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Japanese Plum (*Prunus salicina* L.) Fruit Growth: Seasonal Pattern of Source/Sink Limitations

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Abstract

The seasonal pattern of Japanese plum (*Prunus salicina* L.) fruit growth and source/sink limitations to fruit growth were analyzed by a functional approach. The study was based on the comparison between unthinned and heavily-thinned trees of two plum cultivars, 'Black Amber' and 'Royal Diamond' (early- and late maturing cultivars, respectively). Individual fruit size, expressed as fruit dry weight, was significantly higher in trees with lower crop loads. The analysis of the relative growth rate patterns indicated that plum fruit growth is limited by resource and genetic limitations (source and sink limitations, respectively). Both plum cultivars appeared to have a source-limited fruit growth period occurring in the stage I of the double-sigmoid fruit growth curve and a sink-limited stage occurring during the stage II. Although the fruits of the early-maturing cultivar accumulated less dry matter during their developmental time, compared to those of the late-maturing cultivar, they appear to have a higher potential net sink strength during their growth period.

Introduction

Although the fruit growth pattern of pome and stone fruits has been studied for many years, the pattern of Japanese plum (*Prunus salicina* L.) fruit growth has not been intensively studied. Studies of fruit growth rate of stone fruits have often been guided by the hypothesis that developmental changes in the pericarp are linked with changes in the seed or with competition with the vegetative growth (3). Chalmers and Van Ende (3) showed that fruit dry mass development did not necessarily correspond with fresh mass development in a late-maturing clingstone peach cultivar.

The carbohydrate availability to individual organs depends on the supply of resources from source organs and the demand for resources by sink organs. Although little is known about the mechanisms governing the partitioning of carbohydrates to individual sink organs (19), it is generally agreed that individual sink organs control carbohydrate partitioning by reciprocal competition based on their sink demand and on the relative ability of the translocation system to deliver carbohydrates to them (6). The basis of sink demand is the maintenance respiration and the maximum organ growth potential defined as the genetically determined growth attained when an organ is grown under optimal environmental conditions in the presence of non-limiting supply of carbon and other resources (21). Under these conditions, the organ growth is limited only by endogenous characteristics of the organ and it is termed sink-limited growth (20). In contrast, growth that is limited by resource supply is termed source-limited growth. Fruits are considered to be major sinks for carbohydrates in fruit trees. The analysis of source and sink limitations on peach fruit growth was performed previously using the classical approach to growth analysis (15) and using the functional approach to growth analysis (10). Although there are many reports of resource limitation on growth over the course

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of the season for other tree fruits (9), and plum fruit growth (24) can be source-limited on unthinned trees as in peaches (12), little is known about the seasonal patterns of resource limitation on growth of plum fruits.

Plum bloom and fruit set are approximately synchronous and fruit number is set shortly after bloom. For this reason, 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 flower produces only one fruit, simplifying the potential number for competitive interactions among fruits. As in most perennials, fruit and vegetative growth are simultaneous, suggesting that individual plum fruits compete with each other and with vegetative growth for resources.

The aim of this work was to attempt a quantitative analysis of the seasonal dry matter accumulation of plum fruits in terms of their sink activity and to determine the seasonal pattern of sink and source limitations on fruit growth using the functional approach to growth analysis. In particular this study focuses on the production of smaller fruits as a consequence of resource limitation on reproductive growth and it characterizes the maximum organ growth potential, the seasonal patterns of resource limitation and the resource availability during growth using individual plum (*Prunus salicina* L.) fruits.

Material and Methods

The plum trees used in this study were a mid-June maturing plum cultivar (*Prunus salicina* L. cv. 'Black Amber') and a mid-July maturing plum cultivar (*Prunus salicina* L. cv. 'Royal Diamond') planted in 1984 at the University of California Kearney Agricultural Center in Parlier, California. The field experiment was carried out in 1999. The trees were grown with a Kearney Agricultural Center V (KAC-V) training system in a North-South orientation (the trees were spaced 5.7 m (1.9 m). Routine horticultural care suitable for commercial fruit production was provided, including pruning, fertilization, irrigation and pest control. The trees were not summer pruned. For both cultivars, two thinning treatments were performed: heavily-thinned trees and unthinned trees. On heavily-thinned trees most of the flowers were removed at bloom. In addition these trees were further thinned one month after bloom, leaving less than 420 fruits per tree. Crop load on unthinned trees was greater than 930 fruits per tree (Table 1). Each treatment was replicated four times for the early cultivar and three times for the late cultivar. Each replicate consisted of four trees located in contiguous rows.

The seasonal patterns of dry fruit weight were determined in both cultivars and thinning treatments. At ten day intervals, a 10 fruit sample was harvested from each thinning treatment and each replicate. Each sample consisted of 2 groups of five fruits from two trees taken at random. Care was taken to spread the sampling over the trees so that sampling would not drastically alter the crop load of any one tree. After each harvest, fruit were immediately cut up and dried at 75°C.

At the final harvest, the total number of fruits was determined and the initial number of fruits per tree was calculated from the final number of fruits per tree at harvest and the number of fruits removed from the sampling.

Since temperature has long been recognized as a major environmental factor affecting fruit growth and because Fischer (7) showed that heat-unit accumulation could be used effectively to measure developmental time in stone fruits, degree-days were used to measure the developmental time. Minimum and maximum air and soil temperatures and solar radiation data were obtained from the California Irrigation Management Information System (CIMIS) weather station located at the Kearney Agricultural Center. The calculation of the degree-days was done by the single sine, horizontal cutoff method, with critical temperatures at 7 and 35°C (4, 25). Degree-day data were accumulated from full-bloom to harvest for each cultivar and thinning treatment.

Whole fruit growth analysis was performed by a functional approach. This technique allows the instantaneous estimation of fruit growth and it has been demonstrated to be useful in fruit growth analysis of peaches (10). Growth curves were obtained by fitting cubic splines to logarithmically-transformed fruit dry weight on each measurement date versus the degree-days accumulated after bloom. The splines are particular polynomial functions with the property that the first n-1 derivative functions are continuous. The discontinuity points of the 7th derivative function are called knots (17). The general form of the cubic splines used in this work is:

$$y = a + bx + cx^2 + dx^3 + (x > i)e(x - i)^3 + (x > j)f(x - j)^3 + (x > k)g(x - k)^3 \qquad [1]$$

with knots at $x = i$, $x = j$, and $x = k$, whereas the general equation of the cubic splines fitted to the data from thinned and unthinned 'Royal Diamond' trees is:

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

with knots at $x = i$ and $x = j$. The cubic splines equations were computed by SAS statistical software (SAS Institute, Inc., SAS Circle Box 8000, Cary, NC, USA).

Fruit absolute growth rate (AGR) and fruit relative growth rate (RGR) were analyzed since they were considered the most important parameters to describe the growth of an organ. The AGR can be defined as the rate of increase of the fruit dry weight per unit time and is considered to represent the net sink strength (21, 22). Mathematically the AGR can be defined as:

$$\mathrm{AGR} = \mathrm{d}w/\mathrm{d}t \quad ; \qquad [3]$$

or if we consider the degree-days (*dd*) as a measure of developmental time:

$$\mathrm{AGR} = \mathrm{d}w/\mathrm{d}dd \ . \qquad [4]$$

The RGR can be defined as the rate of increase of the fruit dry weight per unit time and per unit dry weight and can be considered as a measure of net sink activity (21, 22). Mathematically the RGR can be defined as:

$$\mathrm{RGR} = (1/w)(\mathrm{d}w/\mathrm{d}t) = \mathrm{d}(\ln w)/\mathrm{d}t \quad ; [5]$$

or if we consider the degree-days (dd) as a measure of developmental time:

$$\mathrm{RGR} = (1/w)(\mathrm{d}w/\mathrm{d}dd) = \mathrm{d}(\ln w)/\mathrm{d}dd \ .[6]$$

The functions representing the seasonal patterns of RGR and AGR were obtained using derivations of the fitted growth equations and the exponential form of the fitted growth equations, respectively.

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

CRUR = [AGR+(specific respiration rate x individual fruit weight)] x fruit number = (net sink strength + fruit respiration rate) x fruit number ; [7]

where the units for crop resource usage rate, AGR, specific respiration rate, individual fruit weight, and fruit number are g dry mass per degree-day per tree, g dry mass per degree-day per fruit, g dry mass per g dry mass per degree-day, g dry mass per fruit, and fruits per tree, respectively.

The specific respiration rate for plum fruit was assumed to be similar to peaches (10) and so was estimated from DeJong and Goudriaan (4):

Specific respiration rate = [(0.309 RGR) +0.000184] 0.68182 ; [8]

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

In order to check the precision of the functional approach in modeling the AGR, RGR and CRUR seasonal patterns, the fruit AGR, RGR and CRUR were also computed by a classical approach applying the equations [4], [6] and [7] to fruit dry weight experimental data, respectively.

Results and Discussion

Seasonal patterns of fruit growth

The equations of the fitted splines to logarithmically-transformed fruit dry weight computed for unthinned and heav-

Table 1. Mean number of fruits harvested on heavily-thinned and unthinned trees of the cultivars 'Black Amber' and 'Royal Diamond' (± standard errors of the mean).

	Number of fruits per tree	
Cultivar	Heavily-thinned trees	Unthinned trees
'Black Amber'	220.1±9.8	1225.4±107.3
"Royal Diamond'	319.2±23.5	1537.9±127.5

ily-thinned trees of both cultivars are reported in Table 2. Mean fruit dry weight increased rapidly with degree-days after bloom (Figure 1). Significant weight differences between fruits on heavily-thinned and unthinned trees of both cultivars were first detected at 254 and 213 degree-days after bloom, for the early- and late-maturing cultivars, respectively, and persisted through to harvest. The mean final dry weight of individual fruits on unthinned trees of the early-maturing cultivar (5.71 g fruit^{-1}) was 51.8% of that of fruits on heavily-thinned trees, (11.03 g fruit^{-1}). Similarly, the final mean dry weight of individual fruits on unthinned trees of the late-maturing cultivar (8.93 g fruit^{-1}) was 61.8% of that of fruits on heavily-thinned trees (14.44 g fruit^{-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 cultivars (Figure 1).

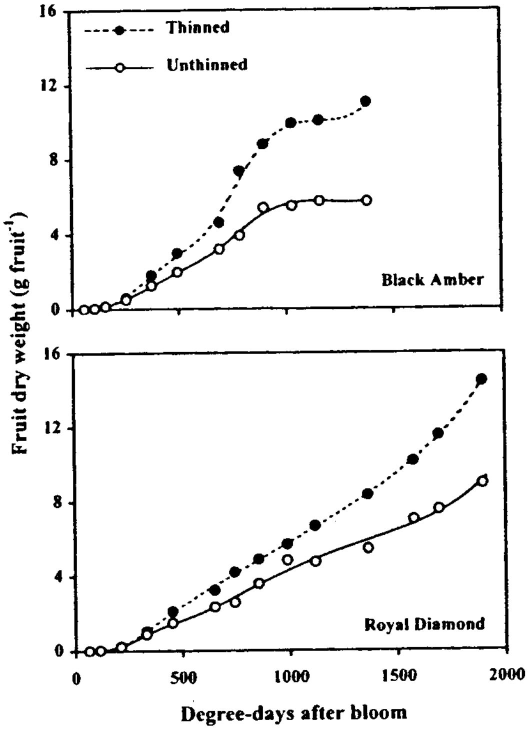

Figure 1. Seasonal patterns of mean individual fruit dry weight on heavily-thinned and unthinned trees of 'Black Amber' and 'Royal Diamond' plum cultivars. The points represent the fruit mean dry weights evaluated with the experimental data at each harvest. Bars indicate the standard errors of the means. The equations of the splines are given in the Table 2.

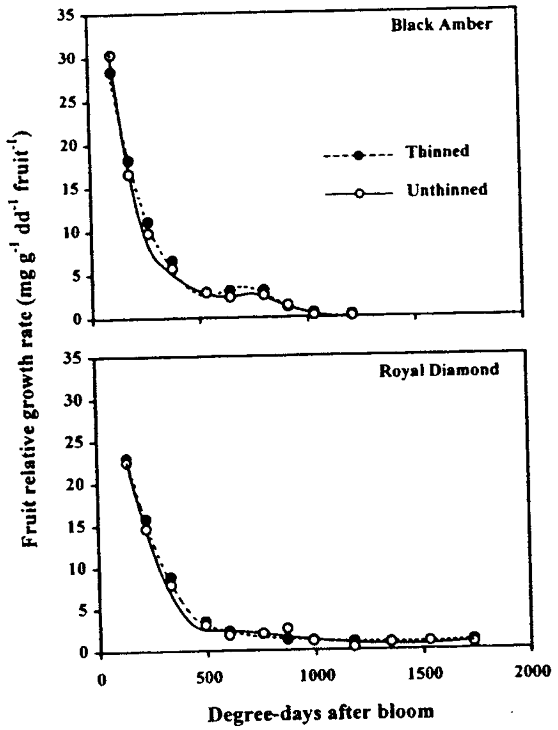

Figure 2. Seasonal patterns of relative growth rate (RGR) for fruits on heavily-thinned and unthinned trees of 'Black Amber' and 'Royal Diamond' plum cultivars. The points indicate the fruit RGR values computed applying the equation (5) to fruit dry weight experimental data.

The shape of the 'Royal Diamond' fruit growth curve was similar to that previously found for 'Cal Red' peach (10, 15). In 'Royal Diamond' the dry matter accumulation dramatically increased in the last part of the fruit growth season. But in the early-maturing plum cultivar, 'Black

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

Cultivar	Thinning	Spline equations	R^2
'Black Amber'	Heavily-thinned	$\ln dw=-6.88652+0.04454dd-(9.433\times10^{-5})dd^{2}+(7.664926\times10^{-8})dd^{3}-(dd>300)(4.1531\times10^{-8})(dd-300)^{3}-(dd>600)(5.77276\times10^{-8})(dd-600)^{3}+(dd>800)(2.932351\times10^{-8})(dd-800)^{3}$	0.99
	Unthinned	$\ln dw=-7.63013+0.05635dd-(1.5205\times10^{-4})dd^{2}+(1.54148\times10^{-7})dd^{3}-(dd>300)(1.40572\times10^{-7})(dd-(300)^{3}-(dd>700)(4.28038\times10^{-8})(dd-700)^{3}+dd>800)(3.386266\times10^{-8})(dd-800)^{3}$	0.99
'Royal Diamond'	Heavily-thinned	$\ln dw=-7.09967+0.03965dd-(6.902\times10^{-5)}dd^{2}+(4.318547\times10^{-8}(dd^{3}-(dd>500)(3.94886\times10^{-8}(dd-500)^{3}-(dd>800)(3.19429\times10^{-9})(dd-800)^{3}$	0.99
	Unthinned	$\ln dw=-7.15823+0.04109dd-(7.741\times10^{-5)}dd^{2}+(5.165427\times10^{-8})dd^{3}-(dd>500)(5.38926\times10^{-8})(dd-500)^{3}+(dd>800)(3.257082\times10^{-9})(dd-800)^{3}$	*0.99*

Amber', the shape of the fruit growth curve was different from the 'Royal Diamond' plum or peaches (15). The main difference occurred in the last phase of fruit growth when the fruit growth curve in 'Black Amber' unthinned trees was almost flat.

Seasonal patterns of fruit relative growth rate

A generally decreasing seasonal pattern of fruit RGR was observed for both the plum cultivars (Figure 2). This result is similar to that reported for peach (10, 15), apple (1, 13, 16) and other species (8, 18). Fruit of both plum cultivars showed a first phase of rapid decline in RGR but unlike 'Royal Diamond' and peaches the RGR of 'Black Amber' had a second marked decline a few weeks prior to harvest.

Seasonal patterns of crop resource usage rate

In order to achieve its maximum growth potential, an organ must grow under non-limiting conditions at its potential RGR throughout development. Under source-limited growth conditions the RGR is reduced below the potential RGR (11). The Crop Resource Usage Rate (CRUR) represents the rate of accumulation of dry matter plus the respiration rate of all the fruits on a tree (10). The general shape of the CRUR curves was different in the two cultivars (Figure 3).

In both cultivars the CRUR was significantly lower on heavily-thinned trees than on unthinned trees for most of the developmental time (Figure 3). Since the CRUR is higher on unthinned trees than on heavily-thinned trees, the individual fruit RGR curves for the heavily-thinned trees should approximate the maximum fruit growth potential at any time during the fruit growth period (Figure 3). The CRUR pattern in heavily-thinned trees was similar for the late-maturing plum cultivar, 'Royal Diamond', and the late-maturing peach cultivar, 'Cal Red', analyzed by Grossman and DeJong (10). Similarities between plums and peaches were not as clear for the early-maturing cultivars.

Seasonal patterns of resource limitation on individual fruit growth

The large difference in final fruit dry weight between unthinned and heavily-thinned trees of both the cultivars indicated that resource limitation occurred during one or more stages of the fruit developmental period. Analysis of seasonal RGR curves can be useful for locating periods of source- and sink-limited fruit growth in

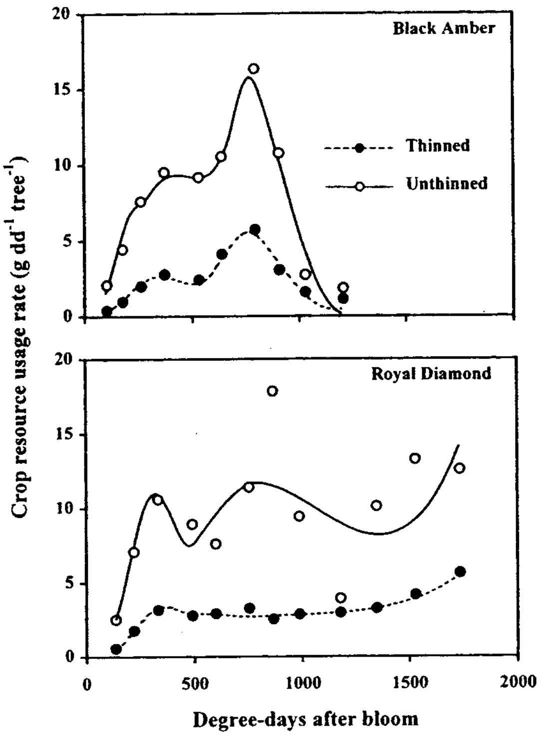

Figure 3. Seasonal patterns of crop resource usage rate (CRUR) on heavily-thinned and unthinned trees of 'Black Amber' and 'Royal Diamond' plum cultivars. The points indicate the fruit CRUR values computed applying the equation (6) to fruit dry weight experimental data.

peach (10, 15). During the source-limited stages of the fruit growth, the RGR in heavily-thinned trees is significantly higher than that in unthinned trees, while during sink-limited stages of the fruit growth there are no significant differences in RGR. In the analysis of seasonal patterns of fruit RGR, the compounding effect of RGR has to be taken into account, especially in the late stage of fruit growth when a high number of degree-days is accumulated each day (10). These conditions occurred between day 175 (1030 degree-days after bloom for 'Black Amber' and 990 degree-days after bloom for 'Royal Diamond') and the harvest date of both cultivars (1380 degree-days after bloom for 'Black Amber' and 1896 degree-days after bloom for 'Royal Diamond'). During this period an average of 18.4 and 17.1 degree-days per day were accumulated for the early- and the late-maturing cultivars, respectively, against an average of 9.8 and 9.7 degree-days per day accumulated earlier in the season.

In order to analyze the seasonal patterns of the resource limitation on individual fruit growth for both plum cultivars, the difference between the fruit RGR of heavily-thinned and unthinned trees was analyzed. At the beginning of the season the differences in fruit RGR between the two treatments were found for both cultivars. After that the differences were much less. These data suggest a first stage of source-limited fruit growth during the first stage of the fruit development for both cultivars. This appeared to be followed by a sink-limited period in both cultivars. After the sink limited period, the fruit appeared to return to a source limited state. This source limitation during the later growth appeared to be less than during the first period but this could be partially due to the compounding effect of high degree-day accu-

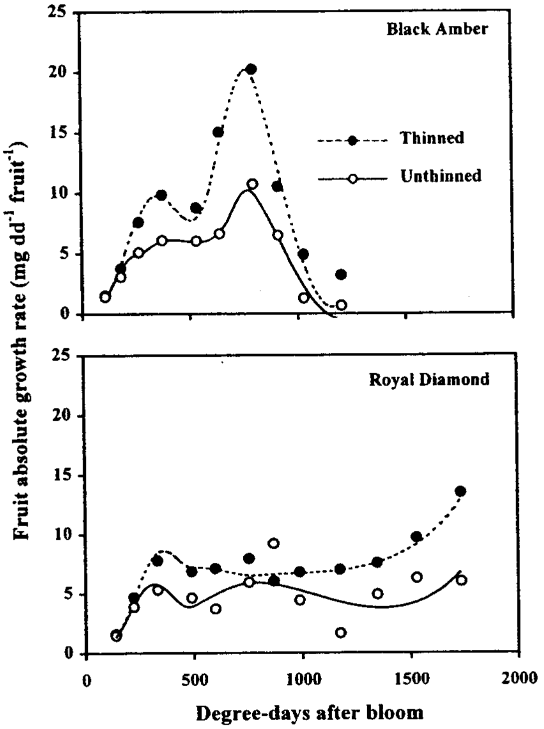

Figure 4. Seasonal patterns of absolute growth rate (AGR) for fruits on heavily-thinned and unthinned trees of 'Black Amber' and 'Royal Diamond' plum cultivars. The points indicate the fruit AGR values computed applying the equation (3) to fruit dry weight experimental data.

mulation during this period. Even though the seasonal pattern of source/sink limitations looked to be similar in the two cultivars, both source- and sink-limited periods appeared to be shorter in the early maturing cultivar than in 'Royal Diamond'.

Pavel and DeJong (15) studied the seasonal patterns of resource limitations in three peach cultivars with different ripening dates (early-, midseason- and late-maturing cultivars). They found that in midseason- and in late-maturing cultivars, fruit growth was characterized by two source-limited stages separated by a sink-limited stage. However a sink-limited stage was not found in the early-maturing cultivar. Similar results were obtained by Grossman and DeJong (10). In our study, both plum cultivars (early- and late-maturing) appeared to have a source-limited fruit growth period occurring in stage I of the double-sigmoid fruit growth curve and a sink-limited stage occurring during stage II. During these two stages of fruit growth the seasonal pattern of resource limitations of the two plum cultivars evaluated in this study appeared to be similar to those of the midseason- and late-maturing peach cultivar ('Flamecrest' and 'Cal Red', respectively) studied by Pavel and DeJong (15). A second source-limited stage was expected in these plum cultivars in stage III, very close to harvest, but it does not appear to be as significant as in peach. (5, 10, 23).

Chalmers and Van den Ende (2, 3) and Nitsch (14) suggested that the slow fruit growth during the stage II of the double-sigmoid fruit growth curve is due to a competition for resources between fruit tissues. Pavel and DeJong (15) and Grossman and DeJong (10) considered this hypothesis unlikely because they did not find any resource limitation in peaches during that stage and they explained the slow fruit growth in the stage II as due to genetic constrains that limit the maximum growth potential (sink-limited stage of fruit growth). Our results in plums support the latter hypothesis. The seasonal pattern of plum fruit growth appeared to be related to the resource availability during the season and also to genetic constraints.

Seasonal patterns of fruit absolute growth rate and potential net sink strength

The seasonal patterns of absolute growth rate for the two plum cultivars were fairly different (Figure 4). The main difference occurred late in the fruit growth season of the two plum cultivars when the 'Royal Diamond' AGR rapidly increased after an almost flat phase of the curve, whereas the 'Black Amber' AGR curve was almost constant very close to harvest after a steep decreasing phase. The seasonal pattern of AGR in 'Royal Diamond' was similar to that previously reported for the 'Golden Queen' peach cultivar (2) and for the 'Cal Red' peach cultivar (10). In both cultivars the AGR on heavily-thinned trees was higher than on unthinned trees throughout the growth period. In 'Black Amber' the patterns on heavily-thinned trees and on unthinned were similar.

The fruit potential net sink strength can be evaluated by fruit AGR when the resources are not limiting (11). In this study the computation of the crop resource usage rate showed that this condition was obtained on the heavily-thinned trees during the fruit growth period of both cultivars. Thus, the AGR for heavily-thinned trees can be considered a measure of the potential net fruit sink strength for both cultivars. The seasonal patterns of potential net fruit sink strength appear to be substantially different for the two cultivars that were studied. These differences could have significant effects on development of optimal management strategies for different plum cultivars that have not been considered previously.

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