

Using L–Systems for Modeling the Architecture and Physiology of Growing Trees: The L–PEACH Model

Mitch Allen¹, Przemyslaw Prusinkiewicz², and Theodore DeJong¹

¹ Department of Pomology, University of California, Davis

² Department of Computer Science, University of Calgary

Introduction

Carbohydrate partitioning represents a central problem of process–based models of tree growth because of the coupling between carbon partitioning, growth, and architecture. PEACH 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 hypothesis 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. Biomass growth was dependent on an experimentally derived growth potential for each organ type. This approach made it possible to avoid the empirical allocation coefficients, functional balance rules, and allometric relationships that were common to most other tree models at the time. However, as pointed out by Le Roux et al., the PEACH model almost entirely ignored the interaction between tree architecture and carbon allocation. 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 requires a more detailed model of carbon economy, in which growth and function of each organ is modeled individually within an architecturally explicit model of canopy growth.

Reference

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Mitch Allen¹, Przemyslaw Prusinkiewicz² and Theodore DeJong¹

¹Department of Pomology, University of California, Davis CA, USA

²Department of Computer Science, University of Calgary, Alberta, Canada

1. 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 hypothesis 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. Biomass growth was dependent on an experimentally derived growth potential for each organ type (Grossman and DeJong 1995a,b, DeJong and Grossman 1995). This approach made it possible to avoid the 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. 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 requires a more detailed model of carbon economy, in which growth and function of each organ is 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, 2004, Prusinkiewicz 2004), were chosen as a platform for tackling the problem of 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.

2. Model description

2.1 General 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 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 the formalism of open L-systems (Mech and Prusinkiewicz, 1996). Simulation proceeds 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. In contrast to the detailed modelling of carbohydrate assimilation, transport, and partitioning, the amount of available water is determined by a user-defined function that globally characterizes water stress as a function of time.

The L-PEACH model is developmental, 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 the 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.

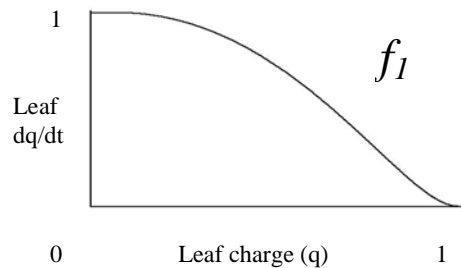
The formalism of L-systems automatically couples the tree structure with the topology and parameters of the electric network that represent the sources, sinks, and conductive elements. L-systems are also used to compute the distribution of charges, potentials, and currents in this network at any instant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

Sources and sinks of carbohydrates are the essential component 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 introduces 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 only describe the general character of functions involved in the definition of sources and sinks.

2.2. Sources of carbon

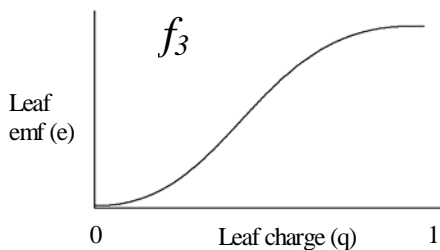
2.2.1. Leaves. In each simulation step, a mature leaf can both gain some amount of carbon due to photosynthesis, and lose some amount due to respiration and export to other parts of the plant. The amount gained depends on two factors: the existing charge (q) and the amount of light reaching the leaf (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. A sample function f_1 is shown on the left. The decrease of the rate of assimilation as charge increases represents the effect of excessive starch accumulation on photosynthesis. A leaf cannot accumulate carbohydrates without limit, and if there is no place for the charge to go, the accumulation in the leaf decreases or even stops.

Function f_2 (plot not shown) captures the relation between the rate of assimilation and the incoming light. It is an increasing function of the light intensity, asymptotically reaching the maximum rate at high illuminations (Rosati and DeJong, 2003).



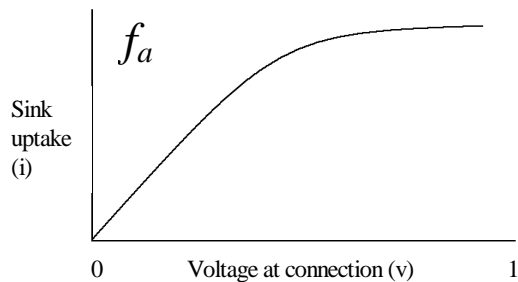
Given the charge accumulated in the leaf, its source strength (in electrical terms, its electromotive force) is determined by a third function, f_3 , as on the left. The charge lost by that leaf during a simulation step (i.e., the current, or flux, out of the leaf) is calculated along with the change in charge of all other components in the tree, based on the interaction of all sources and sinks.

2.2.2. Storage. The model takes into account carbon storage in the stems and roots. The stored carbon can be mobilized in the spring. When this happens, the stem segments, normally sinks, temporarily become sources.

2.3 Carbon allocation.

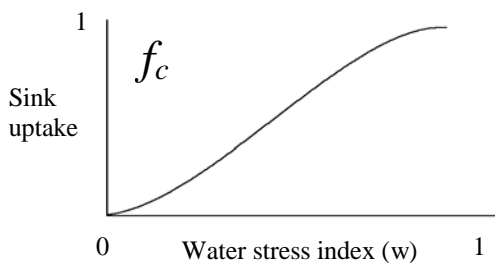
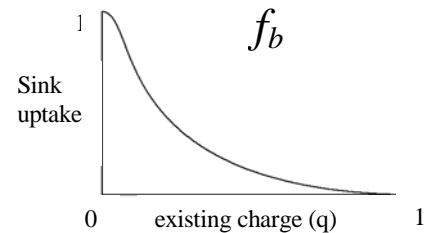
The L-PEACH model includes the following sink types: internodes (further decomposed into three distinct sinks related to elongation growth, girth growth and storage), young leaves, buds, fruits, and roots. The behavior of stem elongation sinks will be described in more detail, to serve as an example of the general methods used in the model.

2.3.1. The stem elongation sink. 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 , of the general character shown on the left, 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 , of the general character shown on the right, 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 (the plant has all the water it can use) to zero (the plant has no water available at all). A sample function f_c is shown on the left.

2.3.2. Other sinks. The behavior of all of the other sinks 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 the pipe model (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.

3. Application example

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 selected 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 model can be used to simulate the simultaneous interactions of multiple factors, including 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. To model responses to 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 (represented by function f_c in the stem elongation sink (Section 2.3.1), and its equivalents in other sinks). During the simulation, water use is calculated based on 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, we have run two different pairs of simulations. In the first pair, fruit set is altered such that the crop load in one tree is twice that of the other. In response to this decrease in initial fruit set, the model produced the following results: an increase in final fruit size, a decrease in the total amount of carbon partitioned to fruit growth, lower variance in fruit size within a tree, and greater partitioning of carbon to vegetative growth (Figure 1).

The second pair of simulations involves two-year-old trees with indeterminate shoot growth under two different irrigation scenarios. One tree is irrigated at regular intervals such that it is never water-stressed at all. The other tree has a limited soil volume from which to extract water, and it is irrigated at long intervals so that it experiences mild water stress. We assumed that shoot growth was more sensitive to water stress than photosynthesis, thus the primary visual effect of the water stress was a reduction in shoot elongation and girth growth (Figure 2). The model also predicted quantitative differences in carbon partitioning (numerical data not shown). Simulations can be further modified by adjusting the functions that characterize the physiology and growth of various plant organs.

4. Conclusions

We consider L-PEACH to be 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, and many postulated mechanisms are hypothetical. Often, there is not enough experimental data to provide a firm foundation for these mechanisms. Thus, L-PEACH is necessarily a work in progress: it already makes it possible to study some relations within a growing plant, but also raises many questions that should be resolved through further experimental studies.

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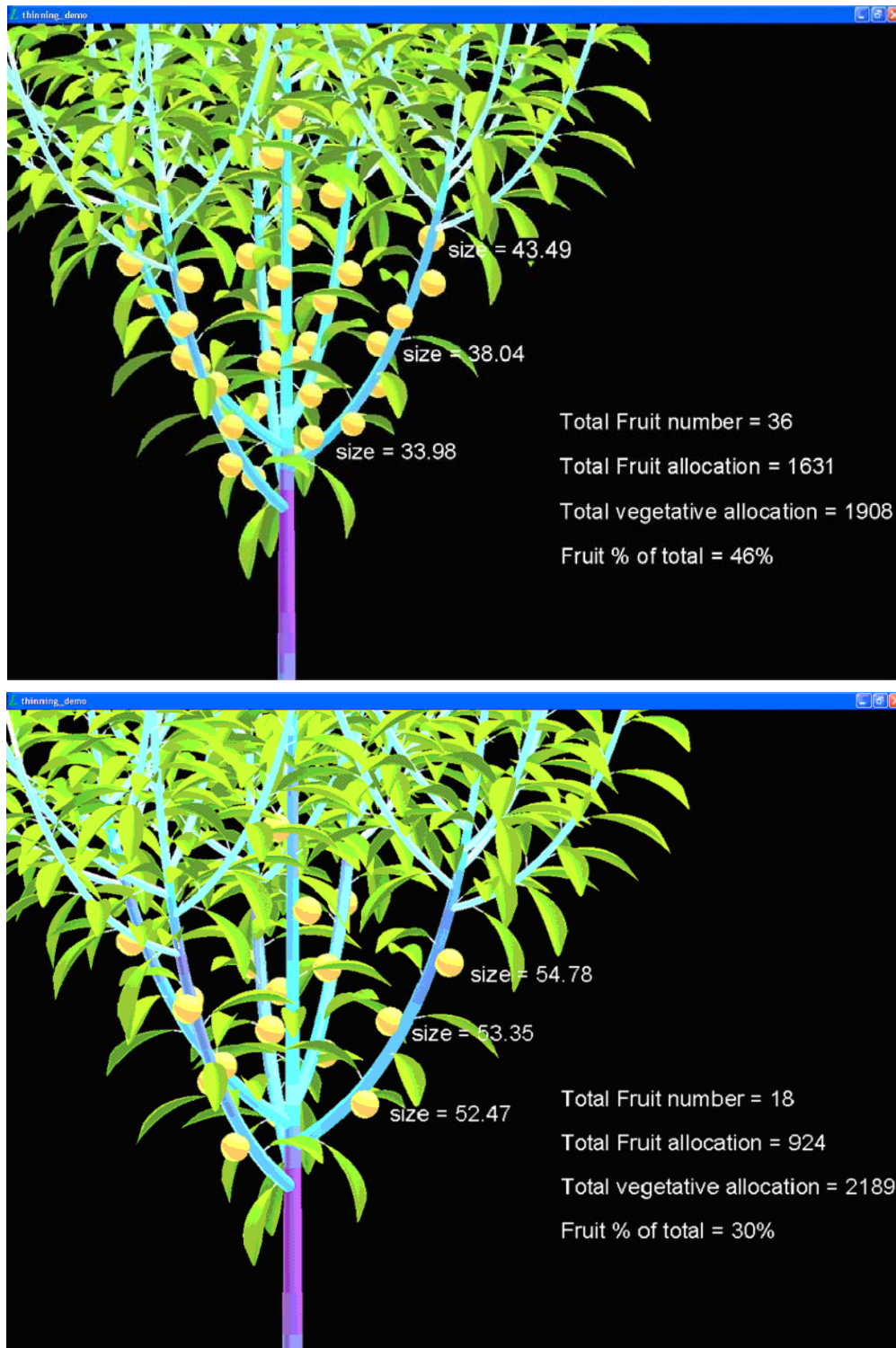


Figure 1. This figure demonstrates the potential of the model to simulate crop load effects on fruit and tree growth, and carbon partitioning. The upper panel is the result of a simulation with a heavy crop load and the lower is a simulation with half as many fruit. Stem colors in these panels are representative of the direction and relative magnitude of carbon flow at the instant the simulation was halted.



Figure 2. This figure demonstrates the potential of the model to simulate the effects of irrigation frequency or mild water stress on tree growth. The tree on the left was simulated under conditions of full irrigation whereas the tree on the right experienced mild water stress during growth. In this simulation leaf initiation and stem elongation rate were both set to be more sensitive to mild water stress than leaf photosynthesis. The model provides the flexibility to set the sensitivities of each of these processes independently to match experimental data available for specific species or circumstances.

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