Using Computer Technology to Study, Understand and Teach How Trees Grow

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Abstract

Studying and understanding fruit tree growth and development is a difficult endeavor. Plants are very complex organisms that are governed and influenced by a multitude of factors. In the past our ability to study and integrate plant function has been largely limited to only dealing with a couple factors at a time and communicating those interactions verbally or with two dimensional diagrams. The subject of studying and understanding carbon partitioning in plants is a good example of this limitation. Modeling carbon partitioning is a complex problem because of the dynamic nature and relationships between carbohydrate partitioning, growth and plant architecture. Until recently there have been no fruit tree simulation models that have attempted to quantitatively model these three processes simultaneously. The L-PEACH model is an attempt to develop a detailed model of tree carbon economy in which growth and function of each organ is modeled individually within an architecturally explicit model of canopy growth. L-PEACH combines the supply/demand concepts of carbon allocation of the previous PEACH model with an L-systems model of tree architecture to create a distributed supply/demand system of carbon allocation in a three dimensional, growing tree. The L-PEACH plant model is expressed in terms of modules that represent plant organs. An organ is represented as one or more elementary sources or sinks for carbohydrates and the whole plant is modeled as a branching network of these sources and sinks, connected by conductive elements. An analogy to an electrical network is used to calculate the flow and partitioning of carbohydrates between the individual components. The model can be used to simulate how crop load, rate of fruit maturity, storage tissue sink capacity, and/or water stress can influence growth and carbohydrate partitioning within a fruit tree.

INTRODUCTION

If someone asked you how trees grow, how would you respond? You might be able to describe how most of the individual organ of a tree work but could you explain how all of the parts of a tree fit together, and are integrated to explain overall tree growth and development? Until recently, attempts to develop systematic approaches to studying, understanding and demonstrating complex physiological and architectural interactions involved in plant growth responses to environmental conditions and horticultural management practices have been largely limited to movie pictures, verbal descriptions, and static two- or three-dimensional displays of pictures or experimental data. An alternative approach is now possible. Recent developments in three-dimensional computer graphics programming have lead to an explosion of possibilities regarding the application of this new technology for studying, modeling and communicating complex plant growth responses in three-dimensional space. Thus, a new field of science has been emerging that is loosely termed functional-structural plant modeling (Godin and Sinoquet, 2005). One approach to using this new technology is by taking multiple sets of experimental data on plant growth and responses to the environment, and integrating all of these data into a complex, virtual plant model with results displayed graphically in three dimensions (Durand et al., 2005). An alternative approach is to start with a set of scientific concepts about how trees grow and respond to their environment, and then try to reconstruct a model tree based on those concepts using whatever empirical data and information are available to parameterize the model. We took the latter approach in constructing the L-PEACH model (Allen et al., 2005).

The central focus of building L-PEACH was to model how carbon partitioning occurs in a growing tree. Carbohydrate partitioning has been a central problem of process-based models of tree growth because of the coupling between carbon partitioning, growth and architecture (Le Roux et al., 2001). PEACH (Grossman and DeJong, 1994) was a sink-driven, compartmental carbohydrate partitioning model for simulating reproductive and vegetative growth of fruit trees. Carbon partitioning in that model was based on the concept that a tree grows as a collection of semi-autonomous but interacting sinks (organs). These organs compete for resources. Organs of the same type were clustered into composite compartments, such as: leaves, fruit, stems, trunk and roots. Carbon was allocated to compartments depending on their competitive ability with respect to other compartments. Biomass growth was dependent on an experimentally derived growth potential for each organ type at specific phenological stages of development. This growth potential or potential carbon demand was quantified as the "genetic" potential growth rate of a sink. Growth potentials were experimentally approximated by determining the maximum growth rate of individual organ types growing under conditions where competition from other sinks was minimized (Grossman and DeJong, 1995a, b, c; DeJong and Grossman, 1995). This approach made it possible to avoid empirical allocation coefficients, functional balance rules, and allometric relationships that were common to most other tree models at the time (Lacointe, 2000). However, as pointed out by Le Roux et al. (2001), the PEACH model almost entirely ignored the interaction 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, and thus all organs of the same type grew at the average rate for that organ. 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, and capture the influence of their performance on patterns of carbon partitioning. Many of these limitations were possible to overcome with the development of L-systems (Lindenmayer, 1968; Prusinkiewicz and Lindemayer, 1990) as implemented in the latest version (4.0) of L-studio (Karwowski and Prusinkiewicz, 2003; Prusinkiewicz, 2004). This new software enabled the development of a more detailed model of carbon economy, in which growth and function of each organ could be modeled individually within an architecturally explicit model of canopy growth. This resulted in the development of the L-PEACH model.

METHODS

As stated previously we did not initiate the development of L-PEACH from the standpoint of what data we had but by formulating hypotheses about how trees work. We were particularly focused on how carbon partitioning might be integrated among organs within a whole plant framework without imposing artificial algorithms or partitioning coefficients on the process.

Model Structure

The L-PEACH plant model is expressed in terms of modules that represent plant organs (Allen et al., 2005). An organ may be represented as one or more elementary sources or sinks of carbohydrates. The whole plant is modeled as a branching network of these sources and sinks, connected by conductive elements. An analogy to an electric network is used to calculate the flow and partitioning of carbohydrates between the individual components. In this analogy, the total amount of carbon corresponds to an electric charge, carbon concentration to electric potential, and carbon fluxes to current flow. Daily photosynthesis of individual leaves is represented as an accumulation of charge. In general, all elements of the network may have a non-linear and time-dependent behavior.

The plant model is interfaced with a model of light environment, which calculates the distribution of light in the canopy using a quasi-Monte Carlo method. This interface is implemented using open L-systems (Mech and Prusinkiewicz, 1996). Simulations proceed in steps representing user-defined time intervals (e.g. days). In each step, the local distribution of light in the canopy is computed as a factor influencing production of carbohydrates by the leaves. The model is also sensitive to the amount of available water, which influences leaf photosynthesis and the growth capacity and thus the uptake of carbohydrates by various sinks. In contrast to the detailed model of carbohydrate assimilation, transport, and partitioning, the amount of water available at each time step is determined by a user-defined irrigation frequency and soil water holding capacity that interacts with calculated plant water use to globally characterize relative water availability over time.

The L-PEACH model is developmental, with the apical buds that are activated to produce new metamers each (simulated) spring. The rate of this process is locally controlled by the amount of carbon accumulated in the bud. Each new metamer has the potential to produce a leaf and three types of lateral buds; flower/fruit buds, lateral shoot buds that can be activated to grow in the current year (sylepsis) or in the following year (prolepsis), and a latent vegetative bud that can be activated after pruning in subsequent years to produce an epicormic shoot (water sprout). The amount of available carbon also controls the growth of organs. If the carbon supply is insufficient, organs (leaves or branches) are shed by the tree. Thus, the development and growth of the branching plant structure (topology and geometry) are closely coupled with the production and partitioning of carbohydrates as well as environmental parameters.

The formalism of L-systems automatically couples the tree structure with the topology and parameters of the electric network that represent the sources, sinks, and conductive elements. L-systems are also used to compute the distribution of charges, potentials, and currents in this network at each instant in time. Efficient implementation of this computation is the main methodological innovation of the L-PEACH model.

Sources and sinks of carbohydrates are the essential components of the model. Their behavior is defined using sets of functions, which in most cases are defined graphically, using the L-studio interactive function editor (Prusinkiewicz, 2004). This definition style introduced a conceptually useful separation between the existence of a functional relation between some variables of the model, and the (often unknown) quantitative details of this relation. The graphically defined functions also provide a very convenient means for experimenting with the model. Consistent with these notions, we describe below the general character of functions involved in the definition of sources and sinks.

Carbon Assimilation and Partitioning

Allen et al. (2005) reported on how the physiological and growth response functions for each organ are coupled with an electrical circuit network to model the generation and movement of fixed carbon within a developing tree. Generally in each simulation step (equivalent to one day of growth) a mature leaf can both gain some amount of carbon due to photosynthesis and loose some due to respiration and export to other plant. The amount gained depends on several factors: the amount of light reaching the leaf over the course of a day (Rosati and DeJong, 2003), ambient temperature, relative water availability and the existing charge in the leaf. The rate of assimilation decreases as a function of increasing charge and represents the effect of excessive starch accumulation on photosynthesis. A leaf cannot accumulate carbohydrates without a limit, and if there is no place for the charge to go (sink-limitation), the accumulation in the leaf decreases or even stops.

The source strength in a leaf (electromotoric force in electrical terms) is determined by the charge accumulated in the leaf. The charge lost by that leaf during a simulation step is calculated along with the change in charge of all other components in the tree, based on the interaction of all sources and sinks. The current (flux) out of the leaf is multiplied by the time step (DT) to give the decrement of charge.

The model also takes into account carbon storage in the stems and roots. The stored carbon can be mobilized in the spring. When this happens, stem segments and roots, normally sinks, temporarily become sources and there are functions to govern this temporary source activity in a manner similar to leaves.

L-PEACH includes the following sink types: internodes (composed of four distinct sinks related to elongation growth, girth growth, maintenance respiration and storage), young leaves, buds, fruits, and roots. The current flowing into a sink is a product of three functions. The voltage (v) at the point where the sink attaches to the tree represents the relationship between the concentration of sugars in the phloem where the sink is attached, and the rate at which those sugars can be unloaded into the sink. This relationship has been described in other phloem models (Minchin et al., 1993; Bidel et al., 2000) using Michaelis-Menten kinetics. The movement of carbon into a sink is not an open-ended process, but will stop (for a given sink) when that sink reaches a mature size. Modeling of sink capacity is thus handled by placing an upper limit on the total charge accumulated by a given sink. As a sink approaches its mature size it will thus take up less and less current, even if a high voltage is present at the point where that sink is attached.

Relative water availability can also influence the sink capacity of each organ. This is achieved through an index of relative water availability, which ranges from one (plant has all the water it can use) to zero (plant has no water available at all). Each sink type has a function defining its sensitivity to this relative water availability index.

In the case of the stem girth sink, the target girth growth is based on pipe model principles (Valentine, 1985). Likewise, storage targets are set relative to girth or stem mass. Buds and leaves grow to set maximum sizes. Fruits have a dynamic maximum growth target as in the original PEACH model. At the present time the root is modeled as an open ended sink (the root module does not include a maximum growth target), although its growth is eventually envisioned to be modulated by functions linking root size, water availability, and canopy water demand.

RESULTS

L-PEACH generates a dynamic visualization of the modeled tree and simultaneously quantifies and displays output data that can be selected by the user (Fig. 1). These data may include global statistics, such as the overall amount of carbon assimilated and allocated to different organ types, as well as local data, characteristic of specific organs specified by the user. The user can thus evaluate, both qualitatively and quantitatively, how different parameters of the model influence the growth and carbon partitioning in the plant and evaluate if the model behaves in a manner that matches field experience or empirically derived data.

In the latest versions of L-PEACH, quantitative data generated during a simulation run can be transferred for the analysis and visualization purposes to an external MATLAB program (Fig. 2). These visualizations complement three-dimensional depictions of the simulated trees generated directly by L-Studio, and represent quantitative output of the model. To date, the graphs produced by MATLAB have been used primarily to verify whether the model outcomes are consistent with expected patterns of tree growth, and to reveal model parameters that have a critical impact on the simulation results. In future applications, with the model parameters more precisely calibrated to experimental data, the quantitative outputs and their graphical visualizations may become an essential element of the model use for predictive purposes, such as the assessment of different pruning strategies on the fruit yield.

The power of this modeling approach becomes clear when simulating the effects of management, genetic, and environmental factors that can influence complex interactions among various organs on the plant. For example, the model can be used to simulate the simultaneous interactions of multiple factors, including (but not limited to):

crop load, rate of fruit maturity, carbohydrate storage capacity, and water availability – and how these factors can influence the growth and carbohydrate partitioning within a fruit tree. The manipulation of the model consists of simple adjustments of parameters, such as the number of fruit, behavior of fruit (rate of maturity) and storage capacity of stems. To model responses to water availability, we have made it possible to run the simulation with varying irrigation regimes. The user specifies the soil volume available for root exploration, an irrigation (or rainfall) interval for replenishing soil water and the relative sensitivities of each organ type to water stress. During the simulation, water use is calculated based on the cumulative leaf exposure to light, and the sink strength of each organ is 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 can be simulated without any empirical rules governing allometry between plant parts.

CONCLUSION

L-PEACH is an L-system-based prototype model for simulating complex interactions within trees, including growth, carbon partitioning among organs, and responses to environmental, management and genetic factors. The use of L-systems allows consideration of both the structural and functional aspects of the modeled plant in an integrated fashion. The model is not yet calibrated to any specific tree and many postulated mechanisms are hypothetical, however it provides a dynamic framework for developing and testing how source-sink interactions in trees can lead to an integrated understanding of plant growth and development. There is not enough experimental data available to provide a firm foundation for all of the proposed mechanisms involved in tree growth but the process of developing the model has provided important insights regarding gaps in our current understanding and highlights critical research to be conducted in the future. Thus, L-PEACH is a work in progress: it already makes it possible to study some relations within a growing plant, but includes many assumptions that should be resolved through further experimental studies.

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Figures

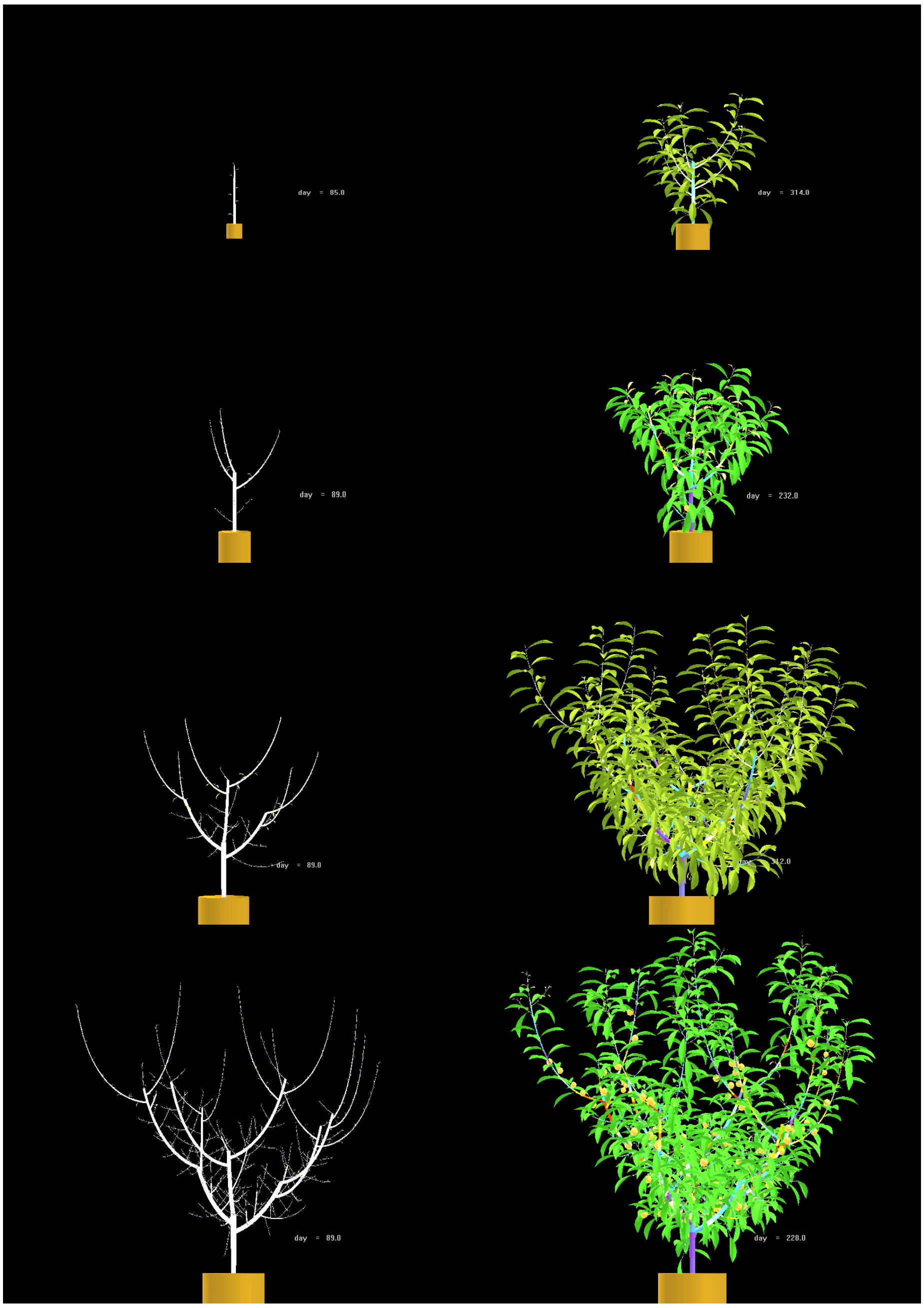

Fig. 1. This figure demonstrates the potential of the model to simulate tree growth, canopy architecture and carbon partitioning over the first four years after planting in the orchard. The left panels show the structure of the trees after dormant pruning prior to the onset of growth in each season. The three upper panels on the right show the simulated growth that resulted until just before leaf fall in years one though three and the bottom panel shows the tree just before fruit harvest in the fourth year. Fruit were thinned automatically with a thinning function that caused random fruit abortion but the model can be set so the operator thins all of the fruit manually. Stem colors in these panels are representative of the direction and relative magnitude of carbon flow at the instant the simulation was halted.

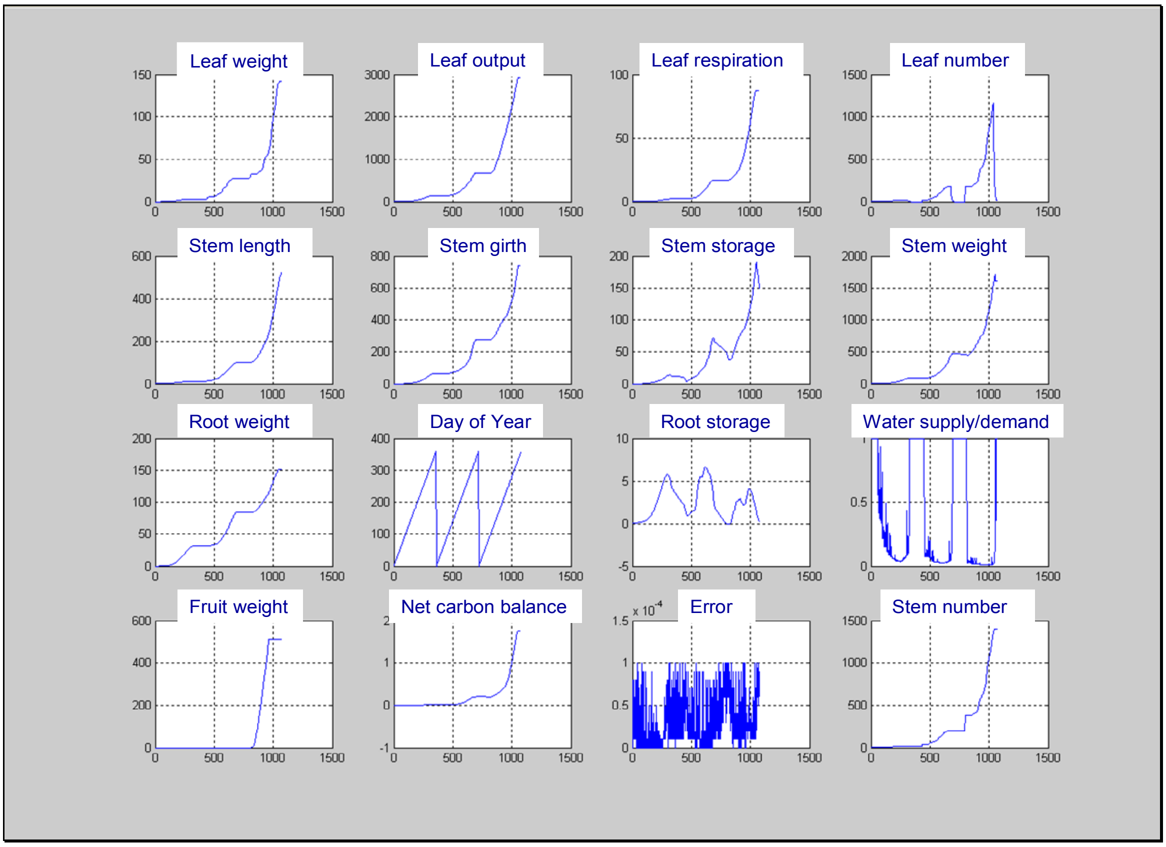

Fig. 2. This figure provides a sample of the type of general data that can be generated by L-PEACH subsequent to a simulation of the first three years of tree growth. If desired quantitative data from individual organs such as leaves can be displayed to evaluate their behavior over time.