Modeling the Vegetative and Reproductive Growth of Plums

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Abstract

The first version of PLUM, a carbon budget computer simulation model was developed by modifying the existing PEACH model (DeJong et al., 1996). Although peaches and plums are closely related, some architectural, anatomical and physiological differences can be observed between these species. Modifications based on these differences were made in the main parts of the model, the carbon supply and demand modules. The results of the first simulations showed that PLUM was able to predict fruit and leaf mass accumulation well throughout the season, but stem mass accumulation was clearly underestimated by the model. More work is needed to re-parameterize the PLUM model according to the vegetative differences between peach and plum trees.

INTRODUCTION

Carbon budget computer simulation models have been used to relate plant growth to environmental conditions for several years (Landsberg et al., 1991). Unfortunately, very few of these models have been developed for fruit tree crops (Lescourret et al., 1998), particularly on a whole tree basis (Buwalda, 1991; Deleuze and Houllier, 1995). PEACH was recently developed in an attempt to model crop production in peach trees (Grossman and DeJong, 1994). PEACH simulates the annual carbon supply and demand for reproductive and vegetative growth of peach trees on a daily basis. It is a state variable simulation model in which fruit, leaf, stem, branch, trunk and root weight are the state variables, and minimum and maximum air and soil temperatures, degree days, solar radiation and canopy light interception are the driving variables.

The central concept behind PEACH is the hypothesis that trees are collections of semi-autonomous but interacting organs whose carbon partitioning is driven by competition based on their growth potential, source proximity and carbohydrate availability. The way the model simulates carbon supply and demand as well as carbon partitioning can be reviewed in detail in previous publications (DeJong and Grossman, 1992; Grossman, 1993; Grossman and DeJong, 1994; DeJong et al., 1996). The assimilated carbon represents the “supply” part of the model; this carbon pool is available for growth and respiration, which represent the “demand” part of the model. Carbon assimilation is simulated as a function of the seasonal patterns of canopy light interception, photosynthesis, and daily maximum and minimum air temperatures. Organ growth simulation is based on experimentally determined maximum achievable growth in trees growing with no limitation of water or nitrogen in which the fruit load was manipulated to minimize competition for carbohydrates (potential growth rates).

Carbon partitioning is simulated first by satisfying the maintenance respiration needs; then, carbon is allocated to organ growth based on sink strength (potential growth rates), source-proximity (fruits, leaves, stems and branches first, then trunk, and roots last), and carbon availability (for details see Grossman, 1993 and Grossman and DeJong, 1994). During the first 200 degree-days, fruits, leaves, stems and branches are left to grow at their potential growth rates, and their cost is subtracted from the trunk and root reserves.

Field validation has shown that PEACH simulates the vegetative and reproductive growth of peach trees growing under different fruit loads and environmental conditions reasonably well (Grossman and DeJong, 1994; DeJong et al., 1996). Subsequent research adapted PEACH to other fruit tree species such as almonds (Esparza et al., 1999). One might presume that PEACH should be easily adapted to species such as plums, which are closely related to peaches. However, some architectural, anatomical and physiological differences can be observed between these species, requiring modification of the two main parts of the model, the supply and demand modules.

The scope of this study was to develop a PLUM carbon budget model and run the first simulations of the carbon supply and demand for reproductive and vegetative growth of plum trees. At the same time, this study serves as a test of the feasibility of adapting the PEACH model to different fruit tree species.

MATERIALS AND METHODS

Field Experiment

The plum trees used to parameterize and test the model 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. Field experiments were carried out in 1999. The trees were planted in a North-South orientation with 1.9 m between trees in the row and 5.7 m between rows and trained with the Kearney Agricultural Center V (KAC-V) training system. Routine horticultural care suitable for commercial fruit production was provided, including pruning, fertilization, irrigation and pest control. The trees were not summer pruned. Three fruit thinning treatments were performed on both cultivars. T1 consisted of heavily thinned trees from which most of the flowers were removed at bloom. These trees were further thinned one month after bloom (<200 fruit per tree). T2 consisted of trees that were left unthinned. T3 consisted of commercially thinned trees. These treatments were replicated four times for the early cultivar and three times for the late cultivar. For each block and thinning treatment, four trees located within individual rows were chosen.

Photosynthetically active radiation penetrating to the orchard floor was measured once a month using a ceptometer (Decagon, Delta-T Devices, Pullman, WA) from bloom to harvest. For each measurement day, radiation penetration was measured seven times from sunrise to sunset, with the fourth measurement occurring at solar noon. Measurements were only made on clear days.

Leaf gas exchange was measured in the field, in spring time, using a CIRAS gas exchange analysis system. Measurements were made on intact mature leaves, of approximately the same age, located at outer, well-exposed part of the canopy. All measurements were made on leaves exposed to direct sunlight above the level required for light saturation.

Fresh and dry fruit weight were monitored for T1 and T2 every ten days by harvesting four samples of 10 fruits each. Each sample had five fruits from two trees. The commercial thinned trees were sampled once a month. The initial number of fruits per tree was estimated by considering the final number of fruit per tree at harvest as well as number of fruit removed during the sampling. At harvest time, total number of fruit and dry and fresh weight were obtained. The fruit were sized by weight using a commercial sizer.

At the end of the season, the final leaf and stem dry weight of current year growth was determined. All the leaves and stems of the current-year growth were removed and dried separately.

Calibration and Initialization

The main change to the carbon supply module of the PEACH model was the modification of the surface response describing the daily and seasonal tree light interception. Response surfaces using a quadratic model were fitted:

$$Qh = a + bx + cy + dx^2 + exy + fy^2 , \quad (1)$$

x being day of year (DOY) and *y* the hour.

Leaf photosynthesis response to temperature was modified according to field data. The leaf photosynthesis at a given temperature (A_t) and the maximum leaf photosynthesis (A_{max}) data were used to compute the A_t/A_{max} ratio.

For the carbon demand module of the model, the peach fruit growth potential curves were replaced by those obtained for heavily thinned trees of the two cultivars. The calibration equations were cubic splines with two knots fitted to logarithmically-transformed fruit dry weight data from bloom through harvest. Initial values for the state variables representing fruit dry weights were calculated from their respective growth potential equations at bloom.

Verification

Verification runs of the model were made from bloom to 3000 degree-days after bloom. Verification data on fruit time-course were obtained from the unthinned and commercially thinned trees. Total estimates of leaf and current stem growth were compared with the vegetative growth data obtained at the end of the season.

Environmental Data

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 for the year 1999, and used for the model simulation. The calculation of the degree-days was done by the single sine, horizontal cutoff method, with critical temperatures at 7 and 35°C (Zalom et al., 1983; DeJong and Goudriaan, 1989). Degree-day data were accumulated from full-bloom to harvest for each cultivar and thinning treatment.

RESULTS AND DISCUSSION

Model Calibration

1. Radiation Interception. The time-course of radiation interception showed an increase from 0.5 early in the season to 0.75 at harvest time. There were slight differences between varieties, the early cultivar having greater values especially during May-June when the incoming radiation was high. After day of year 200 (19 July), the fraction of radiation intercepted by the canopy remained nearly constant. Response surfaces using a quadratic model explained 73 % and 79 % of the variance in light penetration for the early and late cultivar, respectively. The coefficients used in the PLUM model were fairly similar to those of peaches (cv. Ross) having a similar training system, and were different to that of peach in the Standard Open Vase system (data not shown). Thus, the pattern of shoot biomass accumulation in these two plum varieties appeared to be similar to that of Ross peach in a KAC-V training system.

2. Leaf Photosynthesis. The model assumes that leaf photosynthesis varies with time of year, canopy depth and temperature. The relationship between photosynthesis rate and leaf temperature used in the model was obtained from field data. Maximum gross leaf photosynthesis rate was 16.8 μmol m^{-2} s^{-1}. The model uses relative values (A_t/A_{max} ratio) to adjust for leaf temperatures. The response of leaf photosynthetic rate of peaches to temperature has a bell shape with high values between 25 and 30°C. Black Amber plum had a temperature optimum at 35°C and Royal Diamond appeared to have a broad temperature optimum range (25-35°C) (data not shown).

3. Reproductive Growth. Most of the values of the parameters used in the model simulations for Black Amber and Royal Diamond plum cultivars were similar to those used for Ross peach cultivars (DeJong, unpublished data). The primary differences were the initial and final number of fruit, initial fruit weight, thinning, bloom, vegetative bud break and harvest dates (data not shown). The Black Amber cultivar bloomed at 71 DOY (12 March) and was harvested at 194 DOY (13 July). Through this period, 1380 degree-days were accumulated. The late maturing cultivar (Royal Diamond) bloomed at 80 DOY (21 March) and was harvested at 228 DOY (16 August). Through this period, 1890 degree-days were accumulated. The growth patterns of the two varieties were different. Black Amber grew rapidly early in the season while Royal Diamond grew more rapidly at the end of the season (Fig. 1). The PEACH model was modified based on these differences. Field data from heavily thinned trees were used to fit splines between the logarithmically-transformed fruit dry mass and accumulated degree-days (data not shown). Degree-days rather than calendar days were used to account for both time and temperature. Relative growth rates (RGR) of fruits on heavily thinned trees were derived from fruit growth curves and inserted in the model as the new calibration equations for potential fruit growth. Fruit growth estimated using the calculated RGR is showed in Figure 1. The simulated total fruit dry weight at harvest was within one standard error of the mean field value.

4. Vegetative Growth. Vegetative growth data obtained from the heavily thinned trees was compared to simulated data (Table 1). The observed data are not independent from calibration data (all of them came from the same trees), so they can not be used as a true verification of the model, but leaf dry weight at the end of the season was reasonably well predicted for both plum varieties. Stem dry weight was clearly underestimated. The stem growth potential equation does not appear to be accurate because the final stem dry weights were smaller than the observed values. This difference resulted because the model was not explicitly changed to accommodate the differences between peach and plum stem growth. There is a clearly a need to improve the model parameters concerning stem biomass accumulation.

Model Verification

1. Reproductive Growth. The simulated patterns of reproductive and vegetative growth of trees that were thinned to the commercial cropping level or left unthinned, were compared to data from field experiments. For the early maturing cultivar, observed yield was 7.44 kg $tree^{-1}$ for the unthinned trees and 4.06 kg $tree^{-1}$ for the commercially thinned trees. The yield of the late maturing cultivar was substantially higher: 13.8 kg $tree^{-1}$ for unthinned trees and 7.69 kg $tree^{-1}$ for commercially thinned trees (Table 1). Yields estimated by the model were close to observed values in all cases, and the differences between varieties and/or thinning treatments observed in the field data were also reflected in the predicted values (Table 1). The model predicted the time-course of fruit growth fairly well, although there was a slight overestimation for the early cultivar during the phase of rapid fruit growth (Fig. 1).

2. Vegetative Growth. The model predicted an exponentially-shaped curve of leaf mass accumulation and a linear curve for stem mass accumulation (data not shown). For these organs, final dry weights were measured at the end of the season. Observed and simulated final leaf weight were close, but the model consistently underestimated stem dry matter (Table 1). Compared to the values of the parameters used in the original PEACH model, plums exhibit a proportionally more dense above ground structure (trunks, scaffolds, and primary and secondary branches) than peaches. Water sprouts also represent a greater fraction of stem dry weight in plum than in peaches.

The model provides a framework for integrating environmental and physiological factors controlling carbohydrate supply and demand for reproductive and vegetative growth of plum at an orchard level and provides a method to evaluate future potential avenues of research related to growth and productivity of plum. In general, both the model calibration and verification results indicate that the PEACH model could be converted to fairly accurately estimate fruit and leaf growth, but more work is needed to accurately model stem growth.

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Tables

Organ	Cultivar	Organ dry weight (Kg tree^{-1})					
		Heavily thinned		Unthinned		Commercially thinned	
		Observed	Estimated	Observed	Estimated	Observed	Estimated
Fruit	Black Amber	2.43 ± 0.11	2.20	7.44 ± 0.60	7.80	4.06 ± 0.56	3.78
	Royal Diamond	4.61 ± 0.34	4.47	13.80 ± 1.14	15.00	7.69 ± 1.21	8.87
Leaves	Black Amber	3.14 ± 0.30	2.81	2.45 ± 0.14	2.02	2.79 ± 0.09	2.50
	Royal Diamond	2.98 ± 0.50	3.47	2.56 ± 0.51	2.83	2.78 ± 0.39	3.42
Stems	Black Amber	8.94 ± 1.12	2.46	5.14 ± 0.82	1.36	7.03 ± 0.26	1.99
	Royal Diamond	6.51 ± 1.45	3.47	4.46 ± 0.59	2.29	5.49 ± 0.96	3.39

Table 1. Fruit, leaf and stem dry weight per tree (± standard error) experimentally observed and estimated by the model for unthinned, commercially thinned and heavily thinned trees of Black Amber and Royal Diamond plum cultivars.

Figures

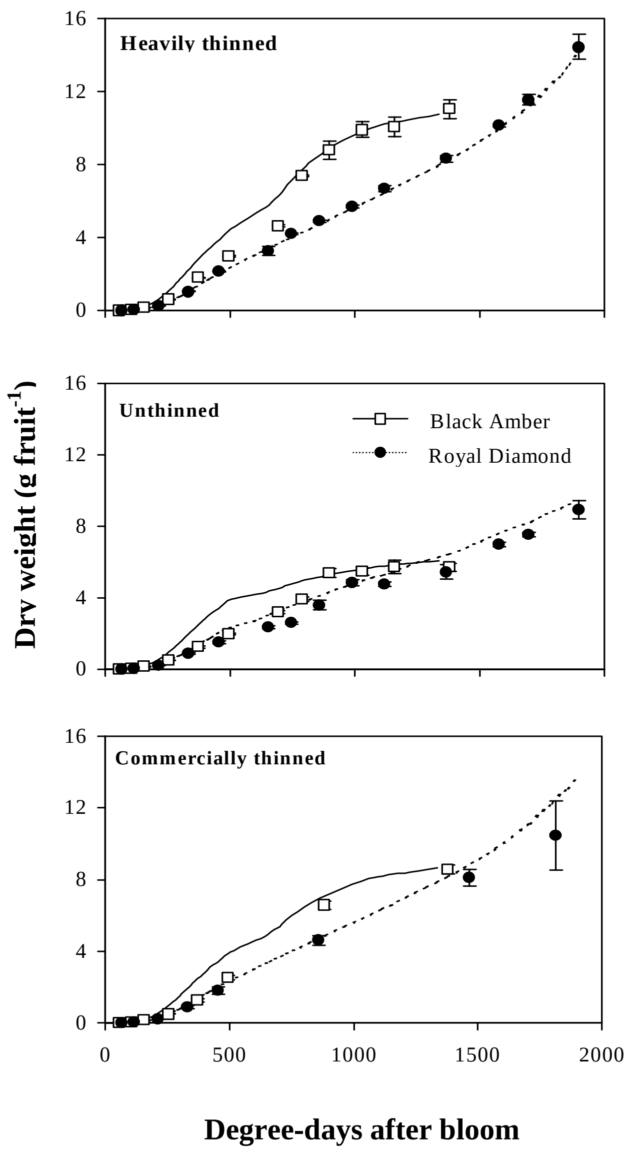

Fig. 1. Simulated (lines) and experimental seasonal patterns of individual fruit dry weight, in heavily thinned (calibration condition), unthinned and commercially thinned trees for Black Amber and Royal Diamond plum cultivars. Bars indicate the standard errors of the means.