs one month after the maximum rate of diameter increase. This was attributed to the secondary and tertiary cell wall thickening that takes place after the stems increase in volume.

Young peach stems have a thick cortex surrounding the vascular cylinder (unpublished micrographs). One layer of the cortex contains chloroplasts. The xylem is characterized by frequent, narrow rays of parenchyma cells separating files of xylem vessels and fibers. The pith, containing parenchyma cells, is interior to the xylem. Most of the cells of the cortex and pith are living, as are those of the xylem ray parenchyma, phloem, and cambium. As the stem ages, additional rings of xylem are added, decreasing the proportion of living cells. Thus, the monotonic decrease in $R_{20}$ from current-year stems to that of one-year-old stems and trunk is probably explained by the decreased proportion of living cells per unit weight, resulting in a decrease in the rate of maintenance respiration per unit weight (Jarvis and Leverenz 1983).

*Temperature response of specific respiration rates*

Specific respiration rates increased with increasing temperature. Figure 2 shows the temperature responses of leaves, current-year stems, and one-year-old stems during May. Repeated measures analysis of variance on $Q_{10,(20-30)}$ and $Q_{10,(30-40)}$ indicated that there were significant range differences within tissues and between tissues (Hotelling-Lawley Trace, $P < 0.001$), but not with time of year. No difference was found between $Q_{10,(20-30)}$ and $Q_{10,(30-40)}$ for leaves, but $Q_{10,(20-30)}$ was significantly greater than $Q_{10,(30-40)}$ for stems (Table 1). No differences were detected between organs for $Q_{10,(20-30)}$, but $Q_{10,(30-40)}$ was significantly greater for leaves than for stems. Because no differences were detected between tissues for $Q_{10,(20-30)}$, the overall mean of 2.00 was used in all calculations of specific respiration rates for temperatures less than 30 °C. Because of the differences in $Q_{10,(30-40)}$ for leaves and stems, mean values of 2.03 for leaves and 1.61 for stems were used in all calculations of specific respiration rates for temperatures greater than 30 °C.

Similar $Q_{10}$s for temperature changes between 20 and 30 °C have been reported for peach fruits (1.90–1.92, DeJong et al. 1987; 2.03, Pavel and DeJong 1993), roots of *Abies lasiocarpa* (Hook.) Nutt. and *Picea engelmannii* Parry (2.0, Sowell and Spomer 1986), and others (summarized in Amthor 1989). Somewhat higher values for $Q_{10,(20-30)}$ have been reported for apple trees (2.32, Butler and Landsberg 1981), and leaves of *Nothofagus truncata* (2.33) and *Pinus radiata* (2.26, Benecke 1985).

A decrease in $Q_{10}$ above 25–30 °C has been reported for some plants (Larcher 1980, Lambers 1985). Maintenance respiration increases exponentially with increas-

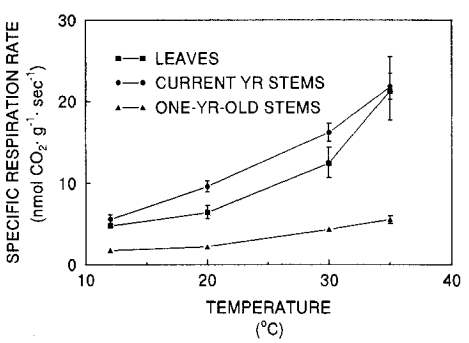


Figure 2. Temperature response of specific respiration rates of leaves, current-year stems, and one-year-old stems in May. Symbols represent the mean ± one standard error.

Table 1. Mean $Q_{10}$s for temperature increases from 20 to 30 °C and from 30 to 40 °C for leaves, current-year stems, and one-year-old stems of peach. Means followed by different letters are significantly different from one another (Tukey's Studentized Range Test, $P < 0.05$).

| | Leaves | Current-year stems | One-year-old stems |
|---|---|---|---|
| $Q_{10,(20-30)}$ | 2.11a | 1.95a | 1.96a |
| $Q_{10,(30-40)}$ | 2.03a | 1.54c | 1.68c |

ing temperature over a fairly broad range; however, the response of growth rate and growth respiration to increasing temperature is not as simple, often failing to increase at the same exponential rate as maintenance respiration (Amthor 1989). A decrease in $R_{20}$ was apparent for stems but not for leaves. Stem respiration included both growth and maintenance respiration, whereas leaf respiration in May, July, and August was primarily maintenance respiration.

No effect of time of year on $Q_{10}$ was detected. Similarly, no trend was detected in $Q_{10}$ for *Nothofagus truncata* or *Pinus radiata* (Benecke 1985). In contrast, the $Q_{10}$ of *Chamaecyparis obtusa* Endl. exhibited a seasonal fluctuation between 1.4 and 3.4, with higher values in winter than in summer (Hagihara and Hozumi 1991). The monthly $Q_{10}$ value showed a negative linear relationship with mean monthly air temperature. Because this study was carried out from April to August, it is not possible to determine whether the $Q_{10}$ of peach vegetative organs changes over the annual range of temperatures.

*Seasonal temperature and respiration patterns*

The daily patterns of temperature and specific respiration rate for current-year stems in July and August were similar (Figure 3). Similar patterns were observed for all organs on all dates (data not shown). The current-year stem $R_{20}$s for July and August were not significantly different, although the higher July temperatures resulted in a higher specific respiration rate in July than in August. The exponential nature of the increase in specific respiration rate with increasing temperature produced a greater divergence in the specific respiration rates at midday than at midnight. The rate of

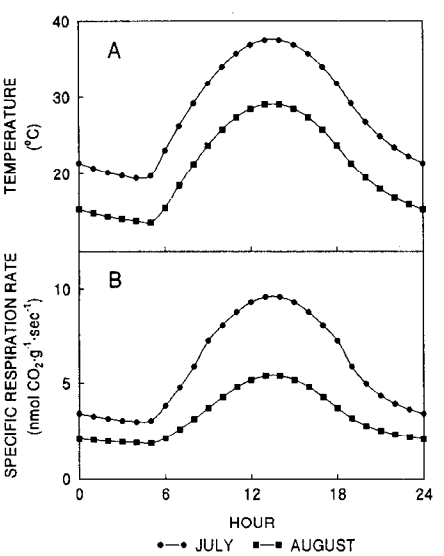


Figure 3. Simulated daily patterns of temperature and specific respiration rate. A: Daily pattern of temperature simulated from average minimum and maximum temperatures for one week in July and August 1990, at the Kearney Agricultural Center, Parlier, California. B: Simulated daily patterns of specific respiration rate for current-year stems in July and August.

increase in specific respiration rate slowed at temperatures above 30 °C because $Q_{10,(20-30)}$ was greater than $Q_{10,(30-40)}$ for stems.

*Standing biomass and annual biomass production*

The standing biomass in October and annual biomass production at the end of the growing season of fruited trees are presented in Table 2. Leaves, current-year stems and fruits accounted for 6, 2 and 16% of the standing biomass, and 21, 8, and 52% of the annual biomass production, respectively. Seventy-six percent of the standing biomass was accounted for by the tree structure (trunk, branches, stump and roots), but only 19% of the annual biomass production was added by these organs.

Table 2. Standing biomass in October and current-year biomass production of fruited trees of the late maturing peach cultivar, Cal Red.

| Organ | Biomass | | Current-year production | |
|---|---|---|---|---|
| | Dry weight (g)[1] | Percent | Dry weight (g) | Percent |
| Leaves | 1930 (149) | 6.2 | 1930 | 20.6 |
| Current-year stems | 761 (139) | 2.4 | 761 | 8.1 |
| Fruits | 4919 (169) | 15.8 | 4919 | 52.4 |
| Branches | 844 (29) | 2.7 | 64 | 0.7 |
| Trunks | 13470 (822) | 43.3 | 1018 | 10.8 |
| Stumps | 3536 (351) | 11.4 | 267 | 2.8 |
| Roots | 5671 (263) | 18.2 | 429 | 4.6 |
| Total | 31131 (1249) | 100.0 | 9388 | 100.0 |

[1] Standard error of the mean in parenthesis.

*Summary of respiration by organ type*

Leaf and current-year stem biomass increased rapidly between April and May (Figure 4A). Leaf biomass reached an asymptote by July, whereas current-year stem biomass continued to increase throughout the season. Branch (stems one-year-old and older and less than 10 mm in diameter) and trunk biomass increased much more slowly than leaf and current-year stem biomass.

Daily (24 h) respiration by organ type did not follow a simple pattern (Figure 4B). Daily respiration by aboveground vegetative organs was higher in April than in May, due to the high $R_{20}$ of young shoots (Figure 1), and highest in July, when temperatures were highest (Table 3, Figure 4B). The $R_{20}$s decreased throughout the season, but increased biomass and temperature tended to increase daily respiration.

Leaves and current-year stems, organs that were produced entirely in the current year, accounted for only 2 and 17% of the aboveground vegetative biomass in April and August, respectively (Figure 4). However, they accounted for 59–80% of daily respiration by aboveground vegetative organs throughout the season. Between May and August, leaves accounted for 10–11% of the aboveground vegetative biomass and 55–61% of the daily respiration by aboveground vegetative organs. In contrast, trunk biomass accounted for 91 and 77% of the aboveground vegetative biomass in

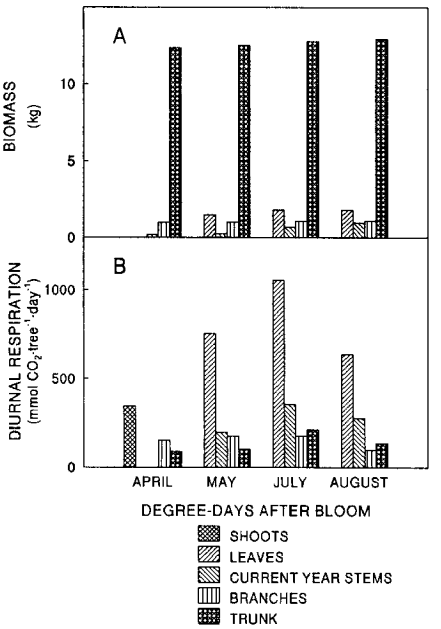


Figure 4. Seasonal patterns of standing vegetative biomass and daily respiration. A: Seasonal pattern of standing biomass of leaves, current-year stems, branches (one-year-old and older and < 10 mm in diameter), and trunks of a mid-August maturing peach cultivar, Cal Red. B: Seasonal pattern of aboveground vegetative respiration per tree per day by organ type. For the April sample period, the value for shoots represents the sum of leaf and current-year stem respiration.

Table 3. Dates, number of degree-days after bloom, and average minimum and maximum temperatures for each sampling period.

| Dates | Degree-days after bloom | Average minimum temperature (°C) | Average maximum temperature (°C) |
|---|---|---|---|
| April 6–12, 1990 | 188–244 | 7.94 | 24.68 |
| May 14–20, 1990 | 624–785 | 8.81 | 26.19 |
| July 8–14, 1990 | 1411–1539 | 19.21 | 37.62 |
| August 15–21, 1990 | 2175–2261 | 13.66 | 29.12 |

April and August, respectively, but accounted for only 8–15% of the daily respiration.

To evaluate the effect of respiration by aboveground vegetative organs on the carbon economy of the tree, daily vegetative respiration was compared to reproductive respiration. The specific respiration rate of peach fruits decreases through the season (DeJong et al. 1987, Pavel and DeJong 1993). Combining the data of DeJong et al. (1987) with the seasonal patterns of peach fruit growth described in Grossman (1993) indicated that daily fruit respiration increased rapidly from April to July. In April, fruit respiration released 54 mmol $CO_2$ per tree per day, less than the amount respired by the trunk. In May, fruit respiration released 248 mmol $CO_2$ per tree per

day, more than that respired by current-year stems, small branches or trunks, but only 33% of that respired by leaves. By July, shortly before fruit harvest, fruit respiration was slightly more than leaf respiration, releasing 1204 mmol $CO_2$ per tree per day. These results are similar to those of DeJong and Walton (1989) for another two peach cultivars.

In contrast to these results, Proctor et al. (1976) concluded that fruit respiration was small relative to respiration of other organs in young apple trees. However, their fruit specific respiration rates were very low, less than 10% of leaf and stem respiration rates, and about 20% of the specific respiration rates for peach fruit reported by DeJong et al. (1987) and Pavel and DeJong (1993).

Peach fruit growth is source-limited during two periods of the growing season (Grossman 1993). The first period of source limitation occurred early in the growing season when fruit specific respiration rates and relative growth rates were high. The data presented in this study indicated that the specific respiration rates of young leaves and stems were also high during this period (Figure 1). Photosynthate production probably was low at the time because few leaves had expanded (Grossman 1993). The high respiratory demand by the vegetative organs and the low photosynthetic fixation rate probably contributed to the establishment of source-limited growth conditions for the fruits.

The second period of source limitation occurred later in the growing season, in July and August, when the respiratory demand by vegetative organs (Figure 4) and reproductive organs was high. In addition, the high temperatures typical of this period increased the respiration rates of all organs. The fruit absolute growth rate was also high, further increasing the carbohydrate demand. Photosynthate production probably was high during this period because the trees had developed a full canopy. Therefore, it was likely that the large demand for carbohydrate imposed by the respiratory needs of the vegetative and reproductive organs, rather than reductions in the photosynthate supply, led to the development of source-limited fruit growth conditions.

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