Maximum Fruit Growth Potential Following Resource Limitation During Peach Growth

YAFFA L. GROSSMAN* and THEODORE M. DeJONG

Department of Pomology, University of California, Davis, CA 95616, USA

To achieve its maximum organ growth potential, an organ must grow at its potential relative growth rate (RGR) throughout development. When resource availability limits growth, the RGR is reduced below the potential RGR. This study examines whether, following a period of resource-limited growth, the RGR is able to increase to the potential RGR when sufficient resources are available. Fruit RGRs of a late maturing peach cultivar were examined following removal of most of the fruits (heavy thinning) from previously unthinned trees in Apr., May, and Jun. The fruit RGRs after imposition of the thinning treatments were higher than those on unthinned trees during source-limited periods of the growing season, suggesting that fruit RGR can increase in response to increased resource availability. In general, the RGRs of fruits on trees thinned in Apr., May, and Jun. did not exceed those of fruits on trees thinned at bloom, suggesting that heavy thinning at bloom provides a reasonable estimate of the potential RGR. There were times, however, when the effects of competition with vegetative sinks were apparent, suggesting that the RGR of fruits on trees that were heavily thinned at bloom may underestimate the potential RGR during these times. The absolute growth rates of fruits on thinned trees were greater than those on unthinned trees, but generally were not greater than those on trees that were thinned at bloom, suggesting that peach fruits are unable to recover potential growth lost during resource-limited growth periods.

© 1995 Annals of Botany Company

INTRODUCTION

Although resource limitations on plant organ growth are widely recognized (Lloyd, 1980; Stephenson, 1981; Patrick, 1988; Ho, Grange and Shaw, 1989) there has been little experimental examination of the seasonal patterns of these limitations. The concept of maximum organ growth potential has been used to detect seasonal patterns of resource limitations on peach fruit growth (Pavel and DeJong, 1993; Grossman and DeJong, 1995). Maximum organ growth potential is genetically determined and is 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; Ho *et al.*, 1989; Farrar, 1993). The maximum organ growth potential represents the potential capacity of an organ to accumulate assimilates.

To achieve its maximum organ growth potential, an organ must grow at its potential relative growth rate (RGR), the potential rate of increase in dry weight per unit dry weight per unit time, throughout development. When resource availability limits growth, 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). The concept of maximum organ growth

potential postulates that, following a period of source-limited growth, the RGR increases to the potential RGR if resource supply exceeds demand. Thus, at a given developmental stage, organs of different sizes and different resource supply histories have the potential to grow at the same RGR.

This hypothesis is supported by the data of Choe *et al.* (1988) indicating that, under comparable conditions, the RGRs of wild radish seedlings (introgressive hybrids of *Raphanus raphanistrum* and *R. sativus*) grown from seeds of differing weights are not significantly different. Further support comes from experiments on potato plants with two fast-growing tubers. The absolute growth rate of one tuber increased when the growth of a competing tuber was slowed by cooling it to 8 °C (Engels and Marschner, 1986). This indicates that tubers are able to increase their relative growth rates in response to increased resource availability.

The hypothesis that the RGR attains the potential RGR under conditions of sufficient resource supply may not be universally applicable (Wardlaw, 1990). It is possible that following a period of resource limitation, the maximum possible RGR of two organs at the same developmental stage might differ if one had previously experienced a resource limitation and the other had not. For example, in many fruits, the majority of cell divisions are completed within the first several weeks after bloom (Denne, 1960; Blanpied and Wilde, 1968; Scorza *et al.*, 1991). If individual fruits are subject to resource limitations during the cell

* For correspondence.

division phase of growth, they might complete fewer cell divisions, reducing their subsequent growth potential.

Many experimental manipulations reduce organ growth over the course of a season. Maximum organ growth potential can be used to investigate whether these reductions result from continuous or episodic reductions in organ growth rate. For example, the timing of resource limitations on fruit growth under a variety of thinning treatments could be examined if the maximum fruit growth potential were known. Estimating growth potentials requires elimination of competing sinks (Wareing and Patrick, 1975; Ho, 1988; Ho *et al.*, 1989). In two studies, maximum growth potential of peach fruits was estimated by removing most of the fruits from the tree at the time of bloom which eliminated most of the fruit–fruit competition but did not eliminate other competing sinks such as developing shoots, roots and cambium (Pavel and DeJong, 1993; Grossman and DeJong, 1995). In fact, vegetative growth was much more vigorous on heavily-thinned trees than on unthinned trees (Grossman and DeJong, 1995, unpubl. res.). This vigorous vegetative growth might have competed with fruit growth, reducing the resource availability to the remaining fruits compared to resource availability on unthinned trees. If this were the case, the RGR of fruits on the heavily-thinned trees would have underestimated the potential RGR.

The present study investigates two questions about the concept of maximum fruit growth potential. The first question is: can previously resource-limited fruits increase their RGR in response to increases in resource availability? This was examined by reducing fruit–fruit competition on previously unthinned trees at several times during the season. The second question is: does heavy thinning at bloom reasonably estimate maximum fruit growth potential? This was addressed by comparing fruit RGRs on trees that were heavily thinned at bloom to fruit RGRs on trees that were heavily thinned later in the season. An ancillary question is: can the absolute growth rate of previously resource-limited fruits exceed that of fruits on trees that were heavily thinned at bloom, allowing their weight to 'catch up' to fruits on earlier thinned trees?

METHODS

Thinning treatments

The fruits analysed in this study were grown in 1991, on trees of a mid-Aug. maturing peach cultivar [*Prunus persica* (L.) Batsch cv. Cal Red] that were planted in 1984 at the University of California Kearney Agricultural Center in Parlier, California, USA. Tree spacing and horticultural care are described in Grossman and DeJong (1995).

Most of the flowers were removed from five replicate trees shortly before full bloom (heavy thinning) in order to estimate maximum fruit growth potential on the remaining fruits (Table 1). To examine the effect of substantially reducing fruit–fruit competition later in the growing season, most of the fruits were removed from five previously unthinned trees in Apr., May, and Jun. (Table 1). Throughout the remainder of the paper, trees that were heavily-thinned at bloom, and in Apr., May, and Jun. are referred to as bloom-, Apr.-, May-, and Jun.-thinned,

TABLE 1. *Treatment dates, average final fruit dry weights, and fruit numbers for a late maturing peach cultivar, Cal Red, that was heavily thinned on different dates*

Thinning time	Date	Degree-days after bloom	Final weight per fruit (g)	Fruit number
Bloom	28 Feb. 91*	−35	52·5[a]†	66[a]
Apr.	9 Apr. 91	166	53·3[a]	57[a]
May	21 May 91	521	39·4[b]	62[a]
Jun.	10 Jun. 91	822	35·2[c]	53[a]
Unthinned	n.a.	n.a.	20·6[d]	378[b]

* Bloom-thinned trees were rethinned on 9 Apr. 1991 to remove fruits missed during initial thinning.

† Different letters indicate significantly different means, Tukey's Studentized Range Test, $P < 0.05$.

n.a., Not applicable.

respectively. Fruit growth on unthinned trees was also monitored.

Fruit dry weights were determined every 2 weeks as described in Grossman and DeJong (1995). All data were expressed on the basis of accumulated degree-days after bloom, a developmental index that integrates the effects of time and temperature on plant growth (Zalom *et al.*, 1983), using weather data acquired by the California Irrigation Management Information System (CIMIS) weather station located at the Kearney Agricultural Center. Degree-days were calculated using the single sine, horizontal cut-off method, with critical temperatures of 7 and 35 °C (DeJong and Goudriaan, 1989*a*).

Data analysis

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 fitted as cubic splines using the method of least-squares regression on logarithmically-transformed dry weight data for each fruit on each measurement day *vs.* degree-days after bloom (SAS REG procedure, SAS Institute, Inc., SAS Circle Box 8000, Cary, NC, USA). Because global equations tend to smooth abrupt changes in the first derivative caused by the imposition of an experimental treatment such as thinning (Wickens and Cheeseman, 1988), thinning date was used as the initial time value for equations fitted to the experimental data for each treatment. Because of the sensitivity of the fitting procedure to the initial time value, companion equations for bloom-thinned and unthinned treatments were calculated using the same initial time values. All statistical comparisons were made between fitted curves with the same initial values.

Instantaneous estimates of relative growth rate (RGR) were obtained as the first derivatives of the fitted growth functions [Grossman and DeJong, 1995, eqn (2)]. Instantaneous estimates of absolute growth rate (AGR) were obtained as the first derivatives of the exponential form of the fitted equations [Grossman and DeJong, 1995, 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 and AGR for the different treatments were based on an asymptotic normal statistic (Z). Tukey's Studentized Range Test was used to make comparisons between mean fruit dry weights for each of the treatments.

RESULTS

Final fruit dry weights were significantly greater on earlier than on later-thinned trees, with the exception that fruit weights on bloom- and Apr.-thinned trees were not different (Fig. 1, Table 1). Significant differences between fruit dry weights on bloom-thinned and unthinned trees were detected within 220 degree-days (6 weeks) after bloom. Differences in fruit dry weights between fruits on thinned and unthinned trees appeared on the day after thinning for the Apr. and May thinnings (7 and 20 degree-days, respectively), and 220 degree-days (2·5 weeks) after thinning for the Jun. thinning. Significant differences in dry weight persisted from the time of initial detection through harvest.

Cubic splines with knots at 700 and 1400 degree-days (12·5 and 18·5 weeks) were fitted to logarithmically-transformed dry weight data vs. degree-days after bloom for the bloom- and Apr.-thinned treatments; cubic splines with a knot at 1400 degree-days were fitted for the May-thinned treatment, and cubic equations with no knots were fitted for the Jun.-thinned treatment (Fig. 1). The fruit RGRs on
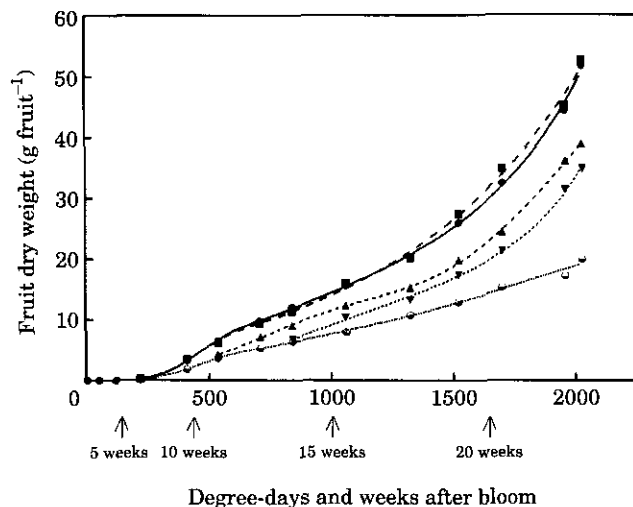

Fig. 1. Seasonal patterns of mean individual fruit dry weight on trees of a late maturing peach cultivar, Cal Red, that were heavily thinned on different dates. Bars representing 1 standard error of the mean fit within the symbols. Lines represent the exponential form of equations fitted to the natural logarithm of dry weight fit beginning 217 degree-days after bloom for bloom-thinned, Apr.-thinned, and unthinned trees, beginning 536 degree-days after bloom for May-thinned trees, and beginning 842 degree-days after bloom for Jun.-thinned trees. Time of thinning: (●), bloom (35 d before bloom); (■), Apr. (166 d after bloom); (▲), May (521 d after bloom); (▼), June (822 d after bloom); ◒, unthinned.
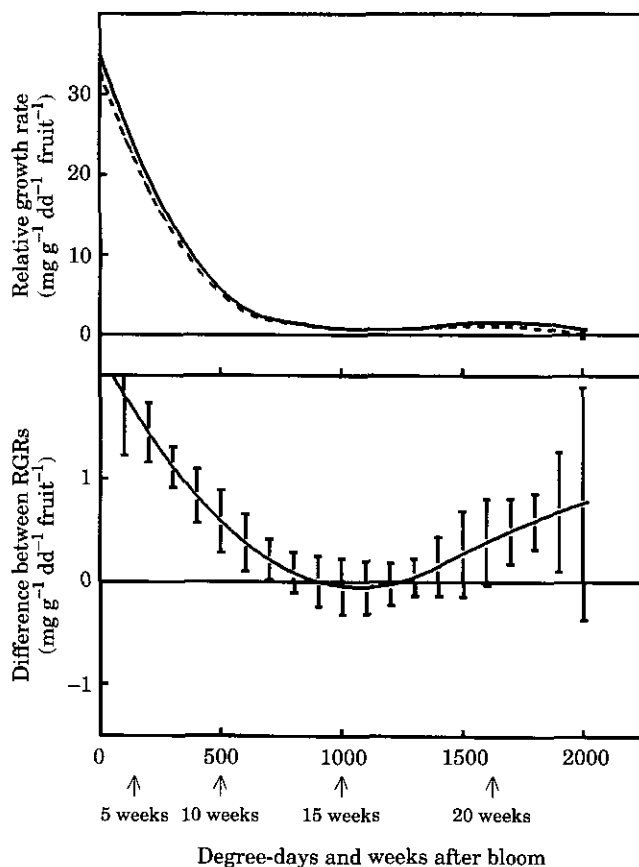

Degree-days and weeks after bloom

Fig. 2. A, Seasonal patterns of relative growth rate (RGR) for fruits on a late maturing peach cultivar, Cal Red, that were heavily thinned at bloom (——) or left unthinned (– – –). Bars indicate one standard deviation of the expected value of RGR at 100 degree-day intervals after bloom (bars fit within line where not visible). B, Seasonal pattern of the difference between the RGR of fruits on bloom-thinned and unthinned trees. Bars represent 95 % confidence limits for the difference. Differences between the means are significant ($P < 0.05$) at time points where bars do not overlap the zero axis.

bloom-thinned and unthinned trees showed a rapid initial decline for the first 400 degree-days after bloom, followed by a slower period of decline until about 650 degree-days after bloom, then a relatively constant RGR until harvest (Fig. 2A). RGRs for fruits on Apr.-, May-, and Jun.-thinned trees showed similar patterns.

Significant differences between the fruit RGRs on bloom-thinned and unthinned trees were detected from bloom until 700 degree-days (0–12·5 weeks) after bloom, and from 1700 to 2000 degree-days after bloom (21–23·5 weeks) (Fig. 2). Similar seasonal patterns were observed when the fruit RGRs on Apr.-, May-, and Jun.-thinned trees were compared with the fruit RGRs on unthinned trees (Fig. 3). However, significant differences between the fruit RGRs on Apr.-thinned and unthinned trees were detected beginning 1000 degree-days after bloom (15 weeks), earlier than they were detected between fruit RGRs on bloom-thinned and unthinned trees (Figs 2 B and 3 A).

Throughout most of the fruit growth period after thinning, the RGRs of fruits on bloom-thinned and later-thinned trees were not significantly different (Fig. 4). The fruit RGR on Apr.-thinned trees was less than the RGR of fruits on
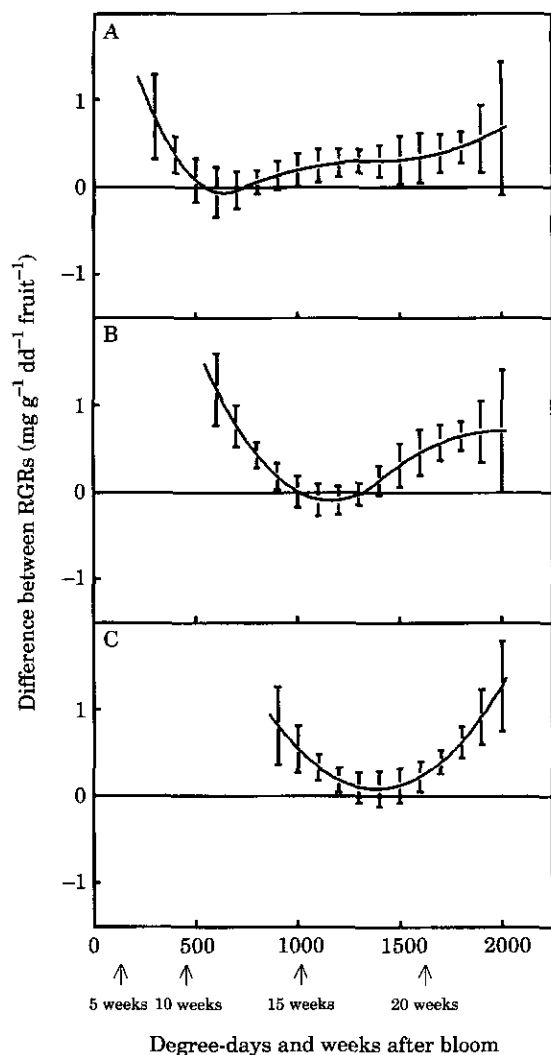
Fig. 3. Seasonal patterns of the differences between the RGRs of fruits on (A) Apr.-, (B) May-, (C) Jun.-thinned and unthinned trees. Bars represent 95% confidence limits for the difference. Differences between the means are significant ($P < 0.05$) at time points where bars do not overlap the zero axis.

Fig. 4. Seasonal patterns of the differences between the RGRs of fruits on bloom-thinned and (A) Apr.-, (B) May-, (C) Jun.-thinned trees. Bars represent 95% confidence limits for the difference. Differences between the means are significant ($P < 0.05$) at time points where bars do not overlap the zero axis.

bloom-thinned trees at 400 and 500 degree-days (9 and 10·5 weeks) after bloom, and was greater than the RGR of fruits on bloom-thinned trees at 1200 and 1300 degree-days (17 and 18 weeks) after bloom (Fig. 4A). The RGRs of fruits on May- and Jun.-thinned trees exceeded the RGR of fruits on bloom-thinned trees for periods of 300 and 400 degree-days (3 and 3·5 weeks) after thinning, respectively (Fig. 4B, C).

The fruit AGRs on bloom-thinned and unthinned trees increased to an initial maximum at about 500 degree-days (10·5 weeks), reached a local minimum at about 1100 degree-days (16·5 weeks), then increased until 1800 degree-days (22 weeks) (Fig. 5). Significant differences between fruit AGRs on bloom-thinned and unthinned trees were detected from 100 to 1900 degree-days (3·5–22·5 weeks). At 2000 degree-days (23·5 weeks) after bloom, the magnitude of the fruit AGR on unthinned trees was lower than that on heavily-thinned trees, however, no significant difference was detected due to the poor predictive ability of the fitted
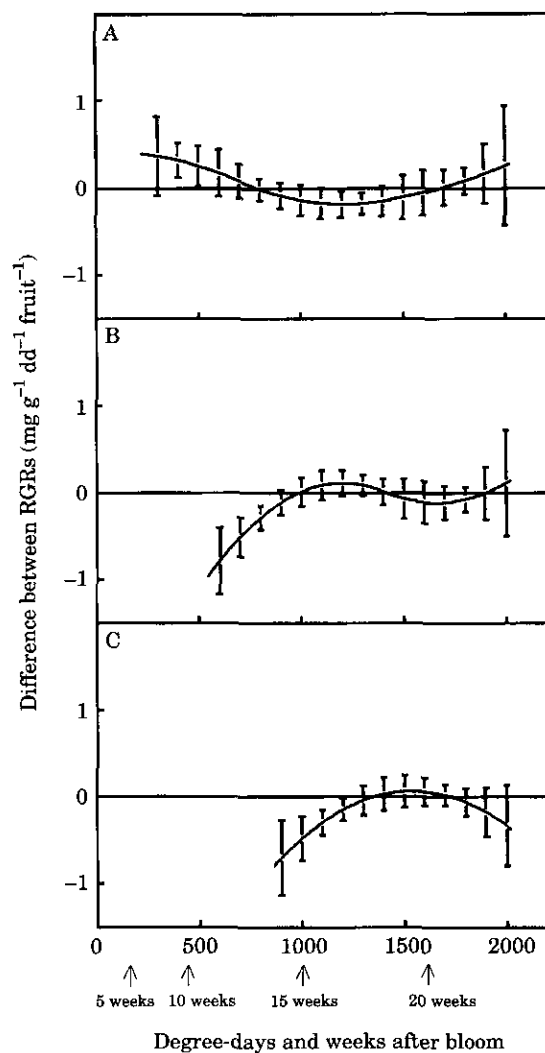
equations near their endpoints. Similar seasonal patterns were observed when the fruit AGRs on Apr.-, May-, and Jun.-thinned trees were compared to the fruit AGR on unthinned trees, and significant differences were detected on all dates tested (Fig. 6).

Throughout most of the season, the fruit AGRs on bloom- and Apr.-thinned trees were not significantly different with the exception of 1200 and 1400 degree-days after bloom (17–18·5 weeks, Fig. 7A). In contrast, significant differences between fruit AGRs on bloom- and May-thinned trees were detected on all dates except 1700 degree-days (21 weeks, Fig. 7B). Significant differences between fruit AGRs on bloom- and Jun.-thinned trees were detected from 1100 to 1900 degree-days (16·5–22·5 weeks, Fig. 7C).

DISCUSSION

Decreasing fruit–fruit competition by removing most of the fruits from the tree increased final fruit dry weight (Fig. 1,
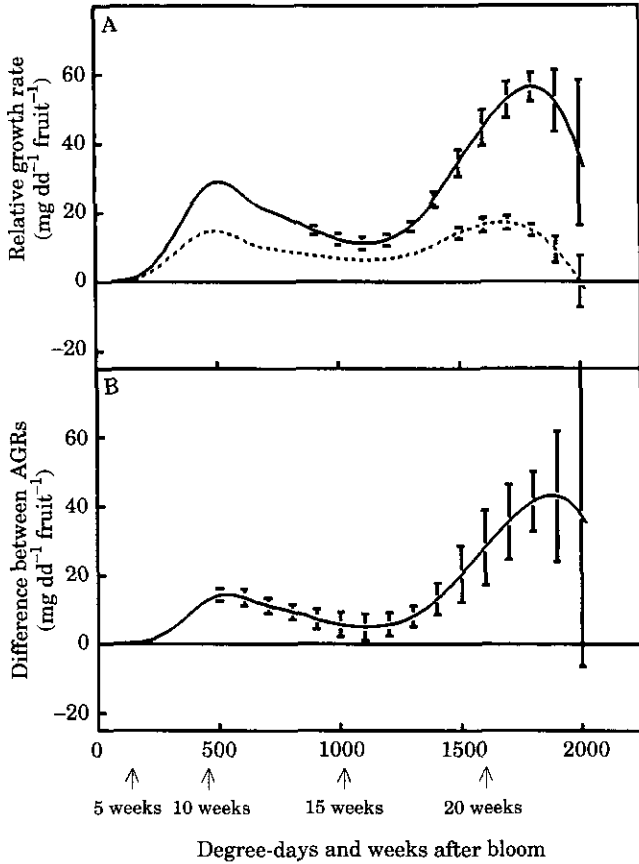
Degree-days and weeks after bloom

FIG. 5. A, Seasonal patterns of absolute growth rate (AGR) for fruits on a late maturing peach cultivar, Cal Red, that were heavily thinned at bloom (———) or left unthinned (---). Bars indicate 1 standard deviation of the expected value of AGR at 100 degree-day intervals after bloom. B, Seasonal pattern of the difference between the AGR of fruits on bloom-thinned and unthinned trees. Bars represent 95% confidence limits for the difference. Differences between the means are significant ($P < 0.05$) at time points where bars do not overlap the zero axis.

Table 1, Johnson and Handley, 1989; Grossman and DeJong, 1994, 1995). This confirms the hypothesis that fruit growth on unthinned trees was resource-limited over the course of the season. As reported previously, source-limited growth periods, periods when fruit RGRs on thinned and unthinned trees were significantly different from one another, alternated with periods when no source limitation was detected (Figs 2 and 3; Pavel and DeJong, 1993; Grossman and DeJong, 1995).

The detection of significant differences between fruit RGRs on Apr.-, May-, Jun.-thinned and unthinned trees gives an affirmative answer to the first question posed in the Introduction: the RGR of previously source-limited fruits (i.e. fruits on previously unthinned trees) increased when additional resources were made available by thinning. Thus, although limited resource availability early in fruit development reduced fruit size and may have reduced cell number and/or cell size compared to bloom-thinned fruits, the fruits retained the ability to respond to increases in resource availability by increasing their RGRs.

In general, increasing resource availability to previously source-limited fruits increased the RGR to near that of
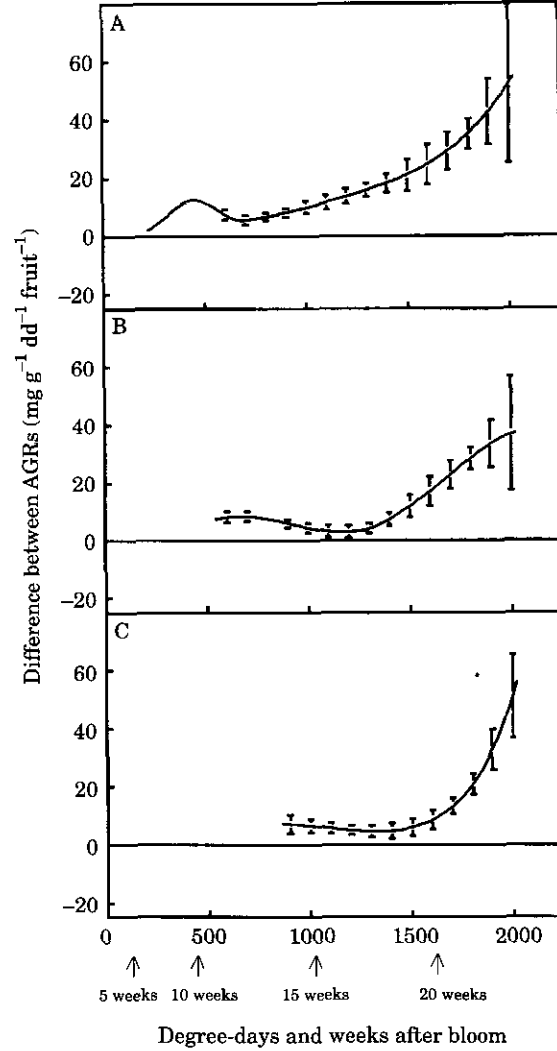

Degree-days and weeks after bloom

FIG. 6. Seasonal patterns of the differences between the AGRs of fruits on (A) Apr.-, (B) May-, (C) Jun.-thinned and unthinned trees. Bars represent 95% confidence limits for the difference. Differences between the means are significant ($P < 0.05$) at time points where bars do not overlap the zero axis.

fruits on bloom-thinned trees (Fig. 4). This suggests that the RGR of fruits on bloom-thinned trees provides a reasonable estimate of the potential RGR. However, the effects of competition with other sinks were apparent, suggesting that the RGR of fruits on bloom-thinned trees may underestimate the potential RGR at certain times. For example, fruit RGRs on May- and Jun.-thinned trees exceeded the fruit RGR on bloom-thinned trees for a period immediately after thinning (Fig. 4B, C). By the May thinning date, shoot extension growth had substantially slowed (Grossman and DeJong, unpubl. res.). Immediately following thinning, the vegetative sink demand was probably lower on the previously unthinned trees than on the bloom-thinned trees, because thinned trees produced more vegetative growth than unthinned trees, and earlier-thinned trees produced more vegetative growth than later-thinned trees (Grossman and DeJong, unpubl. res.). It may have taken several weeks after thinning to activate additional vegetative sink
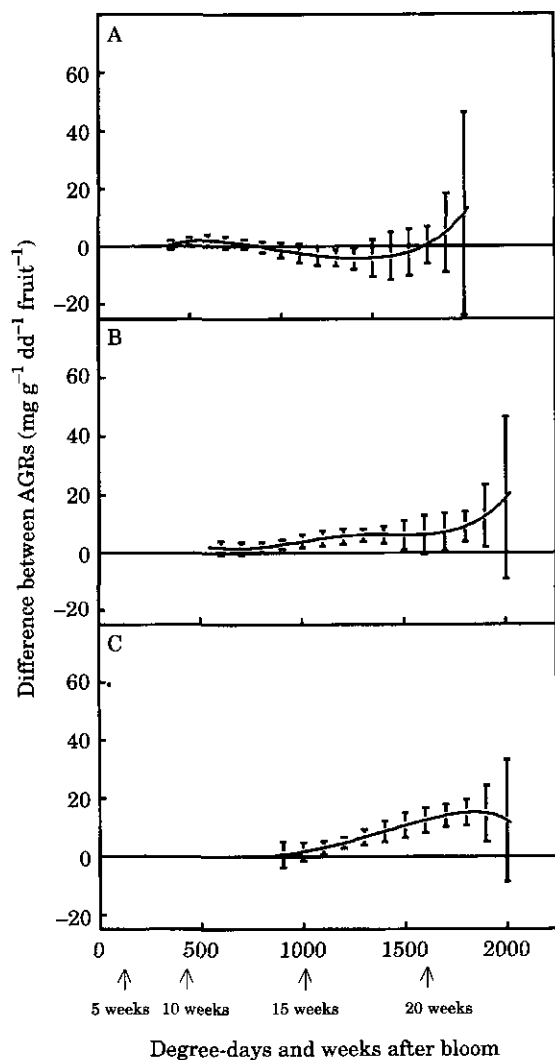
FIG. 7. Seasonal patterns of the differences between the AGRs of fruits on bloom-thinned and (A) Apr.-, (B) May-, (C) Jun.-thinned trees. Bars represent 95% confidence limits for the difference. Differences between the means are significant ($P < 0.05$) at time points where bars do not overlap the zero axis.

demand. Once additional vegetative sinks had developed, the RGRs of fruits on May- and Jun.-thinned trees no longer exceeded the RGR of fruits on bloom-thinned trees. The rapid response of the fruit RGR to heavy thinning suggests that the resource limitations prior to thinning are due to resource supply and not to transport capacity.

The fruit RGR on Apr.-thinned trees was significantly less than the fruit RGR on bloom-thinned trees from 400 to 500 degree-days (9–10·5 weeks), a period of active shoot extension growth (Fig. 4A, Grossman and DeJong, unpubl. res.). It may be that the additional resources made available by removing a large number of fruits were not sufficient to increase the RGR of fruits on Apr.-thinned trees to the level of the RGR of fruits on bloom-thinned trees due to competition from vegetative sinks.

The source-limited fruit growth periods may have been longer than the periods detected because the RGR of fruits

on bloom-thinned trees appears to have somewhat under-estimated the potential RGR. However, the results of this study confirm that a period of growth with no detectable source limitation occurs on unthinned trees (DeJong and Goudriaan, 1989 b; DeJong, Johnson and Castagnoli, 1990; Pavel and DeJong, 1993; Grossman and DeJong, 1995). In all thinning experiments, regardless of the time of thinning, there was a period during which the RGR did not exceed the RGR on unthinned trees (Figs 2 and 3). If fruit growth during this period had been source-limited, one would have expected heavy thinning to increase the fruit RGR on thinned trees above that on unthinned trees. Growth periods without source limitations have also been identified in corn and soybean seeds (reviewed in Patrick, 1988). In these seeds, there are periods when starch accumulation appears to be limited by the capacity for starch synthesis rather than by sucrose concentration in the seed or the rate of sucrose import.

The fruit AGRs represent the rate of dry weight accumulation by individual fruits. All thinning treatments increased the fruit AGRs compared with the fruit AGR on unthinned trees (Figs 5 and 6). Because AGR is the product of dry weight and RGR, the increases in AGR following thinning were caused by increases in fruit dry weight (Fig. 1) and, during some periods, increases in fruit RGR (Fig. 3). Although thinning resulted in increases in fruit RGR, the weight of fruits on later thinned trees could not 'catch up' to the weight of fruits on earlier thinned trees because this would have required that the fruit AGR exceed that on bloom-thinned trees, a situation that occurred only once, briefly, on Apr.-thinned trees (1200–1400 degree-days, 17–18·5 weeks, Fig. 7). Although these fruits were not significantly larger than fruits on bloom-thinned trees (Fig. 1), their RGR was greater from 1200 to 1300 degree-days (17–18 weeks, Fig. 3A). Thus, peach fruits are not able to recover potential growth lost during resource-limited growth periods. At the commercial level, this suggests that fruit thinning should be carried out early in the season, before resource limitations produce irrevocable reductions in fruit absolute growth rate for the remainder of the season (Johnson and Handley, 1989; Yoshikawa and Johnson, 1989; Grossman and DeJong, 1995).

This study supports the hypothesis that resources can be made available to individual organs by reducing competition from other sinks, as suggested by Wardlaw (1968), Wareing and Patrick (1975), Lloyd (1980), Stephenson (1981), and others. It also offers support to the hypothesis that sink regions exercise major control over resource partitioning within the plant by competing with one another (Gifford and Evans, 1981; Ho *et al.*, 1989; Patrick, 1991; DeJong and Grossman, 1992; Grossman and DeJong, 1995 and unpubl. res.). The basis for the competitive ability of a sink is its maximum organ growth potential. However, there are few quantitative descriptions of the seasonal patterns of maximum organ growth potential in the source–sink literature (Warren Wilson, 1967, 1972; Wareing and Patrick, 1975; Ho *et al.*, 1989; Farrar, 1993). The estimate of the maximum growth potential of peach fruits obtained by heavily thinning peach trees at bloom appears to be reasonable for most of the growing season, although it may

underestimate the actual growth potential during periods of heavy competition from vegetative growth. Peach fruits appear to be unable to recover potential growth lost during resource-limited growth periods. A simulation model of peach tree growth that uses estimated fruit and vegetative maximum growth potentials to determine carbon partitioning between reproductive and vegetative growth predicts resource-limited growth periods similar to those described in this experimental study (Grossman and DeJong, 1994).

LITERATURE CITED

Blanpied GD, Wilde MH. 1968. A study of the cells in the outer flesh of developing McIntosh apple fruits. *Botanical Gazette* **129**: 173–183.

Casella G, Berger RL. 1990. *Statistical inference.* Pacific Grove, California: Wadsworth and Brooks/Cole Advanced Books and Software, 328–331.

Choe HS, Chu C, Koch G, Gorham J, Mooney HA. 1988. Seed weight and seed resources in relation to plant growth rate. *Oecologia* **76**: 158–159.

DeJong TM, Goudriaan J. 1989a. Modeling peach fruit growth and carbohydrate requirements: Reevaluation of the double-sigmoid growth pattern. *Journal of the American Society for Horticultural Science* **114**: 800–804.

DeJong TM, Goudriaan J. 1989b. Modeling the carbohydrate economy of peach fruit growth and crop production. *Acta Horticulturae* **254**: 103–108.

DeJong TM, Grossman YL. 1992. Modeling the seasonal carbon economy of deciduous tree crops. *Acta Horticulturae* **313**: 21–28.

DeJong TM, Johnson RS, Castagnoli SP. 1990. Computer simulation of the carbohydrate economy of peach crop growth. *Acta Horticulturae* **276**: 97–104.

Denne MP. 1960. The growth of apple fruitlets, and the effect of early thinning on fruit development. *Annals of Botany* **24**: 397–406.

Elias CO, Causton DR. 1976. Studies on data variability and the use of polynomials to describe plant growth. *New Phytologist* **77**: 421–430.

Engels C, Marschner H. 1986. Allocation of photosynthate to individual tubers of *Solanum tuberosum* L. I. Relationship between tuber growth rate and enzyme activities of the starch metabolism. *Journal of Experimental Botany* **37**: 1795–1803.

Farrar JF, ed. 1993. Forum: Sink strength: What is it and how do we measure it? *Plant, Cell, and Environment* **16**: 1013–1046.

Gifford RM, Evans LT. 1981. Photosynthesis, carbon partitioning, and yield. *Annual Review of Plant Physiology* **32**: 485–509.

Grossman YL. 1993. *The carbon economy of reproductive and vegetative growth of a woody perennial, peach* (Prunus persica (*L.*) Batsch): *Growth potentials, respiratory demand and a simulation model.* Ph.D. Dissertation, University of California, Davis.

Grossman YL, DeJong TM. 1994. Peach: a simulation model of reproductive and vegetative growth in peach trees. *Tree Physiology* **14**: 329–345.

Grossman YL, DeJong TM. 1995. Maximum fruit growth potential and seasonal patterns of resource dynamics during peach growth. *Annals of Botany* **75**: 553–560.

Ho LC. 1984. Partitioning of assimilates in fruiting tomato plants. *Plant Growth Regulation* **2**: 277–285.

Ho LC. 1988. Metabolism and compartmentation of imported sugars in sink organs in relation to sink strength. *Annual Review of Plant Physiology* **39**: 355–378.

Ho LC, Grange RI, Shaw AF. 1989. Source/sink regulation. In: Baker DA, Milburn JA, eds. *Transport of photoassimilates.* Harlow, Essex, UK: Longman Scientific and Technical, 306–344.

Hunt R. 1979. Plant growth analysis: The rationale behind the use of the fitted mathematical function. *Annals of Botany* **43**: 245–249.

Hunt R. 1982. *Plant growth curves.* London: Edward Arnold, 47–120.

Johnson RS, Handley DF. 1989. Thinning response of early, mid-, and late-season peaches. *Journal of the American Society for Horticultural Science* **114**: 852–855.

Lloyd DG. 1980. Sexual strategies in plants I. An hypothesis of serial adjustment of maternal investment during one reproductive session. *New Phytologist* **86**: 69–79.

Miller RG Jr. 1986. *Beyond ANOVA, basics of applied statistics.* New York: John Wiley and Sons, 58–59.

Parsons IT, Hunt R. 1981. Plant growth analysis: a program for the fitting of lengthy series of data by the method of B-splines. *Annals of Botany* **48**: 341–352.

Patrick JW. 1988. Assimilate partitioning in relation to crop productivity. *HortScience* **23**: 33–40.

Patrick JW. 1991. Control of phloem transport to and short-distance transfer in sink regions: an overview. In: Bonnemain JL, Delrot S, Lucas WJ, Dainty J, eds. *Recent advances in phloem transport and assimilate compartmentation.* Nantes, France: Oest Editions, 167–177.

Pavel EW, DeJong TM. 1993. Source- and sink-limited growth periods of developing peach fruits indicated by relative growth rate analysis. *Journal of the American Society for Horticultural Science* **118**: 820–824.

Scorza R, May LG, Purnell B, Upchurch B. 1991. Differences in number and area of mesocarp cells between small- and large-fruited peach cultivars. *Journal of the American Society for Horticultural Science* **116**: 861–864.

Steel RGD, Torrie JH. 1980. *Principles and procedures of statistics: A biometrical approach.* New York: McGraw-Hill Book Company.

Stephenson AG. 1981. Flower and fruit abortion: proximate causes and ultimate functions. *Annual Review of Ecology and Systematics* **12**: 253–279.

Wardlaw IF. 1968. The control and pattern of movement of carbohydrates in plants. *Botanical Review* **34**: 79–105.

Wardlaw IF. 1990. The control of carbon partitioning in plants. Tansley Review Number 27. *New Phytologist* **116**: 341–381.

Wareing PF, Patrick J. 1975. Source-sink relations and the partition of assimilates in the plant. In: Cooper JP, ed. *Photosynthesis and productivity in different environments.* Cambridge: Cambridge University Press, 481–499.

Warren Wilson J. 1967. Ecological data on dry matter production by plants and plant communities. In: Bradley EF, Denmead OT, eds. *The collection and processing of field data.* New York: Interscience Publishers, 77–123.

Warren Wilson J. 1972. Control of crop processes. In: Rees AR, Cockshull KE, Hand DW, Hurd RG, eds. *Crop processes in controlled environments.* New York: Academic Press, 7–30.

Wickens LK, Cheeseman JM. 1988. Application of growth analysis to physiological studies involving environmental discontinuities. *Physiologia Plantarum* **73**: 271–277.

Yoshikawa FT, Johnson RS. 1989. Fruit thinning. In: LaRue JH, Johnson RS, eds. *Peaches, plums and nectarines, growing and handling for fresh market.* Oakland, California: Cooperative Extension, Division of Agriculture and Natural Resources, University of California, Publication 3331, 56–59.

Zalom FG, Goodell PB, Wilson LT, Barnett WW, Bentley WJ. 1983. *Degree-days: The calculation and use of heat units in pest management.* Berkeley, California: Division of Agriculture and Natural Resources, University of California, Leaflet 21373.