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Using L-systems for modeling source–sink interactions, architecture and physiology of growing trees: the L-PEACH model

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Summary

• Functional–structural plant models simulate the development of plant structure, taking into account plant physiology and environmental factors. The L-PEACH model is based on the development of peach trees. It demonstrates the usefulness of L-systems in constructing functional–structural models.

• L-PEACH uses L-systems both to simulate the development of tree structure and to solve differential equations for carbohydrate flow and allocation. New L-system-based algorithms are devised for simulating the behavior of dynamically changing structures made of hundreds of interacting, time-varying, nonlinear components.

• L-PEACH incorporates a carbon-allocation model driven by source–sink interactions between tree components. Storage and mobilization of carbohydrates during the annual life cycle of a tree are taken into account. Carbohydrate production in the leaves is simulated based on the availability of water and light. Apices, internodes, leaves and fruit grow according to the resulting local carbohydrate supply.

• L-PEACH outputs an animated three-dimensional visual representation of the growing tree and user-specified statistics that characterize selected stages of plant development. The model is applied to simulate a tree's response to fruit thinning and changes in water stress. L-PEACH may be used to assist in horticultural decision-making processes after being calibrated to specific trees.

Key words: carbon partitioning, functional–structural plant modeling, L-system, modeling plant growth and development.

Introduction

Historically, two of the most difficult aspects of functional–structural plant modeling have been developing 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. Carbon allocation in plants has been the subject of intense study and debate among plant physiologists for many years (Gifford & Evans, 1981; Brouwer, 1983; Farrar & Gunn, 1998), but there is still no generally accepted theory to explain its underlying mechanisms. Allometric relationships in carbon allocation between roots and shoots clearly exist (Niklas & Enquist, 2002), but the processes involved in creating them are still not well understood. Although the concepts of source and sink strength have appeared in the literature for decades (Warren-Wilson, 1967), there remains a lack of consensus regarding their role in the process of carbon allocation because of the complex quantitative interactions between 'sources' and 'sinks' in a whole-plant system (Farrar, 1993). Consequently, carbohydrate partitioning remains a central problem of process-based models of plant growth. Most early integrated 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 formulae (Le Roux *et al.*, 2001).

PEACH (Grossman & 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 semiautonomous 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 relative proximity to carbon sources. Biomass growth in the model 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. It was approximated experimentally by determining the maximum growth rate of individual organ types under conditions where competition from other sinks was minimized (DeJong & Grossman, 1995; Grossman & 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 (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; thus all organs of a given type (individual fruit, for example) grew at the same rate. 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, or to capture the influence of their performance on patterns of carbon partitioning.

Overcoming these limitations requires a more detailed model of carbon economy, in which the growth and function of organs are modeled individually within an architecturally explicit model of canopy development. The integration of physiological and architectural aspects of plant function is the essential concept of functional–structural plant modeling (Perttunen *et al.*, 1996; Le Dizès *et al.*, 1997; Sievänen *et al.*, 2000). Such models must simulate the architectural growth of a plant, keep track of all of its functional elements as it grows, exchange carbon between all the elements in the plant, and make the individual components sensitive to local availability of carbon and external environmental signals. We propose L-

systems (Lindenmayer, 1968) with subsequent extensions (Prusinkiewicz & Lindenmayer, 1990; Mech & Prusinkiewicz, 1996; Karwowski & Prusinkiewicz, 2003) as a conceptual framework to tackle the difficult problem of integrating all these elements in a systematic and theoretically well founded manner. The carbon source–sink interactions and carbohydrate transport within the plant are modeled using an analogy to electric circuits (Thornley & Johnson, 1990; Minchin *et al.*, 1993; Bidel *et al.*, 2000). The resulting systems of equations describing fluxes and accumulated amounts of carbohydrates are solved numerically within the L-system formalism. The underlying method was proposed by Federl & Prusinkiewicz (2004) for linear circuits, and is extended here for nonlinear 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, results in a conceptually clear integration of functional and structural aspects of the model. The result of our work is L-PEACH, a spatially explicit three-dimensional simulation model that integrates the supply/demand concepts of carbon allocation from the PEACH model and a developmental model of tree architecture into a distributed model of carbon allocation within a growing tree. L-PEACH has been written in the L+C plant modeling language (Karwowski & Prusinkiewicz, 2003) and implemented using the current version (4.0) of the L-system-based modeling 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 modeled as a branching network of these sources and sinks, connected by conductive elements. Our model extends the approach proposed by Thornley & Johnson (1990), and further developed by Minchin *et al.* (1993), according to which the flux of carbohydrates is proportional to osmotically generated differences in hydrostatic pressure, and inversely proportional to a resistance to transport. As (for a given temperature) osmotic pressure is proportional to the concentration of carbohydrates, the fluxes can be related directly to the differences in concentration. In contrast to the previous models, we allow the branching networks representing plants to be arbitrarily large. In general, all elements of the network may have a nonlinear and time-dependent behavior.

The plant model is interfaced with a model of the 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 & Prusinkiewicz, 1996). Simulation proceeds in user-defined time-steps that can correspond to real time (e.g. days). In each

step the local distribution of light in the canopy is computed, and is a factor influencing production of carbohydrates by the leaves. The plant model is also sensitive to the amount of available water, which influences 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 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 root system structural biomass, the soil volume available to the tree, a user-defined soil moisture release curve, and the 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.

The L-PEACH model is developmental, with the buds producing new stem segments, leaves, fruit, etc. Each simulated growing season is initiated with bud break. The growth of organs initiated during the previous season (preformed) as well as the subsequent initiation of new organs (neo-formed) is controlled by the amount of available carbon. If the carbon supply is insufficient for growth and/or maintenance, 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.

The L-PEACH simulation algorithm

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, 1968; Prusinkiewicz & Lindenmayer, 1990), which provides a convenient 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. Efficient implementation of this computation is the main methodological innovation of the L-PEACH model.

Within L-PEACH, the plant is modeled as a growing network comprised of elements that represent individual organs such as leaves, stem segments, fruit, buds and roots. The behavior 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 behavior, 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 nonstationary (the values of parameters associated with the various organs change over time); and is nonlinear (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 (development here denotes changes in the network topology that result from the addition of new segments by buds, or the loss of organs through shedding), 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.

In order to calculate the accumulation, flow and partitioning of carbohydrates between the individual components of this network, we rely on an analogy to electric circuits and employ equations developed in linear circuit theory. The underlying correspondence between biological and electrical quantities is summarized in Table 1. 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 nonintuitive notion is the source/sink strength, the analogue of electromotive force. It can be thought of as 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 connection between the elements of the modeled tree: a serial connection between two consecutive elements, or a parallel connection that occurs at a branch point. Using standard rules for combining components in an electric circuit, it is then possible to reduce any two connected elements into an equivalent single element. For serial connections, the combination is done as shown in Fig. 1a, where r and e (on the right side of the figure) are the resistance

Table 1 Correspondence between biological and electric quantities employed in the model

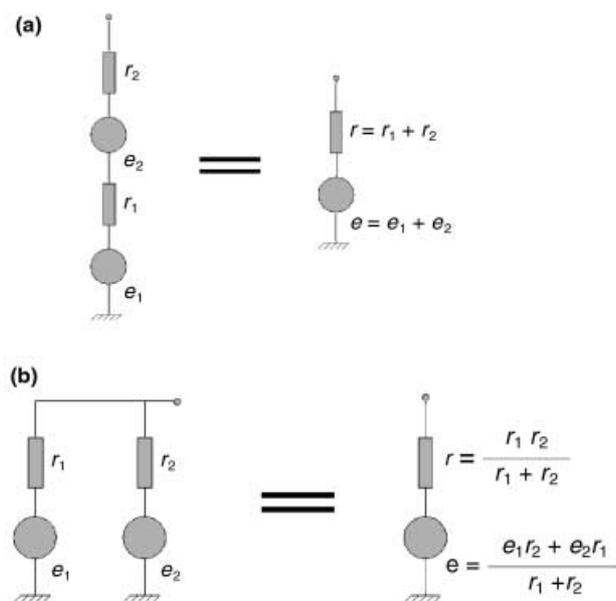| Biological quantity	Electric counterpart	Symbol
Amount (mass) of carbohydrate	Charge	q
Carbohydrate concentration	Potential	v
Carbohydrate flux	Current	i
Rate of photosynthesis	–	dq/dt
Source/sink strength	Electromotive force	e
Resistance (to concentration-driven flow)	Resistance	r

Fig. 1 Schematic representation of how elements of the model are added, in series (a) or parallel (b). Rectangles, resistances; circles, sources or sinks.

and the source/sink strength of the network that results from the combination of the two separate elements shown on the left side of the figure. Following the same labeling conventions, the combination of two parallel elements is shown in Fig. 1b.

Given these two rules, context-sensitive L-system productions are used to calculate fluxes and concentrations at the nodes (i.e. the connection points between elements), given the source/sink strengths and resistances to carbohydrate flow. The calculation is performed in two phases, which we refer to as the folding and unfolding of the network. In the folding phase, information is passed from the tips of branches to the base of the tree. The branching network is then gradually simplified by combining the elements into a sequence of ever more inclusive equivalent networks. For example, let us consider the branching axis comprised of a series of elements, shown in Fig. 2a. Working from right to left in this figure, network elements are combined, or 'folded', into equivalent simpler networks. In the first step, the elements shown in white (Fig. 2b) are combined into a single element. The resulting simplified topology is shown in Fig. 2c, where e' is the source/sink strength of the network equivalent to the combined white elements from Fig. 2b, and r' is the combined resistance. Proceeding in this way, the entire axis can be sequentially simplified to the network shown in Fig. 2d.

As there is nothing to the left of the resistance r_{s1} (Fig. 2d), no carbohydrate will flow through it. Therefore the carbohydrate concentration at the point of the 90° bend (v_1) will be equal to the sink/source strength e'_1. Now that this concentration is known, the network can be 'unfolded', and the fluxes can be determined for the entire branching structure. The first step
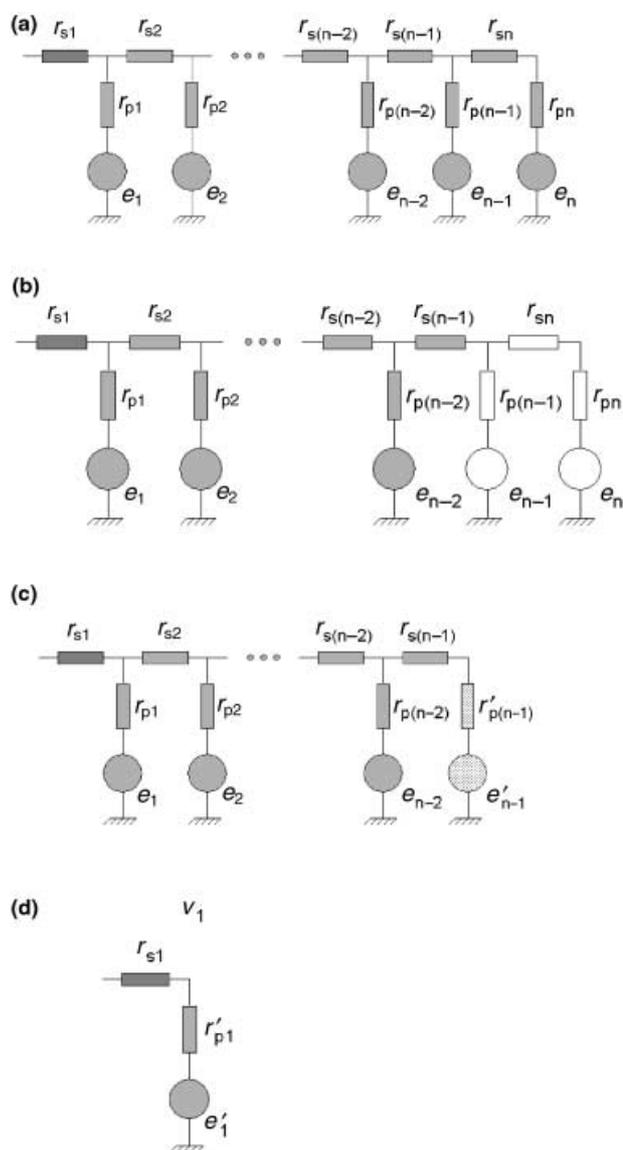

Fig. 2 Schematic representation of the method used for the simplification of a long series of elements. As the process moves from right to left, a simple equivalent circuit is gradually created to represent the entire starting series.

of this process is shown in Fig. 3a. Proceeding to the right, we gradually unfold the entire network into its original form, and calculate values for the concentrations and fluxes in the network (Fig. 3b). While this example deals with a simple nonbifurcating 'branch', structures that include bifurcations can be handled in a similar way.

If the relationship between the carbohydrate flux into a sink and the carbohydrate concentration at the point where that sink is attached were linear for each of the elements in the model, the computation of the fluxes flowing to each element of the network would be completed after the unfolding phase. However, as mentioned above, elements in the model may
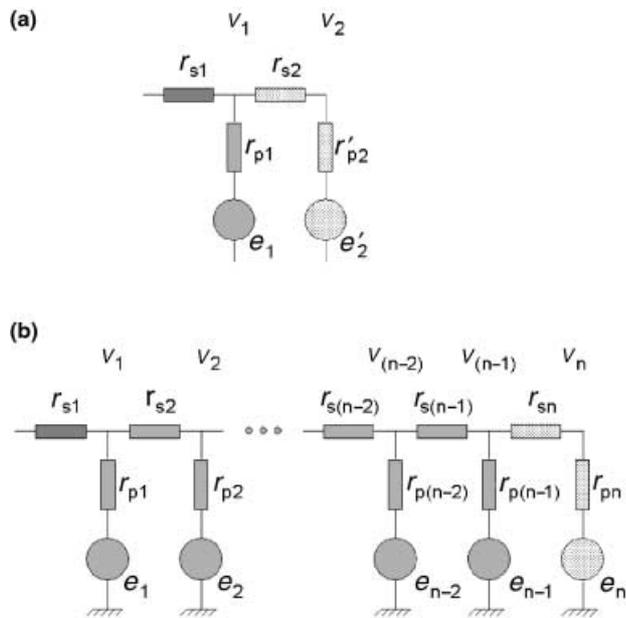
(a)

(b)

Fig. 3 Schematic representation of the method used to 'unfold' the simplified network resulting from the process shown in Fig. 2 into its original form. As this process moves from left to right, concentrations and carbohydrate fluxes throughout the modeled tree are calculated.

Fig. 4 Functions characterizing the behavior of a leaf. These functions are user-defined and can easily be modified in order to simulate different leaf behaviors. Functions representative of 'typical' leaf behavior are shown.

exhibit a nonlinear behavior, which can be thought of as the dependence of resistances and source/sink strengths on concentrations at the attachment points. Because of this, the distribution of concentrations and fluxes in the network is calculated iteratively, using an L-system implementation of the Newton–Raphson method (Press *et al.*, 1992). First, the functional characteristics of sinks and sources are linearized for the values of concentrations obtained in the previous iteration. The resulting source/sink strengths and resistances are then used to compute new values of concentrations in the next iteration of folding and unfolding. Once this process converges on a solution, fluxes out of each source and into each sink are assigned and accounted for, and the simulation advances one time-step.

Functional definitions of sources and sinks

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 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 also provide a very convenient means for experimenting with the model. Consistent with these notions, below we describe only the general character of the functions involved in the definition of a representative source and a representative sink.
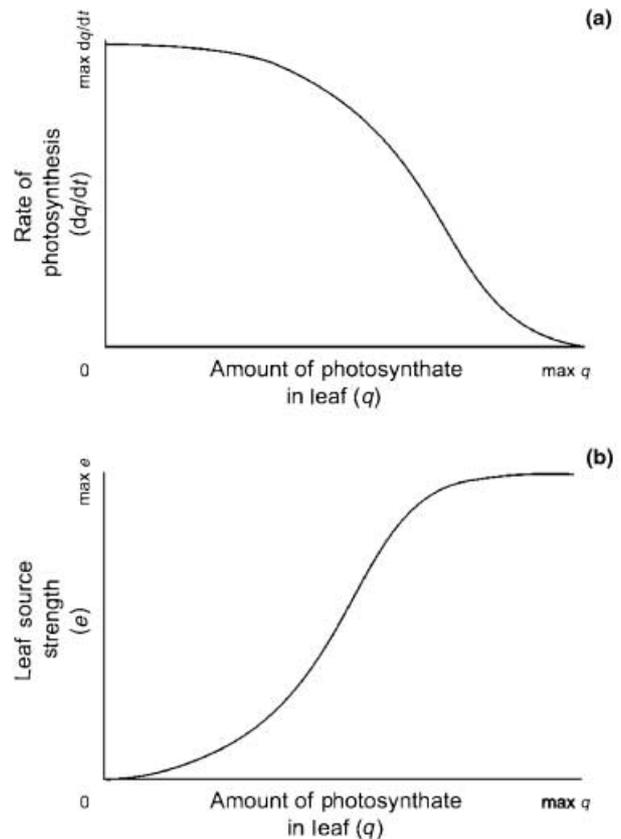
Sources of carbon

Leaves In each simulation step, a mature leaf can both gain some amount of carbohydrates through net photosynthesis, and lose some amount through 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:

$$dq/dt = f_1(q) \times f_2(I) \qquad \text{Eqn 1}$$

Function f_1 relates the rate of assimilation to the amount of carbohydrates (q) already present in the leaf. A sample function of this form is given in Fig. 4a. This decrease in the rate of assimilation as a function of increasing carbohydrate accumulation represents the effect on photosynthesis of excessive starch accumulation. 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 (plot not shown) captures the relation between the rate of assimilation and the incoming light. As photosynthetic carbon assimilation is modeled 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 & DeJong, 2003). Given the carbohydrate accumulated in the leaf, its source strength is determined by a third function f_3, shown in Fig. 4b.

The amount of carbohydrates lost by a leaf 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 (see the following section on carbon allocation for more information on sink behavior). The carbohydrate flux out of the leaf is multiplied by the time-step to give the decrement of accumulated carbohydrate. In the current version of the model, respiration is not handled explicitly. For leaves, photosynthesis is calculated as net photosynthesis, and carbohydrate uptake by individual sinks includes the carbohydrate used by respiration in those sinks. Although this approach ignores some obviously interesting physiology, it does not fundamentally affect the interactions between sources and sinks, and therefore was not simulated. We expect future versions of the model to include explicit functions governing respiration in sources and 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 (nonstructural) 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 nonstructural 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 (but generally not as strong as) other growing organs, as described in the following section. At a user-defined point in the spring, the carbohydrate from the storage compartments is remobilized. When this happens, the storage compartments become carbohydrate sources for a specified time. Their behavior during this time is analogous to the source behavior of leaves as described in the preceding section, except for the inability to 'refill' their carbohydrate charge via photosynthesis.

Carbon allocation (sink behavior)

The L-PEACH model includes the following sink types: stem segments (further decomposed into 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 is described in more detail and serves as an example of the general methods used in the model.
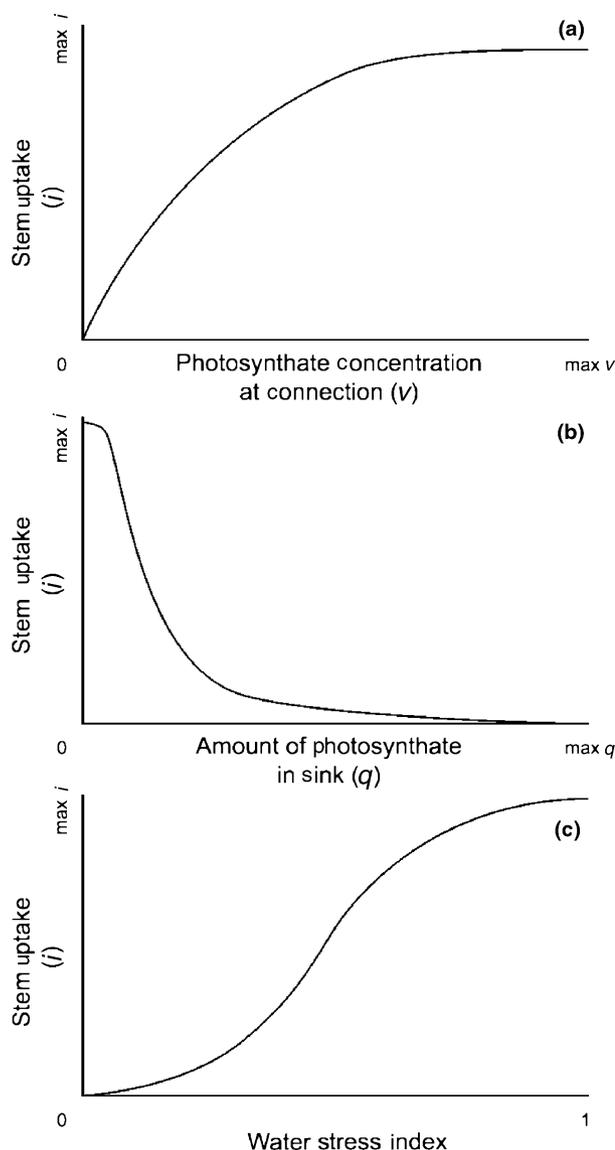
Fig. 5 Functions characterizing the behavior of a representative sink: the stem segment elongation sink. As with leaves, these functions can be easily manipulated by the user in order to simulate different sink behavior.

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

$$i = f_a(v) \times f_b(q) \times f_c(w) \qquad \text{Eqn 2}$$

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. An example of this relationship is given in Fig. 5a. 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, and it should be noted that the function shown in Fig. 5a is of the same form as a Michaelis–Menten function.

The elongation of a stem segment is not an open-ended process, but will stop when that segment reaches a mature length. The 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 shape shown in Fig. 5b, accomplishes this goal. According to this function, as a stem segment approaches its mature size (q approaches 'max q' on the x-axis), 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 1 (the plant has all the water it can use) to 0 (the plant has no water available at all). A sample function f_c is shown in Fig. 5c.

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 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 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 analogous to f_b in the stem-elongation sink), although their growth will eventually be modulated by functions linking root size, water/nutrient availability, and canopy water/nutrient demand.

Application examples

During a simulation, 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 chosen 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 manner in which the model handles carbon partitioning is illustrated in Fig. 6 with several still frames from a simulation run utilizing a highly simplified static 'tree' structure. In this example the modeled plant consists of a small number of stem segments, a root system (shown as a brown cylinder), two leaves, and two peaches. Color coding of the stem segments during the simulation run allows for visualization of carbohydrate fluxes within the plant. Colors ranging from light blue to purple indicate flow 'down' the plant towards the roots, while colors from yellow through red indicate flows 'up' the tree in the direction of the shoot tips (Fig. 6d). At the

beginning of the simulation (Fig. 6a) there is a strong flow of carbohydrates from each leaf out to the rest of the plant (note dark purple color of uppermost stem segments). Each of the fruits (green spheres) is consuming a considerable amount of these carbohydrates, resulting in a noticeably smaller carbohydrate flux down the plant below the fruit (lighter blue color of stem segments below the fruit in Fig. 6a). Fig. 6b shows a still frame taken after the right-hand fruit was 'pruned' before its maturity. Without this strong sink on the right-hand branch, a significant amount of the carbon flow is 'pulled' to the remaining fruit on the left branch (which is the strongest sink remaining on the tree at this time in the simulation). This is indicated by the red color of the stem segment below the left-hand fruit – carbohydrates are now flowing 'up' this segment towards the fruit. When the fruit is fully mature it no longer acts as a sink, and all carbon coming from the leaves goes downwards through the stem system to the roots (Fig. 6c).

The power of L-PEACH becomes clear when simulating the effects of management, genetic and environmental factors that can influence the plant through complex interactions between plant organs. For example, these interactions may include the influence of crop load, rate of fruit maturity, carbohydrate storage capacity, and water stress on 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 simulate responses to canopy management, such as pruning, the model contains a pruning function that allows the user to stop a simulation; prune leaves, fruit or branches at will; and resume the simulation with the adjusted tree structure. 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 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.

As examples, we have run two different pairs of simulations. The first pair involves 2-yr-old trees with indeterminate shoot growth under two different irrigation scenarios. One tree is irrigated at regular intervals such that it is never experiences any water stress. The other tree has a limited soil volume from which to extract water, and is irrigated at long intervals so that it experiences mild water stress. We assumed that shoot growth was more sensitive than photosynthesis to water stress, thus the primary visual effect of the water stress was a reduction in shoot elongation and girth growth (Fig. 7).
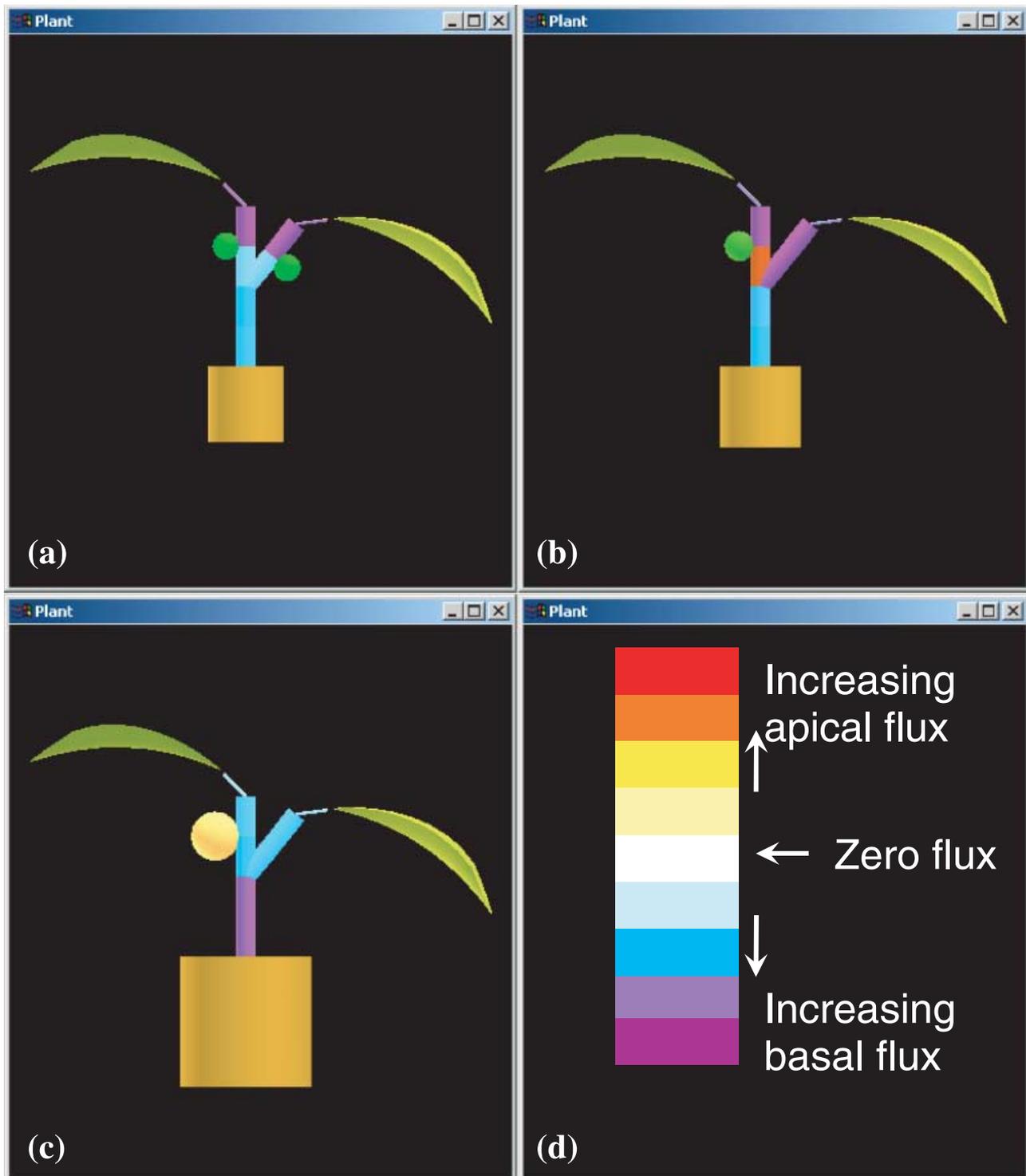
Fig. 6 Model output showing carbohydrate fluxes through a simplified tree structure (a); its changes following selective fruit pruning (b); and fruit maturation (c). (d) Visual key to the colors used to indicate directions and relative magnitudes of the fluxes.

Fig. 7 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 that 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 than leaf photosynthesis to mild water stress. 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.

The model also predicted quantitative differences in carbon partitioning (numerical data not shown).

In the second pair of simulations, fruit set is altered such that 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 (Fig. 8).

Discussion

L-PEACH is an L-system-based functional–structural 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 facilitates several aspects of model construction and operation: the integration of individual organ models

into a growing branching structure; the dynamic updating of the system of equations that characterizes carbon partitioning in this structure; the solution of this growing system of equations; the communication between the plant model and the model of its light environment; and the visual presentation of the simulated trees. L-PEACH has been implemented using the general-purpose plant modeling software L-STUDIO. This makes it possible to keep the model code compact by delegating generic issues (e.g. basic algorithms for simulating development and model visualization) to the general functionality of L-STUDIO. As a result, L-PEACH is easy to maintain and conducive to simulated experimentation. Furthermore, it may serve as a template for constructing other functional–structural models that involve solving complex systems of equations in growing plant structures.

In a comprehensive review of carbon-based tree growth models, Le Roux *et al.* (2001) pointed out that three critical issues have not been adequately addressed by most models:
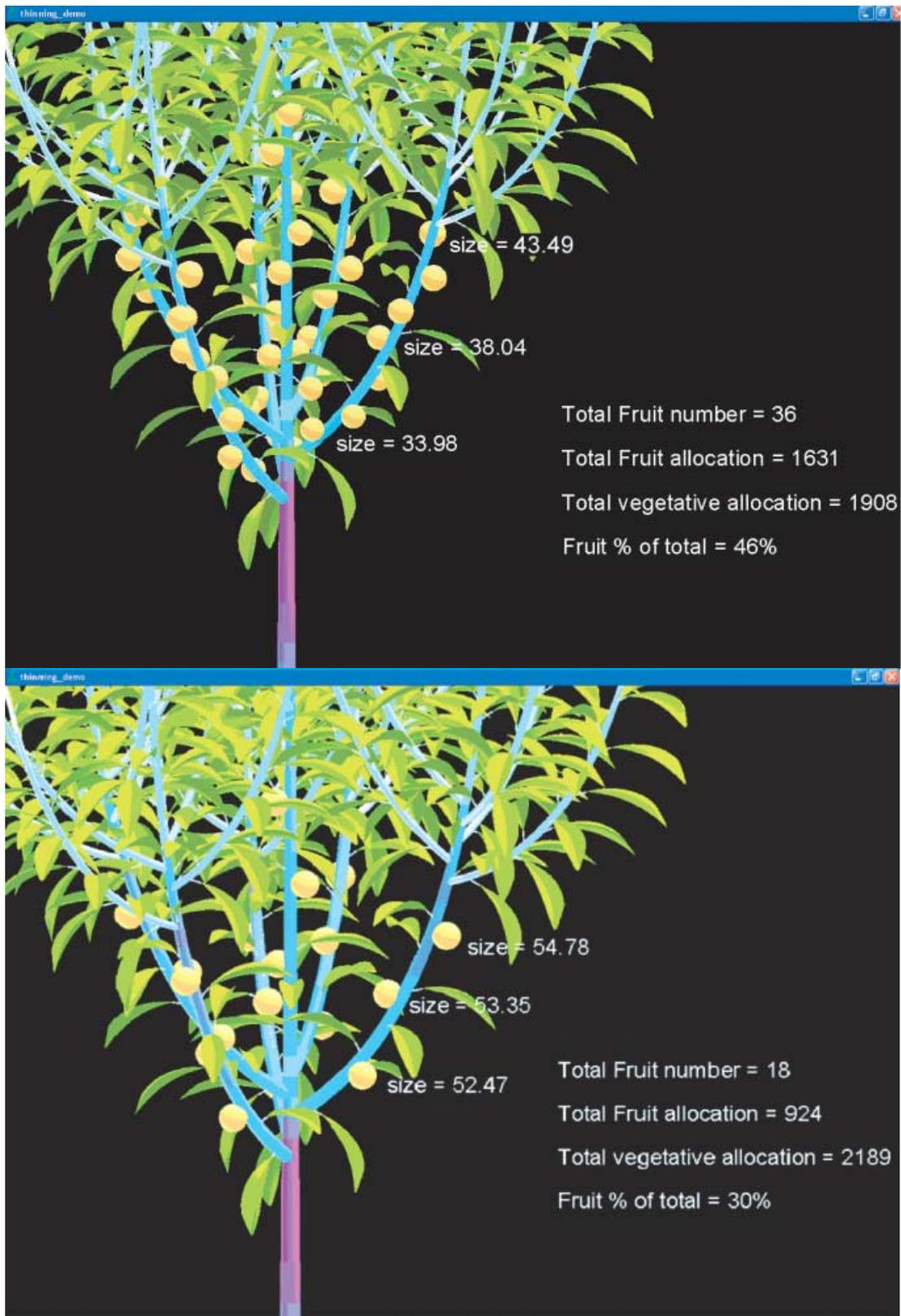
Fig. 8 The potential of the model to simulate crop load effects on fruit and tree growth, and on carbon partitioning. Upper panel, result of a simulation with a heavy crop load; lower panel, a simulation with half as many fruit. Stem colors are representative of the direction and relative magnitude of carbohydrate flow at the instant the simulation was halted.

(1) adequate representation of the dynamic and feedback aspects of carbon allocation on tree structure and carbon acquisition; (2) explicit treatment of carbon storage reserves and remobilization over multiple years; and (3) integration of belowground processes and tree water and nutrient economies into whole-plant function. Although the work is far from complete, the L-PEACH model provides a platform for addressing all these critical issues. By combining the sink-driven carbon partitioning concepts of the original PEACH model (Grossman & DeJong, 1994) into a distributed network of architecturally explicit sources and sinks, factors such as the proximity of individual sinks to other sinks and sources, as well as the transport resistances between these entities, can be accounted for and become involved in growth and carbon allocation outcomes. However, although there are some experimental data to indicate the functional nature of these relationships (Minchin et al., 1993; Lacointe et al., 2002), more data will be required before the model is fully calibrated. Considerable conceptual experimental research will be necessary to provide quantitative data required for this calibration.

This model also explicitly addresses carbohydrate storage in stems and roots during the growing season, and remobilization of stored carbohydrates during the spring growth flush. In the process of developing this model, we became increasingly aware of the lack of information about the quantitative dynamics of carbohydrate reserves in trees. As pointed out by Le Roux et al. (2001), the lack of knowledge of the mechanisms driving reserve deposition and remobilization is a major obstacle for evaluating the carbon available at any given time, or for relating reserve dynamics with internal and external variables in tree growth models. Based on preliminary data on root starch concentrations in peach trees (L.I. Solari & T.M.D.J., unpublished data) we have chosen to treat the starch reserve sinks in stems and root segments as compartments that have sink capacities proportional to their annual growth increment. These reserves then become carbon sources during the spring flush (Loescher et al., 1990). Current model functions related to carbohydrate reserves are based on preliminary data, and it is our intention to test more fully and quantify these aspects of the model in the near future.

The inclusion of the water stress/interaction component in the model is an attempt to demonstrate how root function can be incorporated into a dynamic L-system model of this type. As with carbon storage, the relationships between developing water stress and physiology are based more on published conceptual relationships (Bradford & Hsiao, 1982; Berman & DeJong, 1997; Basile et al., 2003) than on precise quantitative data collected for the purpose of calibrating the model. Nevertheless, the potential of this model to simulate functional interactions between root and shoot processes is readily apparent. Similarly, there is clearly the potential to incorporate additional root processes such as nutrient uptake into the model to more fully capture the functional dynamics of root–shoot interactions. Future developments could also involve the integration of existing architecturally based models of carbon transport and partitioning in roots (Bidel et al., 2000), in order to model root function more explicitly.

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