Using Concept-Based Computer Simulation Modeling to Study and Develop an Integrated Understanding of Tree Crop Physiology

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Keywords: *Prunus persica*, carbohydrate partitioning, crop yield, fruit size, plant architectural modeling, tree growth, tree modeling

Abstract

Studying and developing an integrated understanding fruit tree physiology and growth and development is a difficult endeavor. Plants are very complex organisms that are governed and influenced by a multitude of factors. Traditional experimental approaches to plant function have been largely limited to examining a small number of factors at a time and describing those interactions verbally or with two- or three- dimensional static diagrams. These approaches result in valuable insights into the interactions of a limited number of variables on a similarly limited number of somewhat isolated processes such as organ growth, photosynthesis, or respiration. However it is very difficult to develop and communicate an integrated understanding of natural processes that involve multiple interacting factors. The study and understanding of environmental and endogenous influences on carbon assimilation, partitioning, transport and utilization in plants is a good example of these limitations. The development and testing of hypotheses that explain carbon partitioning and utilization presents complex problems because of the dynamic nature and relationships among carbohydrate partitioning, growth and plant architecture as well as the multitude of factors that can influence each process and organ. One way to dynamically integrate the influence of multiple factors on multiple processes is to use recent advances in computer technology to develop concept-based, computer simulation models of tree crop growth and physiology. For the past two decades research in our laboratories has focused on developing environmental and endogenous influences on carbon assimilation, partitioning, transport and utilization in peach trees. This work has resulted in the PEACH and L-PEACH models. Modeling has allowed us to develop a systematic analysis and integration of hypotheses regarding the factors that control peach fruit growth, crop yield, and tree growth; as well how these processes respond to management practices.

INTRODUCTION

Ultimately crop productivity is dependent on the efficiency of uptake of environmental inputs, energy, CO_2, nutrients and water and their distribution and use toward producing a crop (Cooper, 1981). With horticultural crops there is added emphasis in producing high quality, economically valuable crops. Because of the pivotal importance of the uptake processes related to crop productivity including photosynthesis, nutrient and water uptake, and the relative ease of measuring them with recent technology, much research has been conducted to explore the physiological and environmental limits of these uptake processes in crop plants. However study and understanding of the physiological and environmental limits to the distribution and use of the environmentally derived inputs has been slowed by the absence of a unified theory to explain how assimilated products are partitioned within the plant and because of the complexity of all the interactions that govern the processes involved. As Gifford and Evans (1981) stated, comprehending the development of crop yield requires treating photosynthesis, translocation, growth and storage as an integrated whole since these processes are linked by numerous interactions. The problem becomes even more complex when nutrient inputs and yield quality are considered.

Crop modeling has been used as a tool for estimating rates of photosynthesis of plant canopies, taking into account light distribution, temperature, canopy characteristics, and other factors for many years. These models were fairly successful in predicting yields of deterministic, annual crops by linking the dynamic estimates of canopy photosynthesis up with empirically-derived formulae for partitioning carbohydrates to crop growth (van Keulen et al., 1982). However is was not until the last decade that researchers began to model carbon partitioning of indeterminate crops by using organ, sink-demand driven allocation models (Le Roux et al., 2001). These models required the development of dynamic sub-models not only of the factors governing the uptake processes but also the organ development and growth processes (Grossman and DeJong, 1995a, c). Until the current decade transport processes were merely assumed but not explicitly incorporated in whole plant models. Recent advances in computer graphics simulation technology have facilitated modeling the growth of individual organs within the context of plant canopies and this has provided the opportunity to also explicitly model plant transport and movement of carbon into and out of storage over time (Allen et al., 2005, 2007; Lopez et al., 2008).

The goal of this paper is to describe the development of an integrated computer simulation model of multiple year peach tree growth, including canopy photosynthesis, tree and fruit growth, and crop yield in response to environmental and management factors. The development of this model has allowed us to test hypotheses about the development of yield in peach trees and lead to greater comprehension of the processes involved. This paper will concentrate of the carbon distribution side of the problem rather than the photosynthetic assimilation research associated with the modeling effort.

THE UNDERLYING HYPOTHESES

Over the past three decades there has been a developing consensus that carbohydrate partitioning in plants is primarily driven by growth and development of individual organs (Gifford and Evans, 1981; Ho, 1989; Watson and Casper, 1984). Grossman and DeJong (1994) and Marcelis (1994) reported using this concept as the primary basis for driving carbon partitioning in crop models for peach and cucumber, respectively. The following are the guiding hypotheses for carbon partitioning that evolved in the development of the PEACH model (Grossman and DeJong, 1994).

1) A plant is a collection of semi-autonomous organs and each organ has a genetically determined, organ-specific developmental pattern that governs its growth potential.
2) The genetically determined development/growth potential of an organ is activated (or deactivated) by environmental and/or endogenous signals.
3) Once activated, organ development interacts with current environmental conditions (temperature, light, water statue, nutrients, etc.) to determine conditional organ growth capacity.
4) Realized organ growth is a consequence of conditional organ growth capacity (which may be time-limited), resource availability, and inter-organ competition for the resources.
5) Inter-organ competition for resources is a function of location relative to sources of carbohydrates, transport resistances, organ sink efficiency and organ microenvironment.

The experimental evidence and logical arguments for supporting these five guiding hypotheses have been discussed by DeJong (1999). Their adoption for crop modeling required the development of sub-models for describing the developmentally-based growth patterns of the major organs of the plant of interest, which we did for peach.

These same hypotheses allowed the development of a new computer-graphics based simulation of model of peach tree growth and productivity; L-PEACH (Allen et al., 2005, 2007; Lopez et al., 2008). In this model the location, growth and carbon budget of each organ on the whole tree is modeled individually and carbon is transported from sources to sinks as in the PEACH model.

DEVELOPMENT OF FRUIT MODEL

The most important discovery in the development of the peach fruit model was that the double-sigmoid curve used for describing the growth of peach fruits (Conners, 1919) as well as fruit respiration rates could be derived from dry weight-based relative growth rates per degree-day (DeJong and Goudriaan, 1989). Pavel and DeJong (1993), Grossman and DeJong (1995a) and DeJong and Grossman (1995) subsequently showed how fruit relative growth rate models can be used to identify and quantify source and sink limitations to fruit growth during the fruit development period. More significantly, data from thinning experiments by Grossman and DeJong (1995b) indicated that fruit growth potential generated by the relative growth rate described developmental pattern of a peach cultivar is time dependent. That is, if actual growth does not accompany growth potential over a given time interval, the growth potential is lost and cannot be regained during subsequent growth. This insight has helped us to understand source-sink dynamics of peach fruit growth (DeJong and Grossman, 1995) and has had major implications for recommendations for the timing of fruit thinning practices in commercial stone fruit production (Grossman and DeJong, 1995b). Relative growth rate-based fruit sub-models are fairly easy to establish for various cultivars and can be inserted into larger integrative crop models to simulate effects of cultivar-specific fruit growth patterns on yield (Berman et al., 1998). Such models have been used to determine whether tree nitrogen deficiency and water stress reduce fruit size by reducing fruit sink demands or photosynthate supply (Saenz et al., 1997; Berman and DeJong, 1996).

A second significant advance in the development of our peach growth model was discovering the importance of air temperature during the first month of fruit development in determining the length of the fruit development period (Ben Mimoun and DeJong, 1999). Although we could efficiently model fruit growth using relative growth rate functions based on degree-days, degree-days did not provide a good index for the fruit development period for different cultivars and years. Upon the suggestion of F.P. Marra and P. Inglese (pers. commun.), Ben Mimoun and DeJong (1999) found an excellent relationship between thermal time accumulated shortly after bloom and the length of the fruit development period for peach cultivars in California. Similar relationships were reported for peach in both Italy and California by Marra et al. (2002). This discovery coupled with the relative growth rate model of peach fruit growth has subsequently been used to explain and predict the influence of weather during the first thirty days following bloom on fruit size expectations for a given season (Lopez and DeJong, 2007; Lopez et al., 2007), as well as to create a website for alerting growers during seasons when fruit size is likely to be a problem (Lopez and DeJong, 2009).

THE SHOOT GROWTH MODEL

The original integrated PEACH model (Grossman and DeJong, 1994) was designed as a compartmental model in which the sink capacity of each organ type was modeled as a composite of similar organs for the whole tree. Thus rather than modeling individual leaf and stem growth, it was only necessary to model the general pattern of shoot growth and the influence of the crop on the canopy development. This was accomplished by establishing frequency distribution patterns for several shoot-length categories of primary and secondary stems and developing relative growth rate functions for stems and leaves growing on heavy cropped and de-fruited trees of early and late peach cultivars (Grossman and DeJong, 1994, 1995c). Subsequently, results of studies on the interactions among temperature, water status, crop load and canopy development were incorporated into a diurnal model of shoot growth as a function of temperature and water stress (Berman and DeJong, 1997a) and then extended to include the influence of fruit on the same stem (Berman and DeJong, 1997b). Even though the diurnal shoot growth model was never incorporated in the PEACH model because of the different timeframes for modeling, the diurnal shoot growth model was important for explaining the vegetative growth behavior of peach trees growing on size-controlling rootstocks (Basile et al., 2003; Solari et al., 2006a, b).

The development of the computer graphics-based L-PEACH model required an explicit model of shoot growth because each shoot had to be modeled individually. As the goal of this model was to simulate canopy growth over years and in response to carbon availability, pruning and environmental variables, it was important to be able to predict individual bud fates and how they would respond to various factors. To do this we incorporated the hidden semi-Markov chain (HSMC) methods for analyzing and modeling shoot growth that have been employed by Costes et al. (2008). Collaborations with E. Costes and her colleagues have resulted in multi-year HSMC-based shoot models that can respond to canopy location effects, carbon availability and pruning and simulate realistic peach tree canopy development (Smith et al., 2008). These shoot models incorporate sub-models that regulate elongation and girth growth, carbohydrate storage and maintenance respiration of each node of every shoot over the life of the tree (Lopez et al., 2008).

We have recently modeled water transport through the tree and changed the simulation time steps of the L-PEACH model from days to hours. Currently, we are incorporating nodal growth responses to water stress along the lines of the previous shoot model by Berman and DeJong (1997a). The HSMC shoot modeling methods are also being used to characterize differences in shoot growth and flowering behavior of trees growing on size-controlling compared to vigor-inducing rootstocks.

MODELING CARBOHYDRATE STORAGE

Carbohydrate storage and mobilization of stored carbohydrates were not explicitly modeled in the PEACH model (Grossman and DeJong, 1994) and, in line with prevailing concepts at the time (Kozslowski, 1992), the amount of stored carbon was simply assumed to be sufficient to support early season growth. Le Roux et al. (2001) pointed out the absence of explicit modeling carbohydrate storage as a common weakness of almost all plant growth simulation models. Since the original PEACH model was only used to simulate tree growth and yield over a single season the lack of explicitly modeling carbohydrate storage was a conceptual problem but had minor functional consequences for modeling tree growth during one year. However since the goal of L-PEACH was to simulate tree and fruit growth over multiple seasons, carbohydrate storage had to be more explicitly addressed. We followed the lead of Cannell and Dewar (1994) who argued that tree carbohydrate storage must be treated as an active sink. In L-PEACH temporary storage of carbohydrates can occur in leaves and long-term storage occurs in stem segments and roots (Lopez et al., 2008). The long-term carbohydrate storage in stems is modeled by assuming that stem segments and roots have finite capacities for carbohydrate storage. These capacities were estimated from the concentration of carbohydrates and weight of these organs in the late fall. In the model, carbohydrate storage in stems and roots competes with the carbohydrate demands of other sinks. The potential mobilization of carbon from these organs under normal conditions was characterized by applying treatments that require large amounts of carbohydrate to support growth (such as over-cropping) and measuring stored carbohydrate concentrations during late spring or summer. These concepts have stimulated field studies of carbohydrate storage and mobilization in mature peach trees that appear to verify that such behavior exists (Qin et al., 2009 submitted).

DISCUSSION

In this paper, we have focused attention on the use of integrated growth models as tools for examining complex hypotheses about tree growth and crop yield. Plato wrote, “Necessity is the mother of invention.” Inventions result from putting concepts into practice. The goal of modeling complex biological phenomena creates the necessity for progressively putting concepts into practice in a model and then moving on to the next issues that hinder the further development of the model. This is similar to scientific research in general, except that as the issues are addressed, the solutions can be used to further the model and provide a context for progressively addressing the next issues that are necessary to solve.

Much attention is often paid to whether a model is properly validated or is practically useful while less attention is given to whether the modeling effort provides new insights or opens new questions. The real usefulness of many modeling efforts is not the final product (model) that is produced but the things that are learned during the process. The L-PEACH model is a good example of that. With the multiple sub-models of organ behaviors and the complex computational methods for keeping track of each component and the exchange of carbon, water and information among all the parts, it is unlikely that the model will ever be completely validated with a specific set of data. For similar reasons it is unlikely that the model will ever be practically used for predicting tree growth or crop yield of a specific orchard by a grower. However we believe that it is, and will be increasingly useful for communicating and demonstrating many complexities involved in determining tree growth and yield outcomes under multiple environmental and management conditions. Numerous practical outcomes, such as better understanding of responses to fruit thinning, pruning, rootstocks, water stress, spring and summer temperatures, have already been derived from this long-term modeling project.

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