

CHAPTER 12

L-PEACH, AN L-SYSTEM-BASED MODEL FOR SIMULATING ARCHITECTURE, CARBOHYDRATE SOURCE–SINK INTERACTIONS AND PHYSIOLOGICAL RESPONSES OF GROWING TREES

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Abstract. Carbohydrate partitioning is closely coupled with plant growth and architecture, and therefore constitutes an important aspect of the functional-structural modelling of plants. L-PEACH is an L-system-based tree simulation model that combines supply/demand concepts of carbon partitioning with a developmental model of tree architecture. The model is expressed in terms of modules that represent plant organs. An organ may correspond to one or more elementary sources or sinks for carbohydrates. The whole plant is modelled 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. It can simulate multiple years of tree growth while capturing the effects of irrigation, crop load and pruning on carbon partitioning and the dynamics of architectural development. The growing tree can be visualized in a schematic or semi-realistic manner, while quantitative data characterizing individual organs, organ types or the whole tree can be output for visualization and analysis to an external program, such as MATLAB.

INTRODUCTION

Two of the most difficult aspects of functional-structural plant modelling are the development of a systematic approach for dealing with carbon allocation, and making carbon allocation respond to context-explicit, environmental and endogenous signals within a dynamically growing plant. Most early simulation models of plant growth avoided the issue by using empirically-derived partitioning coefficients or functional balance/allometric relationship rules (Loomis et al. 1979) to arrive at reasonable model outcomes. However, such approaches are more

difficult to apply to models of perennial species, in which indeterminate, multiyear growth makes interactions between carbon partitioning, growth and architecture too complicated to capture using empirical formulas (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 plant grows as a collection of semi-autonomous yet 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 their general, relative proximity to carbon sources. Biomass growth in the model was dependent on 'growth potentials' for each organ type at specific phenological stages of development. Growth potentials were experimentally approximated by determining the maximum growth rate of individual organ types under conditions where competition from other sinks was minimized (DeJong and Grossman 1995; Grossman and DeJong 1995a; 1995b; 1995c). The PEACH model approach made it possible to avoid the empirical allocation coefficients, functional balance rules or fixed 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 interactions between tree architecture and carbon allocation.

A more detailed model of carbon economy was needed, in which the growth and function of organs were modelled individually within an architecturally explicit model of canopy development. Integration of physiological and architectural aspects of plant function has been an essential concept of functional-structural plant modelling (Perttunen et al. 1996; Le Dizès et al. 1997; Sievänen et al. 2000; Godin and Sinoquet 2005). The goal of the L-PEACH functional-structural plant model (Allen et al. 2005) was to simulate the development of a plant architecture, keep track of all of its functional elements as it grew, exchange carbon and other resources between all the elements in the plant, and make the individual components sensitive to local availability of carbon and external environmental signals. L-systems (Lindenmayer 1968a; 1968b) with subsequent extensions (Prusinkiewicz and Lindenmayer 1990; Měch and Prusinkiewicz 1996; Karwowski and Prusinkiewicz 2003) were used to tackle the difficult problem of integrating all these elements. The carbon source-sink interactions and carbohydrate transport within the plant were modelled using an analogy to electric circuits (Thornley and Johnson 1990; Minchin et al. 1993; Bidet et al. 2000). The resulting systems of equations describing fluxes and accumulated amounts of carbohydrates were solved numerically within the L-system formalism. The underlying method was proposed by Federl and Prusinkiewicz (2004) for linear circuits, and was extended in L-PEACH for non-linear circuits. 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 L-PEACH model is a spatially explicit three-dimensional simulation model that integrates the supply/demand concepts of carbon allocation from the previous

PEACH model and a developmental model of tree architecture into a distributed model of carbon allocation within a growing tree. L-PEACH is written in the L+C plant-modelling language (Karwowski and Prusinkiewicz 2003) and implemented using the current version (4.0) of the L-system-based modelling software L-studio (Prusinkiewicz 2004).

MODEL DESCRIPTION

General structure

The L-PEACH plant model is expressed in terms of modules that represent individual plant organs. An organ may be represented as one or more elementary sources or sinks of carbohydrates. The whole plant is modelled as a branching network of these sources and sinks, connected by conductive elements. This model extends proposals by Thornley and Johnson (1990) and Minchin et al. (1993), that the flux of carbohydrates within the phloem is proportional to osmotically generated differences in hydrostatic pressure, and inversely proportional to a resistance to transport. Since (for a given temperature) osmotic pressure is proportional to the concentration of carbohydrates, the fluxes are related directly to the differences in concentration.

The plant model can be 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 (Měch and Prusinkiewicz 1996). Simulation proceeds in user-defined time-steps corresponding to days and real-time environmental data such as daily solar radiation and daily max.-min. temperatures that can be used as inputs to drive assimilation and growth processes. In each daily step, the local distribution of light in the canopy is computed and is a factor influencing local production of carbohydrates by the leaves. Temperature data are used to modulate assimilation, respiration and growth responses of individual model components such as stem segments, leaves and fruit. The model can be also made to be sensitive to the amount of available water, through interactions with 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 are calculated at the whole-canopy level. The water demand for each individual leaf is a function of light exposure, and all of the individual leaf demands are summed to determine the whole-canopy water demand. The ability of the root system to provide water is determined by the root system's structural biomass, the soil volume available 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 provides an index of the water stress in the tree at any given time – as the value of this ratio goes down, the impact of water stress on tree growth and photosynthesis increases.

Simulation of architectural development

The L-PEACH model is developmental, with buds producing new segments to accommodate shoot growth. Each new stem segment consists of an internode with a specified maximum length and a node that has a leaf, a terminal bud, a dormant lateral shoot bud, a dormant flower bud and a lateral latent bud. Shoot length growth is accommodated through creation of new stem segments by the terminal buds on existing shoots. Lateral shoot buds remain dormant until the next season, unless the tip of a shoot above a lateral dormant bud is removed during the growing season. The flower bud also remains dormant in the season in which it has been generated. A specified percentage of the flower buds set a fruit in the next season or abort and fall off the tree. The lateral latent bud remains inactive unless the terminal end of a two-year or older shoot is pruned off. If such pruning occurs, from one to three distal latent buds activate and produce rapidly growing shoots (water shoots in horticultural terms).

Each simulated growing season is initiated with bud break. Shoot growth is controlled by specifying the maximum number of stem segments that an individual shoot can put on in a season and the availability of carbohydrates at the site of growth to support the addition of each segment. The shoots that grow from the lateral buds formed on the previous season's shoots are separated into two categories: long shoots and short shoots. Long shoots are produced from the terminal bud and from a specified number of lateral buds at the distal end of each previous year's long shoot. The maximum number of stem segments of the long shoots can be specified (usually between 20 and 30). All remaining lateral buds on the proximal end of long lateral shoots produce short shoots, with the number of segments ranging from 3 to 10. The number of stem segments on lateral shoots arising from the previous year's short shoots cannot exceed the number of stem segments on that short shoot. A specified percentage of short shoots are aborted each year to avoid overcrowding of shoots. In addition, if the carbon supply is insufficient for growth and/or maintenance over a specified length of time, organs (fruits, 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.

Root growth and architecture are not explicitly modelled in the current versions of L-PEACH; instead, the root is modelled and visualized as a large bucket, with the size proportional to the root system size. In the implementation of the irrigation module of the model, the ability of the root to extract moisture from the soil is a function of total root biomass. While the lack of an explicit representation of root architecture is a limitation of the current model, it does not prevent a functional approach to modelling the above-ground portion of the plant.

Simulation of source-sink interactions and carbohydrate transport within the architectural structure

The formalism of L-systems automatically couples the tree structure with the topology and parameters of the carbohydrate supply network that represents the sources, sinks and conductive elements. At the heart of this coupling lies the notion of context-sensitive L-systems (Lindenmayer 1968a; 1968b; Prusinkiewicz and Lindenmayer 1990), which provides a means of capturing connections between elements of a growing structure at each stage of its development. Given this information, L-systems are used to compute the distribution of carbohydrate, its concentrations and fluxes at each step of the simulation.

Within L-PEACH, the plant is modelled as a growing network comprised of elements that represent individual organs such as leaves, stem segments, fruit, buds and roots. The behaviour of each type of organ is given by a set of user-defined functions. For example, a mature leaf is characterized by its source strength, which in turn depends on the amount of mobilizable carbohydrates that have been accumulated in the leaf as a result of photosynthesis. During each time step, these accumulated carbohydrates can flow into the various sinks within the tree (roots, fruit, etc.). Stem segments, in addition to being potential sources or sinks, act as conduits for the fluxes throughout the tree. The magnitude of these fluxes depends on the differences in carbohydrate concentrations between sources and sinks, and the resistances of the intervening paths. All elements may exhibit nonlinear behaviour, meaning that the resistances may depend on concentrations.

In general, the network representing a growing plant has a dynamically changing structure (its topology changes over time), is non-stationary (the values of parameters associated with the various organs change over time), and is non-linear (the resistance associated with a given sink depends on the potential at the sink's attachment point). L-systems are used to 'develop' the plant and to solve the set of equations defined by the network at any given point in time. These equations are solved numerically, by taking advantage of the branching topology of the network.

The calculation of accumulation, flow and partitioning of carbohydrates between the individual components of this network is analogous to electric circuits using equations developed in linear-circuit theory. The fundamental concept is to identify the amount (mass) of mobilizable carbohydrates with an electric charge. Other correspondences are a straightforward consequence of this identification. The only non-intuitive notion is the source/sink strength, the analogue of electromotive force. Conceptually, it is the concentration of carbohydrates inherent in an organ (a source or a sink), as it would be measured in the absence of flow through resistive conductive elements associated with that organ.

There are two types of connections between the elements (stem segments) of the modelled tree: a serial connection between two consecutive elements, and parallel connections that occur at branch points (nodes). The serial connection of consecutive elements simulates branches formed as sequences of internodes, in which the axial movement of carbohydrates occurs. Parallel connections at the branch points capture ramifications in the branching structure, as well as the

distribution of carbohydrates to the various sinks within a stem segment (length growth, girth growth, carbohydrate storage and maintenance respiration). A general description of the L-PEACH simulation algorithm used to partition carbon according to the electrical-circuit analogue is presented by Allen et al. (2005), and a more detailed description is provided by Prusinkiewicz et al. in Chapter 11 of this book.

Functional definitions of sources and sinks

Sources and sinks of carbohydrates are the essential components of the model. Their behaviour is specified using sets of functions, which can be 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 relationship between some variables of the model, and the (often unknown) quantitative details of this relationship. The graphically defined functions provide a convenient means for experimenting with the model. Consistent with these notions, below we only describe the general character of the functions involved in the definition of a representative source and a representative sink.

Sources of carbon

Leaves In each simulation step, a mature leaf can both gain some amount of carbohydrates due to net photosynthesis, and lose some amount due to export to other parts of the plant. The amount gained depends on two factors: the existing amount of carbohydrates (q) and the accumulated amount of light reaching the leaf (I) during a time-step. We characterize 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 (q) already present in the leaf. The decrease in the rate of assimilation as a function of increasing carbohydrate accumulation represents the effect of excessive starch accumulation on photosynthesis. A leaf cannot accumulate carbohydrates without limit, and if there is no place for the carbohydrate to go (i.e., there is a sink limitation), its accumulation in the leaf will slow down or even stop.

Function f_2 captures the relation between the rate of assimilation and the incoming light. Since photosynthetic carbon assimilation is modelled over time-steps of a day or longer, it is calculated as a linear function of accumulated light exposure of a leaf during a given time-step (Rosati and DeJong 2003). Given the carbohydrate accumulated in the leaf, its source strength is determined by a third function.

The amount of carbohydrates moving from leaf to plant during a simulation step is calculated along with the change in accumulated carbohydrate of all other components in the tree, based on the interaction of all sources and sinks. The carbohydrate flux out of the leaf is multiplied by the time-step to give the decrement

of accumulated carbohydrate. For leaves, photosynthesis is calculated as net photosynthesis, and carbohydrate uptake by individual sinks includes the carbohydrate used by respiration in those sinks.

Storage In addition to having sink compartments for structural carbohydrate (elongation and girth growth), the roots and stem segments each have a compartment dedicated to (non-structural) carbohydrate storage. For most of the year, these storage compartments act as carbohydrate sinks, although the carbon accumulation is not open-ended. The ratio of non-structural to structural carbohydrate in a given segment cannot exceed a user-specified value, and as this limit is approached, the sink strength of the storage compartment decreases. When acting as sinks, the storage compartments compete for carbon in a manner similar to other growing organs, as described in the next section. At a user-defined point in the spring, the carbohydrate from the storage compartments is re-mobilized. When this happens, the storage compartments become carbohydrate sources for a specified time. Their behaviour during this time is analogous to the source behaviour of leaves as described in the preceding section, except for the inability to ‘refill’ their carbohydrate charge via photosynthesis in the short term.

Sinks and their behaviour

The L-PEACH model includes the following sink types: stem segments (further decomposed into four distinct sinks related to elongation growth, girth growth, storage and maintenance respiration), young leaves, buds, fruits and roots. For the purposes of illustration, the behaviour of stem elongation sinks will be described in more detail, serving as an example of the general methods used in the model.

The stem elongation sink The flux of carbohydrates (i) into a stem elongation sink is a product of three functions:

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

Function f_a relates the flow of carbohydrates into the sink to the concentration (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 phloem models (Minchin et al. 1993; Bidel et al. 2000) using Michaelis-Menten kinetics.

The elongation of a stem segment is not an open-ended process, but stops when that segment reaches a mature length. The modelling 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 (as q approaches ‘max q ’), it will accumulate carbohydrates at a decreasing rate, even if the carbohydrate concentration at the point where that segment is attached is high. Function f_c captures the influence of water stress on the model. Its argument is a relative 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).

Other sinks The behaviour 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 pipe-model principles (Shinozaki et al. 1964; Valentine 1985). Likewise, storage targets are set relative to girth or stem mass. Leaves grow to a set maximum size. Fruits have a dynamic growth target determined by experimentally determined relative growth-rate models for specific cultivars as in the original PEACH model. At the present time roots are modelled as an open ended sink (the root model does not include a function analogous to f_b in the stem elongation sink), although it is anticipated that their growth will eventually be modulated by functions linking root size, water/nutrient availability, and canopy water/nutrient demand. Carbon flux for maintenance respiration of each element is modelled using a parallel resistance into each organ or stem segment that is responsive to temperature.

APPLICATION EXAMPLES

Three-dimensional graphic depiction of architectural growth

During a simulation, L-studio generates a dynamic visualization of the modelled tree and simultaneously quantifies and displays the output data selected by the user (Figure 1). Output 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 chosen by the user (only day of year data are printed in Figure 1 to maintain clarity). The user can thus evaluate, both qualitatively and quantitatively, how different parameters of the model influence the growth and carbon partitioning in the plant.

Colour coding of the stem segments during the simulation run allows for visualization of carbohydrate fluxes within the plant. Colours ranging from light blue to purple indicate flow 'down' the plant towards the roots, while colours from yellow through red indicate flows 'up' the tree in the direction of the shoot tips.

The power of L-PEACH becomes clear when simulating the effects of management and genetic and environmental factors that can influence a tree through complex interactions between its organs. For example, these interactions may reflect the influence of pruning, crop load, rate of fruit maturation, carbohydrate storage capacity and water stress on the growth and carbohydrate partitioning within a fruit tree. The manipulation of the model may consist of simple adjustments of parameters, such as the number of fruit, behaviour of fruit (rate of maturity), storage capacity of stems, maximum daily rates of leaf photosynthesis, branch angle, etc., before a simulation begins. In addition, a simulation can be interrupted to perform pruning or fruit-thinning operations, and resumed with the adjusted tree structure. For example, Figure 1a shows a tree that has been pruned to the standard open-vase system (Mücke et al. 1980) and has received fruit thinning on some branches and less on others to show the simulated effect of fruit thinning on fruit size (Figure 1b).



Figure 1. Examples of graphic outputs of L-PEACH. The tree on the left was generated by running the model to simulate growth into the fourth year. The tree was trained to the ‘open vase’ shape by repetitive pruning in the ‘winter’ of each year. Fruit was also selectively thinned early in each fruit growth season. The close-up on the right indicates outcomes of modelled source–sink behaviour on fruit size. Note that fruit size on lightly cropped branches is larger than on the branch with a heavy crop load

To model responses to water stress, the user can specify 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 and its equivalents in other sinks). During the simulation, water demand 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.

Graphic display of quantitative 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. 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 the 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.

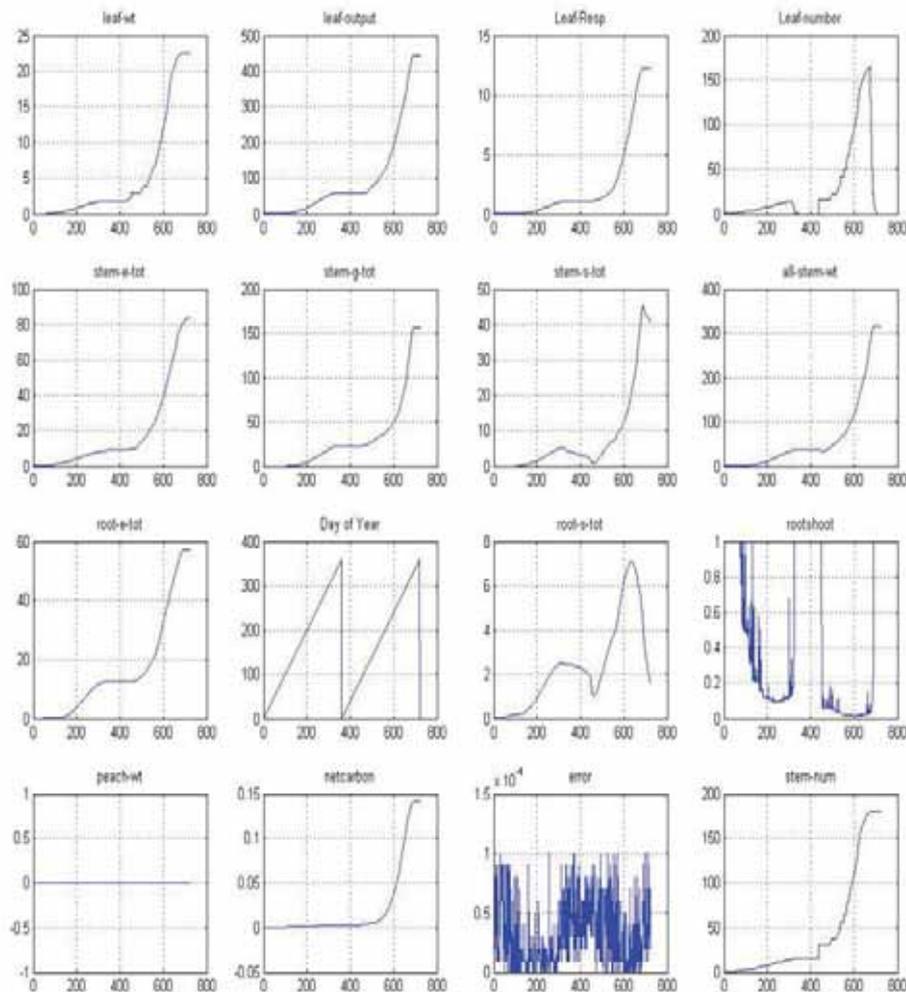


Figure 2. Sample output of quantitative data generated by L-PEACH and visualized using MATLAB after a simulation run. As indicated on the X axis these data are for a simulation of two years. The graphs make it possible for the user to track and quantitatively analyse various aspects of the model behaviour over time

CONCLUSIONS

We believe that L-PEACH demonstrates the potential of L-systems and L-studio for achieving many of the goals of functional-structural plant modelling. Specifically, the model captures and makes it possible to analyse various relationships between carbon partitioning in a growing tree and the resulting architectures. There are also an almost infinite number of possibilities to modify and improve the model, apply it to develop hypotheses and experiments for new avenues of research, calibrate to qualitatively capture features of real peach trees, or adapt it to fit other types or species of plants. Extensions of functional-structural models similar to L-PEACH may also provide a means to link discoveries made at the molecular-genetic level with an integrated understanding of plant structure and function at the whole-plant level. In this context, the key methodological difficulty is the management of the complexity of functional-structural models. Proper modularization is the key to the development and maintenance of any complex software, but proper modularization of complex functional-structural models is an open research problem.

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