

Quantifying sink and source limitations on dry matter partitioning to fruit growth in peach trees

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We describe an approach for determining the degree of sink and source limitations on peach (*Prunus persica* L. Batsch) fruit growth during several growth periods. Source limitations on fruit growth may be due to either a shortfall in assimilate supply within the tree (supply limitation) or to a deficiency in the capacity of the translocation system to deliver assimilates in sufficient quantity to support the maximum fruit growth rate (transport/competition limitation). To ascertain the potential maximum rate of fruit growth, fruit thinning treatments were used. One month after bloom, the number of fruits per tree was adjusted to between 50 and 700 on an early and a late maturing peach cultivar (cvs Spring Lady and Cal Red, respectively). Rates of potential sink demand, potential source supply and actual fruit growth were estimated from sequential harvests of all fruits on 42 trees on two (Spring Lady) and three (Cal Red) dates. These values were used to estimate the proportion of potential growth achieved, and the supply and transport/competition limitations on fruit growth. The results indicated that source limitations were significant on trees with moderate to high fruit numbers. These source limitations were due to supply limitations during all harvest intervals and to transport/competition limitations during the early harvest intervals. Sink limitations occurred to the greatest extent during the mid-period of fruit growth on the later maturing cultivar.

Key words – Partitioning, peach, *Prunus persica*, sink-limited fruit growth, source-limited fruit growth, supply-limited fruit growth, transport/competition-limited fruit growth, yield.

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Introduction

Source-sink relationships and the regulation of carbon allocation determine crop yield in plants. The growth of individual plant organs may be restricted by assimilate availability (source limitation) or by the organs' ability to utilize assimilates (sink limitation, Wareing and Patrick 1975, Patrick 1988). Source and sink limitations may be separated in time so that organ growth is primarily source-limited at certain periods during development and primarily sink-limited at other times. Source limitation may result from insufficient assimilate availability to support potential organ growth (supply limitation). Source limitation may also result from the inability of the translocation system to deliver available assimilates to

the growing organ as the result of long distance or high translocation resistance (transport limitation) or competition from other sinks (competition limitation). This accords with numerous studies indicating that the proximity of a sink to assimilate sources is a factor determining its growth rate (Wardlaw 1990). Thus, yield can be said to be simultaneously source- and sink-limited because the sinks are not strong enough to draw assimilates equally from everywhere in the plant and the source is not plentiful enough to equally supply potential organ growth.

In the present study we develop a technique for determining the degree of source and sink limitations during different periods of fruit growth. DeJong and Goudriaan (1989a) determined that the seasonal patterns of peach (*Prunus persica* L. Batsch) maximum fruit growth po-

tential are governed by a developmentally determined pattern of fruit relative growth rates (RGRs). Maximum fruit growth potential is defined as the genetically determined growth attained by a fruit when it is grown under optimal environmental conditions in the presence of a nonlimiting supply of carbon and other resources (Warren Wilson 1967, 1972, Wareing and Patrick 1975, Ho 1984, 1988, Grossman and DeJong 1995a). Potential fruit RGRs and sink demand of a late maturing peach cultivar have been determined experimentally from fruit growth on trees with very few fruits (Pavel and DeJong 1993b, Grossman and DeJong 1995a). Comparison of fruit RGRs on trees with many fruits to the potential RGRs indicates that fruit growth is source-limited during early and late periods of fruit development (Pavel and DeJong 1993b, Grossman and DeJong 1995a). No source limitation was detected during the middle period of fruit growth, suggesting that fruit growth may be sink-limited during this time.

These previous studies have indicated that source limitations (including supply and transport/competition limitations) and sink limitations tend to be important at different times during the fruit growth period. However, there are no experimental data indicating the effect of intermediate fruit numbers on the relative importance of sink, supply and transport/competition limitations during different periods of fruit growth. The goals of our research were to: (1) quantify the effects of fruit number on the relative importance of sink, supply and transport/competition limitations on the growth of peach fruit, (2) determine the growth periods when these limitations are the most important and (3) describe how the limitations differ on early and late maturing peach cultivars.

Approach

In order to quantify the timing and degree of sink and source limitations on fruit growth, the rates of potential source supply for fruit growth and the potential fruit sink demand must be quantified (Grossman and DeJong 1995a). The potential fruit demand rate can be quantified using the maximum fruit growth potential determined on trees with very few fruits per tree (Grossman and DeJong 1995a). The potential relative growth rate (potRGR) of individual fruits is calculated as:

$$\text{potRGR} = \frac{\log_e W_{2(x_{\min})} - \log_e W_{1(x_{\min})}}{T_2 - T_1} \quad (1)$$

where W_2 and W_1 are the mean individual fruit dry weights at harvest dates T_2 and T_1 , x_{\min} is the fruit number per tree on trees with a minimum number of fruits and potRGR has units $\text{g}^{-1} \text{day}^{-1}$. Using the potRGRs for a given cultivar and harvest interval, the total potential fruit sink demand rates (PSINK) for trees with different numbers of fruits per tree is calculated as:

$$\text{PSINK} = \frac{(W_{1(x)} e^{\text{potRGR} \cdot (T_2 - T_1)} - W_{1(x)}) \cdot x}{T_2 - T_1} \quad (2)$$

where x is the fruit number. The term $W_{1(x)} e^{\text{potRGR} \cdot (T_2 - T_1)}$ is the maximum potential weight at time T_2 of fruits on trees with x fruits. The units for PSINK are $\text{g} \text{day}^{-1}$.

The potential source supply rate (PSOURCE) is estimated from fruit growth under source-limited conditions, such as occurs on trees with high fruit numbers during portions of the growing season (Grossman and DeJong 1995a) as:

$$\text{PSOURCE} = \frac{(W_{2(x_{\max})} - W_{1(x_{\max})}) \cdot x_{\max}}{T_2 - T_1} \quad (3)$$

where x_{\max} is the number of fruits on trees with the maximum fruit number (i.e. trees that set heavy fruit loads and are left unthinned so that the fruit growth rate is frequently source-limited). PSOURCE has units $\text{g} \text{day}^{-1}$. The rate of actual total fruit dry weight growth rate (ACTUAL) during a growth period is calculated as:

$$\text{ACTUAL} = \frac{(W_{2(x)} - W_{1(x)}) \cdot x}{T_2 - T_1} \quad (4)$$

where x is the fruit number per tree. ACTUAL has units $\text{g} \text{day}^{-1}$.

During a growth interval, the proportion of potential growth achieved (GRWTHACH) is:

$$\text{GRWTHACH} = \frac{\text{ACTUAL}}{\text{PSINK}} \quad (5)$$

the source limitation (SOURLIM) is:

$$\text{SOURLIM} = \frac{\text{PSINK} - \text{ACTUAL}}{\text{PSINK}} \quad (6)$$

and the sum of the proportion of potential growth achieved and the source limitation is one:

$$\text{GRWTHACH} + \text{SOURLIM} = 1. \quad (7)$$

As discussed earlier, the source limitation may be due to the assimilate availability (PSUPPLYLIM) and transport/competition limitations (TRANS/COMPLIM). These two limitations may be obtained from the source limitation by algebraic rearrangement:

$$\text{SOURLIM} = \frac{\text{PSINK} - \text{PSOURCE}}{\text{PSINK}} + \quad (8)$$

$$+ \text{PSOURCE} - \text{ACTUAL} / \text{PSINK}$$

The first term represents limitation due to assimilate supply (PSUPPLYLIM) and the second term represents the limitation due to transport and competition (TRANS/COMPLIM). That is:

$$\text{PSUPPLYLIM} = \frac{\text{PSINK} - \text{PSOURCE}}{\text{PSINK}} \quad (9)$$

and

$$\text{TRANS/COMPLIM} = \frac{\text{PSOURCE} - \text{ACTUAL}}{\text{PSINK}} \quad (10)$$

If the potential sink demand rate is greater than the po-

tential source supply rate ($PSINK \geq PSOURCE$), fruit growth may be limited by both supply limitation and transport/competition limitation. However, when the potential sink demand rate is less than the potential source supply rate ($PSINK < PSOURCE$), source supply does not limit fruit growth; that is:

$$PSUPPLYLIM = 0 \quad (11)$$

and the entire source limitation is due to transport/competition limitation; that is:

$$TRANS/COMPLIM = \frac{PSINK - ACTUAL}{PSINK} \quad (12)$$

Abbreviations – ACTUAL, actual total fruit dry weight growth rate; GRWTHACH, proportion of potential growth achieved; PSINK, potential fruit sink demand rate; PSOURCE, potential source supply rate for fruit growth; PSUPPLYLIM, supply limitation due to assimilate supply; RGR, relative growth rate; SOURLIM, source limitation; TRANS/COMPLIM, source limitation due to transport/competition limitation.

Materials and methods

The experiments were conducted at the University of California Kearney Agricultural Center, Parlier, CA, with two peach (*Prunus persica* L. Batsch) cultivars (cvs Spring Lady and Cal Red, early and late maturing, respectively) grown on cv. Nemaguard rootstock during the 1992 growing season. The 9-year-old trees of both cultivars were trained to a high-density central-leader system with trees spaced 2.0 by 4.0 m. Cultural management practices, such as fertilization, pruning, and irrigation were conducted as in a commercial orchard. Nutrients and water were assumed to be nonlimiting.

On 9 April, approximately 1 month after full bloom, 84 and 126 trees of Spring Lady and Cal Red, respectively, were selected for uniformity. Five-sixths of the trees were differentially thinned to a range of fruit numbers from 50 to 400. One-sixth of the trees were left unthinned with higher numbers of fruits per tree. Subsamples of 50 thinned fruits from each cultivar were

weighed, dried at 65°C for ca 4 days, and reweighed to determine mean fruit dry weight on the thinning date.

The Spring Lady fruits were harvested on two subsequent dates: on 6 May, just before the Spring Lady fruits began their final period of maximal absolute growth rates (Pavel and DeJong 1993b, Grossman and DeJong 1995a) and on 21 May, when most fruits had reached commercial maturity and prior to natural fruit abscission. The first of these dates was chosen to represent the end of stage I. Early maturing cultivars such as Spring Lady do not have a detectable stage II (Pavel and DeJong 1993a). One-half of the experimental trees were harvested and weighed on each date. Subsamples of 10 fruits per tree were weighed, dried at 65°C for ca 4 days, and reweighed to determine mean fruit dry weight on each harvest date.

The Cal Red trees were treated similarly except that there were 3 harvest dates after fruit thinning. The first was approximately at the end of stage I of fruit growth (20 May; Connors 1919); the second was near the end of stage II of fruit growth (26 June); and the final was at fruit maturity (31 July). One-third of the experimental trees were harvested on each date in the same manner as was described for the Spring Lady fruits.

Data from the fruit harvests were used to develop regression equations for total fruit dry weight vs fruit number per tree for each cultivar and harvest date. The estimated total fruit dry weights for trees with 100 fruits were then used to calculate the potRGR (Eq. 1) and PSINK (Eq. 2) for trees with 100–700 fruits. The estimated total fruit dry weights for trees with 700 fruits were used to calculate the PSOURCE (Eq. 3). The estimated total fruit dry weight per tree for trees with 100–700 fruits per tree were used to calculate the ACTUAL (Eq. 4).

Results and discussion

The mean dry weights per fruit at the time of thinning on 9 April were 0.517 ± 0.019 g and 0.290 ± 0.018 g for Spring Lady and Cal Red, respectively. The larger dry

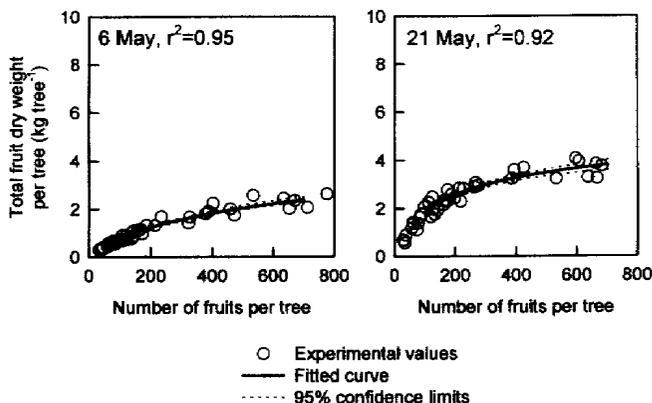


Fig. 1. Relationship between fruit number per tree and total fruit dry weight per tree on two harvest dates for an early maturing peach cultivar, Spring Lady. Individual points represent data values, solid line represents the quadratic polynomial regression line for logarithmically transformed fruit number vs total fruit dry weight per tree, dashed lines represent 95% confidence interval for the fitted curve.

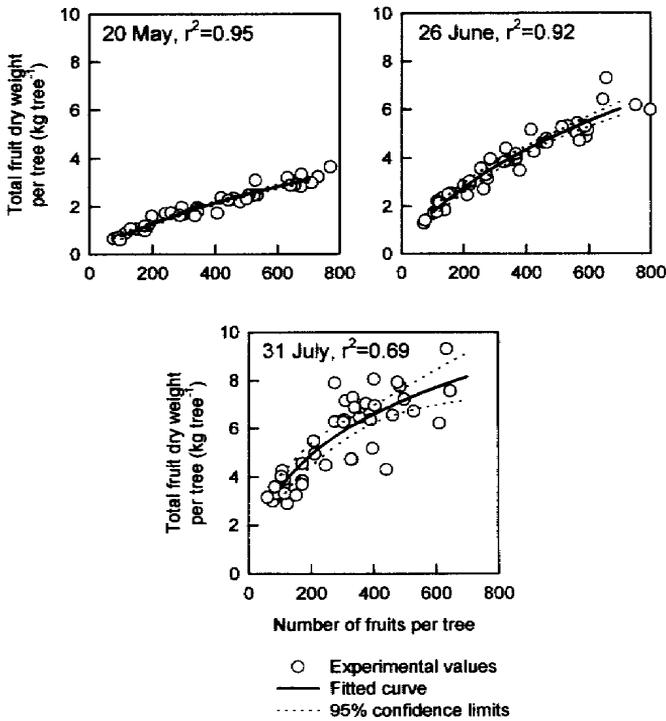


Fig. 2. Relationship between fruit number per tree and total fruit dry weight per tree on three harvest dates for a late maturing peach cultivar, Cal Red. Individual points represent data values, solid line represents the quadratic polynomial regression line for logarithmically transformed fruit number vs total fruit dry weight per tree, dashed lines represent 95% confidence interval for the fitted curve.

weight of the earlier maturing cultivar reflects both an earlier bloom date and larger initial ovary size at bloom (Grossman and DeJong 1995a). Regressions of total fruit dry weight vs fruit number per tree resulted in ascending curvilinear relationships regardless of cultivar and fruit harvest date (Figs 1 and 2).

The potential sink demand rate increased with fruit number for all harvest periods (Figs 3 and 4). During the first harvest interval for both cultivars, the relationship between potential sink demand rate and fruit number was linear because mean fruit weight at the beginning of

the interval was independent of fruit number per tree (Figs 3 and 4). During the later harvest intervals, the curvilinear relationship between fruit number and fruit weight resulted in a curvilinear relationship between potential sink demand rate and fruit number (Figs 1–4). Actual total fruit growth rate increased with fruit number, reaching an asymptote in the final harvest intervals for both cultivars (Figs 3 and 4).

For the early maturing cultivar, Spring Lady, potential sink demand rate on trees with 200 or more fruits significantly exceeded actual total fruit growth rate ($P < 0.05$,

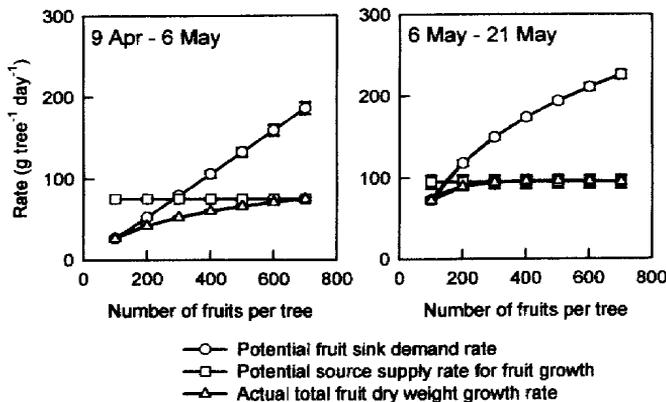
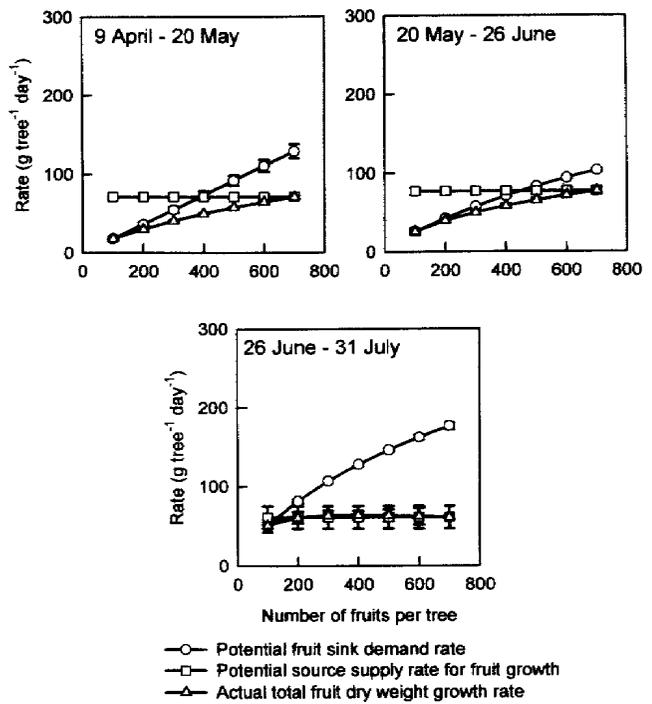


Fig. 3. Relationship between fruit number per tree and rates of potential sink demand, potential source supply and actual total fruit dry weight growth for two harvest intervals on an early maturing cultivar, Spring Lady. SE bars fit within symbols where not visible.

Fig. 4. Relationship between fruit number per tree and rates of potential sink demand, potential source supply, and actual total fruit dry weight growth for three harvest intervals on a late maturing cultivar, Cal Red. SE bars fit within symbols where not visible.



Bonferroni multiple pairwise comparisons) during both harvest intervals (Fig. 3). For the late maturing cultivar, Cal Red, potential sink demand rate significantly exceeded actual total fruit dry weight growth rate on trees with more than 300, 400 and 200 fruits for the first, second and third harvest intervals, respectively (Fig. 4).

During the first harvest interval for the early maturing cultivar, Spring Lady, and the first and second harvest intervals for the late maturing cultivar, Cal Red, potential source supply rate significantly exceeded ($P < 0.05$) actual total fruit growth rate for trees with 100–500 (first interval Spring Lady and second interval Cal Red) and 100–600 (first interval Cal Red) fruits per tree. During the final harvest interval for both cultivars, rates of potential source supply and actual total fruit dry weight growth were not significantly different ($P < 0.05$) for trees with 200 (Spring Lady) or 100 (Cal Red) or more fruits.

For both cultivars, the potential sink demand rate was significantly less ($P < 0.05$) than the potential source supply rate on trees with lower fruit numbers, but was significantly higher than the potential source supply rate on trees with higher fruit numbers (Figs 3 and 4). The fruit number per tree at which the potential sink demand line crossed the potential source supply line was higher during the early harvest intervals than during the final harvest intervals.

The relationships among the rates of potential sink demand, potential source supply and actual total fruit dry

weight growth described above were reflected in the proportion of potential growth achieved, the supply limitation and the transport/competition limitation (Figs 5

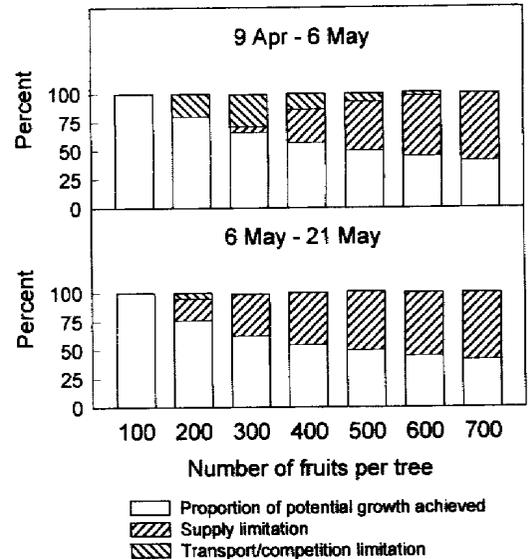


Fig. 5. Relationship between number of fruits per tree and the proportion of potential fruit growth achieved, supply limitation and transport/competition limitation for two harvest intervals (see Eqs 4–9) on an early maturing peach cultivar, Spring Lady.

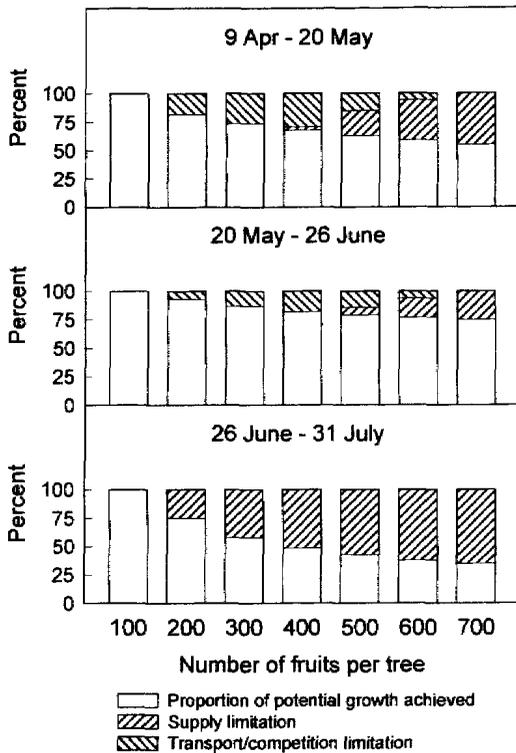


Fig. 6. Relationship between number of fruits per tree and the proportion of potential fruit growth achieved, supply limitation and transport/competition limitation for three harvest intervals (see Eqs 4–9) on a late maturing peach cultivar, Cal Red.

and 6). The proportion of potential growth achieved declined with increasing fruit number for both cultivars during all harvest intervals. This pattern was due to significant differences between the rates of potential fruit sink demand and the potential source supply at moderate and high fruit numbers (supply limitation) during all harvest intervals. At moderate fruit numbers, there were also significant differences between the rates of potential source supply and actual total fruit dry weight growth (transport/competition limitation) during the first harvest interval for the early maturing cultivar and the first two harvest intervals for the late maturing cultivar (Figs 3 and 4). Transport/competition limitations were not apparent during the final harvest interval except on the early maturing cultivar on trees with 200 fruits (Figs 5 and 6). This suggests that during the final fruit growth period, fruits have a greater ability to compete for resources relative to other sinks compared to that at the initial stages of growth. Previous studies indicate that competition between fruit and vegetative growth during the early growth interval, which coincides with the primary period of shoot extension growth, is sufficient to reduce vegetative growth on unthinned trees (DeJong et al. 1987, Grossman and DeJong 1995b). It is also possi-

ble that changes may occur in anatomical and/or phloem unloading capacities during fruit development.

During the middle harvest interval of Cal Red fruits, transport/competition limitations but not supply limitations on fruit growth were detected on trees with fruit numbers between 100 and 400 fruits (Fig. 6). This finding is consistent with other experimental comparisons of the RGR on heavily thinned and unthinned trees in which no source limitations on fruit growth were detected during this period (Pavel and DeJong 1993b, Grossman and DeJong 1995a), and with the results of simulation studies (DeJong and Goudriaan 1989b, DeJong et al. 1990, Grossman and DeJong 1994).

The central leader trees used in the present experiment were substantially overcropped when they carried 700 fruits per tree. This might have caused an underestimate of the potential source supply, because high loads retarded vegetative growth, leaf area expansion (unpublished data) and possibly total tree photosynthesis. Therefore, it might be expected that the actual total fruit dry weight growth rate on trees with fewer than 700 fruits would exceed the actual total fruit dry weight growth rate on trees with 700 fruits. Although this did occur during the final harvest interval for Cal Red for trees with 300 or more fruits, the differences were very small and not significant.

The approach described in the present study used experimentally acquired data to estimate the sink and source limitations on fruit growth and separated the source limitation into supply and transport/competition components. The general conclusions were: (1) source limitations were significant on trees with moderate to high fruit numbers, (2) these source limitations were due to supply limitations during all harvest intervals and to transport/competition limitations during the early harvest interval, and (3) sink limitations occurred to the greatest extent during the mid-period of fruit growth on the later maturing cultivar.

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