

Maximum Vegetative Growth Potential and Seasonal Patterns of Resource Dynamics during Peach Growth

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The maximum vegetative growth potential of two peach [*Prunus persica* (L.) Batsch] cultivars that differ in the timing of resource demand for reproductive growth was determined in terms of stem extension, stem and leaf dry weight accumulation, and trunk radial increment on defruited trees. The maximum vegetative growth potentials were similar on the two cultivars indicating that the greater partitioning of dry weight to vegetative growth frequently observed on early maturing cultivars compared to late maturing cultivars is the result of a shorter period of competition between reproductive and vegetative growth, rather than a genetic difference in vegetative growth potential. On both cultivars, stem extension and leaf dry weight accumulation ceased in mid-summer, however stem dry weight accumulation and trunk radial increment increase continued through the autumn.

The presence of fruit did not have a detectable effect on the final stem length, stem dry weight or leaf dry weight on the early maturing cultivar, but it reduced final stem length and dry weight by 43 and 56%, respectively on the late maturing cultivar. The presence of fruit did decrease stem length, stem dry weight and leaf dry weight on the early maturing cultivar for 1 month prior to and 1 month after fruit harvest. Fruit decreased final trunk radial increment by 42 and 77% on the early and late maturing cultivars, respectively. These reductions in vegetative growth indicate that resource partitioning to vegetative growth was reduced by competition with fruit growth.

Comparison of stem relative extension rates and stem and leaf relative growth rates on fruited and defruited trees indicated that vegetative growth was resource-limited shortly after vegetative bud break on fruited trees of both cultivars. This period of resource-limited vegetative growth corresponded to a period of resource-limited fruit growth identified in an earlier study. During the period of resource-limited vegetative growth, assimilate supply was low due to low leaf area index, and carbohydrate demand was relatively high due to high vegetative and reproductive growth potentials, creating resource-limited growth conditions. © 1995 Annals of Botany Company

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

INTRODUCTION

Vegetative and reproductive growth often occur simultaneously in perennial plants. In many instances, resources are not sufficient to support growth at maximum potential rates, resulting in competition for these resources. Such competition occurs continuously and is generally agreed to be the basis for the partitioning of resources to reproductive and vegetative organs (Ho, Grange and Shaw, 1989; Wardlaw, 1990; Farrar, 1993). For example, developing fruits suppress vegetative growth in apple (Maggs, 1963; Avery, 1969, 1970; Quinlan and Preston, 1971; Heim *et al.*, 1979), peach (Proebsting, 1958; Miller and Walsh, 1988), cherry (Kappel, 1991), and birch (Tuomi, Niemelä and Mannila, 1982), but vegetative growth suppresses fruit growth in red raspberry (Waister and Wright, 1989). Although resource availability appears to limit vegetative and/or reproductive growth in each of these studies, little is known about the timing of resource limitations on growth (Geiger and Shieh, 1993; Grossman and DeJong, 1995a).

The potential sink demand of reproductive and vegetative organs depends upon the number and type of organs, their

maximum growth potentials and maintenance requirements, and environmental factors affecting growth (Warren Wilson, 1967, 1972; Wareing and Patrick, 1975; Ho, 1984, 1988; Ho *et al.*, 1989; DeJong and Grossman, 1992; Farrar, 1993; Grossman and DeJong, 1995a). Maximum growth potential is the genetically determined maximum biomass increase of an organ when grown under optimal environmental conditions in the presence of a non-limiting supply of photoassimilates and other resources. Under these conditions, growth is only limited by the endogenous characteristics of the organ and not by resource availability. Wareing and Patrick (1975) used the term sink-limited growth to characterize growth under these conditions.

In order to achieve its maximum growth potential, an organ must grow at its potential relative growth rate (RGR), the rate of increase in dry weight per unit dry weight per unit time throughout development (Warren Wilson, 1967, 1972; Wareing and Patrick, 1975; Ho, 1984, 1988; Ho *et al.*, 1989). Under resource-limited growth conditions, the observed RGR is reduced below the potential rate. Thus, resource limitations on growth can be detected by comparing the RGR of an organ to its potential RGR. When this approach was applied to individual peach fruit growth, resource limitations were found during discrete periods of

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fruit growth (Pavel and DeJong, 1993; Grossman and DeJong, 1995a, b).

Above-ground vegetative growth in woody plants consists of current year stem extension and dry weight gain, leaf dry weight gain and wood increment added to the trunk and branches. Most studies of the seasonal patterns of partitioning to vegetative growth have examined vegetative growth in terms of stem extension only and have reported that vegetative growth ceases in mid-summer (Westwood, 1978). However, stem, branch and trunk dry weight gain continue after stem extension ceases, and partitioning to vegetative growth continues throughout the growing season (Heim *et al.*, 1979; Forshey *et al.*, 1983; Miller and Walsh, 1988; Kappel, 1991). For these reasons, the present study examined the seasonal patterns of above-ground vegetative growth in terms of current year stem length, current year stem and leaf dry weight, and trunk radial increment.

As in most perennials, fruit and vegetative growth are simultaneous in peach, making competition for resources between fruits and vegetative organs likely to occur (DeJong, Doyle and Day, 1987). This study asked the questions: (1) does competition for resources among reproductive and vegetative organs cause resource limitations on growth? and (2) do the seasonal patterns of these limitations differ on early and late maturing peach [*Prunus persica* (L.) Batsch] cultivars?

MATERIALS AND METHODS

Trees

Vegetative and reproductive growth data were obtained in 1990 and 1991 on two peach [*Prunus persica* (L.) Batsch] cultivars, Spring Lady and Cal Red, with fruit maturity dates in late May and mid-August, respectively. The trees were planted in 1984 at the University of California Kearney Agricultural Center in 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 pruning. For this reason, the early maturing cultivar was pruned more heavily, thinned earlier, and carried fewer fruits to maturity than the late maturing cultivar.

Defruited and fruited treatments were established on each cultivar. For the defruited treatment, blossoms were removed at the time of bloom. Late blossoms were removed 4 weeks after bloom. For the fruited treatment, fruits were removed 4 and 8 weeks after bloom leaving approximately 90 and 200 fruits per tree on the early and late maturing cultivars, respectively. At commercial fruit maturity, fruits were harvested, counted, and weighed. Subsamples (ten fruits per tree) were weighed, dried at 55 °C and weighed to estimate the fresh weight to dry weight ratio.

Stem and leaf measurements

The seasonal patterns of stem extension were determined by tagging a stratified random sample of branches repre-

senting 25% of the branches on each of five trees for each cultivar/treatment combination. The length of every current year stem on each tagged branch was recorded at 2 week intervals, in 1990, from 6–22 weeks after bloom and in Oct. In 1991, stems were measured at 2 week intervals from bloom to 11 weeks after bloom. Five defruited trees of each cultivar were destructively sampled in early Apr., late May, early Jul. and mid-Oct. 1990, to obtain stem length, and stem and leaf dry weight data. In the destructive samplings, 25% of the branches of each tree were removed, separated into leaves, current year stems, and older stems, and dried to a constant weight at 70 °C. The relationships between logarithmically-transformed stem length per branch and stem and leaf dry weight per branch were determined by linear regression for each sample date. Stem length and stem and leaf dry weight data were analysed on a whole tree basis because vegetative growth on many woody plants is not homogeneous and is subject to the effects of apical dominance, light exposure, and other environmental influences (see, for example Forshey and Elfving, 1989).

Trunk measurements

Trunk radial increment was measured on five defruited and five fruited trees at approximately 2 week intervals from Mar. to Oct. 1990 using a microdendrometer (A.B. Pulco, Manufacturer, Lund, Sweden). The mounting pins for the microdendrometer were installed into heartwood at 40 cm above the soil surface. Readings were taken between 0700 and 0830 h Pacific Standard Time to minimize the impact of diurnal trunk shrinkage and swelling due to transpiration (Larson and DeJong, 1988).

Temperature information

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

Data analysis

The functional approach, employing mathematical functions to fit observed data, was used to obtain instantaneous estimates of stem length, stem and leaf dry weight accumulation, and trunk radial increment (Elias and Causton, 1976; Hunt, 1979, 1982; Parsons and Hunt, 1981). Cubic splines with knots at 1000 and 2000 degree-days were fit to logarithmically-transformed length and dry weight data *vs.* degree-days after bloom using the least-squares method (SAS REG procedure, SAS Institute, Inc., SAS Circle Box 8000 Cary, NC, USA).

Stem relative extension rate (RER) and stem and leaf relative growth rates (RGRs) were obtained by differentiation of the fitted growth functions for stem length and

stem and leaf dry weights, respectively. Stem absolute extension rate (AER) and stem and leaf absolute growth rates (AGRs) were obtained as the first derivatives of the exponential form of the fitted growth functions. Variances of the estimates of all growth rates were calculated from the variance-covariance matrix (Steel and Torric, 1980; Miller, 1986; Casella and Berger, 1990; see Grossman, 1993, for details). 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 between treatments ($P < 0.05$) for expected values of the growth rates were based on an asymptotic normal statistic (Z). For each sample date, Student's t -test was used to compare logarithmically-transformed stem lengths, logarithmically-transformed stem and leaf dry weights, and trunk radial increments on defruited and fruited trees.

RESULTS

The early maturing cultivar, Spring Lady, bloomed on 13 Mar. 1990 and 28 Feb. 1991. The late maturing cultivar, Cal Red, bloomed on 17 Mar. 1990 and 6 Mar. 1991. The early and late maturing cultivars were harvested on 24 May 1990 and 9 Aug. 1990, respectively. The mean dry weight of individual fruits on the early maturing cultivar, 15.9 g, was 64% of the final dry weight of individual fruits on the late maturing cultivar 24.8 g (Table 1). At harvest, the total fruit dry weight on the early maturing cultivar was 28% of that on the late maturing cultivar.

Stem extension

Vegetative bud break occurred in early Mar., about 50 degree-days (1 week) after full bloom on both the early and late maturing cultivars. Stem extension began at about 200 degree-days (3 weeks) after bloom, increased rapidly until 500 degree-days (7 weeks) after bloom, and neared an asymptote by 1500 degree-days (4 months) after bloom

TABLE 1. Mean fruit load and mean fruit dry weight at harvest of fruited trees of the early maturing peach cultivar, Spring Lady, and the late maturing peach cultivar, Cal Red

Cultivar	Mean fruit load* (number per tree)	Mean total fruit dry weight† (kg per tree)
Spring Lady	92 (12)‡	1.3 (0.04)
Cal Red	209 (8)	4.7 (0.26)

* Thinning dates were 12 Apr. 1990 (274 degree-days after bloom) and 10 May 1990 (581 degree-days after bloom) for Spring Lady and Cal Red, respectively.

† Harvest dates were 24 May 1990 (758 degree-days after bloom) and 9 Aug. 1990 (2069 degree-days after bloom) for Spring Lady and Cal Red, respectively.

‡ Standard error of the mean.

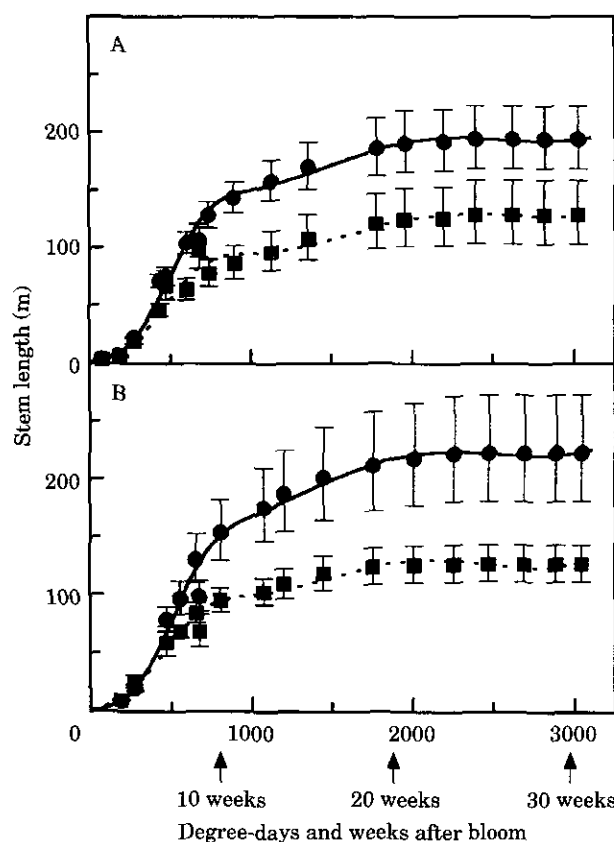


FIG. 1. Seasonal patterns of stem length per tree for defruited (●) and fruited (■) trees of the early maturing cultivar, Spring Lady (A), and the late maturing cultivar, Cal Red (B). Means and standard errors, indicated by error bars, were calculated using the natural logarithm of stem length, resulting in apparent asymmetry in the error bars. Lines represent the exponential form of cubic splines fit to the natural logarithm of stem length vs. degree-days after bloom.

(Fig. 1). All stem growth occurred at nodes that began growing within the first 2 weeks after bloom, that is, no vegetative nodes broke bud later in the growing season. After mid-May (800 degree-days after bloom, 11 weeks), the majority of stems had set terminal buds and the remaining stem extension was due to a small number of stems that continued to extend.

Stem length on defruited trees of the early maturing cultivar exceeded that of fruited trees from 450 to 1125 degree-days (6.5–14 weeks) after bloom in 1990 (Fig. 1). On the late maturing cultivar, stem length on defruited trees exceeded that on fruited trees from 800 to 1200 degree-days (11–14.5 weeks) and 2250 degree-days to the end of the season (22–32 weeks) in 1990. Differences from 1200 to 2250 degree-days (14.5–22 weeks) were significant at the $P < 0.06$ level. At the end of the growing season, the total stem length on fruited trees of the late maturing cultivar was 57% of that on defruited trees. No significant differences between fruited and defruited trees were detected on either cultivar in 1991 when stems were measured from vegetative bud break until 600 degree-days (11 weeks) after bloom.

The mean number of new stems per tree on the early maturing cultivar was 62% of that on the late maturing

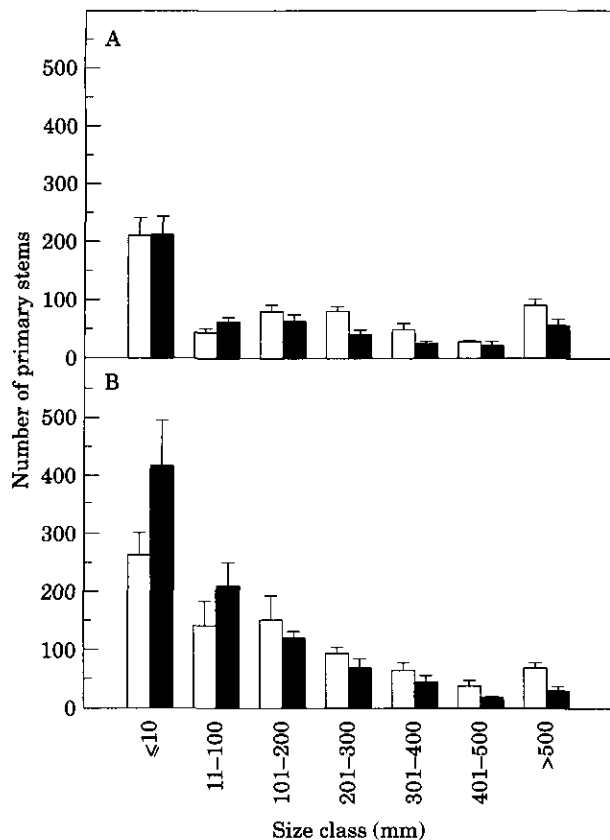


FIG. 2. Frequency distributions of primary stems per tree on defruited (\square) and fruited (\blacksquare) trees of the early maturing cultivar, Spring Lady (A), and the late maturing cultivar, Cal Red (B). Standard errors of the mean are indicated by error bars.

cultivar. Defruiting did not cause differences in the number of new stems within each cultivar, however, the size distributions of these stems differed (Figs 2 and 3). Defruited trees of both cultivars produced more primary stems 200 mm long and longer than did fruited trees (Fig. 2). On the early maturing cultivar, there was no difference between treatments in the number of primary stems less than 10 mm long, however, on the late maturing cultivar, there were fewer stems in this size class on defruited trees than on fruited trees. Defruited trees of the late maturing cultivar produced more secondary stems 200 mm long and longer than did fruited trees (Fig. 3).

Cubic splines for logarithmically-transformed stem length *vs.* degree-days explained more than 95 and 87% of the variation in stem length for defruited and fruited trees of the early maturing cultivar, respectively, and more than 85% of the variation in stem length for defruited and fruited trees of the late maturing cultivar (Fig. 1).

The seasonal patterns of stem relative extension rate (RER) on defruited trees of both cultivars were similar, declining rapidly for the first 750 degree-days (10.5 weeks) after bloom, and remaining relatively constant after 1000 degree-days (13 weeks, Fig. 4). The stem RER on fruited trees was significantly less than that on defruited trees at 400 degree-days (6 weeks) on the early maturing cultivar and from 400–600 degree-days (6–8.5 weeks) on the late maturing cultivar.

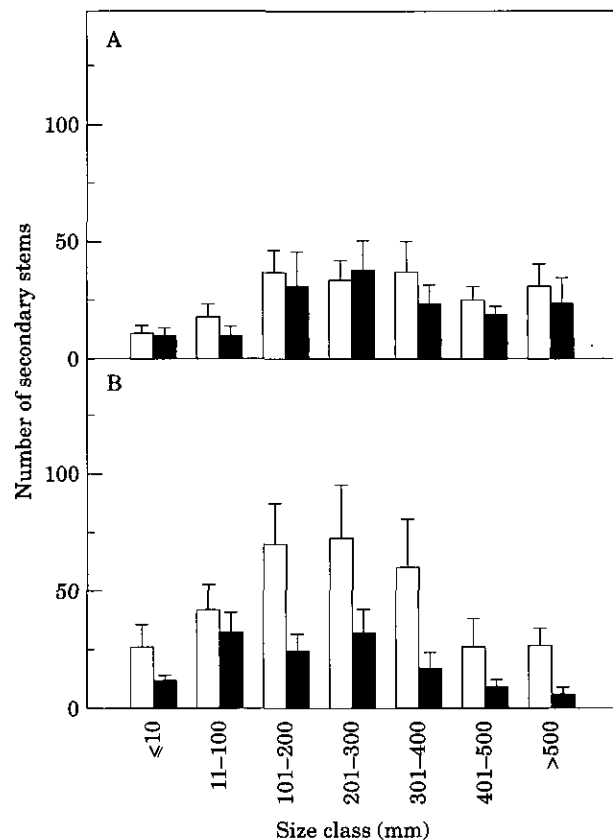


FIG. 3. Frequency distributions of secondary stems per tree on defruited (\square) and fruited (\blacksquare) trees of the early maturing cultivar, Spring Lady (A), and the late maturing cultivar, Cal Red (B). Standard errors of the mean are indicated by error bars.

The seasonal patterns of stem absolute extension rate (AER) on fruited and defruited trees of both cultivars were similar, peaking at approximately 500 degree-days (7 weeks) after bloom (Fig. 5). Significant differences in stem AER were detected between fruited and defruited trees of both cultivars for the period from 300 to 700 degree-days (4.5–10 weeks) after bloom, with fruited trees achieving 65 and 59% of the maximum stem AER on defruited trees of the early and late maturing cultivars, respectively. The peak stem AERs on fruited trees occurred 40 and 80 degree-days (3 and 7 d) earlier than the peak stem AERs on defruited trees of the early and the late maturing cultivars, respectively.

Stem dry weight accumulation

In contrast to the seasonal patterns of stem extension, stem dry weight increased throughout the season on trees of both cultivars (Fig. 6). At the end of the growing season, the total stem dry weight on defruited trees of the early maturing cultivar was not significantly different from that of the late maturing cultivar. Mean stem dry weight on defruited trees of the early maturing cultivar was significantly higher on defruited trees than fruited trees from 450 to 750 degree-days (6.5–10.5 weeks) after bloom in 1990. On the late maturing cultivar, mean stem dry weight on defruited trees significantly exceeded that on fruited trees from 560 degree-days after bloom through the end of the season

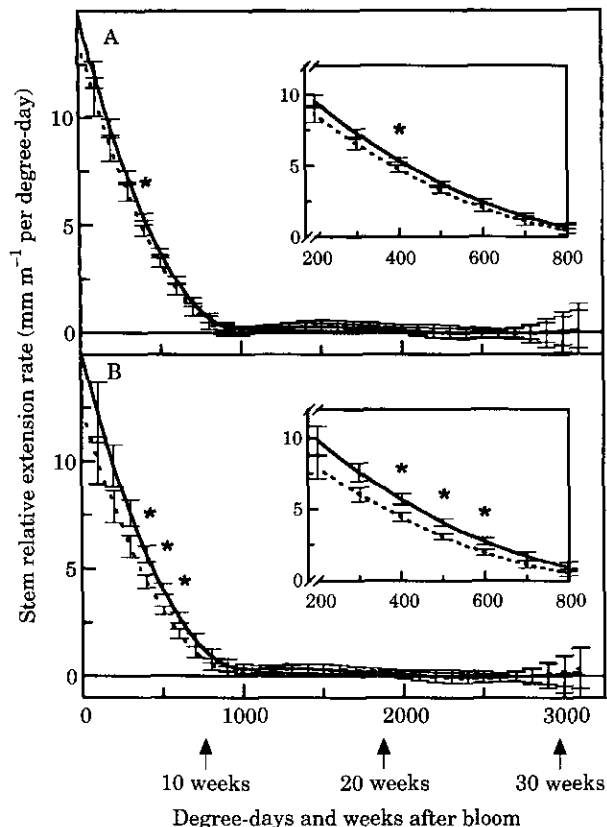


FIG. 4. Seasonal patterns of stem relative extension rate (RER) for defruited (—) and fruited (---) trees of the early maturing cultivar, Spring Lady (A), and the late maturing cultivar, Cal Red (B). Bars indicate one standard deviation of the expected value of stem RER at 100 degree-day intervals after bloom. Significant differences ($P < 0.05$), indicated by stars, were detected based on an asymptotic normal statistic (Z) of RER for stems on defruited and fruited trees.

(7.5–32 weeks) in 1990. At the end of the growing season, the total stem dry weight on fruited trees of the late maturing cultivar was 44% of that on defruited trees. Stem dry weight on fruited and defruited trees did not differ significantly on either cultivar in 1991 when stem dry weight was estimated from vegetative bud break until 600 degree-days (11 weeks) after bloom.

Cubic splines for logarithmically-transformed stem dry weight *vs.* degree-days explained more than 90% of the variation in stem dry weight for both treatments on both cultivars (Fig. 6). The seasonal patterns of stem relative growth rate (RGR) on defruited trees of both cultivars were similar, declining rapidly for the first 750–1000 degree-days (10.5–13 weeks) after bloom, then remaining relatively constant after 1000 degree-days (13 weeks, Fig. 7). Stem RGRs did not differ on fruited and defruited trees of the early maturing cultivar. The stem RGR of fruited trees of the late maturing cultivar was significantly lower than that of defruited trees from 300–600 degree-days (4.5–8.5 weeks) after bloom.

The stem absolute growth rates (AGRs) on defruited trees exceeded those on fruited trees during portions of the growing season, from 400 to 1200 and 1300 degree-days (6–15 weeks) after bloom on the early and late maturing

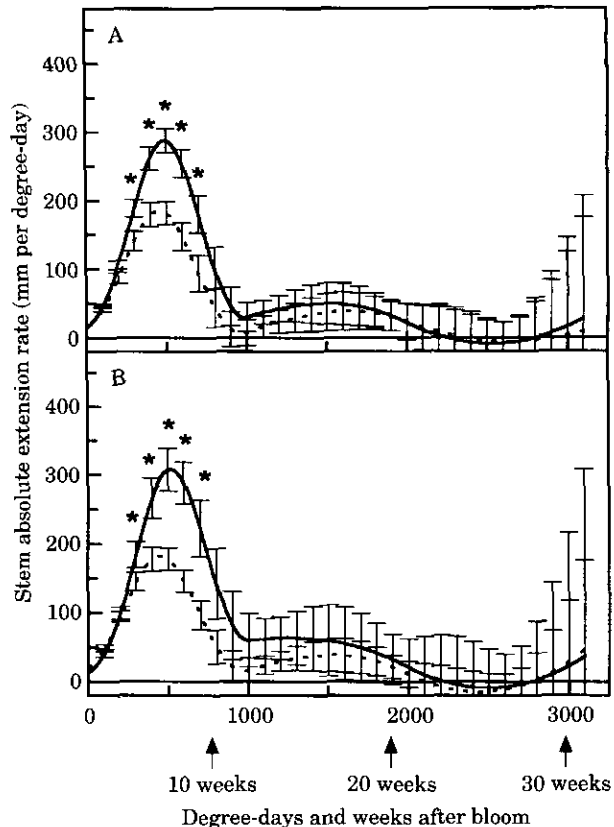


FIG. 5. Seasonal patterns of stem absolute extension rate (AER) for defruited (—) and fruited (---) trees of the early maturing cultivar, Spring Lady (A), and the late maturing cultivar, Cal Red (B). Bars indicate one standard deviation of the expected value of stem AER at 100 degree-day intervals after bloom. Significant differences ($P < 0.05$), indicated by stars, were detected based on an asymptotic normal statistic (Z) of AER for stems on defruited and fruited trees.

cultivars, respectively (Fig. 8). The magnitude of the maximum stem AGR on fruited trees was 54 and 44% of that on defruited trees of the early and late maturing cultivars, respectively.

Leaf dry weight accumulation

Leaf dry weight increased rapidly for approximately the first 1000 degree-days (13 weeks) after bloom, reaching an asymptote by 2000 degree-days (21 weeks) after bloom (Fig. 9). At the end of the growing season, the total leaf dry weight on defruited trees of the early maturing cultivar was not significantly different from that of the late maturing cultivar.

Leaf dry weight on defruited trees of the early maturing cultivar exceeded that of fruited trees from 450 to 1350 degree-days (6.5–16 weeks) after bloom in 1990 (Fig. 9). On the late maturing cultivar, differences were significant at the $P < 0.06$ level from 1075 degree-days after bloom (13.5 weeks) through the end of the season. Leaf dry weight on fruited and defruited trees did not differ significantly in 1991 on either cultivar.

Cubic splines for logarithmically-transformed leaf dry weight *vs.* degree-days explained more than 85% of the

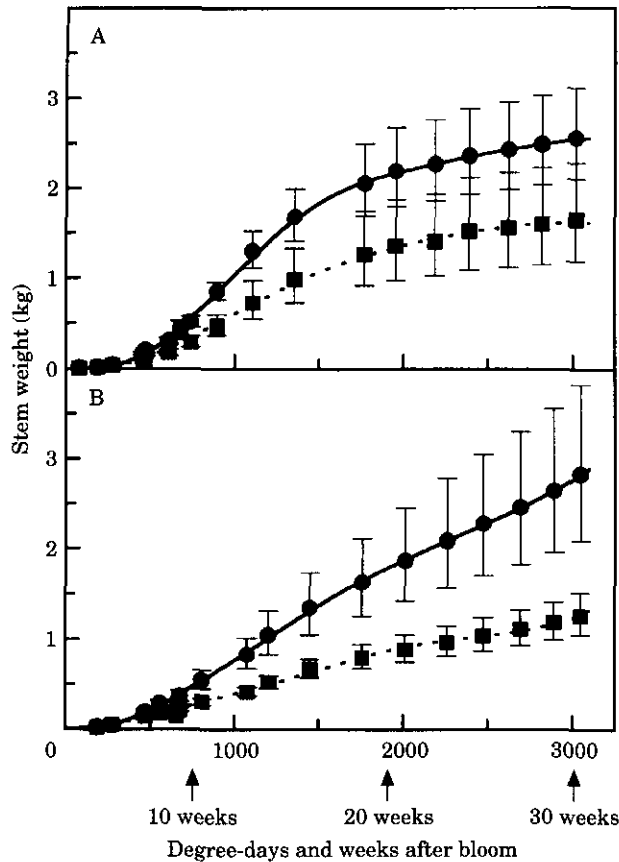


FIG. 6. Seasonal patterns of stem dry weight per tree for defruited (—●—) and fruited (---■---) trees of the early maturing cultivar, Spring Lady (A), and the late maturing cultivar, Cal Red (B). Means and standard errors, indicated by error bars, were calculated using the natural logarithm of stem dry weight, resulting in apparent asymmetry in the error bars. Lines represent the exponential form of cubic splines fit to the natural logarithm of stem dry weight *vs.* degree-days after bloom.

variation in leaf dry weight for both treatments on both cultivars (Fig. 9). Leaf RGRs decreased for the first 1200 degree-days (15 weeks) after bloom, then approached zero (Fig. 10). Leaf RGRs were significantly lower on fruited than on defruited trees from 400 to 500 and 400 to 600 degree-days (6–7 and 6–8.5 weeks) after bloom on the early and late maturing cultivars, respectively. Leaf AGRs on defruited trees exceeded those on fruited trees from 200 to 800 and 400 to 700 degree-days (3–11 and 6–10 weeks) after bloom on the early and late maturing cultivars, respectively (Fig. 11). The magnitude of the maximum leaf AGR on fruited trees was 65 and 67% of that on defruited trees of the early and late maturing cultivars, respectively.

Trunk growth

Significantly greater trunk radial increment was detected on defruited trees than on fruited trees beginning 600 and 700 degree-days (8 and 10 weeks) after bloom on the early and the late maturing cultivars, respectively (Fig. 12). Linear equations were fitted to trunk radial increment *vs.* degree-days after bloom because the highest order

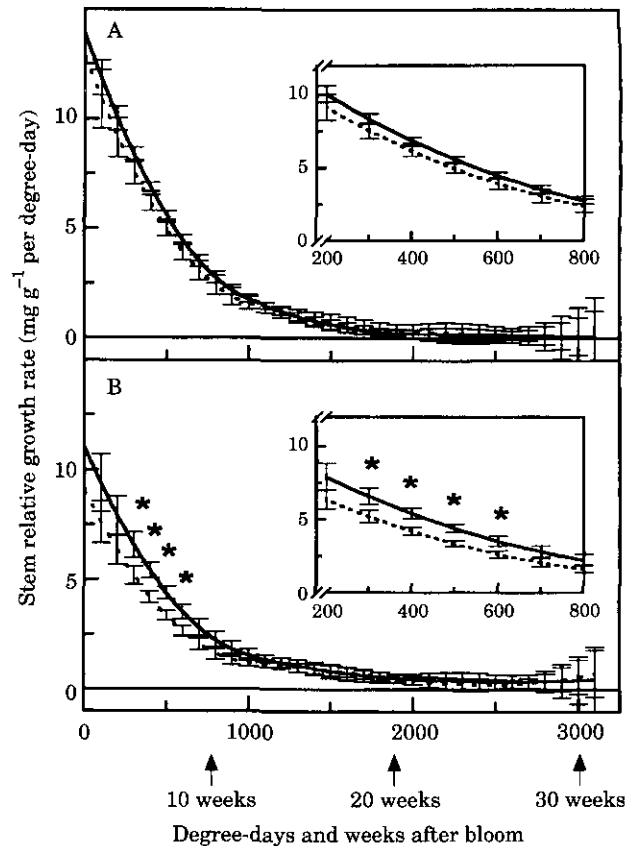


FIG. 7. Seasonal patterns of stem relative growth rate (RGR) for defruited (—●—) and fruited (---■---) trees of the early maturing cultivar, Spring Lady (A), and the late maturing cultivar, Cal Red (B). Bars indicate one standard deviation of the expected value of stem RGR at 100 degree-day intervals after bloom. Significant differences ($P < 0.05$), indicated by stars, were detected based on an asymptotic normal statistic (Z) of RGR for stems on defruited and fruited trees.

coefficients of quadratic and cubic splines were not significantly different from zero (Elias and Causton, 1976). These equations explained more than 78 and 68% of the variation in trunk radial increment for the defruited and fruited trees of both cultivars, respectively.

The slopes of the fitted equations for defruited trees of the two cultivars did not differ, but the slopes for fruited trees were lower than the slopes for defruited trees of both cultivars (Fig. 12). Trunk radial increment on fruited trees was 58 and 23% of that on defruited trees of the early and late maturing cultivars, respectively.

DISCUSSION

Maximum vegetative growth potential

To estimate maximum vegetative growth potential, vegetative organs must be grown under conditions of non-limiting resource availability. Because vegetative growth on defruited trees exceeded that on fruited trees (Figs 1, 6, 9 and 12), the stem relative extension rate (RER) and stem and leaf relative growth rates (RGRs) on defruited trees provide an estimate of the maximum stem and leaf growth potentials (Figs 4, 7 and 10). These estimates represent

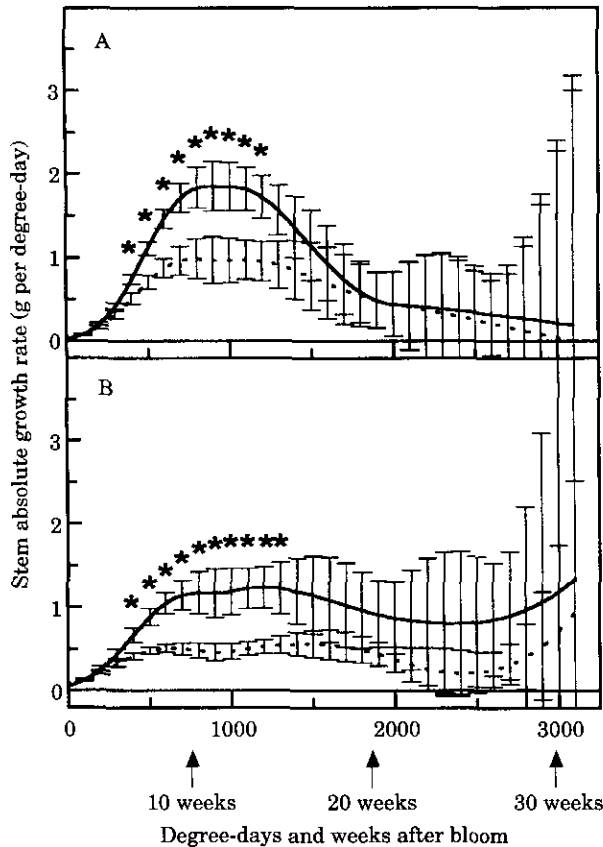


FIG. 8. Seasonal patterns of stem absolute growth rate (AGR) for defruited (—) and fruited (---) trees of the early maturing cultivar, Spring Lady (A), and the late maturing cultivar, Cal Red (B). Bars indicate one standard deviation of the expected value of stem AGR at 100 degree-day intervals after bloom. Significant differences ($P < 0.05$), indicated by stars, were detected based on an asymptotic normal statistic (Z) of AGR for stems on defruited and fruited trees.

lower limits for the maximum growth potentials because observed stem, leaf and trunk growth may have been reduced by competition with one another or with the roots. Maximum fruit growth potential was estimated in a similar manner by heavily thinning peach trees at bloom (Pavel and DeJong, 1993; Grossman and DeJong, 1995*a, b*).

The seasonal patterns of potential stem RER and potential stem and leaf RGRs estimated on defruited trees were very similar for the early and the late maturing peach cultivars examined in this study. In addition, the number of long stems on defruited trees of the two cultivars were similar although the total number of growing stems on the early maturing cultivar was 62% of that on the late maturing cultivar due to differences in dormant-season pruning. These results suggest that the genetic differences that determine the timing of fruit maturation do not affect the maximum vegetative growth potential. Similarly, an earlier study found that differences in the timing of fruit maturity do not alter the ability of the tree to provide resources for fruit growth (Grossman and DeJong, 1995*a*). Thus, the greater partitioning of dry weight to vegetative growth frequently observed on early maturing cultivars compared to late maturing cultivars is apparently the result of a

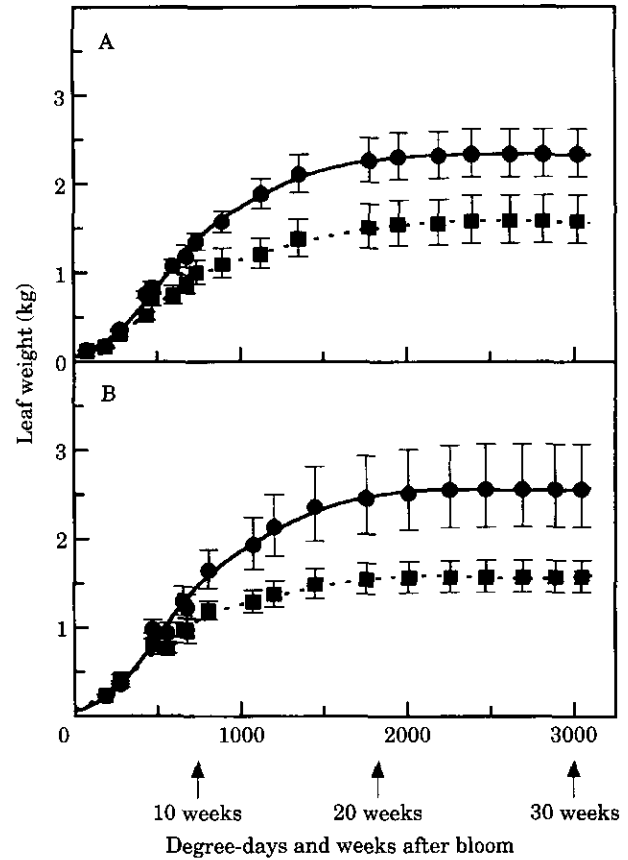


FIG. 9. Seasonal patterns of leaf dry weight per tree for defruited (—) and fruited (---) trees of the early maturing cultivar, Spring Lady (A), and the late maturing cultivar, Cal Red (B). Means and standard errors, indicated by error bars, were calculated using the natural logarithm of leaf dry weight, resulting in apparent asymmetry in the error bars. Lines represent the exponential form of cubic splines fit to the natural logarithm of leaf dry weight vs. degree-days after bloom. Leaf area index may be determined by multiplying by 1.75.

shorter period of competition between reproductive and vegetative growth, rather than a genetic difference in maximum vegetative growth potential.

Stem extension vs. stem dry weight accumulation

Current year stem extension ceased in mid-season, however, stem dry weight accumulation continued through the autumn, indicating continued girth growth (Figs 1, 6). These results together with similar findings for apple (Heim *et al.*, 1979; Forshey *et al.*, 1983), peach (Miller and Walsh, 1988) and cherry (Kappel, 1991), emphasize that measurements of stem length alone are insufficient for estimation of carbon partitioning to stem growth. Therefore, because most studies of stem growth measured stem length without estimating stem dry weight, one must be cautious when reading statements such as 'most mature trees complete a single, relatively short, annual period of shoot growth well before the end of the growing season, and growth remains arrested for the remainder of the year' (Borchert, 1991). Inferences about dry matter partitioning must be based on dry weight data.

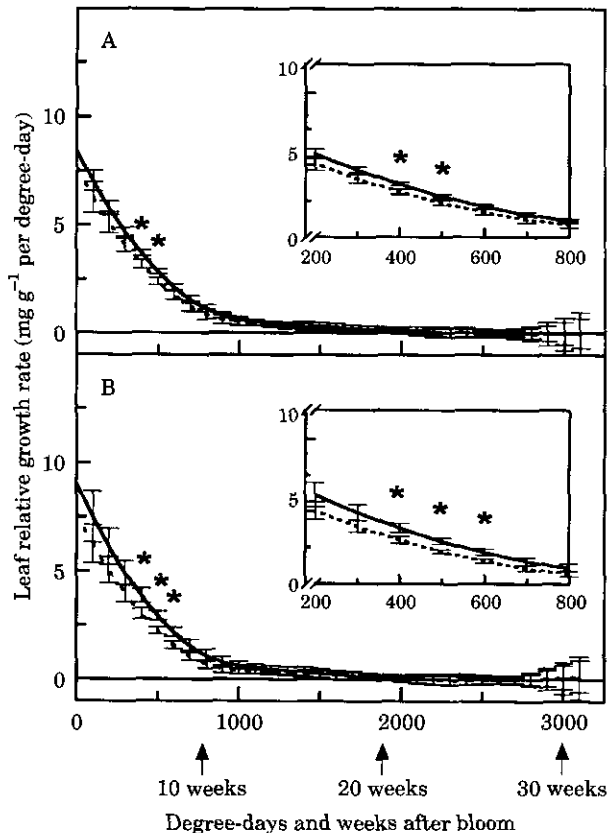


FIG. 10. Seasonal patterns of leaf relative growth rate (RGR) for defruited (—) and fruited (---) trees of the early maturing cultivar, Spring Lady (A), and the late maturing cultivar, Cal Red (B). Bars indicate one standard deviation of the expected value of leaf RGR at 100 degree-day intervals after bloom. Significant differences ($P < 0.05$), indicated by stars, were detected based on an asymptotic normal statistic (Z) of RGR for leaves on defruited and fruited trees.

Seasonal patterns of resource limitation on vegetative growth

The reduction in vegetative growth on fruited trees compared to defruited trees implies that, over the course of the growing season, resource availability for vegetative growth was more limited on fruited trees than on defruited trees. The longer period of fruit growth and greater final crop weight on the late maturing cultivar resulted in greater reductions in stem extension, stem and leaf dry weight and trunk increment than were observed on the early maturing cultivar (Figs 1, 6, 9 and 12, Table 1).

Comparison of the seasonal patterns of stem RER and stem and leaf RGRs on fruited trees to the potential RER and RGRs estimated from defruited trees of both cultivars indicated that the resource limitation on vegetative growth was not continuous throughout the growing season (Figs 4, 7 and 10). On the late maturing cultivar, resource limitation on stem growth was detected from 400 to 600 degree-days (6–8.5 weeks) after bloom when stem RGR and stem RER were lower on fruited trees than on defruited trees. This time period corresponds to the period of rapid stem elongation, during which stem and leaf dry weight accumulation were also rapid (Figs 1, 6 and 9). On the early maturing cultivar,

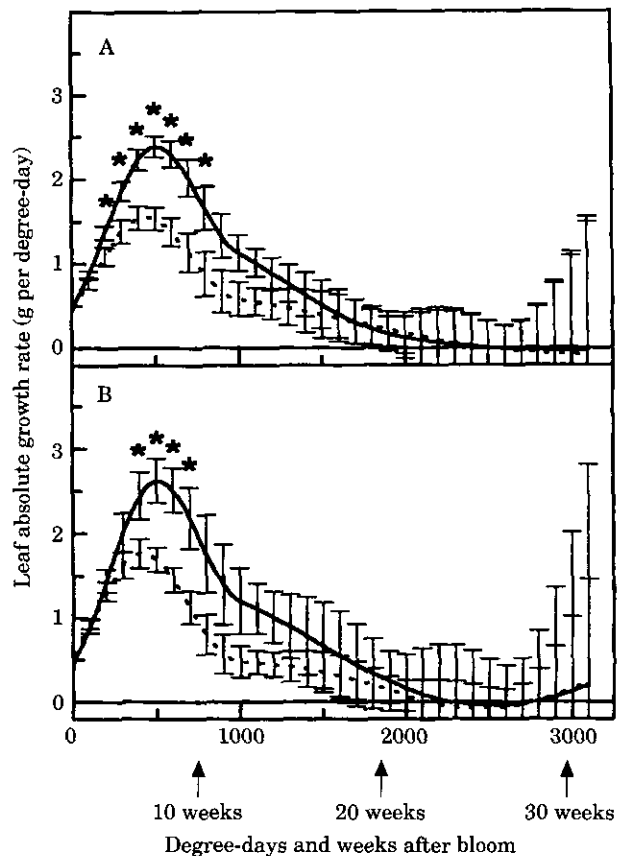


FIG. 11. Seasonal patterns of leaf absolute growth rate (AGR) for defruited (—) and fruited (---) trees of the early maturing cultivar, Spring Lady (A), and the late maturing cultivar, Cal Red (B). Bars indicate one standard deviation of the expected value of leaf AGR at 100 degree-day intervals after bloom. Significant differences ($P < 0.05$), indicated by stars, were detected based on an asymptotic normal statistic (Z) of AGR for leaves on defruited and fruited trees.

resource limitations on stem RER and leaf RGR were detected during this period, but no differences in stem RGR were found (Figs 4, 7 and 10). Stem and leaf dry weights on fruited trees fell below that on defruited trees during this period (Figs 6 and 9).

Within each cultivar, the number of nodes that began growing at vegetative bud break was not affected by fruiting, indicating that the differences in stem RER on fruited and defruited trees were not due to a fruit effect on the number of stems present in each treatment. Individual stems grew to greater length and produced more and longer secondary stems on defruited trees than on fruited trees (Figs 2 and 3).

Strong competition between reproductive and vegetative growth was found in a number of other systems. The presence of fruits decreased the number, but not the average length, of long stems on apple (Barlow, 1966; Forshey and Marmo, 1985), leading Barlow to conclude that the first 3–4 weeks after bloom is a period of intense internal competition between developing fruits, stems, leaves, roots and cambium. Reducing competition by removing whole shoots or shoot tips above the youngest unrolled leaves at 2 week intervals increased the retention of young apple fruits in the early

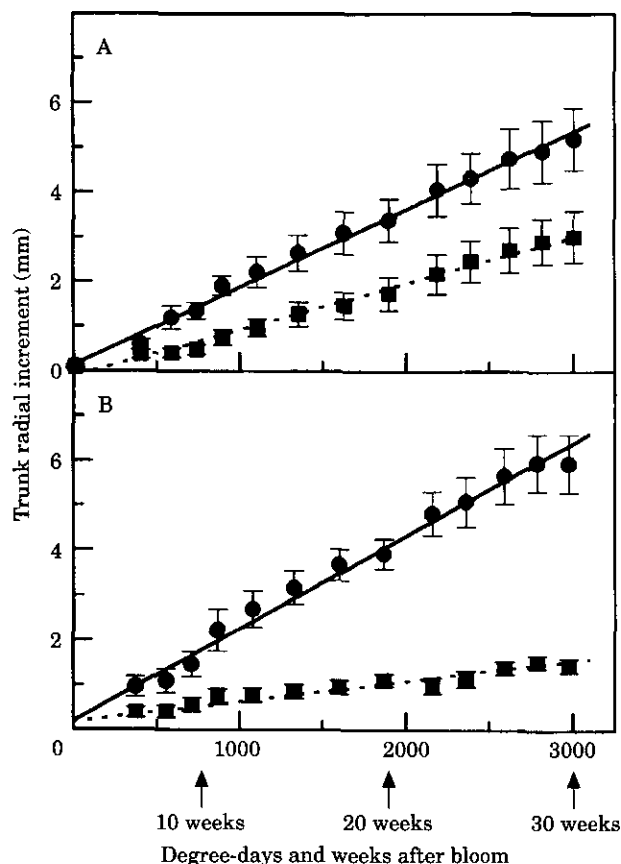


FIG. 12. Seasonal patterns of trunk radial increment for defruited (—●—) and fruited (---■---) trees of the early maturing cultivar, Spring Lady (A), and the late maturing cultivar, Cal Red (B). Error bars indicate standard error of the mean radial increment. Lines represent linear equations fit to trunk radial increment vs. degree-days after bloom.

part of the season (Quinlan and Preston, 1971). Defruiting at bloom increased stem length of potted apple trees within 10 d (Maggs, 1963). These data are consistent with the estimate that apple shoots do not become net exporters of carbohydrates until 15–19 d after bud break (Johnson and Lakso, 1986).

Fruit growth on an early and a late maturing peach cultivar was also found to be resource-limited during similar periods, from 300 degree-days to harvest (4.5–10 weeks) and 200–900 degree-days (3.5–12 weeks) after bloom, respectively (Grossman and DeJong, 1995a). The present study indicates that stem AER and stem and leaf AGRs were near their maxima during this time (Figs 5, 8 and 11). The magnitudes of the maximum potential biomass demand for stem and leaf growth were approximately 1.5 g per degree-day per tree and 2.5 g per degree-day per tree, respectively (Figs 8 and 11), compared to 2.9 and 3.3 g per degree-day per tree for fruit growth on the early maturing and late maturing cultivars, respectively [calculated from potential fruit RGR (Grossman and DeJong, 1995a) multiplied by experimental fruit dry weight at 500 degree-days and fruit number]. Similarly, during the generative stage of growth, cucumber fruits were stronger sinks for assimilates than were vegetative organs (Marcelis, 1992).

During the period of resource-limited vegetative growth, leaf area index was low (Fig. 9), suggesting that daily carbon assimilation would have been limited relative to the high vegetative and reproductive growth potentials during this period (Grossman and DeJong, 1994). This interaction between high demand and low supply probably resulted in the resource limitations detected on both vegetative and reproductive growth. Vegetative growth continued during periods of resource-limited fruit growth, indicating that the sink strength of vegetative organs was sufficient to compete with the high sink strength of growing fruits.

The dynamics of carbohydrate supply and demand have been integrated into a simulation model of carbon assimilation, growth, and respiration by peach trees (Grossman and DeJong, 1994). In a simulation for the late maturing cultivar, resource availability limited fruit and vegetative growth on fruited trees shortly after bloom and again near the time of harvest. The model used maximum fruit and vegetative growth potentials to simulate competition and resource partitioning among vegetative and reproductive organs during peach tree growth. The fit between model predictions and the field data was reasonable, supporting the hypothesis that resource partitioning to the various reproductive and vegetative organs is based upon competition among sinks based upon their maximum growth potentials (Warren Wilson, 1967, 1972; Wareing and Patrick, 1975; Bloom, Chapin and Mooney, 1985). Thus, resource partitioning is apparently determined by individual organs acting as autonomous units which compete with one another for resources and not by a set of fixed priorities for resources.

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