

Source- and Sink-limited Growth Periods of Developing Peach Fruits Indicated by Relative Growth Rate Analysis

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Abstract. Peach [*Prunus persica* (L.) Batsch] fruit thinning was used to reduce the competition for assimilates among peach fruits and to identify periods of source- and sink-limited growth during development. Individual fruit size, based on diameter or calculated dry matter accumulation, increased in trees with lower crop loads compared to fruits of unthinned trees in three peach cultivars. Relative growth rate analysis indicated that peach fruit growth was apparently limited by the assimilate supply (source-limited) or by its genetic growth potential (sink-limited) during specific growth periods. In stage I and at the beginning of stage III of the double-sigmoid growth curve, periods of source-limited growth occurred in the later-maturing cultivars Flamecrest and Cal Red. Peach fruit growth was apparently sink-limited during stage II of the growth curve when fruit relative growth rates were similar for the thinning treatments. Fruit growth in 'Spring Lady', an early maturing cultivar, appeared to be primarily source-limited during the season. Although total fruit dry matter production was reduced by thinning, individual fruit dry weight on thinned trees was higher than that on trees with a heavy crop load. This typical thinning response was apparently caused by the differences in the amount of time that fruits grew under sink- vs. source-limited conditions with different crop loads. Final crop yield depended on fruit count per tree and on the available assimilate supply, and was affected by the individual fruit growth potential.

To improve the understanding of crop physiology and the influence of yield-limiting factors on crop production, it is useful to study source-sink relationships and the regulation of carbon partitioning among sinks in plants. Leaves are regions of assimilate production and are referred to as sources. A developing leaf, however, can represent both-a source by producing assimilates itself, as well as a sink, by importing assimilates from other parts of the plant. Sinks import and use assimilates in respiration, growth, and storage material (Wareing and Patrick, 1975). Within a tree, reproductive organs, such as fruits, compete for assimilates with each other, especially in trees with high crop loads, and with vegetative organs, shoots, leaves, and roots (Dann et al., 1984; DeJong et al., 1987; Hansen, 1971; Maggs, 1963; Weinberger, 1931). High crop loads reduce the growth of roots, shoots, and leaves in citrus trees and can account for 50% of the total dry matter production of a tree at harvest. Fruits, therefore, represent strong sinks within a tree and can compete successfully for assimilates with vegetative organs (Lenz, 1977). Reducing the number of fruits per tree by thinning increases the leaf : fruit ratio and also increases fruit size (Dorsey and McMunn, 1927; Haller and Magness, 1925; Martin et al., 1964; Weinberger, 1931).

Many studies have been conducted to explain the control of assimilate partitioning between sinks competing for a limited supply of assimilates. Sinks change their competitive ability with growth, leading to diversion towards the stronger sinks (Ho, 1980; Wright, 1989). The strength of a fruit sink (i.e., its potential capacity to accumulate assimilates) depends on its size, the time of its initiation relative to other sinks, its location, and distance from the source (Bangerth and Ho, 1984; Cook and Evans 1978; Engels and Marschner, 1986; Ho, 1980). In contrast to annual plants, in most fruit trees the buds are formed and differentiated to flower buds in the year before fruiting. This differentiation generally occurs during the fruit growing season in pome fruits and at the end or after

the fruit growing period in stone fruits (Feucht, 1982). Environmental as well as endogenous factors within the tree (i.e., assimilate reserves) affect the fruit growth potential between flower bud formation and anthesis (Feucht, 1982). The final fruit size is also related to cell count and, to a lesser extent, cell size in apples (*Malus domestica* Borkh.) (Bain and Robertson, 1951; Denne, 1961). Factors such as temperature and assimilate competition between fruits during the cell division period apparently affect the fruit growth potential (Blanpied and Wilde, 1968; Quinlan and Preston, 1968). Early thinning, at bloom or within the first weeks after pollination, results in larger fruit in peaches and apples (Quinlan and Preston, 1968; Weinberger, 1941) indicating that, during this period, fruit growth can be source-limited. Fruit growth may also be source-limited later in the season, at the beginning of stage III of the double-sigmoid growth curve in peaches and after the "June drop" in apples (Denne, 1961; Dorsey and McMunn, 1927; Preston and Quinlan, 1968; Weinberger, 1941).

DeJong and Goudriaan (1989a, 1989b) hypothesized that, for any given time interval over the season, peach fruit growth is a function of potential relative growth rate for that time interval and the fruit mass at the beginning of the time interval. Recently, Pavel and DeJong (1993) showed that the seasonal relative growth rate pattern of later-maturing peaches is related to changes in growth of individual fruit tissues and the relative nonstructural carbohydrate composition of the mesocarp. The following experiments were designed to determine if fruit relative growth rate analysis could also be used to identify when fruit growth is limited either by sink growth potential or by a limited assimilate supply. Hereby, relative growth rates of fruits from trees with different crop loads were compared.

Materials and Methods

The experiments were conducted at the Univ. of California's Kearney Agricultural Center, Parlier, with three peach cultivars

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Abbreviations: °D, degree day; °DAF, degree days after flowering; DAF, days after flowering.

['Spring Lady' (early), 'Flamecrest' (midseason), and 'Cal Red' (late) grown on Nemaguard rootstock] during the 1988 growing season. The growing period lasted 94 days (883^oD) for 'Spring Lady', 134 days (1531^oD) for 'Flamecrest', and 171 days (2238^oD) for 'Cal Red'. The 5-year-old 'Spring Lady' and 'Cal Red' trees were trained to a high-density central-leader system (2.0 × 4.0 m). Twelve-year-old trees of 'Flamecrest' were trained to a low-density open-vase system (6.1 × 6.1 m). Cultural management practices, such as fertilization, winter pruning, and irrigation, were conducted as in a commercial orchard. Nutrients and water were assumed to be nonlimiting.

After the cell division period, the trees were hand-thinned [232^oD after flowering (^oDAF) or 31 days after flowering (DAF) in 'Spring Lady', 365^oDAF or 44 DAF in 'Flamecrest', and 404^oDAF or 49 DAF in 'Cal Red']. The cell division period ceases ≈4 weeks after anthesis in peaches (Addoms et al., 1930). Three thinning treatments per each cultivar were applied (Table 1). Four trees were used for each thinning treatment randomized in a block. Fruit count per tree was determined or calculated by total yield per tree and mean fruit fresh weight at harvest. The diameter of 20 fruits (five fruits per tree) was measured weekly beginning at 186^oDAF (26 DAF) after flowering in 'Spring Lady', 193^oDAF (27 DAF) in 'Flamecrest', and 165^oDAF (24 DAF) in 'Cal Red', until harvest. Fruit dry weight was determined at harvest, and seasonal fruit dry weight accumulation was estimated by regression analysis of weekly diameter and dry weight measurements of 10 individual fruits of each peach cultivar from a separate set of 20 trees. These trees were hand-thinned to a normal commercial level. Seasonal mean fruit dry weight accumulations were used to calculate relative growth rates according to the method of Hunt (1982). The effect of temperature on fruit growth was considered by integrating degree-day accumulations into the equation instead of standard time intervals. Ambient air temperatures were monitored at a California Irrigation Management Information System weather station located on the research station (within 1 km of the study site). Degree-day accumulations were calculated from daily minimum and maximum temperatures by the single-sine method (Zalom et al., 1983) with lower and upper temperature thresholds at 7 and 35C. Fruit relative growth rate data were tested with analysis of variance (one factor, completely randomized) at each sampling date. Tukey's mean separation test was used to compare mean fruit relative growth rates among thinning treatments.

Total fruit dry matter was estimated for the trees with different crop loads at each sampling date by using the calculated mean dry weights per fruit and the fruit counts per tree. Because the trees were planted and trained in different systems, fruit dry matter production was expressed on a per-hectare basis.

Results and Discussion

Seasonal patterns of peach fruit diameter and calculated dry weight accumulations showed that, with declining tree crop load, individual fruit sizes increased (Figs. 1 and 2), similar to results reported for peach and apple fruits by Preston and Quinlan (1968)

Table 1. Number of fruits per tree for the thinning treatments.

Cultivars	Thinning		
	None	Normal commercial	Heavy
Spring Lady	268 ± 49 ²	124 ± 8	15 ± 0
Flamecrest	3058 ± 226	1471 ± 133	583 ± 74
Cal Red	386 ± 10	219 ± 8	15 ± 0

²Mean ± SE of four trees.

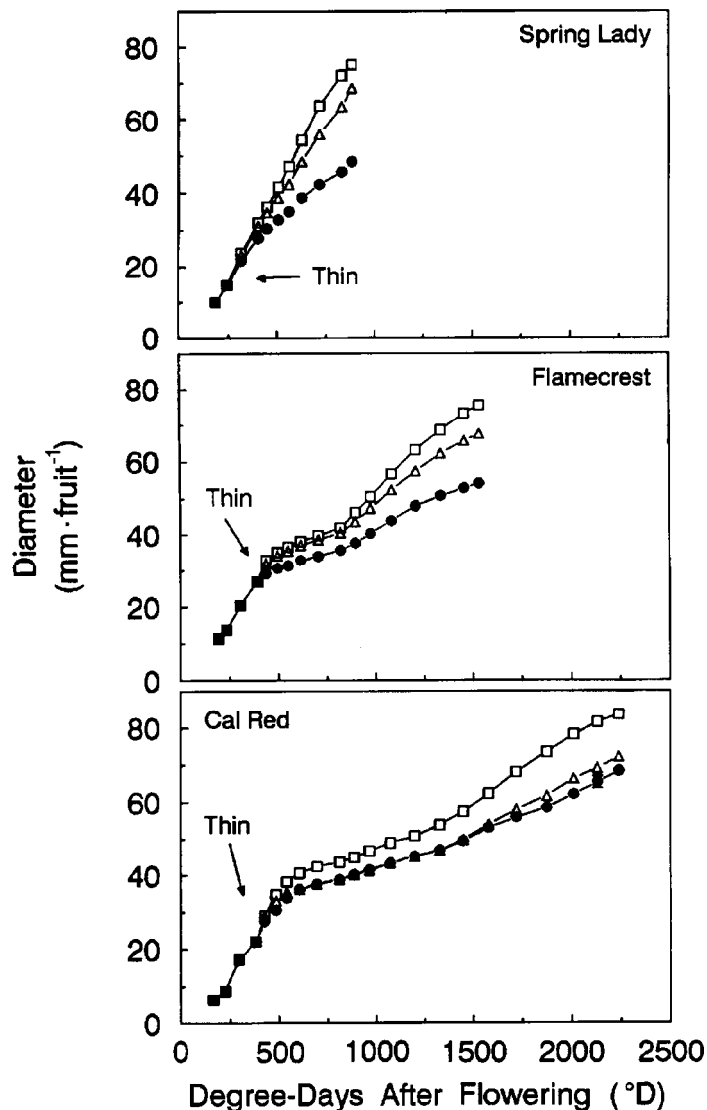


Fig. 1. Patterns of fruit diameter of early ('Spring Lady'), midseason ('Flamecrest'), and late-maturing ('Cal Red') peaches with differing crop loads during the 1988 growing season (data points represent means ± SE of 20 fruits measured on each sampling date; SE bars are visible when larger than the symbols depicting data points; thin = thinning date). Fruit count per tree: 'Spring Lady': (solid circle) 268/unthinned, (open triangle) 124/normal commercial thinning, (open square) 15/heavily thinned; 'Flamecrest'—(solid circle) 3058/unthinned, (open triangle) 1471/normal commercial thinning, (open square) 583/heavily thinned; 'Cal Red'—(solid circle) 386/unthinned, (open triangle) 219/normal commercial thinning, (open square) 15/heavily thinned.

and Tukey and Einset (1939). Shortly after thinning (317^oDAF in 'Spring Lady', 437^oDAF in 'Flamecrest', and 427^oDAF in 'Cal Red'), and also later in the season, at the beginning of stage III of the growth curve, fruits on thinned (normal commercial and heavy thinning) trees grew more rapidly than fruits on unthinned trees of the three cultivars (Figs. 1 and 2). The difference in growth between fruits on thinned and unthinned trees remained nearly constant during stage II. However, in 'Cal Red', there was no significant difference in fruit growth increases between trees with 386 (unthinned) and 219 (normal commercial thinned) fruits during stage II, although thinning initially affected the growth of fruits on trees with the lower crop load (Figs. 1 and 2).

Peach fruit growth is limited by the availability of current photosynthates before thinning and again before harvest, as DeJong and Goudriaan (1989a) suggested with their simulation model. In these experiments, the assumption was made that the growth of

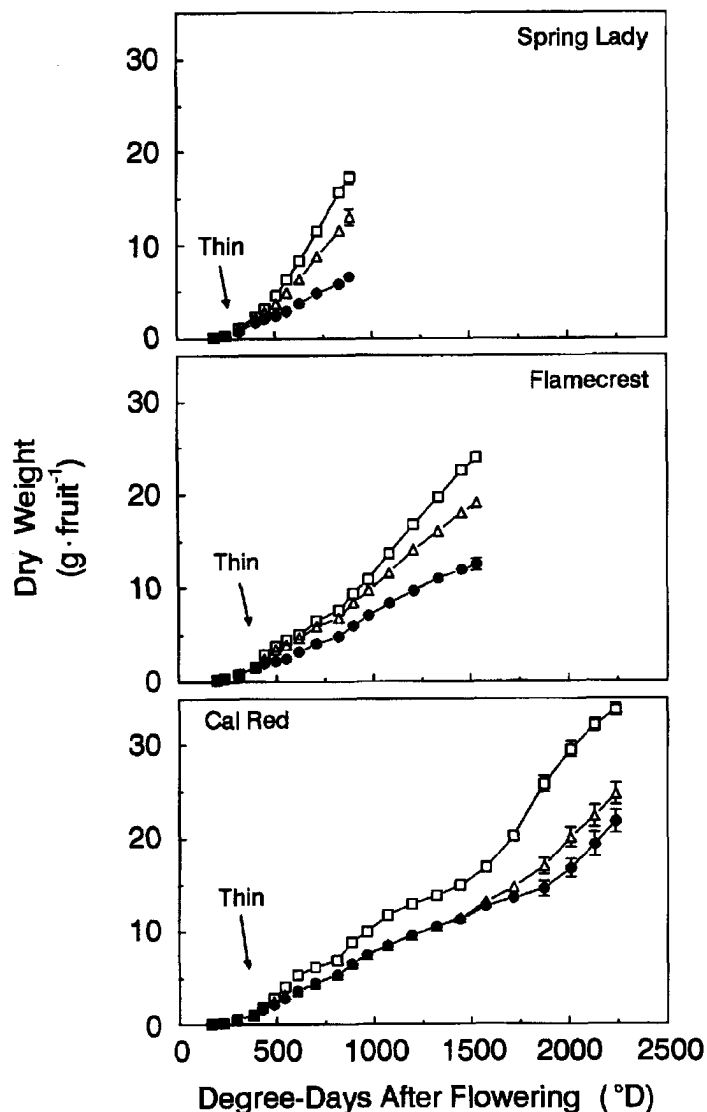


Fig. 2. Seasonal patterns of fruit dry weight accumulation of early ('Spring Lady'), midseason ('Flamecrest'), and late-maturing ('Cal Red') peaches (data points represent means \pm SE of 20 fruits calculated for each sampling date from the fruit diameter by regression; SE bars are visible when larger than the symbols depicting data points; thin = thinning date). Symbols represent different crop loads after thinning (see Fig. 1).

fruits on heavily thinned trees (15 fruits on 'Spring Lady' and 'Cal Red', or 583 fruits on 'Flamecrest') was not limited by the availability of photosynthates (source-limited). Those fruits would then have indicated mean maximum relative growth rates; i.e., maximum individual sink demands. If fruit growth was not source-limited, then there would be no differences in relative growth rates between fruits on thinned (heavily thinned, normal commercial thinned) and unthinned trees. Significant differences between relative growth rates of fruits on unthinned and thinned trees indicate that fruit growth was source-limited at specific periods (Fig. 3).

The first apparent period of source-limited growth occurred in stage I of the growth curve (at 281°DAF in 'Spring Lady', 414°DAF in 'Flamecrest', and 456°DAF in 'Cal Red') (Fig. 3). Dry weight relative growth rates increased promptly after thinning in fruits of thinned trees in comparison to fruits on unthinned trees, apparently as a result of the reduction of fruit competition for assimilates in each of the three cultivars.

A second period of source-limited growth took place later in the

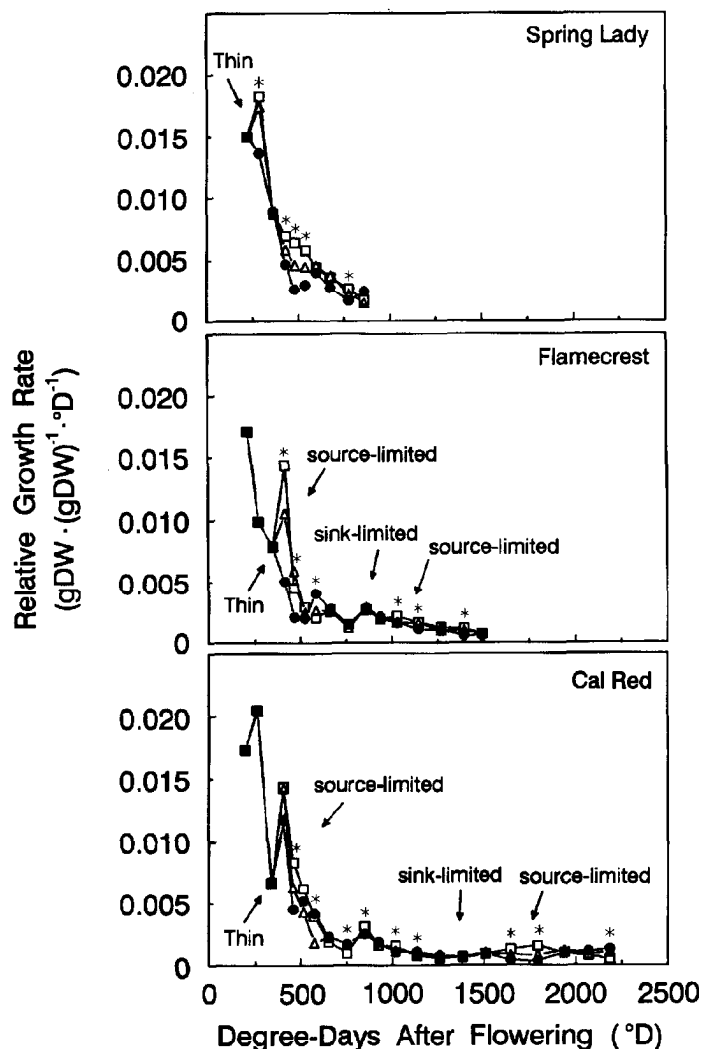


Fig. 3. Seasonal patterns of mean fruit dry weight relative growth rates of early ('Spring Lady'), midseason ('Flamecrest'), and late-maturing ('Cal Red') peaches (thin = thinning date). Asterisks indicate significant differences among fruit relative growth rates of the thinning treatments at each sampling date analyzed by Tukey's mean separation test at $P = 0.05$ ($df = 57$; replications per treatment, $n = 20$). Symbols represent different crop loads after thinning (see Fig. 1).

season, at the beginning of stage III of the growth curve (Fig. 3). In 'Flamecrest', this period occurred between 1028 and 1144°DAF and in 'Cal Red' between 1647 and 1795°DAF. The second period of source-limited peach fruit growth apparently results in a competition for assimilates between fruits, as reported previously by Dorsey and McMunn (1927) and Weinberger (1941). Relative growth rates indicated that fruit growth of the early 'Spring Lady' appeared to be source-limited over almost the entire growing season in trees with a heavy crop load. At the last sampling date, fruit relative growth rates on trees with 15 ('Spring Lady', 'Cal Red') or 583 ('Flamecrest') fruits declined, indicating fruit maturity.

Sink-limited growth of a plant organ occurs when the sink demand is saturated by assimilate supply (Patrick, 1988). Wareing (1979) suggested that the growth rate of a sink is limited by itself in response to low temperatures. The carbon import into tomato (*Lycopersicon esculentum* Mill.) fruits is inhibited by low temperatures, and very large fruits even export carbon under these conditions (Walker and Ho, 1977). In our study, the temperature effect of sink activity was taken into account by calculating fruit relative growth rates on a degree-day basis. The relative growth

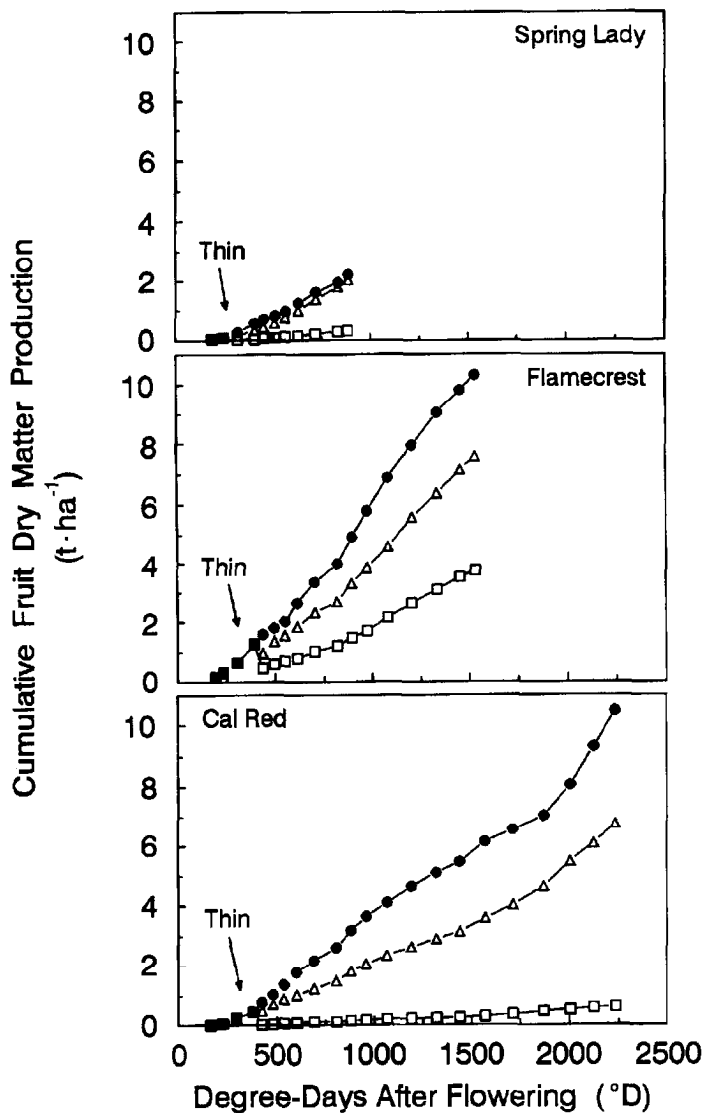


Fig. 4. Seasonal patterns of cumulative fruit dry matter production per hectare of early ('Spring Lady'), midseason ('Flamecrest'), and late-maturing ('Cal Red') peaches during the 1988 growing season (thin = thinning date). Symbols represent different crop loads after thinning (see Fig. 1).

rate analysis in the later-maturing cultivars indicated that peach fruit growth was apparently sink-limited by its genetic potential. The period of sink-limited growth took place between 660 and 935°DAF in 'Flamecrest' and between 1134 and 1510°DAF in 'Cal Red' and represented stage II of the growth curve. During this period, there were no differences of fruit relative growth rates between the different thinning treatments. Chalmers and Van den Ende (1975, 1977) and Nitsch (1953) suggest that the slow peach fruit growth in stage II is caused by a competition for assimilates between fruit tissues. This situation seems unlikely because competition between compartments should not affect the growth potential of the whole fruit. Further, competition for assimilates requires a limited supply of assimilates, but in heavily thinned trees (15 fruits on 'Cal Red' or 583 fruits on 'Flamecrest'), the availability of photosynthates likely was not limited. A phase of sink-limited growth could not clearly be distinguished in the early 'Spring Lady' by relative growth rate analysis, but fruit growth might have been sink-limited at 360°DAF.

Cumulative fruit dry matter production per hectare increased over the season (Fig. 4). 'Spring Lady', the early cultivar, accumulated less fruit dry matter per hectare than the later-maturing

cultivars because of the short time to fruit maturity and the few fruits per tree. The calculated values of total fruit dry matter per hectare under different crop levels might be slightly underestimated because abscised fruits were not included in the calculations. Fruit count and total yield per hectare are positively correlated with each other and both are reduced by thinning in apple and peach trees (Forshey and Elfving, 1977; Preston and Quinlan, 1968; Tukey and Einset, 1939). Trees with a heavy crop load accumulated more fruit dry matter over the season than thinned trees. However, individual fruit were considerably smaller in unthinned trees than trees with lower crop loads. If final crop yield only depended on the assimilate supply, then fruit count per tree would not have affected the final crop yield. The individual fruit growth potential would then be infinite. However, thinning would not affect fruit size, if final crop size were solely dependent on fruit growth potential. Therefore, fruit growth potential (demand for assimilates) and the available photosynthate supply must both limit the final crop yield of trees. Consequently, the response of fruit size to thinning, typically observed in peaches, is a result of differences in the amount of time that fruits grow under sink- vs. source-limited conditions in response to different crop loads.

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