

L-PEACH, an L-Systems Based Model for Simulating the Architecture and Carbon Partitioning of Growing Fruit Trees

Mitch Allen and Theodore DeJong
Dept. of Pomology
University of California
Davis, CA 95616
USA

Przemyslaw Prusinkiewicz
Dept. of Computer Science
University of Calgary
Alberta, T2N 1N4
Canada

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Abstract

Modeling carbon partitioning is a complex problem because of the dynamic nature and relationships between carbohydrate partitioning, growth and plant architecture. To date there have been no fruit tree simulation models that have attempted to quantitatively model these three processes simultaneously. In this paper we report on 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-systems was chosen as the platform for tackling the problem of simultaneous modeling of architecture, carbon partitioning and physiology of growing trees and here we introduce the L-PEACH model. 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

Carbohydrate partitioning represents 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 an early, sink-driven, 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), and that these organs compete for resources. Organs of the same type were clustered into composite compartments, such as: roots, fruit, or stems. Carbon was allocated to compartments depending on their competitive ability with respect to other compartments, and relative proximity to carbon sources. Growth potential or potential carbon demand of each sink type was quantified as the “genetic” potential growth rate of a sink. It was 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). Actual realized growth of each organ is then derived from interactions between organ growth potentials and the availability of carbon for each organ. 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. Overcoming these limitations required 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.

L-systems (Lindenmayer, 1968; Prusinkiewicz and Lindenmayer, 1990), as implemented in the latest version (4.0) of L-studio (Karwowski and Prusinkiewicz, 2003; Prusinkiewicz, 2004) were chosen as a platform for tackling this problem of simultaneously modeling architecture, carbon partitioning and physiology of growing trees. The result was the development of L-PEACH. It combines the supply/demand concepts of carbon allocation from the PEACH model with an L-system model of tree architecture to create a distributed supply/demand system of carbon allocation within a growing tree.

METHODS

Model Structure

The L-PEACH plant model is expressed in terms of modules that represent plant organs. 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, most 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 the formalism of 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 plant model is also sensitive to the amount of available water, which influences the uptake of carbohydrates by various sinks. Water demand by the tree is calculated as a function of the collective light exposure of each individual leaf, and water supply is based on an interaction between the tree's allocation to roots and the user defined soil volume and irrigation schedule. Water stress is then calculated at the whole tree level, and subsequently affects each module type according to user defined water stress functions.

The L-PEACH model mimics developmental processes, with the buds producing new metamers every (simulated) spring. The rate of this process is locally controlled by the amount of carbon accumulating in the bud. The amount of available carbon also controls the growth of organs in size. 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.

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, below we describe the general character of functions involved in the definition of sources and sinks.

Sources of Carbon

In each simulation step (equivalent to one day of growth), a mature leaf can both gain some amount of carbon due to photosynthesis, and lose some amount due to respiration and export to other parts of the plant. The amount gained depends on two factors: the existing charge (q) and the amount of light reaching the leaf (I). We capture this by expressing the rate of assimilation dq/dt as a product of two functions:

$$dq/dt = f_1(q) * f_2(I)$$

Function f_1 relates the rate of assimilation to the amount of carbohydrates (charge) already present 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.

Function f_2 captures the relation between the rate of assimilation and the incoming light. It is a linear function relating a leaf's daily assimilation rate with its daily accumulated light exposure (Rosati and DeJong, 2003).

Given the charge accumulated in the leaf, its source strength (electromotoric force in electrical terms) is determined by a third function, f_3 . 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 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.

Carbon Allocation

The L-PEACH model includes the following sink types: internodes (composed of three distinct sinks related to elongation growth, girth growth and storage), young leaves, buds, fruits, and roots. For the purposes of illustration, the behavior of stem elongation sinks will be described in more detail, serving as an example of the general methods used in the model. The current i flowing into a stem elongation sink is a product of three functions:

$$i = f_a(v) * f_b(q) * f_c(w)$$

Function f_a states that the flow of assimilates into a sink depends on the voltage (v) at the point where the sink attaches to the tree. In biological terms, this can be thought of as 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 elongation of stem segments is not an open-ended process, but will stop (for a given segment) when that segment reaches a mature length. Modeling of stem elongation

is thus handled by placing an upper limit on the total charge accumulated by a given segment. Function f_b , accomplishes this goal.

According to this function, as a stem segment approaches its mature size (q approaches 1 on the x-axis), it will thus take up less and less current, even if a high voltage is present at point where that segment is attached. Function f_c captures the influence of water stress on the model. Its argument is an index of water stress, which ranges from one (plant has all the water it can use) to zero (plant has no water available at all).

The behavior of all of the other sinks in is defined by a similar set of functions, based on the physiological principles that characterize the type of sink in question. In the case of girth growth the target girth 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 growth target as in the original PEACH model. At the present time roots are modeled as an open ended sink (the root model does not include function f_b), although their growth will eventually be modulated by functions linking root size, water availability, and canopy water demand.

RESULTS

Given an input L-system, L-studio generates a dynamic visualization of the modeled tree and simultaneously quantifies and displays the output data selected by the user. 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.

The power of this modeling approach becomes clear when simulating the effects of management, genetic, and environmental factors that can influence complex interactions between 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 stress – 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 fruits, behavior of fruit (rate of maturity), and storage capacity of stems. To model responses to water stress, we have made it possible to run the simulation with varying degrees of water stress. 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.

As an example of model results, we have run a simulation of tree growth out through the third year and left the tree unpruned. For the purpose of this example the conditions were set so that the crop load would be fairly high (Fig. 1). Although it is difficult to visually see the differences in fruit size on the simulated tree because of the scale of the figure the graph at the right shows the size distribution of the fruit on the tree. The differences in simulated fruit sizes are a function of the proximity of the various fruit to source leaves, inter-fruit and inter-organ competition for carbon within the tree and local differences in simulated light environment within the tree canopy. For the sake of simplicity and clarity the simulations for this example were run as if the trees were well-watered.

CONCLUSIONS

L-PEACH is an L-system-based template 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 allowed us to consider both the structural and functional aspects of the modeled plant in an integrated fashion. The model is not yet calibrated to any specific tree species, and the exact parameters of some postulated mechanistic functions are hypothetical. In some cases there is not enough experimental data to provide a firm foundation for these functions. Thus, L-PEACH is necessarily a work in progress: it already makes it possible to study functional relationships within a growing plant, but also includes assumptions that need to be resolved through further experimental studies.

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Figures

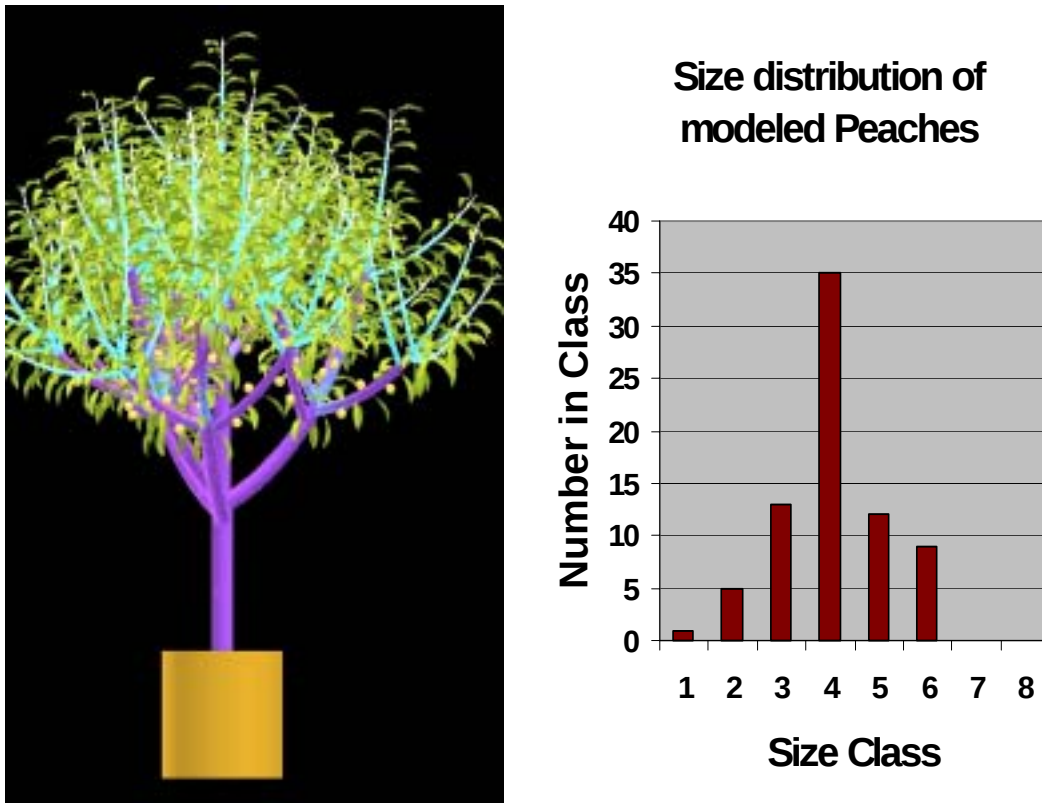


Fig. 1. This figure demonstrates the potential of the model to simulate crop load effects on fruit and tree growth, and carbon partitioning. The figure on the left is the result of a simulation through the third year of growth with a heavy crop load. The histogram on the right depicts the distribution of fruit sizes present on the simulated tree.