

Simulating fruit tree growth, structure, and physiology using L-systems

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Abstract

Simulation modeling of perennial fruit tree growth, structure, and physiology over multiple years is particularly difficult and has lagged behind modeling of other crops because fruit trees are indeterminate organisms that grow over several growing seasons, vary widely among individuals, and have their structures modified by variable pruning practices. Nearly 30 yr of research have been devoted to developing a mechanistic, virtual tree model to simulate peach [*Prunus persica* (L.) Batsch] fruit tree growth, structure, and physiology. Details of much of this work have been published in several research papers in a variety of journals over a couple decades. The goal of this review is to report on the entire project and provide an overview of the approach we took in such an endeavor. This review contains excerpts of numerous previously published papers and some comments and conclusions about the value of the modeling that has occurred.

1 | INTRODUCTION

Carbon balance models of plant growth have been used to identify environmental factors limiting plant growth and yield for many years (Loomis et al., 1979; Penning de Vries & van Laar, 1982). Many mechanistic models of carbon assimilation and distribution within plants have been developed, and various approaches to modeling carbon partitioning have been taken. Early models depended on the use of empirical partitioning coefficients (de Wit, 1978; van Kraalingen & Spitters, 1986), whereas some later models were based on determination of the maximum possible growth rates of each sink type (Loomis et al., 1979; Ng & Loomis, 1984; Penning de Vries & van Laar, 1982; Vos et al., 1982), an assumption of the maintenance of a functional balance between the size and activity of roots and shoots (Thornley & Johnson, 1990), and the development of transport coefficients for individual sources and sinks (Rauscher et al., 1990). Most early models were focused on annual crops whose growth could be described

in one growing season and partitioning coefficients could be developed by doing sequential destructive harvests as the crop grew.

The hypothesis that plants grow as collections of semi-autonomous, interacting organs that compete for resources (Harper, 1980; Sprugel et al., 1991; Watson & Casper, 1984; White, 1979) provided a mechanistic basis for modeling carbohydrate distribution within plants. 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 & 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 discovery that peach [*Prunus persica* (L.) Batsch] fruit growth could be modeled as a relative growth rate function (DeJong & Goudriaan, 1989) and that, using empirically defined relative growth rate patterns, the growth potential of individual fruit could be predicted at any time during

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a growing season, made it possible to model carbohydrate demands for the most economically important carbohydrate sinks of mature, fruit-bearing peach trees (Grossman & DeJong, 1994a). The potential growth of fruit, leaves, new shoots, older branches, and trunks was estimated from field experiments on very lightly cropped trees (for potential fruit growth estimations) and de-fruited trees (for potential vegetative growth estimations; Grossman & DeJong, 1995a, 1995b, 1995c).

The resulting PEACH model simulated carbohydrate partitioning based on sink strength, proximity to sources, and the quantity of carbohydrate available derived from calculations of canopy photosynthesis (Grossman & DeJong, 1994a). The sink strength of each organ was based on its estimated organ growth potential, the maximum rate at which the organ could accumulate dry matter per unit of thermal time (degree-days), which was assumed to be related to the ability to unload assimilates from the phloem (Warren Wilson, 1967, 1972; Wareing & Patrick, 1975; Wardlaw, 1990; DeJong & Grossman, 1992). The potential net sink strength (S_{NET} , g dry weight/degree day) was the product of sink size (S_{SIZE} , g dry weight) and potential sink activity ($S_{ACTIVITY}$) expressed as the relative growth rate (g dry weight/g dry weight/degree day)

$$S_{NET} = S_{SIZE} \times S_{ACTIVITY} \quad (1)$$

The estimated potential gross sink strength (S_{GROSS} , g dry weight/degree day) was the sum of the potential net sink strength and the respiratory losses of the growing organ:

$$S_{GROSS} = S_{NET} + R_g + R_m \quad (2)$$

where R_g (g dry weight/degree day) was growth respiration and R_m (g dry weight/degree day) was maintenance respiration. Respiration coefficients were derived from field measurements (Grossman & DeJong, 1994b). The sink strength of an organ could be decreased by suboptimal environmental conditions or insufficient resource availability, or both. The conditional sink strength was the rate of change determined from the potential sink strength by varying environmental conditions such as temperature and water availability, and the apparent sink strength was the rate of change determined from the conditional sink strength and resource availability (Warren Wilson, 1967, 1972; Wareing & Patrick, 1975; Ho et al., 1989; DeJong & Grossman, 1992).

The PEACH model had hierarchical priorities for distributing recently assimilated carbon. It initially distributed carbohydrates to supply the calculated respiration needs for maintaining the existing biomass at the beginning of each daily time step. Then it added up carbon required to supply the collective potential growth of fruit, leaves, shoots, and branches in a daily time step and divided the calculated available daily assimilated carbohydrate by this total demand. If the supply was greater than the calculated demand, all

Core Ideas

- Modeling tree crops is especially difficult because they are long-lived and highly variable.
- L-systems are ideally suited to deal with the complexity of tree structure and function.
- Carbon partitioning in trees can be modelled as collections of semi-autonomous organs.
- Similar processes can be used to model water relations of trees.
- Estimates of woody biomass of trees can be used to model annual dynamics of tree carbohydrate storage.

entities grew according to their potential but if the supply was less than demand, each sink type received a portion of the supply proportionate to their relative demand. Excess supply for each time step was first distributed to support potential trunk growth and any remaining carbohydrate was distributed to root growth.

Although this model performed reasonably well in demonstrating the effects of crop load on total tree yield and average fruit size, as well as some of the interactions between crop load and vegetative shoots and leaves, it was wholly unsatisfactory in realistically modeling carbohydrate distribution to roots. It also totally ignored carbohydrate distribution to long-term storage. Thus, it could also only simulate one season's growth and the model had to be initialized with data that represented a mature tree at the beginning of a growing season.

2 | INITIAL DEVELOPMENT OF THE FSPM L-PEACH MODEL

The original PEACH model almost entirely ignored interactions between tree architecture and carbon allocation (other than giving trunk and root growth lower priority for carbon allocation than crown organs such as fruit, leaves, stems, and branches). In addition, each organ type was treated collectively as a single compartment; thus, all organs of a given type (individual fruit, for example) grew at the same rate. Because of these limitations, there was no potential to simulate differences in organ size or quality as a function of location in the canopy. It was also impossible to use this model structure to simulate the function of individual organs, capture the influence of their performance on patterns of carbon distribution, or model the architectural development of trees over time. Overcoming these limitations required a more detailed model of carbon economy, in which the growth and function of organs are modeled individually within an architecturally explicit model of canopy development. This

required integration of physiological and architectural aspects of plant function which is an essential concept of virtual plants (Room et al., 1996) and functional–structural plant modeling (Perttunen et al., 1996; Le Dizès et al., 1997; Sievänen et al., 2000).

We chose to use L-systems (Lindenmayer, 1968) with subsequent extensions (Prusinkiewicz & Lindenmayer, 1990; Mech & Prusinkiewicz, 1996; Karwowski & Prusinkiewicz, 2003) to simulate the architectural growth of a peach tree, track all of its functional elements as they grew, exchange carbon between all the elements of the tree, and make the individual components sensitive to local availability of carbon and external environmental signals. The carbon source–sink interactions and carbohydrate transport within the plant were modeled using an analogy to electric circuits (Thornley & Johnson, 1990; Minchin et al., 1993; Bidet et al., 2000). The resulting system of equations describing fluxes and accumulated amounts of carbohydrates were solved numerically within the L-systems model. The underlying method was proposed by Federl and Prusinkiewicz (2004) for linear circuits and was extended for nonlinear circuits (Prusinkiewicz et al., 2007). The use of L-systems to both simulate the development of plant architecture and solve the (dynamically changing) systems of differential equations for carbon accumulation and fluxes, resulted in a conceptually clear integration of functional and structural aspects of the model.

The result of this work was L-PEACH (Allen et al., 2005), a spatially explicit three-dimensional simulation model that integrated the supply and demand concepts of carbon allocation from the PEACH model and a developmental model of tree architecture, into a distributed model of carbon allocation within a growing tree. L-PEACH was written in the L+C plant modeling language (Karwowski & Prusinkiewicz, 2003) and implemented using the 4.0 version of L-STUDIO (Prusinkiewicz, 2004).

The L-PEACH model was expressed in terms of modules that represented individual plant organs. An organ could be represented as one or more elementary sources or sinks for carbohydrates. The whole plant was modeled as a branching network of sources and sinks, connected by conductive elements. All elements of the network could have a nonlinear and time-dependent behavior.

The plant growth model was interfaced with a model of the light environment, which calculated the distribution of light in the canopy using a quasi-Monte Carlo method (Cieslak et al., 2008). This interface was implemented using the formalism of open L-systems (Mech & Prusinkiewicz, 1996). Simulation proceeded in user-defined time-steps (1-d minimum). In each step the local distribution of light in the canopy at the level of individual leaves was computed and used as a factor influencing production of carbohydrates by the leaves. The plant model was also sensitive to the amount of available water, which influenced both the production of carbohydrates

by the leaves and the uptake of carbohydrates by various sinks. In contrast to the architecturally detailed model of carbon assimilation, transport, and partitioning; tree water use and water stress were calculated at the whole-canopy level. The water demand for each individual leaf was a function of light exposure, and all the individual leaf demands were summed to determine the whole-canopy water demand. The ability of the root system to provide water was determined by root system structural biomass, the soil volume assigned to the tree, a user-defined soil moisture release curve, and a user-defined irrigation schedule. The ratio of canopy water demand and root water supply capability provided an index of the water stress in the tree at any given time; as the value of this ratio went up, the impact of water stress on tree growth and photosynthesis increased.

The L-PEACH model was developmental, with the buds producing new stem segments, leaves, fruit, etc. Each simulated growing season was initiated with a user-defined date of bud break. The growth of organs initiated during the previous season (performed) as well as the subsequent initiation of new organs (neo-formed) was influenced by the calculated amount of available carbon. If the carbon supply was insufficient for growth and/or maintenance, organs (fruits, leaves, or branches) were shed by the tree. Thus, the development and growth of the branching plant structure (topology and geometry) were closely coupled with the production and distribution of carbohydrates.

L-systems automatically coupled the tree structure with the topology and parameters of the carbohydrate supply network that represented the sources, sinks, and conductive elements. At the heart of this coupling was the notion of context sensitive L-systems (Lindenmayer, 1968; Prusinkiewicz & Lindenmayer, 1990), which provided a convenient means of capturing connections between elements of the growing structure at each stage of its development. Given this information, the L-system computed the distribution of carbohydrate, its concentrations, and fluxes at each step of the simulation. Efficient implementation of this computation was a major methodological innovation of the L-PEACH model. Within L-PEACH, the plant was modeled as a growing network comprised of elements that represented individual organs such as leaves, stem segments, fruit, buds, and roots. The behavior of each type of organ was given by a set of user-defined functions. For example, a mature leaf was characterized by its source strength which, in turn, depended on the amount of mobilizable carbohydrates that were accumulated in the leaf as a result of photosynthesis. During each time-step, these accumulated carbohydrates could flow into the various sinks within the tree (roots, fruit, etc.). Stem segments, in addition to being potential sources or sinks, acted as conduits for the fluxes throughout the tree. The magnitude of these fluxes depended on the differences in carbohydrate concentrations between sources and sinks, and the resistances of the intervening paths. All elements could exhibit

nonlinear behavior, meaning that the resistances could depend on concentrations.

In general, the network representing a growing plant had a dynamically changing structure (its topology changed over time); was nonstationary (the values of parameters associated with the various organs changed over time); and was nonlinear (the resistance associated with a given sink depended on the potential at the sink's attachment point). The L-system model "developed" and solved the set of equations defined by the network at any given point in time. The equations were solved numerically, by taking advantage of the branching topology of the network. For details concerning the algorithms and equations used to simulate growth and distribution of carbohydrates in this first version of the L-PEACH model see Allen et al. (2005) and Prusinkiewicz et al. (2007).

L-PEACH provided the ability to test and better understand the fundamental mechanisms underlying peach tree responses to specific management practices as well as environmental factors that can influence a tree through complex interactions among its organs. For example, these interactions could reflect the influence of pruning, crop load, rate of fruit maturation, and water stress on growth and carbohydrate partitioning within a fruit tree (Figure 1). The model could be manipulated by simple adjustments of parameters, such as the number of fruit set, behavior of fruit (rate of maturity), storage capacity of stems, maximum daily rates of leaf photosynthesis, branch angle, etc. before a simulation began. In addition, a simulation could be interrupted to perform pruning or fruit thinning operations and then resumed with the adjusted tree structure.

To simulate responses to water stress, the user could specify the soil volume available for root exploration and water holding capacity of the soil, an irrigation (or rainfall) interval for replenishing soil water, and the relative sensitivities of each organ type to water stress. During the simulation, water demand was calculated based on the cumulative leaf exposure to light, and the sink strength of each organ was modified in response to the developing water shortage within the plant. Thus, the differential effects of a developing water stress on root, shoot, and fruit growth, as well as on carbon assimilation and partitioning, could be simulated without any empirical rules governing allometry among plant parts. This version of the model was useful for testing hypotheses and demonstrating an integrated understanding of how fruit trees grow (DeJong et al., 2008) and produce fruit of a range of sizes in response to crop load (Lopez et al., 2008b).

3 | IMPROVING SIMULATION OF THE ARCHITECTURAL DEVELOPMENT OF PEACH TREES

Substantial improvements to the original L-PEACH model were needed to increase the realism of the simulated trees

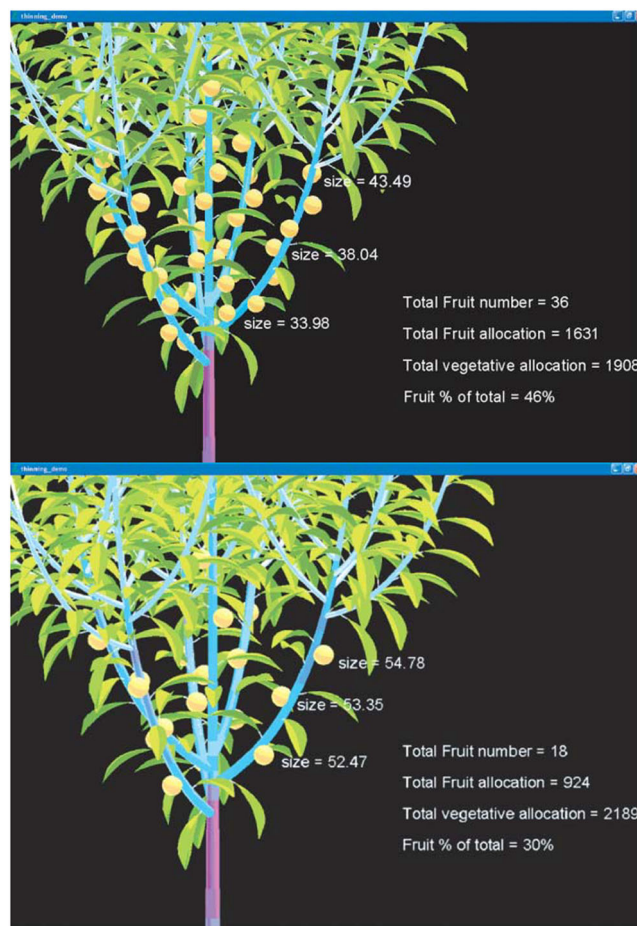


FIGURE 1 L-PEACH simulation of crop load effects on fruit and tree growth and on carbon partitioning. The upper panel shows the result of a simulation with a heavy crop load. The lower panel shows a simulation with half as many fruit. Stem colors are representative of the direction and relative magnitude of carbohydrate flow at the instant the simulation was halted (from Allen et al., 2005)

because the topology and geometry of the modelled trees (Allen et al., 2005) and the quantitative outputs generated by early versions of L-PEACH (Allen et al., 2007) did not correspond closely with observations of peach trees growing under field conditions. To develop a more realistic model of tree architecture, Markovian models of shoot topology and bud fates were incorporated into the model (Lopez et al., 2008a). A similar approach was used to simulate the architectural development of fruiting apple (*Malus domestica*) trees by incorporating Markovian models into another L-system-based architectural tree model (Renton et al., 2006; Costes et al., 2008).

This new version of L-PEACH (Lopez et al., 2008a) was implemented using the L-system-based plant simulator LPFG included in L-studio (http://www.algorithmicbotany.org/virtual_laboratory; Karwowski & Lane, 2006) combined with Markovian models (Durand et al., 2005) that were developed in V-Plants software (<http://www.sop.inria.fr/>)

[virtualplants](#); Guédon et al., 2001). Like the original model, the conceptual framework of L-systems was used to simulate carbohydrate distribution and to integrate all of the architectural elements of the plant, whereas the statistically based Markovian models were used to define patterns of vegetative and floral buds as well as the succession of shoots along an axis. The Markovian models provided probabilities for the location of branching and flowers, and the L-system-based carbon distribution model determined the amount of carbohydrate available to support the flowering and branching as the tree developed. This strategy was previously developed to insert Markovian models into the mAppleT model (Costes et al., 2008).

In L-systems, a plant is treated as a collection of semi-autonomous modules (Prusinkiewicz, 2004) and the modelled tree is described as a branching network of phytomers. Each phytomer consisted of an internode with a specified initial length and a node that had a leaf and different types of buds attached to it. The bud modules played a significant role in the tree architectural model: vegetative buds produced new phytomers which accommodated shoot growth, whereas floral buds produced flowers which accommodated reproductive growth. Buds could be terminal or axillary. Terminal buds were always vegetative. With regard to the axillary buds, each phytomer had a central axillary bud that could be either blind (failing to produce phytomers or flowers), floral or vegetative, with zero to two lateral floral axillary buds. The number and characteristics of the axillary buds, within a specific phytomer and along the parent shoot, were modelled according to bivariate statistical models estimated for three shoot types characterizing unpruned peach trees (brindles [short shoots], mixed shoots and vigorous shoots; Fournier et al., 1998) and adjusted based on observations of shoots from pruned trees. In the bivariate models, the first variable controlled the fate of the central bud, and the second variable controlled the fate of the lateral buds associated with the central bud. Branching organization was modelled by hidden semi-Markov chains that were indexed by the node rank from the base to the tip of the shoot as a succession of zones that differed in their axillary bud fates.

L-PEACH was initiated with a root and a stem segment that had a leaf, a vegetative terminal bud, a vegetative axillary bud, and an axillary latent bud that could be stimulated to produce an epicormic shoot. Simulation began with terminal bud break, and shoot growth was simulated by the creation of new phytomers. At this point the branching pattern of the tree was modelled with hidden semi-Markov chains in a two-step process: selection of the shoot type and generation of a succession of zones within each shoot, as determined by the bivariate model described above. The shoot types were categorized by their length (number of phytomers in the shoot) as small (5), medium-small (7–17), medium (16–35), long (36–56), and very long (59–87). Small shoots were assumed

to have five blind nodes. The remaining shoots had different lengths, but they all started with a blind zone and ended with floral and blind zones. Despite this similarity, shoots differed in the number of zones and the number of vegetative and flower buds. These vegetative buds could become active in the same season (syllaptic shoots), in the next growing season (proleptic shoots) or remain dormant. With regard to terminal bud fates, the potential length of the new shoots was based on the concept that succeeding shoots have less vigor than their parent shoot (Durand et al., 2005). This was modelled by a transition matrix representing a first-order Markov chain, as proposed in mAppleT (Costes et al., 2008). In addition, potential shoot length was reduced for shoots produced late in the season (Costes et al., 2007). Once the type of shoot was determined either by the Markov chain for terminal buds or the hidden semi-Markov chains for axillary buds, if there was no carbohydrate limitation the shoot grew to its full size. If there was a carbohydrate limitation, the realized length was reduced (Costes et al., 2007). Flower buds remained dormant in the season in which they were generated, and anthesis and fruit set occurred in the next season.

The architectural model was governed by calendar time for ease of relating to end users. The time parameters included dates of floral bud break, vegetative bud break, full bloom, initiation of bud dormancy in the late summer or autumn, and the start and end of leaf abscission. These parameters could be easily specified by the user and provided flexibility for simulating experiments that were conducted for model evaluation.

The use of hidden semi-Markov chain concepts for modelling branching structures in L-PEACH successfully reproduced trees that were similar to the peach trees observed in orchards (Figure 2). The improved architectural model, along with several improvements in the carbohydrate-partitioning algorithms, significantly improved the results related to carbon assimilation and respiration as well as carbohydrate distribution that supported organ growth (Figure 3). The model results were in general agreement with observations of peach trees growing under field conditions, but strict quantitative validation was lacking because of inherent variability among orchard trees and lack of detailed data from actual trees growing in the field.

4 | INTRODUCING A XYLEM CIRCUIT INTO L-PEACH

The version of L-PEACH described above did not explicitly take plant water relations into account while simulating physiological functioning or growth during a day. Water availability is a key factor governing tree development that affects growth directly and indirectly through reduced organ growth and decreased production and transport of

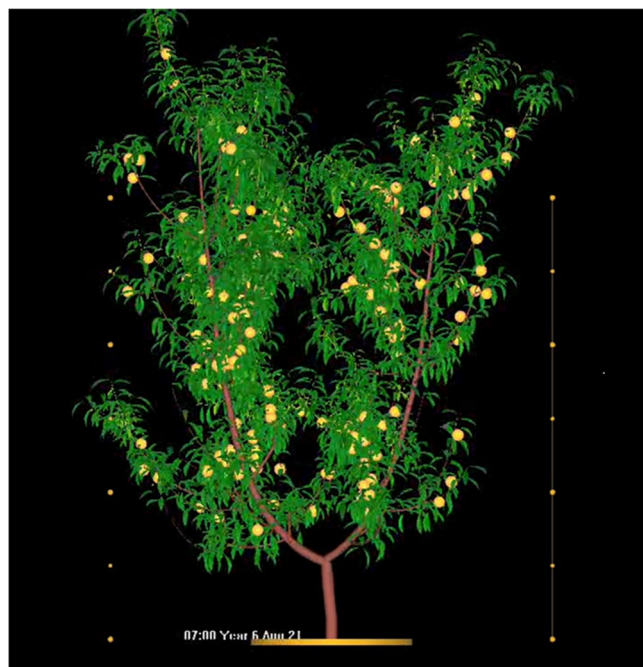


FIGURE 2 L-PEACH model virtual tree output after improvements in simulating tree architecture (Lopez et al., 2008a) showing 3D depiction of a two-leader peach tree after 6 yr of growth. The model was halted, the tree was virtually pruned each “dormant season,” and the fruit were virtually thinned each “spring” after initial fruit set

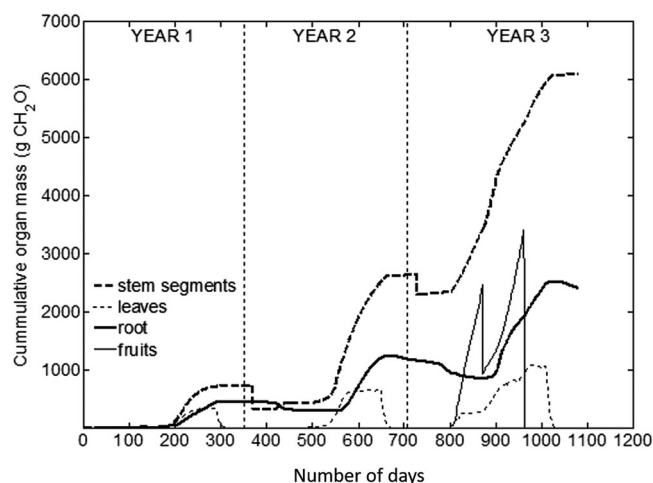


FIGURE 3 L-PEACH estimated organ mass during three consecutive years for simulated peach trees. Sudden drops in the cumulative mass of stems and fruits were the result of simulated pruning, fruit thinning, and fruit harvest (from Lopez et al., 2008a)

carbohydrates. Many physiological processes such as photosynthesis, respiration, and transpiration can be strongly influenced by environmental variables such as light, temperature, relative humidity, soil water availability, etc., that can vary dramatically during a day (Nobel, 1999). Thus, in order to realistically simulate interactions between environ-

mental inputs and physiological function, a new version of L-PEACH that had hourly time-steps (L-PEACH-h) was modified to include a xylem circuit so that the diurnal water potential of each organ could be simulated along with its physiological functioning and growth (Da Silva et al., 2011). In addition, the canopy light distribution sub-routine was simplified to speed up estimations of light extinction within the tree canopy by using a layered turbid medium approach (Da Silva et al., 2008).

In plants, water moves from soil through roots, up through the xylem circuit of the stems, and eventually evaporates from the leaves. Therefore, in addition to adding a xylem circuit, modelling water transport in a tree required simulating both water uptake from the soil and leaf transpiration; that is, modelling soil water availability and the soil–plant–atmosphere interactions (Slatyer, 1967; Thornley & Johnson, 1990). A tree growth model based on carbon partitioning coupled with water transport offered a framework for simulating water stress effects on tree growth, yield, and fruit size (Da Silva et al., 2011).

To model water transport, a natural decomposition of the tree into phytomers was used and each organ was associated with a sub-circuit for transporting water using the electrical analogy similar to the carbohydrate-allocation modelling already present in L-PEACH (Allen et al., 2005; Prusinkiewicz et al., 2007; Lopez et al., 2008a). In the water-transport electrical-circuit analogy, the xylem vessels of each organ (internodes, leaves, fruits, and root) were represented by conductances, and interfaces with the environment were represented as sources (soil interface) and sinks (atmosphere interface). Conductance, transpiration, and water availability were modelled as nonlinear functions that changed with time. Thus, water potential at each point in the circuit was evaluated by means of the fold–unfold procedure described by Prusinkiewicz et al. (2007). Using estimated water potentials, the flow of water could be computed through each organ (Figure 4). To model water transport into and through the tree, three necessary components were modelled: (a) leaf transpiration, (b) soil water availability at the soil–plant interface, and (c) the xylem circuit.

Leaf transpiration was computed by the leaf submodel implemented in the L-PEACH-h version of the model. The leaf submodel was a coupled model of instantaneous photosynthesis and transpiration based on Kim and Lieth (2003) and Collatz et al. (1991). The coupled model included submodels of photosynthesis (Farquhar et al., 1980), stomatal conductance (Ball et al., 1987), and an energy budget. The submodels were interdependent, and a nested iteration process was used to resolve their functioning. The association of the submodels allowed transpiration rates to be calculated as a function of leaf properties and environmental variables (intercepted radiation, air temperature, air relative humidity, wind speed, and leaf water potential).

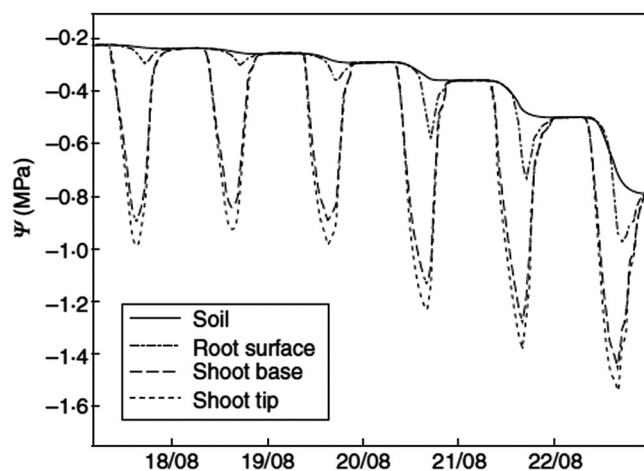


FIGURE 4 L-PEACH simulation outputs showing patterns of water potential at four locations (soil, root surface, at the base of a large shoot, and at the tip of the same shoot) over 6 d as the soil began to dry out. The difference between curves at any specific time indicates the gradient of water potential within the water transport model, from soil to the apex of a stem (from Da Silva et al., 2011)

Water availability and consequently soil water potential were directly related to the water inputs (rainfall or irrigation) and water used by the tree. Therefore, these parameters could not be simple inputs to the model but had to be estimated at each step of the simulation. This was achieved by adding a soil submodel connected to the root of the tree. The soil was modelled in a manner identical to the root, as an underground cylinder that grew with the root. The radius of the cylinder followed the radius of the canopy, whereas the depth depended on root weight and root density in the soil. This virtual growing cylinder defined a volume of soil accessible to the root. Depending on the soil, a maximum soil relative water content was an input parameter. This parameter defined the maximum quantity of water per cubic meter of soil, and consequently the maximum amount of available water. At each step of the simulation, the water transpired by the leaves was removed from the soil, thus changing the available water and the simulated relative water content of the soil.

Water depletion during a day was faster than water movement within the soil. This generated a local lack of water around the root known as the soil–root air gap (Nobel, 1999). This air gap reduced the root ability to take up water over a day and consequently induced a reduction of the root water potential. This effect was accounted for in the modeling of the soil–plant conductance at the root level. The soil hydraulic conductivity differed as a function of soil type and the air gap. Irrigation events that reset the soil water content to its maximum level were programmed to simulate irrigation scheduling either at specified time intervals or at specific thresholds of soil water availability or plant water stress. Thus,

virtual irrigation experiments could be conducted to simulate a variety of commercial irrigation practices.

The network of xylem vessels that simulated transport of water throughout the tree was represented as a network of conductances connected in series. The core of the network was composed of the conductances of the internodes (stems); the root at one end that provided the water, and the leaves at the other end that generated the driving force for water movement in the plant through transpiration. The fact that a large amount of water was present in the tree and that rehydration of plant tissues rather than leaf transpiration could act as an auxiliary driving force had to be accounted for. To do this, the xylem circuit was divided into three zones: the stems, the leaves, and the root zone.

The internode component for the xylem circuit was a conductance that accounted for the water transport capacity of each stem segment. Transpiration was computed by the leaf submodel as a function of the environment, local carbohydrate availability, and water potential; and acted as a sink in the xylem circuit. Although there can be multiple factors governing water movement through plant roots and a detailed model of root water transport would consider multiple root conductance parameters (Steudle & Peterson, 1998), we chose to use a simplified model that only specified one variable root conductance for water transport.

Water potentials simulated by the xylem circuit were linked with the carbohydrate assimilation and transport circuit in three ways: through their influence on leaf net carbon assimilation, transpiration, and individual organ growth. It is widely recognized that leaf water potential can affect leaf CO_2 assimilation directly by influencing carboxylation efficiency, or indirectly, by influencing stomatal conductance; thus, also influencing transpiration (Schulze, 1986).

In L-PEACH-h as in the original PEACH model, the potential growth rate of individual organs was determined by relative growth rate functions (RGR; Warren-Wilson, 1967, 1972; Grossman & DeJong, 1995a, 1995b). As shown by Solari et al. (2006) and Solari and DeJong (2006), decreases in water potential directly affect the RGR of individual organs. Therefore, an actual growth rate function (AGR) was defined for each type of organ as: $\text{AGR} = \text{RGR}f(C)$ where $f(C)$ was a function that decreased with a reduction in stem water potential. Similarly, $f(C)$ functions for net CO_2 assimilation and transpiration responses were adapted from the linear relationship described in Solari et al. (2006). For fruit and leaves, the value of water potential used for growth rate modification was the water potential value of the phytomer bearing an individual organ. The coupling with the carbohydrate sources (through net CO_2 assimilation) and sinks (through growth) established the phloem–xylem interactions, whereas the coupling through transpiration constituted the feedback loop necessary for auto-regulation of the xylem.

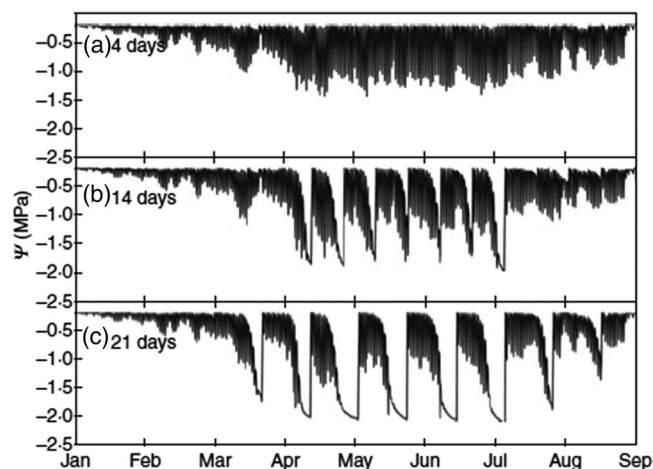


FIGURE 5 Simulated annual patterns of stem water potential at the basal leaf of a scaffold branch for trees subjected to the three different irrigation schedules: (a) every 4 d, (b) every 14 d, (c) every 21 d. Changes in diurnal patterns are clearly visible as the soil dries out between simulated irrigations (from Da Silva et al., 2011)

The L-PEACH-h model was very complex and provided useful insights into numerous interactions among environmental parameters such as diurnal and seasonal irradiance, temperature, and water availability; and physiological processes such as CO_2 assimilation, transpiration, stomatal conductance, plant water potential, and fruit and vegetative growth. Although testing the quantitative accuracy of the L-PEACH-h model was limited and validation of the model was difficult as with previous models because of the inherent structural variability among individual trees in an orchard and a lack of detailed validation data, the model provided novel opportunities for doing virtual experiments that tested concepts about how plant water stress can affect growth and productivity of peach trees (Figures 4, 5, 6). It marked a milestone in functional–structural mechanistic plant modeling of interactions between plant water relations, carbon assimilation and transport, and tree growth and productivity at the whole-plant level. Note that because the L-PEACH model simulates growth of individual fruit, it could simulate the final fruit dry weight distributions in response to differences in irrigation strategy (Figure 6).

5 | MODELING SEASONAL PATTERNS OF CARBOHYDRATE STORAGE AND MOBILIZATION

The L-PEACH-h functional–structural plant model simulated the development and growth of a peach tree's architecture and tracked all functional elements during growth and exchanges of carbon and water (Da Silva et al., 2011). This model had no set carbohydrate allocation patterns; instead, carbohydrate

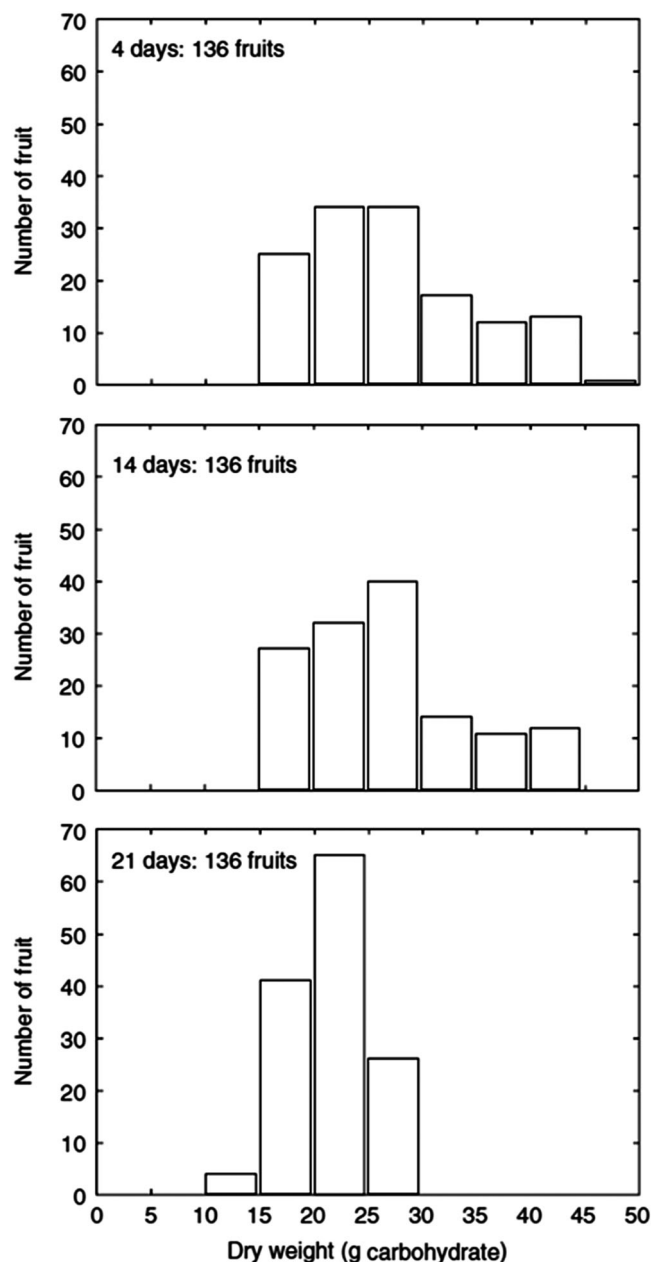


FIGURE 6 Simulated dry weight fruit size distributions on a 3-yr-old peach tree subjected to the three different irrigation treatments shown in Figure 5. Note: all simulations yielded the same number of fruit because the water stress occurred after fruit set, but simulated fruit-size distributions changed as a function of irrigation treatment (from Da Silva et al., 2011)

distribution was governed by the relative carbon demands of each carbohydrate sink, the proximity of the sinks to carbohydrate sources, and resistances along the transport pathways. Early versions of this model included the concept that carbohydrate storage is an active sink (and a source during a remobilization period in the spring; Allen et al., 2005; Lopez et al., 2008a). However, the processes involved were never explicitly implemented or validated because of lack of

understanding and quantitative information about the dynamics of this long-term storage sink and source. Treating carbohydrate storage reserves as an active sink (and a source in the spring) in a dynamic carbon distribution system required that the potential carbohydrate demand of the storage sink (and the potential source when carbohydrates are mobilized) be defined and quantified. The most important carbohydrate storage organs in deciduous trees are the major roots, trunk, and major branches (Kozlowski, 1992). Although mass fractions of carbohydrates can be greater in phloem tissue than in xylem, the relative mass of active xylem tissue is much greater than that of active phloem tissue; thus, sapwood is the primary storage tissue of large trees (Kozlowski, 1992). Furthermore, virtually all of the xylem carbohydrates capable of being stored and subsequently mobilized are stored in radial and axial xylem and phloem parenchyma (Oliveira & Priestley, 1988; Kozlowski, 1992), and the distribution of xylem parenchyma in trees is characteristic of specific taxonomic groups (Zimmermann, 1971). This means that the upper limit of long-term carbohydrate storage in a deciduous tree is mainly determined by the mass fraction of xylem parenchyma characteristic of the sapwood of that species. Thus, the storage potential of perennial tissues of deciduous trees can be quantified by determining the mass fraction of stored carbohydrates in the sapwood of a tree under conditions in which the storage sink would be expected to be saturated and by quantifying the total amount of sapwood in the tree. By the same reasoning, the potential source of xylem carbohydrates that are available for mobilization would be represented by the difference between the maximum mass fraction of carbohydrates in the bark and sapwood and the minimum mass fraction at the end of spring, under conditions when it would be expected that all available reserves have been mobilized.

A detailed analysis of nonstructural carbohydrates stored in the phloem and sapwood at different times during the year in mature, field-grown peach trees was conducted to determine the maximum and minimum mass fractions of nonstructural carbohydrates in bark and different ages of xylem tissue of the major branches and roots in late autumn and late spring, respectively (Table 1). These data were used to parameterize a carbohydrate storage submodel in the L-PEACH-h FSPM (Da Silva et al., 2014). Thus, the carbohydrate storage capacity (csc) of above- and belowground tree biomass was estimated from a weighted mean of the roots and shoots and potential (maximum), and minimum carbohydrate mass fractions measured in the field. We assumed that the potential csc of the storage sink could be estimated from the biomass of the simulated woody structures of the shoot and root and the potential total nonstructural carbohydrate mass fraction of those structures. Furthermore, we assumed that the amount of storage available for mobilization at any time could be deduced from the experimentally estimated percentage decline as the

difference between the actual storage and the product of the csc and the percentage decline.

Simulations depicting carbohydrate storage and mobilization behavior results were obtained on a virtual tree that was grown on the computer, where the potential and minimal total nonstructural carbohydrate mass fractions were set according to the values measured in field-grown trees. The model successfully simulated storage accumulation and remobilization under orchard conditions over five simulated growing seasons (Da Silva et al., 2014). The simulation of shoot storage behavior was somewhat better than the behavior of the root, which probably reflects the fact that the development of the L-PEACH model has concentrated on simulating shoot growth much more than root growth; this was a recognized limitation of the model.

The addition of the carbohydrate storage submodel to the L-PEACH-h model represented a conceptually simple approach to modelling carbohydrate storage and mobilization in trees but did require collection of substantial amounts of field data. The data set used in the study (Table 1) was rather limited and more accurate results could probably have been obtained if more frequent carbohydrate sampling had been done in an accompanying field experiment.

The empirical and modelling results of this study were consistent with the concept of active carbohydrate reserve sinks and sources proposed by Cannell and Dewar (1994). The modelling approach used provided a path forward for understanding and modelling annual carbohydrate storage behavior in trees and addressed a major limitation of almost all previous perennial plant models identified by Le Roux et al. (2001).

6 | CONVERSION OF L-PEACH INTO AN L-ALMOND MODEL

The most recent development in the L-PEACH modeling project was to convert the model into an L-ALMOND model (DeJong et al., 2017) to demonstrate the utility of the approaches used in functional-structural modeling of peach trees for modeling other tree species. Because almond [*Prunus dulcis* Mill. (D.A. Webb)] is a close relative of peach (Martínez-Gómez et al., 2007), the same overall structure of the L-PEACH model was used to construct an L-ALMOND model. The modular nature of the L-PEACH model allowed the parameters of the submodels to be simply adjusted for factors such as leaf characteristics (size, specific leaf weight, leaf photosynthesis characteristics), potential fruit growth rates over the season and seasonal phenology (bloom date, leaf-out date, beginning of leaf drop and dormancy). When possible, parameters from an earlier ALMOND model (Esparza et al., 1999) that was an adaptation of the original PEACH model, were used for this transition. Otherwise, the data used

TABLE 1 Mean (\pm standard error) nonstructural carbohydrate mass fractions (% dry weight) for inner bark and 1-, 3- and 5-yr xylem rings of root crown and trunk tissues of peach trees prior to bud-break (March) and at the sampling date when the minimum over all treatments was measured (June or August), and percentage decline in mass fraction between the two sampling dates (from Da Silva et al., 2014)

	March	Minimum	Decline
	% dry weight		%
Scion			
Bark	12.43 \pm 0.62b	8.37 \pm 0.67ab	32.66
Year 1	7.33 \pm 0.60c	4.53 \pm 0.61 cd	38.20
Year 3	7.93 \pm 0.33c	3.97 \pm 0.19 cd	49.94
Year 5	7.80 \pm 0.17c	3.47 \pm 0.14d	55.51
Root			
Bark	15.90 \pm 0.51a	10.33 \pm 0.38a	35.03
Year 1	13.30 \pm 0.62ab	6.60 \pm 0.92bc	50.38
Year 3	12.17 \pm 0.85b	6.63 \pm 0.52bc	45.52
Year 5	11.40 \pm 0.62b	6.40 \pm 0.46bc	43.86

Note. Within a column, values not sharing a common letter are significantly different ($P < .01$).

came from more recent studies on almond (Basile et al., 2003; Lampinen et al., 2011). Because the architectural growth in the L-PEACH model relied on statistically based Hidden semi-Markov Chain models of bud fates on different types of shoots, detailed field studies of shoot architecture and bud fates of almond trees were carried out to develop a series of submodels for various types of almond shoots (Negron et al., 2013). Once obtained, these almond-shoot architectural submodels were used to replace the peach shoot submodels (Lopez et al., 2018b).

A more difficult problem encountered when converting the L-PEACH model to L-ALMOND was the incorporation of a more robust canopy light distribution subroutine into the model that could be used to drive shade-dependent shoot and spur mortality in the denser areas of the simulated tree canopies. This was not a problem in the previous L-PEACH simulations because, when running simulations in L-PEACH, the trees were always heavily pruned during each year of simulation to mimic what is traditionally done in commercial peach orchards. Thus, there was no need to program shoot death to run realistic simulations. However, in California, almond trees are rarely pruned after the second or third year in the orchard and even then, pruning is much lighter than with peaches. This leads to much natural small shoot mortality in the most shaded portions of the canopy. Therefore, we attempted to simulate shade-dependent shoot death based on field studies of spur mortality (Lampinen et al., 2011). This required a more robust canopy light distribution subroutine than the rather simple estimation of light extinction using the layered turbid medium approach used in later versions of L-PEACH (Da Silva et al., 2011). To do this we incorporated a shadow propagation method to compute a course estimate of the exposure of each bud to light (Palubicki et al., 2009) and then used a combination of field data and visual evaluation to determine

appropriate levels of shading that caused shade induced shoot and spur mortality.

The L-ALMOND model provided a reasonable simulation of the architectural tree growth, seasonal patterns of accumulated photosynthesis and respiration, accumulation of stem segments (internodes) and their dry weight, as well as general patterns of tree productivity. The total accumulated stem biomass in carbohydrate equivalents per tree in simulated trees growing without water or nutrient stress were very similar to the total harvested biomass of almond trees growing under field conditions in the southern San Joaquin Valley of California. Simulated fruit yields and number of nuts per tree were also similar to what would be expected for comparable aged trees in the field (DeJong et al., 2017).

This project successfully created a working version of an L-ALMOND model that appeared to function fairly satisfactorily, and thus verified the utility of the modeling approach used in the L-PEACH model for simulating other fruit tree species. Subsequent research demonstrated that the L-ALMOND model that was originally developed to simulate growth of 'Nonpareil' trees could be relatively easily modified to simulate the architectural growth of other cultivars with distinctly different growth habits (Figure 7; Lopez et al., 2018b).

7 | DISCUSSION

There is no better way to test one's understanding of how something is put together and functions than to try to build that object. That is the challenge that this mechanistic functional-structural plant modeling effort attempted to resolve. The L-PEACH and L-ALMOND modeling efforts attempted to build virtual functional tree models that represented what

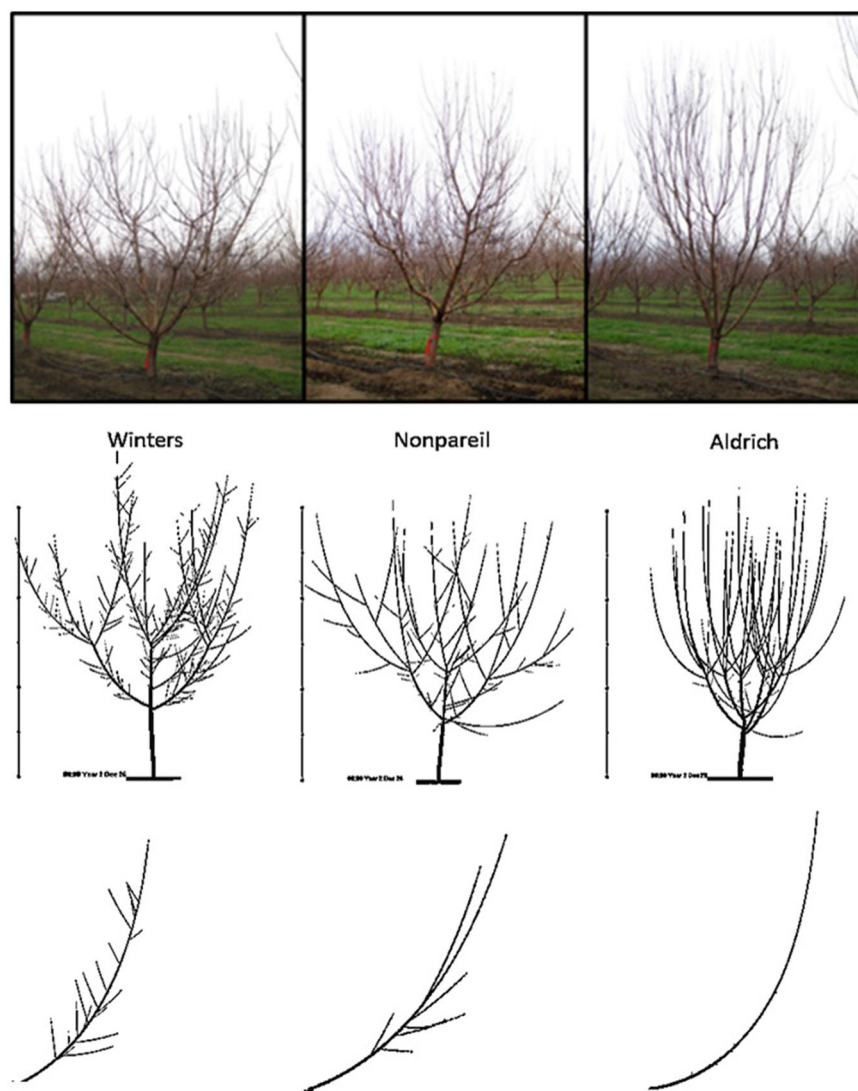


FIGURE 7 L-ALMOND simulations of the tree structures of three different almond cultivars resulting from the characteristic branching habits of the cultivars, compared with pictures of actual trees in the field (from Lopez et al., 2018b)

trees do in the field. An additional model derived from the modelling approaches used in L-PEACH (and its resistance-based carbon allocation model) was the development of a functional-structural kiwifruit (*Actinidia chinensis* Planch.) vine model that integrated architecture, carbon dynamics, and environmental responses (Cieslak et al., 2011). Although the resulting models are still lacking in some areas, the modeling process provided valuable insights into key areas where knowledge was lacking for turning static physiological models presented in textbooks into dynamic functional models that operate through virtual time and space. Overall, these modeling efforts were successful in providing approaches to understanding and implementing many such connections, but they are still fairly rudimentary. There are still many aspects of the models that could be improved upon or added to.

The current models do not have effective methods for modeling the onset of tree dormancy or the initiation of anthesis

and regrowth in the spring. Recent research by Sperling et al. (2019) may provide a way forward on this topic that could tie into the carbohydrate storage submodels described for L-PEACH. Adapting the models to better simulate the onset of bloom and tree growth in the spring based on weather patterns would enhance the capacity of the models to simulate the effect of climate change (warmer winters) on seasonal tree growth and potential productivity.

Another interesting aspect of modeling tree growth is that there is very little understanding of something as fundamental as what factors drive the rate of the addition of new nodes on a shoot (the plastochron) in trees. Models of annual crops often assume that the plastochron is primarily driven by temperature (Dennett et al., 1978), but recent research indicates that the plastochron of peach tree shoots varies by shoot type, carbohydrate availability, and season (Davidson et al., 2017, 2019). The significance of understanding what drives the

plastochron in the tree becomes very apparent when attempting to build functional–structural plant models like L-PEACH and L-ALMOND.

Another potentially interesting addition to this modeling effort would be modeling the uptake and distribution of nitrogen and perhaps other nutrients in trees. In an earlier effort, the PEACH model was used to describe the seasonal dynamics of nitrogen in peach trees (Rufat & DeJong, 2001). The addition of a nitrogen submodel in L-PEACH or L-ALMOND could improve insights into dynamic interactions of nitrogen status with carbon assimilation and growth in trees beyond what is known from static studies (DeJong & Doyle, 1985; DeJong et al., 1989; Rosati et al., 2000). Better understanding of the dynamics of nitrogen uptake and distribution in fruit trees is critical to efficient management of nitrogen fertilizers and increasing sustainability of fruit production (Muhammad et al., 2018). Because L-PEACH-h simulates water uptake and flow through a tree, the model may also be useful in simulating movement of xylem mobile nutrients through trees.

One drawback of the detailed functional–structural plant modeling approach used in these studies is that the resulting models are so complex that they have limited value for direct application in providing guidance for farm management. Rather, the value of these types of models is to refine and test understanding about how plants function and then this understanding can be used to provide concepts that guide grower practice and identify research targets for genetic improvements.

This modeling project clarified some of the major differences between modeling annual crops and perennial fruit crops. It is possible to fairly accurately model seasonal growth patterns and yields of many annual crop species because seeds of annual species are planted in the field and their crop development is highly dependent on field environmental conditions that can be readily monitored. Furthermore, plant-to-plant variability is minimal if the crop is well managed. The crop initially grows and then flowers during a period when temperatures are relatively stable and thus the amount of crop is fairly predictable. In contrast, temperate deciduous tree crops are managed so that there are no two trees in a field that are exactly alike and the trees bloom and set a crop early in the spring when temperatures and other environmental factors are highly variable, making fruit set very difficult to predict. Thus, the best that can be hoped for in modeling these tree crops at present is simulating potential yields under specific sets of parameters. A complete understanding of the precise factors that determine and/or limit fruit set in temperate deciduous fruit trees is a major limiting factor for accurate yield predictions derived from these types of models.

However, these models are still very valuable for identifying key factors that can limit potential yields and indicating

how different management practices such as pruning (DeJong et al., 2012; Lopez et al., 2018a) and fruit thinning (Lopez et al., 2008b) affect tree performance. They have also been used to identify why the effects of breeding for early harvested varieties (Berman et al., 1998) and warmer spring weather (Lopez et al., 2011) tend to decrease yields. In addition, they have provided a means for testing how differences in xylem anatomy of rootstocks can influence the vigor of scions grafted on various rootstocks (Da Silva et al., 2015; Basile & DeJong, 2019).

An additional benefit of embarking on a wholistic plant modeling project that attempts to mechanistically integrate numerous processes forces one to identify and collect data on processes that have not been thoroughly investigated. Thus, it can provide novel questions and avenues for research. Some examples of this are the following: patterns of fruit growth and respiration (DeJong & Goudriaan, 1989; Grossman & DeJong, 1995a, 1995b), importance of fruit photosynthesis (Pavel & DeJong, 1993a, 1993b), vegetative organ respiration and growth potentials (Grossman & DeJong, 1994b, 1995c), water stress and cropping effects on shoot (Berman & DeJong, 1997) and fruit growth (Berman & DeJong, 1996), and distinguishing the characteristics of specific shoot types (Gordon et al., 2006a, 2006b; Gordon & DeJong, 2007; Negron et al., 2013; Prats-Llinàs et al., 2019).

It is often assumed that the primary goal of plant and crop modeling is to predict crop yields but that should not be the goal of structural–functional tree models like L-PEACH. Their most valuable contribution is to provide a dynamic tool to develop and test understanding of how trees develop and function. This understanding can be used to manage and genetically improve trees overall. Such models could be invaluable to plant breeders, plant genetic engineers and molecular biologists who are searching for “the quantitative trait locus” that will make quantum improvements in their crop of choice.

An unforeseen outcome of this long-term modeling project was the simultaneous development and virtual testing of a set of fundamental concepts for understanding how fruit trees function and grow (DeJong, 2022). These concepts can be useful for future modeling research as well as horticultural management of fruit crops.

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AUTHOR CONTRIBUTIONS

Theodore DeJong: Conceptualization; Data curation; Formal analysis; Funding acquisition; Investigation; Methodology; Project administration; Resources; Software; Supervision; Validation; Visualization; Writing – original draft; Writing – review & editing.

CONFLICT OF INTEREST

The authors report no conflict of interest.

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