# **PEACH: A simulation model of reproductive and vegetative growth in peach trees**

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#### Summary

The hypothesis that carbohydrate partitioning is driven by competition among individual plant organs, based on each organ's growth potential, was used to develop a simulation model of the carbon supply and demand for reproductive and vegetative growth in peach trees. In the model, photosynthetic carbon assimilation is simulated using daily minimum and maximum temperature and solar radiation as inputs. Carbohydrate is first partitioned to maintenance respiration, then to leaves, fruits, stems and branches, then to the trunk. Root activity is supported by residual carbohydrate after aboveground growth.

Verification of the model was carried out with field data from trees that were thinned at different times. In general, the model predictions corresponded to field data for fruit and vegetative growth. The model predicted that resource availability limited fruit and stem growth during two periods of fruit growth, periods that had been identified in earlier experimental studies as resource-limited growth periods. The model also predicted that there were two periods of high carbohydrate availability for root activity. The fit between model predictions and field data supports the initial hypothesis that plants function as collections of semiautonomous, interacting organs that compete for resources based on their growth potentials.

Keywords: carbohydrate partitioning, carbon demand, organ growth potential, peach simulation model, photosynthetic carbon assimilation, respiration.

## Introduction

Carbon balance models of plant growth have been used to identify environmental factors limiting plant growth (Loomis et al. 1979, Penning de Vries and van Laar 1982*a*). Many detailed mechanistic models of photosynthetic processes within the plant canopy have been developed, but much less is known about the physiological processes involved in carbohydrate partitioning (Wardlaw 1990). Various approaches to modeling carbon partitioning have been taken, including the use of empirical partitioning coefficients (de Wit 1978, van Kraalingen and Spitters 1986), determination of the maximum possible growth rate of each sink type (Loomis et al. 1979, Penning de Vries and van Laar 1982*b*, Vos et al. 1982, Ng and Loomis 1984, Wermelinger et al. 1991, Buwalda 1991), the maintenance of a functional balance between the size and activity of roots and shoots (Thornley and Johnson 1990), and the development of detailed transport coefficients for individual sources and sinks (Rauscher et al. 1990).

The hypothesis that plants grow as collections of semiautonomous, interacting organs that compete for resources (White 1979, Harper 1980, Watson and Casper 1984, Sprugel et al. 1991) provides a mechanistic basis for modeling carbohydrate

partitioning. Carbohydrate moves in the phloem, from supply regions (sources) to demand regions (sinks). Sink regions exercise control over carbon partitioning, competing with one another for carbon based on their sink strengths (Gifford and Evans 1981, Ho et al. 1989, Patrick 1991). In general, sinks are supplied with carbohydrate from nearby sources (Ho et al. 1989, Wardlaw 1990).

The PEACH model simulates carbohydrate partitioning based on sink strength, proximity to sources, and the quantity of carbohydrate available. The sink strength of each organ is based on its genetically determined organ growth potential, the maximum rate at which the organ can accumulate dry matter per unit time, which is closely related to the ability to unload assimilates from the phloem (Warren Wilson 1967, 1972, Wareing and Patrick 1975, DeJong and Goudriaan 1989*a*, Wardlaw 1990, DeJong and Grossman 1992). The potential net sink strength ( $S_{\text{NET}}$ ,  $g_{\text{DW}}$  dd<sup>-1</sup>) is the product of sink size ( $S_{\text{SIZE}}$ ,  $g_{\text{DW}}$ ) and potential sink activity ( $S_{\text{ACTIVITY}}$ ,  $g_{\text{DW}}$   $g_{\text{DW}}^{-1}$  dd<sup>-1</sup>) expressed as the relative growth rate:

$$S_{\text{NET}} = S_{\text{SIZE}} \times S_{\text{ACTIVITY}},\tag{1}$$

where  $g_{DW}$  and dd represent gram dry weight and degree-day, respectively. The potential gross sink strength ( $S_{GROSS}$ ,  $g_{DW}$  dd<sup>-1</sup>) is the sum of the potential net sink strength and the respiratory losses of the growing organ:

$$S_{\text{GROSS}} = S_{\text{NET}} + R_{\text{g}} + R_{\text{m}},\tag{2}$$

where  $R_g$  ( $g_{DW}$  dd<sup>-1</sup>) is growth respiration and  $R_m$  ( $g_{DW}$  dd<sup>-1</sup>) is maintenance respiration.

The potential sink strength of an organ can be decreased by suboptimal environmental conditions or insufficient resource availability, or both. The conditional sink strength is the rate of change determined from the potential sink strength by environmental conditions such as temperature and water availability, and the apparent sink strength is the rate of change determined from the conditional sink strength by resource availability (Figure 1, Warren Wilson 1967, 1972, Wareing and Patrick 1975, Ho et al. 1989, DeJong and Grossman 1992).

## Model design

PEACH is a state-variable model in which fruit, leaf, current-year stem, branch, trunk and root weight are the state variables, and minimum and maximum air and soil temperatures, degree-days and solar radiation are the driving variables. The rate variables that characterize carbohydrate assimilation and utilization are derived from previous studies on photosynthesis, respiration and growth potential in peach trees (DeJong and Goudriaan 1989*b*, DeJong et al. 1990, Grossman 1993, Grossman and DeJong 1994). The model assumes that the trees are optimally irrigated and fertilized.

The model was written in CSMP (Continuous System Modeling Program III for

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Figure 1. Defining equations for sink strength.

personal computers, IBM), a Fortran-based simulation package. The source code is presented in the Appendix to Grossman (1993) and may be obtained from the authors.

#### Carbohydrate supply

The photosynthetic carbon assimilation submodel was modified from an annual crop growth model, SUCROS '86 (Simple and Universal Crop Growth Simulator, van Keulen et al. 1982, van Kraalingen and Spitters 1986), which explicitly simulates total daily canopy photosynthesis by Gaussian integration of the instantaneous rate of leaf photosynthesis over canopy depth and diurnal light conditions (Goudriaan 1986, Kropff et al. 1987).

The assimilation module of SUCROS '86 was modified to account for the discontinuous canopy within a peach orchard using empirical data on the seasonal pattern of daily light interception within peach orchards to adjust the effective leaf area index throughout the day (DeJong and Goudriaan 1989b). The light-saturated instantaneous photosynthetic rate (DeJong and Doyle 1985, DeJong et al. 1989) is adjusted for the effect of air temperature (Grossman, unpublished data), leaf age (DeJong and Doyle 1984) and leaf nitrogen concentration as a function of canopy depth (DeJong and Doyle 1985). Leaf area index is calculated from simulated leaf weight.

#### Carbohydrate demand

*Maintenance* Leaf maintenance respiration rates were estimated from previously determined leaf specific respiration rates by the mature tissue method (Table 1, Amthor 1989, Grossman and DeJong 1994). Stem, branch and trunk maintenance respiration rates were estimated by the regression method:

$$R_{\rm S} = R_{\rm M} + (G \,\rm RGR), \tag{3}$$

where  $R_{\rm S}$  is the specific respiration rate ( $g_{\rm CHO} g_{\rm DW}^{-1} {\rm s}^{-1}$ ),  $R_{\rm M}$  is the maintenance respiration rate ( $g_{\rm CHO} g_{\rm DW}^{-1} {\rm s}^{-1}$ ), G is the growth respiration coefficient ( $g_{\rm CHO} g_{\rm DW}^{-1}$ 

Organ	Maintenance respiration rate $(ng_{CHO} g_{DW}^{-1} s^{-1})$	Method of estimation
Leaf	105.00	Mature tissue <sup>1</sup>
Current-vear stem	68.61	Regression <sup>1</sup>
Branch <sup>2</sup>	24.00	Regression <sup>1</sup>
Trunk <sup>2</sup>	2.40	Regression <sup>1</sup>
Root	24.00	Branch value
Fruit	18.87	Regression <sup>3</sup>

Table 1. Maintenance respiration rates (at  $20 \,^{\circ}$ C) of peach leaves, current-year stems, branches, trunk and fruits.

<sup>1</sup> Data from Grossman and DeJong (1994).

<sup>2</sup> Branch wood is distinguished from trunk wood by diameter: branch wood consists of all stems one-year-old and older less than 10 mm in diameter; all other wood including the stump is trunk wood.
<sup>3</sup> Data from Dataset of Condition (1090a)

<sup>3</sup> Data from DeJong and Goudriaan (1989*a*).

s<sup>-1</sup>), RGR is the relative growth rate  $(g_{DW} g_{DW}^{-1} s^{-1})$ , and subscript CHO is carbohydrate (Table 1, Amthor 1989). The growth respiration coefficient, *G*, for peach fruits was used in the calculation (0.211 g<sub>CHO</sub> g<sub>DW</sub><sup>-1</sup>, DeJong and Goudriaan 1989*a*). Current-year stems, branches and trunk specific respiration rates, *R*<sub>S</sub>s, and relative growth rates, RGRs, were obtained experimentally (Grossman 1993, Grossman and DeJong 1994). The fruit maintenance respiration rate was determined from DeJong and Goudriaan (1989*a*). The maintenance respiration rate for roots was set to the rate determined for branches of similar size.

The model calculates temperature and maintenance respiration hourly because maintenance respiration is sensitive to temperature, approximately doubling when the temperature increases from 20 to 30 °C (Amthor 1989, Grossman and DeJong 1994). Hourly temperatures are calculated from air and soil minimum and maximum temperatures assuming a sinusoidal temperature pattern during the day and an exponential temperature decline during the night (van Kraalingen and Rappoldt 1987). The daily carbohydrate cost of maintenance respiration is determined as the sum of the products of the hourly respiration rates and the dry weights for each organ type.

*Growth* The model determines daily potential net sink strength for each organ type from experimentally determined seasonal patterns of organ growth potential (Grossman 1993). The daily conditional net sink strength, reflecting the effect of temperature on growth, is determined from the potential net sink strength and the number of degree-days accumulated on each day (Figure 1). The carbohydrate cost of daily growth is calculated as the sum of the carbohydrate equivalent weight of the dry weight added by growth (sink strength) and the respiratory cost of that growth:

$$C_{\rm G} = ({\rm CE}_{\rm DM} + G){\rm DM},\tag{4}$$

where  $C_G (g_{CHO} day^{-1})$  is the carbohydrate cost of the dry matter added,  $CE_{DM} (g_{CHO} g_{DW}^{-1})$  is the carbohydrate equivalent weight of the dry matter, DM  $(g_{DW} day^{-1})$  is

the weight of the dry matter added, and G is the growth respiration coefficient. The carbon equivalent weights of leaves, current-year stems, trunk and roots were calculated from carbon concentrations determined by pyrolysis (Microanalytical Laboratory, Department of Chemistry, University of California, Berkeley, CA) (Table 2).

*Partitioning* PEACH simulates carbohydrate partitioning on a daily basis (Figure 2). The model supplies carbohydrate for maintenance respiration requirements before supplying carbohydrate for growth (Crapo and Ketellapper 1981). The carbohydrate requirements for growth are satisfied based on the conditional net sink strengths of the growing organs and their proximity to a source. Similar approaches to partitioning have been taken in modeling the growth of potatoes, (Ng and Loomis 1984), grapevines (Wermelinger et al. 1991) and kiwifruit (Buwalda 1991). All carbohydrate partitioning is characterized in terms of dry weight gain, representing the weight of structural growth and carbohydrate storage reserves.

Sink strength is calculated by grouping organs of the same type together, rather than making calculations for individual organs, although it is recognized that transport occurs to individual organs. The fruits, leaves, stems and branches are modeled as being closest to the source, followed by the trunk, and finally the roots. Daily carbohydrate availability after maintenance respiration and the carbohydrate cost of daily potential fruit, leaf, stem and branch growth are calculated. Growth occurs at the potential rate if sufficient carbohydrate is available. If this is not possible, the fraction of potential growth that can be supported is calculated as the ratio of the carbohydrate available after maintenance respiration to the carbohydrate requirement for potential growth. This fraction is multiplied by the daily potential growth of each organ type to determine organ growth. Trunk growth is determined by calculating the ratio of the carbohydrate available after fruit, leaf, stem and branch growth to the carbohydrate cost of daily trunk growth potential.

The daily carbon budget is balanced by assigning remaining carbohydrate to root growth. No attempt is made to account for loss of carbohydrate from the roots by fine root turnover, exudation, and increased respiration during active transport of nutrients. For this reason, although the model calculates root growth, the values should

Organ	Carbon concentration $(g C g_{DW}^{-1})^1$	Carbon equivalent weight <sup>2</sup>
Leaf	45.3%	1.13
Current-year stem	45.7%	1.14
Trunk	47.5%	1.19
Root	45.8%	1.14
Fruit <sup>3</sup>	47.5%	1.19

Table 2. Carbon concentration of peach tree organs.

<sup>1</sup> Determined by pyrolysis at the Microanalytical Laboratory, Department of Chemistry, University of California, Berkley, CA.

<sup>2</sup> Ratio of carbon concentration of organ to carbon concentration of carbohydrate.

<sup>3</sup> Data from DeJong and Walton (1989).



Figure 2. Relational diagram illustrating carbohydrate partitioning by the model. Boxes are state variables and valves are rate variables. Solid lines represent carbon flows and dashed lines represent information flows.

more reasonably be attributed to root function, including metabolic processes and structural and storage biomass gain.

For the first 150 degree-days after bloom (approximately two weeks), fruits, leaves, stems and branches are allowed to grow at their conditional growth rates, unrestricted by carbohydrate availability. If the carbohydrate available from current photosynthesis is not sufficient to support this growth, it is provided by stored carbohydrate and deducted from the dry weight of the trunk and roots (Ryugo and Davis 1959, Johnson and Lakso 1986). During the rest of the season, the carbohydrate demand is met by daily carbon assimilation.

# Model parameterization

## Input data

The trees used in the development and testing of the model were a mid-August

maturing peach cultivar (*Prunus persica* (L.) Batsch cv. Cal Red) planted in 1984 at the University of California Kearney Agricultural Center in Parlier, California. Field data were obtained from unthinned trees and from trees from which fruits were selectively removed at three levels: defruiting, removal of all fruits at the time of bloom; heavy thinning, removal of most fruits at the time of bloom; and commercial thinning, removal of a sufficient number of fruits to leave approximately 200 fruits per tree (Table 3). Commercial thinning treatments were carried out at approximately two, four and eight weeks after bloom.

Calibration data on fruit and vegetative growth potentials were obtained on trees that had been heavily thinned and defruited at bloom, respectively (Table 4, Grossman 1993). Respiration data were obtained on trees that had been thinned eight weeks after bloom (Grossman and DeJong 1994). Verification data on fruit and trunk growth were obtained for all treatments. Data on leaf and current-year stem growth were obtained for the defruited trees and trees that had been thinned eight weeks after bloom.

Minimum and maximum air and soil temperatures, and solar radiation were obtained from the California Irrigation Management Information System (CIMIS) weather station located at the Kearney Agricultural Center. Degree-days were calculated by the single sine, horizontal cutoff method, with critical temperatures of 7 and 35 °C (Zalom et al. 1983, DeJong and Goudriaan 1989*a*).

State variable	Value	
Fruit number at bloom	400	
Fruit number at thinning		
Defruited	0	
Heavily thinned at bloom	59	
Thinned at two weeks	196	
Thinned at four weeks	239	
Thinned at eight weeks	219	
Unthinned <sup>1</sup>	289	
Individual fruit weight	0.614 mg	
Leaf weight	0.810 g	
Current-year stem weight	10.4 g	
Branch weight <sup>2,3</sup>	844 g	
Trunk weight <sup>3</sup>	15.721 kg (includes stump)	
Root weight <sup>3</sup>	5.237 kg	

Table 3. Initial values for state variables.

<sup>1</sup> Fruit number on unthinned trees adjusted to reflect fruit drop during first two months of fruit growth.

<sup>2</sup> Branch wood is distinguished from trunk wood by diameter: branch wood consists of all stems one-year-old and older less than 10 mm in diameter; all other wood including the stump is trunk wood.

<sup>3</sup> Data from Grossman and DeJong (1994).

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Table 4. Calibration equations for fruit, leaf, current-year stem, branch and trunk potential growth. FWT, LWT, SWT, BWT and TWT represent fruit, leaf, stem, branch and trunk dry weight, respectively, in units of g<sub>DW</sub>. DD represents degree-days after bloom.

Fruit FWT =  $\exp(-7.39 + 0.032DD - (3.81 \times 10^{-5})DD^2 + (1.65 \times 10^{-8})DD^3 - (DD>700)(1.44 \times 10^{-8})(DD-700)^3 - (DD>1400)(2.73 \times 10^{-9})(DD-1400)^3)$ Leaf LWT =  $\exp(8.84 + 0.0091DD - (7.94 \times 10^{-6})DD^2 + (2.49 \times 10^{-9})DD^3 - (DD>1000)(2.38 \times 10^{-9})(DD-1000)^3 - (DD>2000)(2.87 \times 10^{-11})(DD-2000)^3)$ Stem SWT =  $\exp(1.61 + 0.011DD - (8.56 \times 10^{-6})DD^2 + (2.55 \times 10^{-9})DD^3 - (DD>1000)(2.32 \times 10^{-9})(DD-1000)^3 - (DD>2000)(1.21 \times 10^{-10})(DD-2000)^3)$ Branch BWT =  $\exp(8.44 + (5.50 \times 10^{-5})DD)$ Trunk TWT =  $\exp(15721 + (5.04515 \times 10^{-5})DD)$ 

#### Model predictions

#### Calibration conditions

Reproductive and vegetative growth were simulated under the conditions used to obtain the calibration equations for the various organ growth potentials. The seasonal pattern of simulated fruit growth on trees that were heavily thinned at bloom was similar to the seasonal pattern of fruit growth potential used to calibrate the model, except during the final week before harvest, when simulated individual fruit weights fell below the calibration and field values (Figure 3). Examination of the fraction of potential growth allowed by the model for heavily thinned trees indicated that carbon assimilation limited simulated growth during the final phase of fruit growth, resulting in an underestimate of final individual fruit weight.

Simulated leaf, stem and branch growth on defruited trees followed the calibration equations for growth potential. The simulated pattern of trunk growth was of lower magnitude than the calibration curve.

The correspondence between the simulation results for defruited trees and the calibration equations indicates that simulated daily carbon assimilation generally provided sufficient carbohydrate to support aboveground growth at the rates observed in the field experiment (Figure 3).

## Other conditions

Simulations were made of reproductive and vegetative growth on trees that were thinned two, four and eight weeks after bloom and on unthinned trees. Simulated individual fruit weights were lower on later thinned trees than on earlier thinned trees (Figures 4 and 5). Similar results were obtained in field experiments (Grossman 1993). Simulated total fruit dry weight at harvest was within one to two standard



# CALIBRATION

DAY OF THE YEAR

Figure 3. Simulated and experimental seasonal patterns of organ dry weight per tree under calibration conditions: individual fruit dry weight and the fraction of potential growth allowed by the model for peach trees that were heavily thinned at bloom, and leaf, stem, branch and trunk dry weight per tree for defruited trees. Leaf area index can be calculated from leaf weight by multiplying by 1.75.

errors of the field values (Table 5).

Simulated leaf weights on trees thinned eight weeks after bloom were similar to the field weights during the first two months after bloom, then continued to increase after the field weights had reached their maximum value (Figure 4). Simulated weights for stems and trunk diverged from the field values early in the season. In the case of stem growth, the growth potential calibration equations may not be accurate because of the high standard errors in the estimate of mean stem weight on defruited trees (Figure 3). Small errors, particularly errors early in the season, become large by the end of the season because the rate of increase in stem dry weight is calculated by multiplying the stem dry weight by the relative growth rate.

In most treatments, the seasonal patterns of simulated trunk growth followed the field values until fruit harvest, then exceeded field values for the rest of the growing season (Figures 4 and 5). In the thinned at eight weeks treatment, simulated trunk growth exceeded field values on an earlier date than in other treatments; however, the field values for the eight week thinning were also low compared to the field values for other thinning treatments (Figures 3-5).



# THINNED AT EIGHT WEEKS

Figure 4. Simulated and experimental seasonal patterns of individual fruit dry weight, the fraction of potential growth allowed by the model, and leaf, stem, branch and trunk dry weight per tree for peach trees that were thinned eight weeks after bloom.

The seasonal pattern of the fraction of potential growth allowed by the model in the simulation of trees thinned eight weeks after bloom indicated two periods of carbohydrate limitation on growth (Figure 4). Field studies indicated similarly timed periods of resource limitation on reproductive and vegetative growth (Pavel 1991, Grossman 1993). The periods of simulated carbohydrate limitation on growth were longer on later thinned trees than on earlier thinned trees (data not shown).

The seasonal pattern of simulated root weight reflected its residual status in the model, reaching higher values at the end of the season on earlier thinned trees than on later thinned trees (Figure 6). The root weight accumulated by the model undoubtedly exceeds actual root growth because nutrient uptake, exudation, and fine root turnover are not modeled. However, the prediction that simulated root growth was reduced on trees with large numbers of fruits compared to defruited or heavily thinned trees is supported by numerous studies indicating that the presence of a fruit sink decreases annual root growth (Head 1969, Avery 1970, Heim et al. 1979, Williamson and Coston 1989, Kappel 1991).

Simulated carbohydrate availability to the roots was high during two periods (Figure 6). The first period corresponded to late spring when simulated carbohydrate availability did not restrict aboveground growth. The second period occurred after



## FRUIT AND TRUNK WEIGHTS

Figure 5. Simulated seasonal patterns of individual fruit and trunk dry weights for peach trees thinned two and four weeks after bloom and for unthinned trees.

Treatment	Simulated fruit weight	Experimental fruit weight (standard error)
Heavily thinned at bloom	2271	2363 (209)
Thinned 2 weeks after bloom	5298	4899 (701)
Thinned 4 weeks after bloom	5878	5465 (314)
Thinned 8 weeks after bloom	4652	4736 (258)
Unthinned	5655	5193 (102)

Table 5. Simulated and field total fruit weights at harvest for all treatments.

fruit harvest. These conclusions are supported by experimental results obtained for apple and peach trees, indicating the root growth rates are high during two similarly-timed periods (Head 1969, Miller and Walsh 1988, Williamson and Coston 1989).

## Carbohydrate supply and demand

The simulated seasonal pattern of daily carbon assimilation for trees thinned eight weeks after bloom (Figure 7) was similar to simulated daily carbon assimilation reported for individual potato plants (Ng and Loomis 1984) and grapevines



Figure 6. Simulated seasonal patterns of root dry weight per tree for peach trees that were defruited, heavily thinned at bloom, thinned at two, four and eight weeks after bloom, and unthinned.



# SIMULATED CARBOHYDRATE SUPPLY AND DEMAND

Figure 7. Simulated seasonal patterns of daily carbon assimilation, maintenance respiration, growth respiration, and growth of peach trees that were thinned eight weeks after bloom. Values can be converted to  $g_{CHO} m^{-2} day^{-1}$  by dividing by 8.

(Wermelinger et al. 1991). On a ground area basis, the maximum rate of simulated daily carbon assimilation for peach was 27.9  $g_{CHO}$  m<sup>-2</sup> day<sup>-1</sup>, similar to the simulated value of 30  $g_{CHO}$  m<sup>-2</sup> day<sup>-1</sup> reported for potato (Ng and Loomis 1984).

Total simulated seasonal carbon assimilation from bloom to mid-October on trees thinned eight weeks after bloom was 33 kg<sub>CHO</sub> per tree (4.1 kg<sub>CHO</sub> m<sup>-2</sup> year<sup>-1</sup>), in the range between simulated gross annual photosynthesis in a cool, wet coniferous forest (3 kg<sub>CHO</sub> m<sup>-2</sup> year<sup>-1</sup>, Running and Gower 1991) and estimated gross annual photosynthesis in a *Liriodendron tulipifera* L. woodland, including understory and ground flora (5.4 kg<sub>CHO</sub> m<sup>-2</sup> year<sup>-1</sup>, Harris et al. 1975).

Simulated daily maintenance respiration accounted for an increasing proportion of daily carbon assimilation as the season progressed due to increases in whole-tree biomass and temperature (Figures 7 and 8). In contrast, by two months after bloom, simulated daily growth respiration accounted for a relatively constant amount of carbohydrate usage except during periods when growth was limited by carbohydrate availability.

Simulated daily growth accounted for 22–86% of carbon assimilation (Figure 7). The simulated partitioning of this growth to individual organs was highly dynamic (Figure 9). The simulated seasonal total carbohydrate cost (dry matter plus growth respiration) of fruit growth (8410 g) was about 36% times greater than the simulated seasonal total cost of leaf growth (3056 g), stem growth (2938 g) and trunk growth (2494 g). The simulated seasonal cost of branch growth (212 g) was much lower. The simulated total carbohydrate availability for root activity over the growing season on trees thinned at eight weeks after bloom (8198 g) represented 32% of the carbohydrate available after simulated seasonal carbohydrate assimilation. Approximately one-third of total simulated carbon assimilation was utilized for maintenance respiration, and approximately two-thirds was utilized for growth and growth respiration. Sim-



### **ENVIRONMENTAL PARAMETERS**

# DAY OF THE YEAR

Figure 8. Seasonal patterns of solar radiation, air temperature, soil temperature and degree-day accumulation at the Kearney Agricultural Center during 1990.



DAY OF THE YEAR

Figure 9. Seasonal patterns of the simulated partitioning coefficient for fruits, leaves, stems, branches, trunk and roots of peach trees that were thinned eight weeks after bloom.

ulated fruit growth, above ground vegetative growth and root activity each consumed about one-third of the carbohydrate used for growth.

# Conclusion

Simulation models are useful tools for integrating information about plant processes that are measured on time scales of seconds and minutes, such as photosynthesis and respiration rates, with data on processes that are measured over longer time intervals, such as reproductive and vegetative growth. The PEACH model developed here estimates carbon assimilation, maintenance respiration, and the growth of reproductive and vegetative organs of peach trees. Growth was simulated using experimentally determined seasonal patterns of growth potential of fruits, leaves, stems, branches and trunk (Grossman 1993).

Model predictions corresponded to observed field values for fruit and vegetative growth under conditions that differed greatly from those used to develop the growth potential equations. In particular, changes in the seasonal patterns of fruit and vegetative growth due to differences in the time of fruit thinning were accurately simulated by the model. The model predicted periods of carbohydrate limitations on fruit and stem growth which coincided with resource-limited growth periods identified by previous experimental studies (Grossman 1993). Thus, the model accurately simulated the balance between carbohydrate supply and aboveground carbohydrate demand and supports the hypothesis that plants function as collections of semiauton-

SIMULATED PARTITIONING COEFFICIENT

omous, interacting organs that compete for resources based on their potential sink strengths.

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