

Maximum Fruit Growth Potential and Seasonal Patterns of Resource Dynamics During Peach Growth

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Maximum fruit growth potential, the growth attained by fruits when they are grown under optimal environmental conditions in the presence of a non-limiting supply of resources, was estimated for two peach [*Prunus persica* (L.) Batsch] cultivars that differ in the timing of resource demand for reproductive growth. Maximum potential fruit growth was estimated on trees that were heavily thinned at bloom. On these trees, resource availability exceeded resource demand for fruit growth.

For both cultivars, the mean dry weights of fruits grown on unthinned trees were approximately half the mean dry weights of fruits grown on trees that were heavily thinned at bloom, indicating that fruit growth was source-limited on unthinned trees. Comparison of the seasonal patterns of relative growth rate of fruits on unthinned and heavily thinned trees indicated that source-limited fruit growth occurred during distinct periods of the growing season. On the early maturing cultivar, source-limited fruit growth occurred from 300 degree-days after bloom until harvest (4.5–10 weeks after bloom). On the late maturing cultivar, source-limited fruit growth occurred from 200–900 and 1600–1900 degree-days (3.5–12 and 18–20 weeks) after bloom.

Although the final dry weight of fruits on the early maturing cultivar was only half that of fruits on the late maturing cultivar, the potential net sink strength of fruits was significantly higher on the early than the late maturing cultivar throughout the entire growth period of the early maturing cultivar. Resource availability for fruit growth was similar on the early and late maturing cultivars, indicating that selection for early maturing fruits has not changed the patterns of resource availability for fruit growth.

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Key words: Maximum fruit growth potential, carbon economy, partitioning, resource availability, resource limitation, source-limited growth, sink activity, sink strength, growth analysis, relative growth rate, *Prunus persica* (L.) Batsch, peach.

INTRODUCTION

The availability of carbohydrate resources limits reproductive growth in many plants species (Lloyd, 1980), resulting in decreased flower initiation (reviewed in Monseville and Goldschmidt, 1982), abortion of flowers or immature fruits (reviewed in Stephenson, 1981), or production of smaller fruits (Wright, 1989). This study focuses on the third consequence of resource limitation on reproductive growth: reduction in individual fruit weight.

The availability of carbohydrates to an individual fruit is dependent upon the supply of resources from source organs and the demand for resources by sink organs. Very little is known about the mechanisms governing the partitioning of carbohydrates to individual sink organs (Wardlaw, 1990), however, its importance is underscored by the observation that the majority of historical increases in crop yield have been due to changes in partitioning patterns rather than changes in the rates of photosynthetic carbon assimilation or respiration (Gifford and Evans, 1981).

It is generally agreed that individual sink organs control carbohydrate partitioning by competing with one another based upon their sink demand and the relative ability of the

translocation system to deliver carbohydrates to them (Gifford and Evans, 1981; Ho, Grange and Shaw, 1989; Wardlaw, 1990; Farrar, 1993). Sink demand is the sum of the carbohydrate requirements for maintenance and growth of the sink organ. The bases for sink demand are maintenance respiration and the maximum organ growth potential, the genetically determined growth attained when an organ is grown under optimal environmental conditions in the presence of a non-limiting supply of carbon and other resources (Warren Wilson, 1967, 1972; Wareing and Patrick, 1975; Ho, 1984, 1988). Under these conditions, organ growth is limited only by endogenous characteristics of the organ, and is termed sink-limited growth (Warren Wilson, 1967, 1972; Wareing and Patrick, 1975). In contrast, growth that is limited by resource supply is termed source-limited growth. Although there are many reports of resource limitations on growth over the course of a season (see, for examples, Maggs, 1963; Wareing and Patrick, 1975; Forshey and Elfving, 1989), little is known about the seasonal patterns of resource limitation on growth.

This study characterizes the maximum organ growth potential and the seasonal patterns of resource limitation and resource availability during growth using individual peach [*Prunus persica* (L.) Batsch] fruits as the model system. Peach fruit growth was chosen for this study

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because it is source-limited on unthinned trees (Johnson and Handley, 1989; Pavel and DeJong, 1993*b*). Peach bloom and fruit growth are approximately synchronous and fruit number is set at bloom. That is, experimental manipulations that reduce the number of fruits on a tree after bloom do not cause the production of additional flowers and fruits in the current season. Each inflorescence produces only one fruit, simplifying the potential number of competitive interactions among fruits. As in most perennials, fruit and vegetative growth are simultaneous, suggesting that individual peach fruits compete with other fruits and with vegetative growth for resources (DeJong, Doyle and Day, 1987).

The maximum organ growth potential of individual fruits was determined on trees which were manipulated to create approximately sink-limited conditions for fruit growth (Pavel and DeJong, 1993*b*; Grossman and DeJong, 1995). This maximum fruit growth potential was used to determine the seasonal pattern of resource limitation on fruit growth on unthinned trees. Seasonal patterns of resource availability for fruit growth were assessed on unthinned trees of two peach cultivars that differ substantially in the timing of reproductive growth, with one cultivar maturing its fruits during the period of stem extension and the other maturing its fruits 2 months after the cessation of stem extension.

METHODS

Fruit measurements

The fruits analysed in this study were grown in 1990, on two peach [*Prunus persica* (L.) Batsch] cultivars, Spring Lady and Cal Red, with fruit maturity dates in late May and mid-Aug., respectively. The trees were planted in 1984 at the University of California Kearney Agricultural Center, Parlier, California, USA. Trees were spaced at 4 × 2 m, pruned to retain a vertical central leader with fruit-bearing branches, and topped at 3 m. Routine horticultural care suitable for commercial fruit production was provided, including fertilization, irrigation, pest control, and dormant-season but not summer pruning.

Maximum fruit growth potential was determined using fruits grown on heavily-thinned trees from which most of the flowers were removed at bloom. These trees were further thinned 1 month after bloom. Fruit growth was also measured on trees that were left unthinned. The numbers of fruits harvested from each treatment and cultivar are given in Table 1.

Fruit dry weight was monitored weekly. During the first 4 weeks after bloom, fruit dry weight was determined directly by harvesting two groups of 20 (week 1) or 10

(weeks 2–4) fruits from each of five heavily-thinned and five unthinned trees. Flower parts were removed by dissection, then the fruits were dried at 70 °C, and weighed. Beginning in week 4, fruit dry weight was estimated indirectly from fruit diameter. Suture diameter measurements were made on ten tagged fruits per tree (four in the lower canopy, six in the upper canopy) on each of five heavily-thinned and five unthinned trees with Mitutoyo digital calipers (MTI Corporation, City of Industry, California, USA). Tagged fruits that dropped off were replaced by average sized fruits in a nearby location on the same tree.

On each measurement day, an independent determination of the relationship between fruit diameter and dry weight was made for each treatment using linear regression. Data for the regressions were obtained from additional trees treated in the same manner as the trees with tagged fruits. Five fruits per tree (two from the lower canopy, three from the upper canopy) on each of four trees per treatment were measured on the tree, harvested, dried at 70 °C, and weighed. A sufficient number of trees were available so that the fruit load on the harvest trees never varied more than 20% from that on the trees with tagged fruits. At commercial fruit maturity, tagged fruits were harvested, dried at 55 °C (to prevent sugar caramelization in ripe fruit) and weighed.

Information on ambient air temperatures was obtained from the California Irrigation Management Information System (CIMIS) weather station located at the Kearney Agricultural Center. All data were expressed on the basis of accumulated degree-days from time of bloom, a developmental index that integrates the effects of time and temperature on growth (Zalom *et al.*, 1983). Degree-days were calculated using the single sine, horizontal cut-off method, with critical temperatures of 7 and 35 °C (DeJong and Goudriaan, 1989).

Data analysis

Relative growth rate (RGR) and absolute growth rate (AGR) are two parameters that may be used to characterize organ growth through time. The RGR is the rate of increase in dry weight per unit dry weight per unit time and represents net sink activity (Warren Wilson, 1967, 1972):

$$\text{RGR (net sink activity)} = (1/w)(dw/dt) \quad (1)$$

$$= d(\ln w)/dt \quad (2)$$

where w and t represent organ dry weight and time, respectively. Gross sink activity is the sum of net sink activity and specific respiration rate, the amount of carbohydrate respired per unit dry weight per unit time. The AGR is the rate of increase in dry weight per unit time and represents the net sink strength:

$$\text{AGR (net sink strength)} = dw/dt \quad (3)$$

$$= \text{RGR } w. \quad (4)$$

Gross sink strength is the sum of net sink strength and organ respiration rate, the amount of carbohydrate respired by an organ per unit time.

In order to achieve its growth potential, an organ must grow under non-limiting conditions at its potential RGR

TABLE 1. The number of fruits at harvest on heavily-thinned and unthinned trees of an early maturing peach cultivar, Spring Lady, and a late maturing peach cultivar, Cal Red. Standard errors of the mean are given in parenthesis

Cultivar	Heavily-thinned	Unthinned
Spring Lady	33.2 (1.4)	240.0 (13.4)
Cal Red	60.9 (2.9)	288.0 (6.2)

throughout development. Under source-limited growth conditions the RGR is reduced below the potential RGR (Warren Wilson, 1967, 1972; Wareing and Patrick, 1975; Ho, 1984, 1988; Ho *et al.*, 1989; Farrar, 1993). In contrast, because the AGR is a function of both RGR and organ weight, a reduction in AGR compared with potential AGR may result from current source limitation and reduction in RGR or from reduced organ weight due to a previous period of source-limited growth.

The functional approach, employing mathematical functions to fit observed data, was used to obtain instantaneous estimates of fruit growth (Elias and Causton, 1976; Hunt, 1979, 1982; Parsons and Hunt, 1981). Fruit growth curves were obtained by fitting cubic polynomial functions (Spring Lady) and cubic splines (Cal Red) to log-transformed dry weight data for each fruit on each measurement day *vs.* degree-days after bloom using the method of least-squares regression (SAS REG procedure, SAS Institute, Inc., SAS Circle Box 8000, Cary, NC, USA). A spline is a piecewise continuous n th order polynomial equation with the additional property that the first $n-1$ derivatives are continuous. The points at which the n th derivative is discontinuous are called knots (Smith, 1979; Parsons and Hunt, 1981). Splines of the form

$$y = a + bx + cx^2 + dx^3 + (x > i)e(x-i)^3 + (x > j)f(x-j)^3 \quad (5)$$

with knots at $x = i$ and $x = j$ were used.

Instantaneous estimates of relative growth rate (RGR) were obtained as the first derivatives of the fitted growth functions [eqn (2)]. Instantaneous estimates of absolute growth rate (AGR) were obtained as the first derivatives of the exponential form of the fitted equations [eqn (3)]. Variances of the estimates of fruit dry weight, RGR, and AGR were calculated from the variance-covariance matrix (Steel and Torrie, 1980; Miller, 1986; Casella and Berger, 1990; Grossman, 1993). All statistical comparisons of the derivative curves were made using the expected values and variances from the fitted equations at 100 degree-day intervals. Tests for significant differences ($P < 0.05$) between expected values of RGR for fruits on heavily-thinned and unthinned trees were based on an asymptotic normal statistic (Z).

The crop resource usage rate, the rate at which dry weight is used for growth and respiration by all of the fruits on a tree, was determined from the following equation:

$$\text{crop resource usage rate} = \left[\text{AGR} + \left(\frac{\text{specific respiration rate} \times \text{individual fruit weight}}{\text{fruit number}} \right) \right] \quad (6)$$

$$= \left(\frac{\text{net sink strength} + \text{fruit respiration rate}}{\text{fruit number}} \right) \times \text{fruit number} \quad (7)$$

where the units for crop resource usage rate, AGR, specific respiration rate, individual fruit weight, and fruit number

are g dry weight per degree-day per tree, g dry weight per degree-day per fruit, g dry weight per g dry weight per degree-day, g dry weight per fruit, and fruits per tree, respectively.

The specific respiration rate for peach fruits was estimated from DeJong and Goudriaan (1989):

$$\text{Specific resp rate} = [(0.309 \times \text{RGR}) + 0.000184] \times 0.68182 \quad (8)$$

with specific respiration rate expressed as g dry weight (carbohydrate) per g dry weight per degree-day and RGR expressed as g dry weight per g dry weight per degree-day.

RESULTS

Seasonal patterns of fruit growth

Mean fruit dry weight increased rapidly with degree-days after bloom (Fig. 1). Significant dry weight differences between fruits on heavily-thinned and unthinned trees of both cultivars were first detected at 340 degree-days (5 weeks) after bloom and persisted through harvest (Fig. 1). The final mean dry weight of individual fruits on unthinned trees of the early maturing cultivar, 9.8 g, was 49% of that of fruits on heavily-thinned trees, 20.0 g (Fig. 1). Similarly,

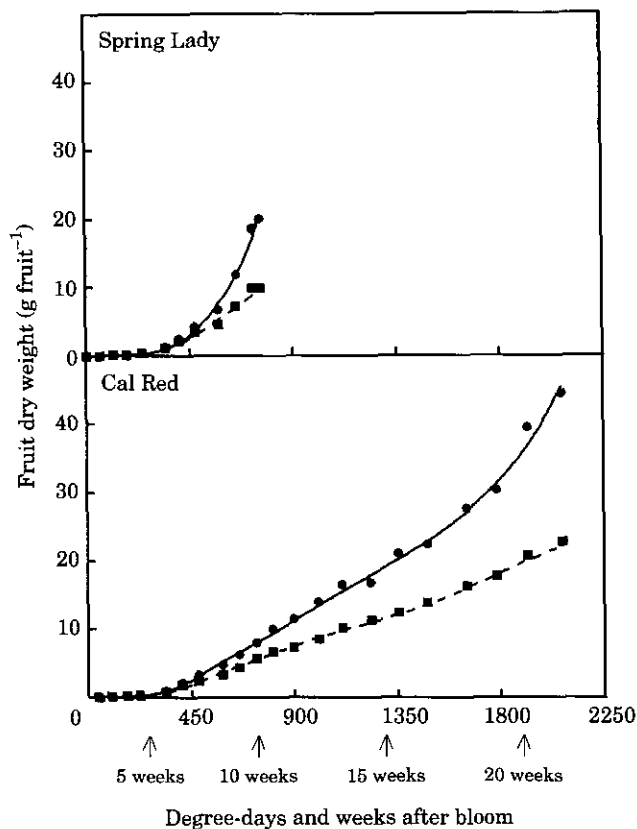


FIG. 1. Seasonal patterns of mean individual fruit dry weight on heavily-thinned (—) and unthinned (---) trees of the early maturing cultivar, Spring Lady, and the late maturing cultivar, Cal Red. Bars indicating 1 standard error of the mean fit within the symbols. Lines represent the exponential form of polynomial equations (Spring Lady) or cubic splines (Cal Red) fit to the natural logarithm of dry weight *vs.* degree-days after bloom. Equations for the lines are given in Table 2.

TABLE 2. Equations fitted to logarithmically-transformed fruit dry weight data (*Indw*) vs. degree-days after bloom (*dd*)

Spring Lady, heavily thinned:	$Indw = -6.55 + 0.029dd - (3.25 \times 10^{-5})dd^2 + (1.51 \times 10^{-8})dd^3$
Spring Lady, unthinned:	$Indw = -6.69 + 0.030dd - (3.61 \times 10^{-5})dd^2 + (1.62 \times 10^{-8})dd^3$
Cal Red, heavily thinned:	$Indw = -7.39 + 0.032dd - (3.81 \times 10^{-5})dd^2 + (1.65 \times 10^{-8})dd^3$ $-(dd > 700)(1.44 \times 10^{-8})(dd - 700)^3 - (dd > 1400)(2.73 \times 10^{-9})(dd - 1400)^3$
Cal Red, unthinned:	$Indw = -7.45 + 0.032dd - (3.96 \times 10^{-5})dd^2 + (1.76 \times 10^{-8})dd^3$ $-(dd > 700)(1.61 \times 10^{-8})(dd - 700)^3 - (dd > 1400)(2.18 \times 10^{-9})(dd - 1400)^3$

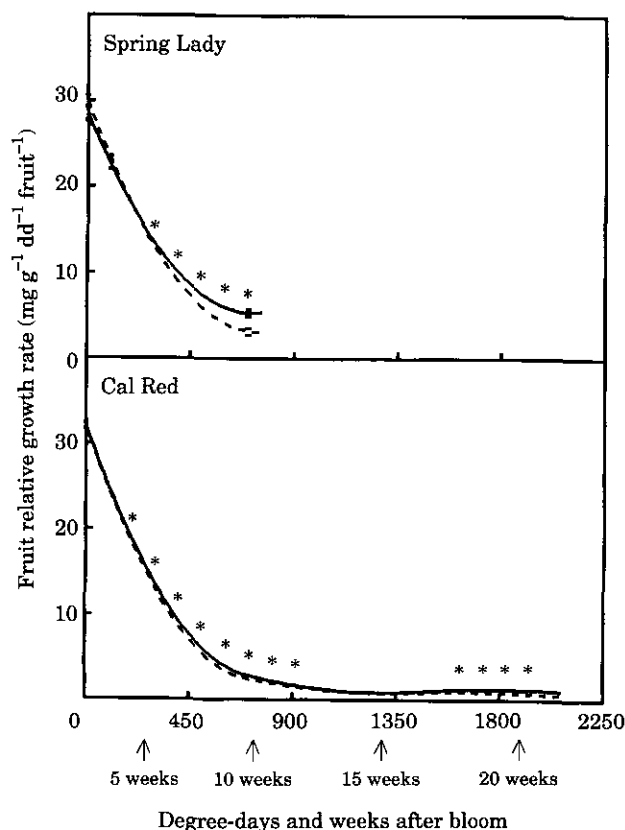


FIG. 2. Seasonal patterns of relative growth rate (RGR) for fruits on heavily-thinned (—) and unthinned (---) trees of the early maturing cultivar, Spring Lady, and the late maturing cultivar, Cal Red. Bars indicate 1 standard deviation of the expected value of RGR on heavily-thinned trees at 100 degree-day intervals after bloom (bars fit within line where not visible). Significant differences ($P < 0.05$) between treatments are indicated by stars.

the final mean dry weight of individual fruits on unthinned trees of the late maturing cultivar, 22.6 g, was 51% of that of fruits on heavily-thinned trees, 44.3 g (Fig. 1). The mean dry weight of fruits from heavily-thinned trees of the early maturing cultivar was significantly higher than that of the late maturing cultivar throughout development of the early maturing cultivar (Fig. 1).

Cubic polynomial equations for logarithmically-transformed fruit dry weight vs. accumulated degree-days explained 97.6 and 98.0% of the variance in the data for heavily-thinned and unthinned trees, respectively, of the early maturing cultivar, Spring Lady (Fig. 1, Table 2).

Cubic splines with knots at 700 and 1400 degree-days (10 and 16.5 weeks) fitted to logarithmically-transformed fruit dry weights explained 99.2 and 98.8% of the variance for heavily-thinned and unthinned trees, respectively, of the late maturing cultivar, Cal Red (Fig. 1, Table 2).

Seasonal patterns of fruit relative growth rate

The fruit relative growth rates [RGRs, eqns (1) and (2)] for fruits on heavily-thinned trees of both cultivars declined rapidly for approximately the first 400 degree-days (6 weeks) after bloom (Fig. 2). On the late maturing cultivar, Cal Red, the period of declining RGR was followed by a period of relatively constant RGR. On the early maturing cultivar, Spring Lady, the rate of decline in the RGR also decreased, however, fruit harvest occurred before the period of relatively constant RGR began on the late maturing cultivar. At the time of harvest of the early maturing cultivar, the magnitude of the RGR of fruits on heavily-thinned trees of the early maturing cultivar was approximately twice that on the late maturing cultivar.

These seasonal patterns of RGR, obtained using the functional approach to growth analysis, were similar to those described for several peach cultivars using the classical approach to growth analysis in which the RGR is determined by a difference equation (DeJong and Goudriaan, 1989; Pavel and DeJong, 1993a, b). The seasonal patterns obtained using the functional approach were smoother than those obtained using the classical approach. The seasonal patterns for peach were generally similar to tomato (Monselise, Varga and Bruinsma, 1978; Bangerth and Ho, 1984) and cucumber (Marcelis, 1992), although peaches lacked the initial increase in RGR reported for the other fruits.

On the early maturing cultivar, Spring Lady, the RGR of fruits from heavily-thinned trees was significantly higher than the RGR of fruits from unthinned trees beginning at 300 degree-days after bloom and continuing through harvest (4.5–10 weeks after bloom, Fig. 2). Similarly, on the late maturing cultivar, the RGRs were significantly different for the period from 200 to 900 degree-days (3.5–12 weeks) after bloom (Fig. 2). An additional period of significantly higher RGR for fruits on heavily-thinned trees occurred during the latter portion of the period of relatively constant RGR, from 1600 to 1900 degree-days (18–20 weeks) after bloom (Fig. 2). Near the time of harvest, the magnitude of the RGR of fruits on unthinned trees was lower than that on heavily-thinned trees, however, no significant differences

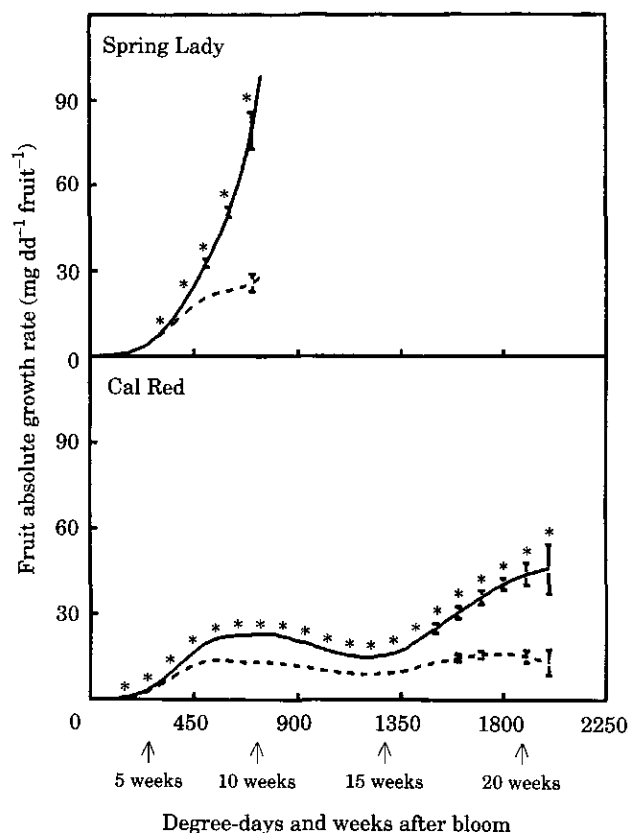


FIG. 3. Seasonal patterns of absolute growth rate (AGR) for fruits on heavily-thinned (—) and unthinned (---) trees of the early maturing cultivar, Spring Lady, and the late maturing cultivar, Cal Red. Bars indicate 1 standard deviation of the expected value of AGR on heavily-thinned trees at 100 degree-day intervals after bloom (bars fit within line where not visible). Significant differences ($P < 0.05$) between treatments are indicated by stars.

were detected at 2000 degree-days (21 weeks) after bloom due to the poor predictive ability of the fitted equations near their endpoints.

Seasonal patterns of fruit absolute growth rate

The fruit absolute growth rate [AGR, eqns (3) and (4)] on heavily-thinned trees of the early maturing cultivar, Spring Lady, increased rapidly from bloom to harvest while the AGR of fruits on unthinned trees increased more slowly (Fig. 3). Significant differences in AGR were first detected at 300 degree-days after bloom and continued through harvest (4.5–10 weeks after bloom).

The AGR of fruits on the late maturing cultivar, Cal Red, increased to an initial maximum at about 600 degree-days (8.5 weeks), reached a local minimum at about 1250 degree-days (15 weeks), then increased through harvest. This pattern was similar to that reported for the Golden Queen peach cultivar (Chalmers and van den Ende, 1975). The AGR of fruits on heavily-thinned trees was significantly greater than that of fruits on unthinned trees throughout the growth period. The AGR of fruits on the early maturing cultivar was greater than the AGR of fruits on the late maturing cultivar from bloom until harvest of the early maturing cultivar.

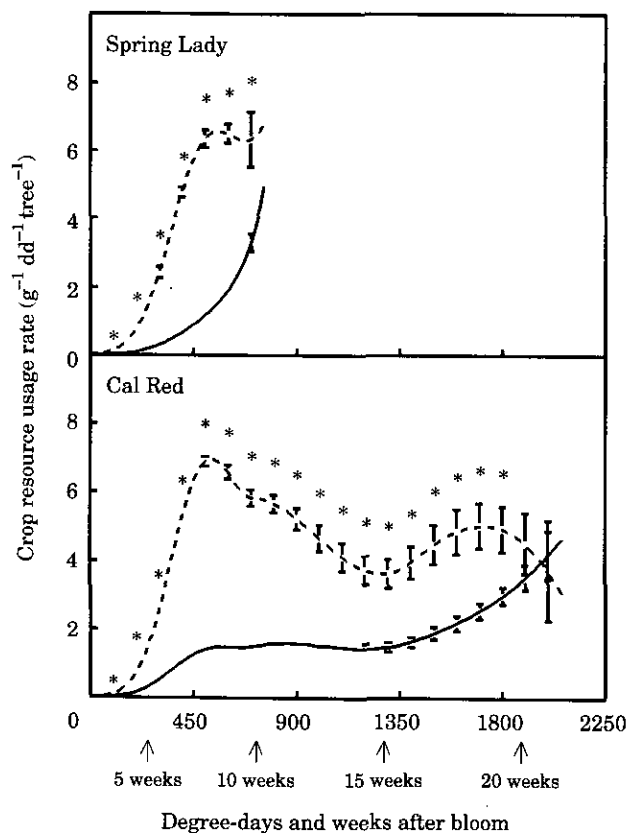


FIG. 4. Seasonal patterns of crop resource usage rate on heavily-thinned (—) and unthinned (---) trees of the early maturing cultivar, Spring Lady, and the late maturing cultivar, Cal Red. Bars indicate 1 standard deviation of the expected value of the crop resource usage rate on unthinned trees at 100 degree-day intervals after bloom (bars fit within line where not visible). Significant differences ($P < 0.05$) between treatments are indicated by stars.

Seasonal patterns of crop resource usage rate

The crop resource usage rate, the rate of accumulation of dry weight plus the respiration rate of *all* the fruits on the tree [eqns (6) and (7)], was significantly lower on heavily-thinned trees than on unthinned trees throughout most of the growth period, with the exception of the last two sample dates tested for the late maturing cultivar (Fig. 4). The crop resource usage rate on unthinned trees was similar for both cultivars through the time of harvest of the early maturing cultivar. On the unthinned trees of the late maturing cultivar, the crop resource usage rate peaked between 500 and 600 degree-days (7–8.5 weeks), decreased to a low at 1250 degree-days (15 weeks), then increased slightly.

DISCUSSION

Maximum fruit growth potential

To estimate maximum fruit growth potential, individual fruits must be grown under conditions of non-limiting resource availability. Assuming that vegetative sink demand was similar on unthinned and heavily-thinned trees, the crop resource usage rate, the rate of accumulation of dry weight plus the respiration rate of *all* the fruits on the tree, represents an estimate of the resources available for fruit

growth when it is determined on unthinned trees. The crop resource usage rate was significantly higher throughout the growing season on unthinned trees than on heavily-thinned trees of the early maturing cultivar, Spring Lady, and the late maturing cultivar Cal Red, except during the last 2 weeks before harvest (Fig. 4). Thus, because resource availability for fruit growth exceeded resource usage on heavily-thinned trees, individual fruit growth on heavily-thinned trees represents the maximum fruit growth potential (Fig. 1). The seasonal patterns of RGR of these fruits represents the potential RGR except that values obtained during the last 2 weeks before harvest may underestimate maximum fruit growth potential and the potential RGR on the late maturing cultivar (Fig. 2).

Seasonal patterns of resource limitation on individual fruit growth

The harvest weights of fruits grown on unthinned trees of both cultivars were about 50% of the weights of fruits grown on heavily-thinned trees, indicating that resource availability limited individual fruit growth on unthinned trees during at least some portion of the growing season (Fig. 1). Statistically significant differences between the RGRs of fruits on unthinned trees and the potential RGRs of both cultivars were detected during discrete time periods (Fig. 2). Although the differences in RGR were small, they were biologically significant due to the compounding effect of RGR, which was calculated on a degree-day basis. During the summer, there were as many as 23 degree-days per day, thus, the RGR was compounded up to 23 times per day.

The periods when significant differences in RGR occurred represent periods of source-limited fruit growth on unthinned trees (Fig. 2). Fruits on unthinned trees of both cultivars experienced a period of source limitation beginning 3–4 weeks after bloom. This source-limited period lasted through harvest for the early maturing cultivar and through 12 weeks after bloom for the late maturing cultivar. A second period of source-limited fruit growth was detected on the late maturing cultivar during the month prior to harvest. The patterns of resource limitation found in this study using the functional approach to estimate RGR were similar to those determined using the classical approach in which RGR is calculated during discrete time intervals (Pavel and DeJong, 1993*a, b*).

During both source-limited growth periods, fruits grew by cell enlargement, as the majority of post-anthesis cell divisions in peach occur within the first 3–4 weeks after bloom (Addoms, Nightingale and Blake, 1930; Ragland, 1934). During the first source-limited growth period, shoot extension was rapid, competing with fruits for resources (Grossman and DeJong, unpubl. res.). In apple, shoot growth competes strongly with young fruits during the early part of the growing season (Maggs, 1963; Barlow, 1966; Quinlan and Preston, 1971). The late maturing cultivar experienced a second period of source-limited growth during the month before harvest. This is a period of rapid cell enlargement, intercellular space decrease, and soluble solids increase (reviewed in Zucchini, 1986).

Girdling, the removal of a thin strip of bark down to the cambium to prevent movement of assimilates to the roots, is frequently performed on early maturing peach cultivars to increase final fruit size and dry weight (Fernandez-Escobar *et al.*, 1987). The response to girdling is optimum when girdling is performed at a time corresponding to the source-limited period of fruit growth on the early maturing cultivar (Day and DeJong, 1990).

The occurrence of discrete source-limited periods of peach fruit growth is further supported by the results of a simulation model that estimated daily carbon assimilation, respiration and growth by peach trees (Grossman and DeJong, 1994). When the model was parameterized for the late maturing cultivar, it predicted that carbohydrate supply restricted fruit growth during the periods of time when source-limited growth was detected in this experimental study.

Peach fruit growth has only recently been analysed using relative growth rates (DeJong and Goudriaan, 1989). The traditional description of peach fruit growth divides growth, usually measured as diameter increase, into three stages (Connors, 1919; Lilleland, 1932; Tukey, 1933; Chalmers and van den Ende, 1975). The first and third stages are periods of rapid diameter increase, while the second stage is a period of slower diameter increase. On the early maturing cultivar, the source-limited period of fruit growth began during Stage I and continued through Stage III. On the late maturing cultivar, the first source-limited growth period occurred during Stage I and the beginning of Stage II and the second source-limited growth period occurred during Stage III. Early researchers postulated that the slower diameter increase during Stage II is due to competition for resources between the developing embryo and the fleshy mesocarp (reviewed in Nitsch, 1953). However, this data and that of Pavel and DeJong (1993*b*) contradict this hypothesis because no resource limitation on fruit growth was detected during most of Stage II. This suggests that the observed pattern of diameter increase is due to genetic constraints on growth rather than resource competition (Pavel and DeJong, 1993*b*).

Source limitation on fruit growth frequently occurs in the commercial production of peaches, leading to the common horticultural practice of selective thinning. Thinning is carried out approximately 30 and 60 d after bloom for early and late maturing cultivars, respectively (Johnson and Handley, 1989; Yoshikawa and Johnson, 1989). This study suggests that these thinning times are too late because they are well into the first source-limited growth period. Thus, the remaining fruits are unable to take full advantage of the decreased competition for resources caused by thinning and potential yield is lost.

During the times when no resource limitation on growth was detected, fruits may have grown at their potential RGR or the magnitude of source limitation may have been too low to detect with this experimental design. On the late maturing cultivar, periods of source-limited growth alternated with periods when no source limitation was detected. This suggests that a history of source limitation does not prevent a fruit from growing at its potential RGR during periods when resource supply exceeds resource demand. An

experimental test of this observation indicated that the RGR of previously source-limited fruits can increase in response to increases in resource availability (Grossman and DeJong, 1995).

Potential net sink strength

The potential net sink strength of individual fruits may be determined from the absolute growth rate (AGR) of the sink when resources are not limiting (Ho *et al.*, 1989). In this study, these conditions were fulfilled on heavily-thinned trees throughout the entire growth period of the early maturing cultivar, and during most of the growth period of the late maturing cultivar (Fig. 4). Thus, the observed AGR of the fruits on heavily-thinned trees represents the potential net sink strength (Fig. 3), except that the values obtained during the last 2 weeks before harvest on the late maturing cultivar may underestimate potential net sink strength because the observed crop resource usage rates were not detectably different on heavily-thinned and unthinned trees (Fig. 4).

Although the mean final dry weight of fruits of the early maturing cultivar was only about half the mean final dry weight of fruits of the late maturing cultivar, this dry weight was accumulated in approximately one-third the time. This rapid growth was due to the higher potential net sink strength of fruits of the early maturing cultivar, Spring Lady, compared with that of the late maturing cultivar, Cal Red (Fig. 3). At the time of their respective harvests, the potential net sink strength of fruits of the early maturing cultivar was more than twice that of the late maturing cultivar. This genetically determined, higher potential net sink strength near the time of harvest was the result of greater RGR and not larger weight [eqn (4), Figs 1 and 2]. Similar differences in potential net sink strength have been observed in tomato, due to position within a truss and order of fruit induction (Bangerth and Ho, 1984). Wardlaw (1990) listed features of an organ with high net sink strength: the size of the surface area across which metabolites are transferred from the vascular system to the zone of utilization, the efficiency of the transfer of carbon from the vascular system to the sink, and the spatial or biochemical isolation of assimilates in the organ once they leave the vascular system. Studies of sucrose storing fruits have suggested that high net sink strength is correlated with high sucrose phosphate synthase activity (Hubbard, Huber and Pharr, 1989; Miron and Schaffer, 1991).

Seasonal patterns of resource availability

As mentioned earlier, the crop resource usage rate on unthinned trees provides an estimate of resource availability for fruit growth. When fruit grown on unthinned trees was source-limited, the crop resource usage rate equalled the resource availability for fruit growth. When fruit growth on unthinned trees was not source-limited, more resources may have been available for fruit growth than were utilized by the crop. On the late maturing cultivar, resource availability may have exceeded resource usage between 1000 and 1500 degree-days (13–17.5 weeks) after bloom because no source

limitation on fruit growth was detected on unthinned trees. This probably accounts for the dip in crop resource usage observed during this time (Fig. 4).

The seasonal patterns of resource availability for fruit growth were similar on the early and late maturing cultivars until the harvest of the early maturing cultivar, suggesting that although plant breeders have manipulated the schedule of fruit maturity, the ability of the tree to provide resources for fruit growth has not been changed. Other studies indicate that patterns of vegetative growth have not been changed by selective breeding for earliness in fruit maturity (DeJong *et al.*, 1987; Grossman and DeJong, unpubl. res.).

Changes in the timing of fruit development on early and late maturing peach cultivars seem to have resulted from changes in mesocarp development, but not seed and endocarp development because the pattern of seed and endocarp development in early and late maturing cultivars follows approximately the same time course (Tukey, 1933; Pavel and DeJong, 1993a). The genetic changes in the timing of mesocarp development are reflected in the higher potential RGR after the period of steep decline in RGR and in the greater potential net sink strength of the early maturing cultivar throughout development. Thus, greater potential net sink strength due to greater potential RGR and not greater resource availability accounts for the more rapid fruit growth on the early than on the late maturing cultivar.

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