Demonstrative simulations of L-PEACH: a computer-based model to understand how peach trees grow

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Abstract

L-PEACH is a computer-based model that simulates the distribution of light in the peach canopy as the tree grows and carbohydrate assimilation of each leaf. The model integrates important concepts to simulate water and carbon transport within the tree with real environmental input data collected from weather stations. Tree architecture is based on developmental principles governing tree growth and detailed measurements of shoots of peach trees. While running L-PEACH, realistic three-dimensional depictions of simulated growing trees can be displayed on the computer screen for visualization of tree architecture. The L-PEACH model has been widely reported in the literature along with quantitative data generated during simulations. However, demonstrative simulations were never disseminated to the scientific community and they are an essential component for understanding the model and demonstrating principles of tree growth. Along with the modeling work several movies with demonstrative simulations of L-PEACH have been made public in a scientific repository to complement existing references. Demonstrative simulations are related with overall tree growth and the movement of carbon within the tree, detailed growth of leaves and fruit and responses of tree growth to pruning intensity, drought and size-controlling rootstocks. In this work each demonstrative simulation will be accompanied by a physiological and/or horticultural description to demonstrate the value of L-PEACH to study, understand and teach how trees grow.

Keywords: computer simulations, modeling, *Prunus persica*, source-sink relationships, tree growth

INTRODUCTION

L-PEACH is a computer-based model that simulates source-sink interactions, architecture and physiology of peach trees (Allen et al., 2005, 2006, 2007). The model integrates important concepts related to water transport and carbon assimilation, distribution, and use within the tree (DeJong et al., 2011). L-PEACH is able to simulate crop yield responses to commercial practices such as fruit thinning (Lopez et al., 2008a) and pruning (Smith et al., 2008) and can be useful for making fruit growers understand how to optimize these operations. The L-PEACH model has been widely reported in the literature along with quantitative data generated during simulations (Lopez et al., 2008b, 2010; Da Silva et al., 2011). However, demonstrative simulations were never disseminated to the scientific community and they are an essential component for understanding the model and demonstrating principles of tree growth. Several movies with demonstrative simulations of L-PEACH have been made public in a scientific repository by Lopez et al. (2016) and the simulations can be downloaded for visualization using the following link: http://dx.doi.org/10.5281/zenodo.47228.

Selected simulations are related with overall tree growth, the movement of carbon within the tree, detailed growth of leaves and fruit and responses of tree growth to pruning intensity, drought and size-controlling rootstocks. The objective of this work is to provide a detailed description of relevant physiological mechanisms behind each simulation to demonstrate the value of crop modelling to study, understand and teach how trees grow.

TREE GROWTH: INTERACTIONS BETWEEN CARBON ALLOCATION AND TREE ARCHITECTURE

L-PEACH was designed as a functional-structural plant model to simulate carbohydrate assimilation and partitioning within the architectural framework of a peach tree. The model was implemented using the L-system-based plant simulator LPFG included in L-studio (http://www.algorithmicbotany.org/virtual_laboratory). The conceptual framework of L-systems was used to simulate carbohydrate allocation and to integrate all of the architectural elements of the plant. The partitioning of carbohydrates between individual tree components was modeled using an analogy between the flow of resources in a plant and the flow of current in an electric circuit in combination with multiple algorithms that define the physiological functionality of various types of sources and sinks and their interactions (Lopez et al., 2008a, b). Statistically-based Hidden semi-Markov Chain models of bud fates on different types of shoots were used to define patterns of vegetative and floral buds and the succession of shoots along an axis (Costes et al., 2006). The result of the combination of carbon allocation and architectural concepts can be observed when a simulation with L-PEACH is performed over multiple years. This corresponds with the first simulation presented in Lopez et al. (2016) with a version of L-PEACH that runs on a daily time-step (L-PEACH-d) (Lopez et al., 2008a, b, 2010) (Figure 1).

Figure 1. Demonstrative simulations of a tree over three years of growth (simulation 1), detailed section of the tree to observe the realism of individual organ growth (simulation 2), and example of how to prune a tree to a v system (simulation 3) using L-PEACH can be visualized at http://dx.doi.org/10.5281/zenodo.47228.

The simulation shows the growth of a peach tree over three years. In this simulation L-PEACH is initiated with a root and a stem segment that has a leaf. The stem segment has also a vegetative terminal bud, a vegetative axillary bud and an axillary latent bud. The simulation begins with terminal bud break, and shoot growth is simulated by the creation of new phytomers. At this point the branching pattern of the tree is modelled with hidden semi-Markov chains in a two-step process: selection of the shoot type and generation of a succession of zones with different characteristics within each shoot (Lopez et al., 2008a, b). During the first year of tree growth, grafting was simulated by cutting the tree back in early spring and allowing the tree to grow again as it would in a tree nursery. After this first year the tree is cut back to a single trunk in the same manner as is commonly done when a peach tree is transplanted from a tree nursery to a commercial fruit orchard. The simulation was stopped during the dormant season between years and the tree was pruned by the model operator in a manner that is similar to how trees would be pruned when growing in an orchard. Once the type of shoot is determined by the Markov chain, if there is no carbohydrate limitation the shoot will grow to its full size. If there is a carbohydrate limitation, the realized length will be reduced. As can be observed during the first simulation, L-PEACH allows the observation of the movement of carbohydrates within the tree. The color of the stem indicates the direction of the movement of carbon within the tree (white indicates no flux of carbon, increasing apical flux of carbon from light yellow to red, and increasing basal flux of carbon from light blue to deep purple) (see details of colors in

Allen et al., 2005). The combination of carbon allocation and the use of hidden semi-Markov chain concepts for modelling branching structures in L-PEACH is an efficient strategy for successfully reproducing trees that are similar to the peach trees observed in orchards and to facilitate the study of their physiology.

INDIVIDUAL ORGAN GROWTH

One of the most important features of the L-PEACH model is that each leaf, stem segment, and fruit is treated individually within the tree. This follows the concept that carbohydrate distribution and the growth of trees is primarily controlled by the behavior of individual organs and not vice versa (DeJong, 1999). In L-PEACH, leaves are programmed to perform net photosynthesis and to assimilate carbohydrates that are then used by the tree. Thus the collective light exposure of each leaf is the main driver of the plant development. The carbohydrates gained by leaves through photosynthesis are first stored in the leaf. Some of these carbohydrates remain in the leaf, simulating starch accumulation. The remainder is used by the leaf for its growth or is exported to other parts of the tree. From the time of leaf emergence to the time at which the leaf reaches its final size, the gained carbohydrates are used primarily to build the young leaf. Afterwards, the leaf is a net source of carbohydrates, which are exported from the leaf. Carbohydrates assimilated by the leaf are also used for leaf maintenance respiration, which has been programmed to respond to temperature using previously determined leaf-specific respiration rates. Stem segments (internodes) act as conduits for carbohydrate transport within the tree and require significant amounts of carbohydrates for elongation growth, girth growth, storage and maintenance respiration. For most of the growing season the stem segments act as sinks competing for carbon with other growing organs. However, at floral bud break, carbohydrate from storage in the overwintering structures is mobilized and exported to other parts of the tree to support initial leaf and fruit growth before current carbohydrates from photosynthesis can support total tree carbohydrate demand. Fruit growth is programmed following seasonal fruit relative growth rates, as a function of accumulated degree-days after full bloom. The relative growth rate functions provide the growth potential of fruit for each time interval and interact with the amount of carbohydrates available for fruit growth over specific intervals to generate realized fruit growth over time. The second simulation presented in Lopez et al. (2016) corresponds with a detailed section of the tree to better appreciate the realism of leaves, stem segments, and fruit growth and the variability among organ growth (Figure 1). The simulation of the variability in growth of individual organs was only possible because of the capacity of the L-PEACH model to simulate processes at the organ scale as a function of local environment and resource availability, which is a unique feature of this model.

INTERACTION WITH THE MODEL: PRUNING

As L-PEACH developed the necessity to simulate management operations typically conducted in the field became evident. Pruning is one of the most important horticultural practices in peach trees because it defines the training system of the tree with many implications in tree performance and productivity. One of the most important features of the L-PEACH model is that users can interact with the model to prune the tree. Pruning is carried out by directly manipulating the tree displayed on the screen with the LPFG plant modeling program. Tree responses to pruning are modelled using the concepts of apical dominance and reiteration described in Smith et al. (2008) and Lopez et al. (2008a, b). When a pruning cut is made, the fates of the buds between the cut and the next branching point are reassigned. Following reiteration concepts, if axillary vegetative buds are present, the distal buds are assigned to the same shoot category as the shoot that has been removed. Following the apical control concept, only a few axillary buds become active, while the rest remain latent. This follows the idea that the distal buds are no longer under apical dominance, but as they emerge they have a dominance effect on the more proximal buds. The number of activated buds is determined by the stem segment circumference below the pruning cut. If only axillary latent buds are present, then the distal latent buds become active and develop very-long shoots. In any case, if the pruning cut is made during the growing season, the distal buds become active immediately. If pruning is done during the dormant period, the distal buds become active at vegetative bud break. In the third simulation presented by Lopez et al. (2016) a peach tree was pruned to a V-system and it is possible to observe all the necessary pruning cuts (Figure 1). In the simulation the trunk of the tree was cut to half a meter prior to the beginning of the second year. This cut prompted a reiteration response, resulting in the production of new very-long shoots below the cut after bud break. This new shoot growth compensated for the perturbed equilibrium between the shoot and the root after the pruning cut. This response is the key to eventually developing the strong, open structure of commercial peach trees. The rest of the pruning cuts are performed to remove undesirable waterspouts and to avoid an excessive number of fruiting shoots within the tree as is often done with trees in the field.

MOVEMENT OF WATER WITHIN THE TREE: THE EFFECT OF WATER STRESS ON TREE GROWTH

Initial versions of the L-PEACH model simulated tree growth assuming that water was not limiting. However, peach orchards can be exposed to multiple environmental stresses including water stress. In order to simulate the effects of water stress in L-PEACH, a xylem circuit was included into the model that can simulate the diurnal patterns of water potential of each organ along with its physiological functioning and growth (Da Silva et al., 2011). Sub-models for leaf transpiration, soil water potential and the soil-plant interface were also incorporated to provide the driving force and pathway for water flow within the modeled tree (Da Silva et al., 2011). The result was a new version of the model that runs on an hourly time-step (L-PEACH-h). In the fourth simulation presented by Lopez et al. (2016) it is possible to observe the effect of different irrigation treatments (normal irrigation and modest drought) on tree development and growth by using L-PEACH-h (Figure 2). In the simulation water stress causes a gradual growth reduction as a function of induced water-stress for all organs in comparison with control trees. Trees grown under water stress conditions have fewer leaves and stems and their size is smaller than the tree grown under control conditions. The effect of water stress on fruit size can be also observed at the time of fruit harvest when all the fruit drop to the ground in the simulation. With the addition of the modelling of water transport, the L-PEACH-h model increased its capability to understand the complex relationships between the physiological processes and the environmental factors that govern fruit tree growth and development and also to identify gaps in current knowledge such as the effects of drought on shoot structure that need further investigation.

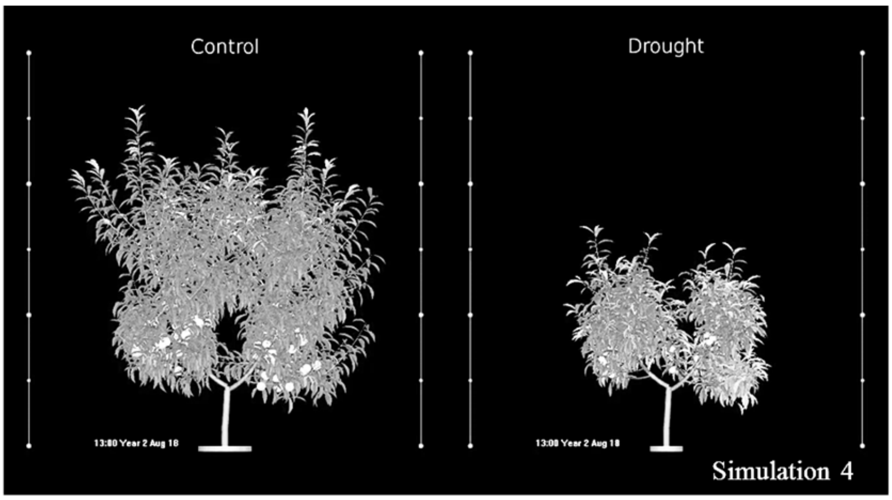

Figure 2. Demonstrative simulation of a tree grown under control and drought conditions with L-PEACH (simulation 4) can be visualized at http://dx.doi.org/10.5281/zenodo.47228.

RESPONSES TO SEVERITY OF PRUNING

The L-PEACH-h model was also used to illustrate the effect of severity of pruning in tree growth as can be observed in the fifth simulation presented by Lopez et al. (2016) (Figure 3). In this simulation three levels of pruning were tested: soft, control, and hard. The simulation indicates how trees that received hard pruning are able to recover a tree size similar to the control and soft pruned trees due to the generation of many vigorous shoots (epicormic shoots) in response to hard pruning (DeJong et al., 2012).

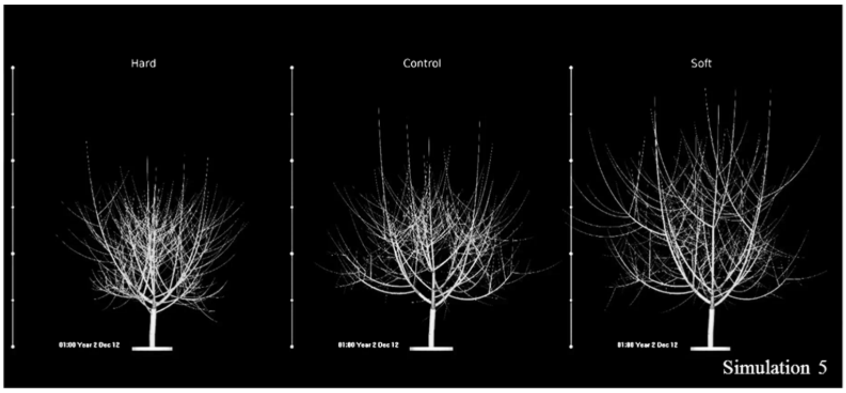

Figure 3. Demonstrative simulation of the responses of tree growth to different levels of pruning (hard, control, soft) with L-PEACH (simulation 5) can be visualized at http://dx.doi.org/10.5281/zenodo.47228.

THE EFFECT OF SIZE CONTROLLING ROOTSTOCK

The sixth simulation presented by Lopez et al. (2016) was generated to demonstrate that L-PEACH-h can be also used to simulate the effect of size-controlling rootstock in tree growth (Da Silva et al., 2015) (Figure 4). In the simulation tree growth with a standard rootstock (Control) and a size controlling rootstock (Rootstock) were modeled by adjusting rootstock hydraulic conductance. In a normal simulated tree, the hydraulic conductance values, assigned to both the "scion" and the "rootstock", are the same. In order to simulate the size controlling effect of a dwarfing rootstock, on tree growth and water relations, the hydraulic conductance of the "rootstock" piece, at the base of the trunk was reduced to simulate a reduction in vessel diameters and their density documented in size-controlling rootstock (Tombesi et al., 2010). The resulting reduction, in hydraulic conductance, was approximately 50%. After four years of simulated growth, the virtual tree on the dwarfing rootstock was substantially smaller than the virtual tree on the control rootstock.

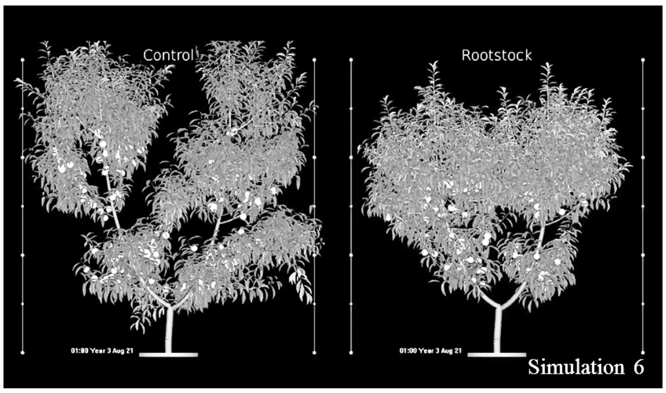

Figure 4. Demonstrative simulation of the effect of size controlling rootstock with L-PEACH (simulation 6) can be visualized at http://dx.doi.org/10.5281/zenodo.47228.

DISCUSSION

In this study several demonstrative simulations of L-PEACH were complemented with a physiological and/or horticultural explanation. The 3-D graphical representations associated with the model makes L-PEACH a highly educational tool for students as well as for growers. The simulations are based on real environmental input data (light, temperature, day length, etc., collected from a real weather station located near a peach orchard) and development of tree architecture is based on developmental principles governing tree growth and detailed measurements of shoots of peach trees. While a model like L-PEACH can always be improved to include more features and be made more accurate, these simulations serve to demonstrate the potential of computer simulation modeling to increase understanding of the dynamics of tree growth and responses of fruit trees to management practices.

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