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Modeling Peach Fruit Growth and Carbohydrate Requirements: Reevaluation of the Double-sigmoid Growth Pattern

T.M. DeJong

Department of Pomology, University of California, Davis, CA 95616

J. Goudriaan

Department of Theoretical Production Ecology, Agricultural University, 6700 AK, Wageningen, Netherlands

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Abstract. Seasonal patterns of fruit growth were measured on early and late-maturing peach (*Prunus persica* L. Batsch) cultivars ('June Lady' and 'O'Henry', respectively). Seasonal relative growth rates of fruit dry matter accumulation were calculated. The relationships between fruit relative growth rates and respiration were used to develop a quantitative carbon budget model of peach fruit growth and sink activity. The resulting model indicates that the double-sigmoid growth pattern of peach fruits involves only two physiologically distinct phases of sink activity instead of the three stages that are traditionally recognized. The traditional stage II of fruit growth is apparently a function of the timing of the shift between these two physiological phases of sink activity.

The cyclic pattern of growth in peach fruits has been studied for many years. In 1919, Connors (6) subdivided what has become known as the double-sigmoid growth curve into three stages, the initial phase of exponential growth (Stage I), the lag phase (Stage II), and the second exponential phase (Stage III). Since those early studies, many attempts have been made to describe the mechanisms that control the changes in fruit growth rate, usually with the hypothesis that developmental changes in the pericarp are linked with changes in the seed or with competition with the vegetative activity of the tree (4, 5, 16, 17, 22).

While some researchers were interested in understanding the mechanisms that triggered or coordinated shifts from one growth stage to another, others have been interested in the environmental and/or endogenous tree factors that affect fruit growth. The importance of temperature on fruit growth and development has been confirmed by numerous researchers (1, 2, 11, 19);

Fischer (10) showed that, under some circumstances, heat unit or degree-day accumulation can be used effectively to measure developmental time in stone fruits.

Because most of the research on peach fruit development has been oriented toward production of fresh fruit, most fruit development studies are based on measurements of fruit diameter or fresh weight. Chalmers and van den Ende (5) showed that the three stages of fruit dry weight development did not necessarily correspond with fresh weight development in a late-maturing clingstone cultivar, but their emphasis was also on the potential factors controlling the three stages of fruit growth.

In spite of the fact that fruits are considered to be major sinks for carbohydrates in fruit trees, there have been few quantitative analyses of the carbohydrate demands of fruit growth in tree crops. DeJong and Walton (9) recently have quantified the daily carbohydrate demands for fruit respiration through the season. The purpose of the current research was to attempt a quantitative analysis of the seasonal dry matter carbohydrate requirements of peach growth and to develop a quantitative carbon budget model of peach fruit growth that could be used to estimate daily potential fruit demands for photosynthates. In other words, we attempted to quantify developing peach fruits in terms of their

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sink activity (17). The primary sink activities of fruits are growth and respiration. In this paper, we present data on a two-phase model of fruit growth using a relative growth rate approach and then indicate how the fruit growth model can be linked to fruit respiration rates to estimate daily fruit carbohydrate demands through the season.

Materials and Methods

The fruits analyzed in this study were grown on mature peach trees planted in 1972 at the Univ. of California's Kearney Agricultural Center, Parlier. Two cultivars were used: the early maturing 'June Lady', which typically matures around the second week in June, and the late-maturing 'O'Henry', which typically matures the first week in August. The trees were planted and trained to a vertical hedgerow configuration and received routine horticultural care suitable for commercial fruit production, including: pruning, fruit thinning, fertilization, irrigation, and pest control.

The seasonal patterns of fruit growth were determined in both cultivars during 1984 through 1986. In 1984, weekly harvests of 10 samples consisting of 10 fruit per sample were made from a uniform set of trees within the study block. Care was taken to spread the sampling over the trees so that weekly sampling would not drastically alter the crop load of any one tree. Each sample consisted of four fruit from the top, four from the mid-section, and two from the bottom of two adjacent trees. For each sample, fruit within each area of the tree were harvested at random, except that visually abnormal fruit were discarded. During 1985 and 1986, five 10-fruit samples were taken per week. After each harvest, fruit were immediately cut up and dried at 75°C.

Since temperature has long been recognized as a major environmental factor affecting fruit growth and because Fischer (10) showed that heat-unit accumulation could be used effectively to measure developmental time in stone fruits, we used degree-days for measuring developmental time. Ambient air temperatures were monitored at a standard California Irrigation Management Information System (CIMIS) weather station (13), located within 1 km of the study site. Degree-days were calculated from daily minimum and maximum temperatures using the single-side method (21), with upper and lower temperature thresholds at 35 and 7°C, respectively. Degree-day data were accumulated from full-bloom to harvest for each cultivar during each year of the study.

Fruit relative growth rates (rate of dry weight increase per unit dry weight per unit time, RGR) were calculated with 1984 data using the formula: $RGR = (1/w)(dw/dt) = \ln W_2 - \ln W_1 / T_2 - T_1$; where W_2 and W_1 are mean fruit dry weights at harvest times T_2 and T_1 , respectively (3). Degree-days were used as the developmental time unit for this analysis.

Log transformations of the RGR data were performed. These transformations clearly delineated two log-linear phases of fruit growth. The regression equations of the two log-linear phases of fruit growth were then combined to develop predictive models of fruit growth potential for the two peach cultivars.

Results and Discussion

Modeling fruit growth. Calculation of 1984 fruit RGR on a degree-day basis and transformation of the data using natural logarithms indicated that dry matter growth in peaches could be separated into two log-linear phases (Fig. 1). In the first phase, there was a negative linear relationship between the natural log

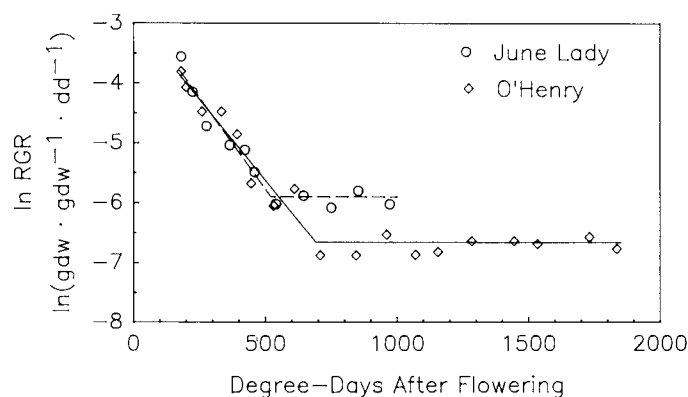


Fig. 1. Log-transformed 1984 fruit relative growth rates (RGR) for 'June Lady' and 'O'Henry' peaches plotted against degree-days after flowering. Lines representing the decreasing phases of relative growth rate were drawn from regression analyses using the first seven and nine points of the fruit dry weight growth curves of 'June Lady' and 'O'Henry', respectively. 'June Lady': $y = -2.73 - 0.00608x$, ($r^2 = -0.95$). 'O'Henry': $y = -2.93 - 0.00540x$, ($r^2 = -0.93$). Lines representing the later phase of stable relative growth rates indicate the mean relative growth rate during the last five and ten points of the fruit growth curves of 'June Lady' ($\bar{x} = -5.96 \pm 0.05$) and 'O'Henry' ($\bar{x} = -6.73 \pm 0.04$), respectively.

of the RGR and degree-day ($r^2 = 0.95$ and 0.93 for 'June Lady' and 'O'Henry', respectively), indicating that the fruit RGR decreased logarithmically with degree-day accumulation. This type of relationship is known as the Gompertz function and has been found to be appropriate in biological work involving sigmoid growth functions (3). In the second phase, the fruit RGR remained relatively constant and consequently the absolute fruit growth rate increased in a logarithmic fashion. The slope of the first phase was slightly different for the two cultivars (0.00608 and 0.00540 for 'June Lady' and 'O'Henry', respectively), but more data are necessary to determine if these differences are statistically significant. The stable RGR of the second phase (Fig. 1) was much higher in 'June Lady' than 'O'Henry' (0.00258 and 0.00119 g/g per degree-day, respectively). The shift between the two phases was also earlier in 'June Lady' than 'O'Henry' (530 and 704 degree-days after flowering, respectively).

Attempts to simulate seasonal fruit growth using mathematical functions describing these two phases were partially successful. The seasonal pattern of growth for a given year could be successfully simulated by using mathematical functions adjusted to that particular year, but the resulting simulated fruit growth pattern did not precisely fit fruit growth data from other years (Fig. 2). It appears that the general concept of a biphasic fruit dry weight accumulation model for fruit growth may be correct, but there are almost certainly other factors such as water stress, carbohydrate availability, and plant nutrition that also influence fruit growth.

Previous studies have tended to emphasize the double-sigmoid nature of peach fruit growth. Stage I is a period of rapid development of the pericarp and seed. Stage II is a period of slower growth and is generally thought to be dominated by the lignification of the endocarp. Stage III is the period of rapid cell expansion/maturation of the mesocarp. There have been numerous attempts to explain the regulation of these sigmoid patterns of peach growth by hormone studies and/or competition for carbohydrates with different parts of the fruit or between the

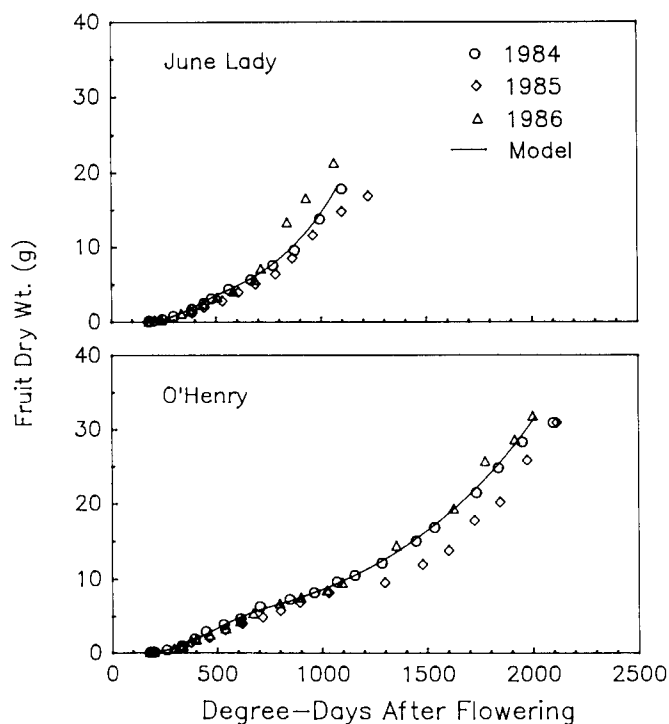


Fig. 2. Predicted cumulative fruit dry weight (solid lines) using models based on 1984 data (Fig. 1) compared with measured dry weight data collected during 1984 through 1986.

fruit and vegetative activity of the tree (5, 22). None of these interpretations appear to explain the range of variation in fruit growth pattern exhibited by different peach cultivars or under different cultural conditions.

Our data do not deny the existence of the three traditional stages of fruit growth. They merely indicate that hormonal regulation or carbohydrate competition need not be invoked as the explanation for the sigmoid pattern of fruit growth. The sigmoid pattern simply appears to be a result of the rate of change in the RGR relative to the RGR itself. As the initial developmental phase (Fig. 1) runs its course, the RGR decreases in a logarithmic fashion. This causes the first sigmoid increase and decrease in absolute growth rate because the initial rate of growth is greater than the rate of decrease in RGR, but, as the RGR decreases in a logarithmic fashion, eventually it decreases more rapidly than fruit size increases. This causes a decrease in the absolute growth rate, typical of the traditional stage II of fruit growth. This type of growth pattern may be expected if one considers that the primary events occurring in this early period of fruit growth are cell division and cell differentiation. Presumably, cell division and differentiation are finite events and, after cell division has ceased, only a limited amount of differentiation can occur before the onset of final fruit cell expansion/maturation. Thus, the RGR of the fruit decreases. Perhaps the primary difference between early and late-maturing cultivars is the length of time required before fruit cell expansion/maturation (phase 2) begins. This time requirement may not be directly linked to the length of the initial cell division and differentiation phase of fruit growth, and data from Tukey (14) indicate that it is probably also independent of embryo development.

The biphasic model presented here may be useful in describing the basic genetic potential for fruit growth in response to degree-day accumulation of a given cultivar, but the actual fruit

growth attained in the field depends on other factors, such as water stress, carbohydrate availability, plant nutrition, or other factors that would limit the fruit from growing to its full genetic potential. This model is attractive because it would also provide a simple basis for understanding the genetic changes required for breeding early or late-maturing cultivars. This model shows that large changes in fruit growth pattern can be achieved by altering the timing of the shift between phase I (when fruit RGR is decreasing at a logarithmic rate) and phase II (when the fruit RGR remains stable at the RGR achieved at the time of the shift). Adjusting total time (accumulated degree-days) to maturity in proportion to the adjustment in timing of the phase change would result in cultivars with different times of maturity. Figure 3 shows the simulated growth patterns for a group of hypothetical cultivars in which the shift from phase I to phase II is set at 400, 500, 600, 700, and 800 degree-days after full bloom. Figure 4 shows the corresponding absolute growth rates for the same five hypothetical cultivars. The model predicts that the double-sigmoid growth pattern should be most pronounced in later-maturing cultivars. This generally is the case in real cultivars (16).

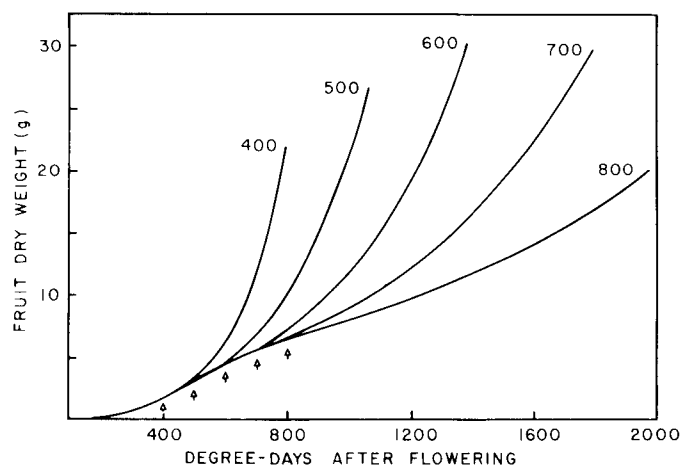


Fig. 3. Simulated cumulative fruit dry weight growth curves for hypothetical cultivars in which the shift (arrows) from the log-linear decrease in relative growth rate occurs at 400, 500, 600, 700, and 800 degree-days after flowering.

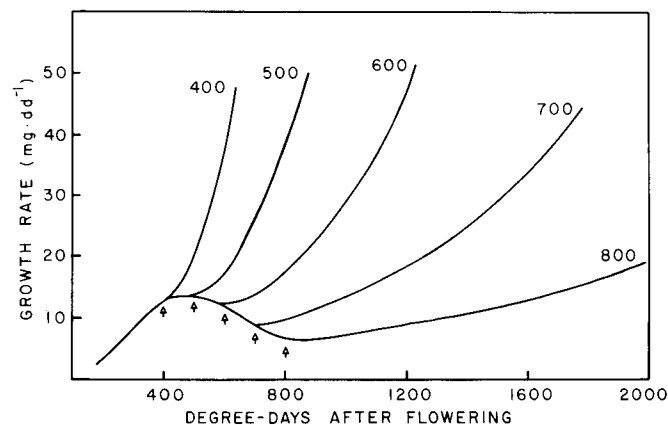


Fig. 4. Simulated absolute fruit growth rates for hypothetical cultivars in which the shift (arrows) from the log-linear decrease in relative growth rate occurs at 400, 500, 600, 700, and 800 degree-days after flowering.

Of course, carrying these generalizations too far is dangerous because general correlations do not offer proof. Nonetheless, the model provides intriguing possibilities for understanding some of the observed cultivar differences in fruit growth. If this model is combined with the knowledge that there are also significant differences in the chilling requirement and time of bloom, it may be possible to analyze the basis for much of the developmental variation between cultivars.

Modeling fruit carbohydrate requirements. The carbohydrate requirements for plant dry matter accumulation can be estimated by assuming that dry peach tissue consists of $\approx 47.5\%$ carbon (9) and then calculating how much carbohydrate (CH_2O) is needed to supply that carbon.

To estimate the carbohydrate requirements needed to sustain fruit respiration, the fruit respiration rates per degree-day calculated from previous research on both 'June Lady' and 'O'Henry' (7, 9) were regressed against the fruit RGR, also expressed on a degree-day basis (Fig. 5). The slope of the resulting linear relationship is an estimate of the growth respiratory coefficient per unit of fruit growth ($0.309 \text{ mg CO}_2/\text{mg}$). The Y-intercept of the same relationship is an estimate of the maintenance respiration coefficient ($0.184 \text{ mg CO}_2/\text{g per degree-day}$) (13, 14).

By using these functions to compute CH_2O requirements for respiration and linking them to the fruit growth models for the 1984 season (Fig. 2), simulation models were constructed that estimate the seasonal pattern of fruit carbohydrate requirements for 'June Lady' and 'O'Henry' on a daily basis (Fig. 6). These are essentially models of potential carbohydrate demands to sustain fruit growth and respiration (sink activity), without regard for the availability of photosynthate. Therefore, the basic functions for the fruit growth models have been developed under circumstances in which carbohydrate limitations are minimized. These functions can be linked to canopy photosynthesis models to predict when fruit growth is limited by photosynthate supply (8).

Although the exact functions in the models presented here may vary with cultivar and environment, growth of peach fruits, from shortly after fruit set to fruit maturity, appears to be functionally divided into two phases. During the first phase, the fruit RGR declines exponentially with developmental time; during the second phase, the fruit maintain a relatively constant RGR. Combining these two phases also yields what has traditionally been described as the double-sigmoid growth curve. Numerous attempts have been made to explain the varying growth rates

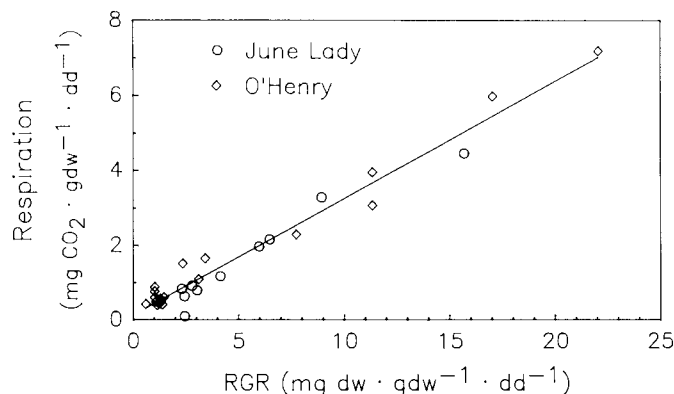


Fig. 5. The relationship between fruit respiration and relative growth rate for 'June Lady' and 'O'Henry' peaches during the 1984 growing season ($y = 0.184 + 0.309x$, $r^2 = 0.96$).

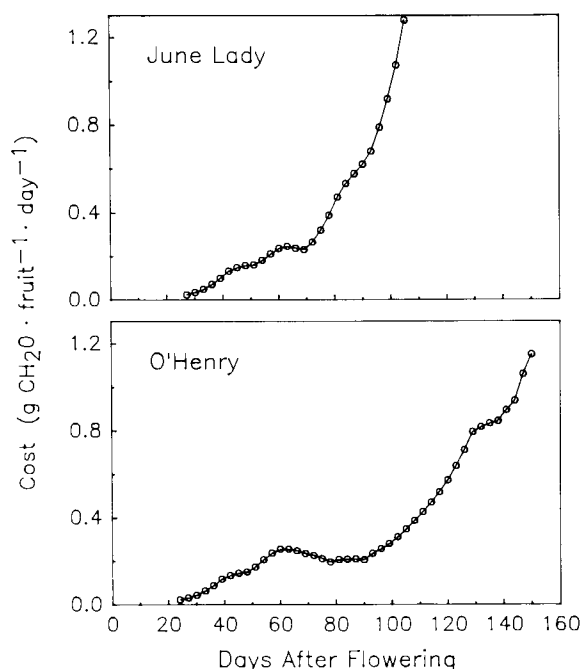


Fig. 6. Calculated daily carbohydrate costs for fruit dry weight growth and respiration from shortly after flowering to harvest of 'June Lady' and 'O'Henry' peach fruits during the 1984 season.

during the three traditional stages of fruit growth. The linkages between these stages and temporally related phenomena should be reevaluated with respect to the biphasic model for fruit growth presented here. Similarly, although the fruit respiration model needs to be validated for other cultivars and situations, fruit growth and maintenance respiration can be estimated from calculations of fruit respiration per degree-day and RGR per degree-day. This approach may also be valid in the modeling of fruit CH_2O requirements of other species.

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