Integrating simulation of architectural development and source–sink behaviour of peach trees by incorporating Markov chains and physiological organ function submodels into L-PEACH

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This paper originates from a presentation at the 5th International Workshop on Functional–Structural Plant Models, Napier, New Zealand, November 2007.

Abstract. L-PEACH is an L-system-based functional–structural model for simulating architectural growth and carbohydrate partitioning among individual organs in peach (*Prunus persica* (L.) Batsch) trees. The original model provided a prototype for how tree architecture and carbon economy could be integrated, but did not simulate peach tree architecture realistically. Moreover, evaluation of the functional characteristics of the individual organs and the whole tree remained a largely open issue. In the present study, we incorporated Markovian models into L-PEACH to improve the architecture of the simulated trees. The model was also calibrated to grams of carbohydrate, and tools for systematically displaying quantitative outputs and evaluating the behaviour of the model were developed. The use of the Markovian model concept to model tree architecture in L-PEACH reproduced tree behaviour and responses to management practices visually similar to trees in commercial orchards. The new architectural model along with several improvements in the carbohydrate-partitioning algorithms derived from the model evaluation significantly improved the results related to carbon allocation, such as organ growth, carbohydrate assimilation, reserve dynamics and maintenance respiration. The model results are now consistent within the modelled tree structure and are in general agreement with observations of peach trees growing under field conditions.

Additional keywords: architectural modelling, carbon allocation, carbon-based model, functional–structural plant modelling, peach tree growth simulation.

Introduction

PEACH (Grossman and DeJong 1994*b*), a mechanistic computer model, was developed to understand the functional carbon economy of peach trees, how fruit trees function in the field environment, and to predict tree growth and crop yield responses of commercial peach trees. Although PEACH was able to simulate the reproductive and vegetative growth of peach trees, responses to variable environmental conditions and crop yield responses to commercial practices, it ignored interactions between tree architecture and carbon allocation. Each organ type was treated collectively as a single compartment and consequently all organs of a given type grew at the same rate. Because of these limitations PEACH did not simulate changes in architecture over time and intra-canopy variability among organs of the same type. These limitations were overcome in L-PEACH (Allen *et al.* 2005, 2007), a more detailed simulation model of carbon economy, in which the growth and function of organs were modelled individually within an architectural model of canopy development. L-systems (Lindenmayer 1968; Prusinkiewicz and Lindenmayer 1990) were used to simulate the architectural development of the tree and keep track of all its functional elements as it grows. The partitioning of carbohydrates between individual tree components was modelled using an analogy between the flow of resources in a plant and the flow of current in an electric circuit (Prusinkiewicz *et al.* 2007*b*).

L-PEACH was designed as a functional–structural plant model that simulated growth and carbon source–sink relationships within the architectural framework of a plant (Allen *et al.* 2005). However, substantial improvements to the model were needed to increase the realism of the simulated trees because the topology and geometry of the modelled tree (Allen *et al.* 2005) and the quantitative outputs generated by L-PEACH (Allen *et al.* 2007) did not correspond closely with observations of peach trees growing under field conditions.

To develop a more realistic model of tree architecture, we incorporated into L-PEACH a Markovian model of shoot topology and bud fate. A similar approach was used to simulate the development of fruiting apple trees by incorporating a Markovian model into L-system-based architectural tree models (Renton *et al.* 2006; Costes *et al.* 2008). The objectives of the present study were to improve the architectural development of simulated trees in L-PEACH by using Markovian models, to evaluate the physiological characteristics of simulated trees within the new architectural model, and to document the most significant improvements in the model algorithms obtained from this evaluation. To demonstrate the potential of the new version, we simulated tree architectural development, individual organ growth and functionality, carbohydrate assimilation, reserve storage and mobilisation, and maintenance respiration of peach trees over three consecutive years.

L-PEACH

Description of the model

The general model structure and simulation algorithm were reported by Allen *et al.* (2005, 2007). Original and subsequent developments to the model design that are necessary to understand the overall concept of the present research are described below.

L-PEACH is written in the L+C plant modelling language (Karwowski and Prusinkiewicz 2003; Prusinkiewicz *et al.* 2007*a*) and implemented using the L-system-based modelling software L-studio (Prusinkiewicz 2004*a*). The model is driven by environmental factors, such as daily solar radiation and daily minimum and maximum temperatures. These environmental drivers interact with four different components of the model: an architectural model of peach (*Prunus persica* (L.) Batsch) tree growth; a set of submodels that define the physiological functionality of various types of sources and sinks; an algorithm that simulates source–sink interactions and carbohydrate transport within the architectural model; and another set of submodels that simulate commercial practices, such as pruning and fruit thinning. The four components of the model interact over time, directing the growth and development of the organs that make up the simulated tree. In each daily step, 3D depictions of the simulated tree can be defined graphically using the L-studio (4.0) software (Karwowski and Lane 200; Fig. 1), while quantitative data generated during a simulation are automatically transferred to MATLAB (version 7.0, release 14; MathWorks, Natick, MA, USA) for data analysis and to display the results in the form of plots.

Tree architecture

The model is implemented using the L-system-based plant simulator LPFG included in L-studio (http://www.algorithmicbotany.org/virtual_laboratory; Karwowski and Lane 2006) combined with Markovian models (Durand *et al.* 2005) that are fully implemented in V-Plants software (http://www.sop.inria.fr/virtualplants; Guédon *et al.* 2001). The conceptual framework of L-systems is used to simulate carbohydrate allocation and to integrate all of the architectural elements of the plant, while the statistically based Markovian models are used to define patterns of vegetative and floral buds and the succession of shoots along an axis. The Markovian models provide probabilities for the location of branching and flowers, and the L-system-based carbon allocation model determines the amount of carbohydrate available to support the flowering and branching as the tree develops. We selected the strategy developed in MAppleT (Costes *et al.* 2008) to insert Markovian models into L-PEACH.

In the L-system formalism, a plant is treated as a collection of semi-autonomous modules (Prusinkiewicz 2004*b*). Specifically, L-PEACH modules represent stem segments (internodes), buds, leaves, flowers or fruits. The root system is treated collectively as a single module. The modelled tree is then described as a branching network of phytomers. Each phytomer consists of an internode with a specified initial length and a node that has a leaf and different types of buds attached to it. The bud modules play a significant role in the tree architectural model: vegetative buds produce new phytomers, which accommodate shoot growth, whereas floral buds produce flowers, which accommodate reproductive growth. Buds can be terminal or axillary. Terminal buds, which are only located at the end of a shoot, are always vegetative. With regard to the axillary buds, each phytomer has a central axillary bud that can be blind (failing to produce phytomers or flowers), floral or vegetative, with zero to two lateral floral axillary buds. The number and characteristics of the axillary buds, within a specific phytomer and along the parent shoot, are modelled according to bivariate statistical models estimated for three shoot types characterising unpruned peach trees (brindles, mixed shoots and vigorous shoots; Fournier *et al.* 1998) and adjusted in L-PEACH based on observations of shoots from pruned trees. In the bivariate models, the first variable controls the fate of the central bud and the second variable controls the fate of the lateral buds associated with the central bud. Branching organisation is modelled by hidden semi-Markov chains (HSMCs) that are indexed by the node rank from the base to the top of the shoot as a succession of zones that significantly differ in their axillary bud fates (Table 1). Four sets of parameters are estimated for each shoot type: initial probabilities that determine the first zone at the base of the shoots, transition probabilities between zones, occupancy distributions representing the length of each zone, and two observation distributions representing the fate of the central bud and the fate of the lateral buds within each zone, respectively (see Guédon *et al.* 2001 and Renton *et al.* 2006 for details). These distributions are the same in a given zone for all the shoot types, whereas transition probabilities depend on shoot type, with the median zones being progressively skipped as shoot length decreases (Table 1; Fournier *et al.* 1998).
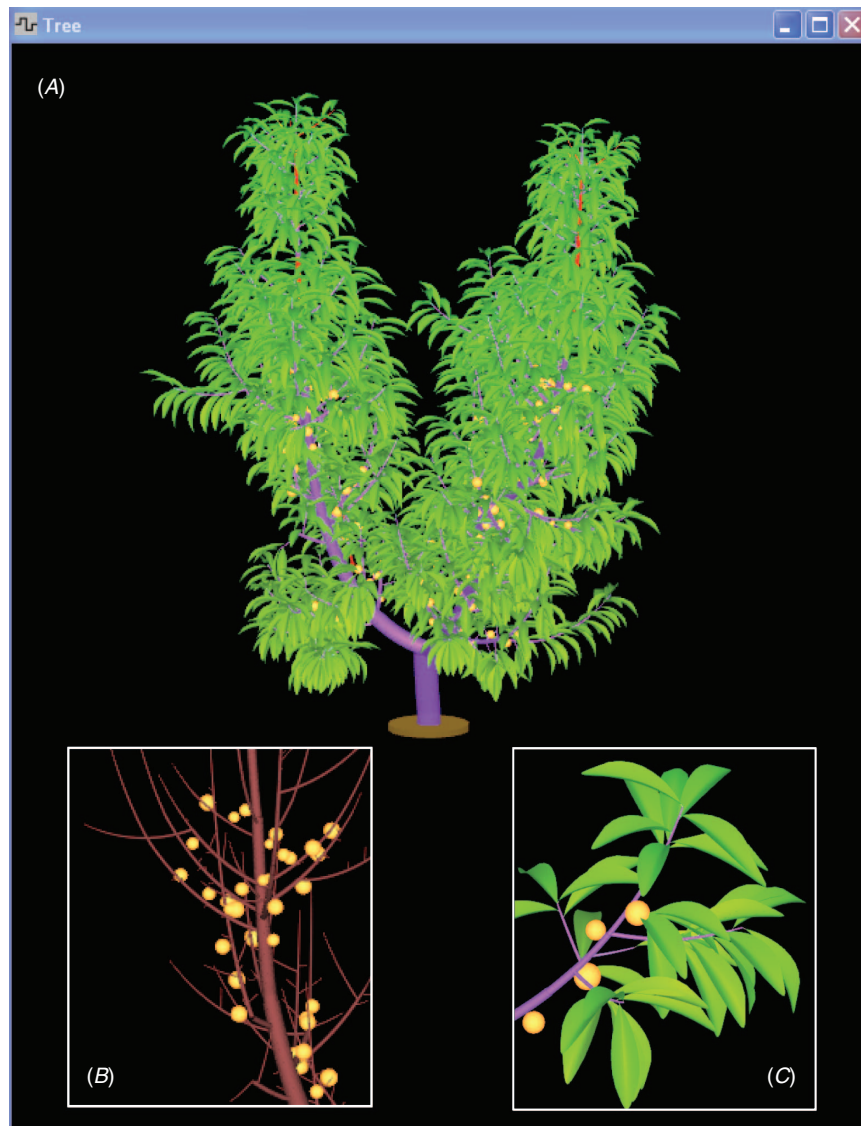
Fig. 1. (*A*) L-studio output showing the potential of L-PEACH to simulate the 3D structure of mature peach trees and (*B, C*) intra-canopy variability among organs of the same type in response to localised source–sink behaviours. L-studio allows modification of the stem's colours to automatically denote directions of net flux of carbohydrates (*A, C*) (see Allen *et al*. 2005 for further details), or a more natural bark-like colour (*B*). In (*B*) leaves were removed to increase the visibility of the fruit.

Table 1. Types of shoots and the succession of zones (from proximal to distal) within each shoot type according to the hidden semi-Markov chains used in L-PEACH

Zone composition represents the type of axillary buds that are the most frequent in that zone. AF, axillary flowers; B, blind buds; F, floral buds; V, vegetative buds

Type of shoot	Zone composition					
	1	2	3	4	5	6
Small	B					
Medium-small	B	V+AF	F	B		
Medium	B	V	V + AF	F	B	
Long	B	V	V + AF	F	B	
Very-long	B	V	V + AF	V + AF	F	B

L-PEACH is initiated with a root and a stem segment that has a leaf, a vegetative terminal bud, a vegetative axillary bud and an axillary latent bud. Simulation begins with the terminal bud break, and shoot growth is simulated by the creation of new phytomers. At this point the branching pattern of the tree is modelled with hidden semi-Markov chains in a two-step process: selection of the shoot type and generation of a succession of zones within each shoot, as determined by the bivariate model outlined above. The shoot types are categorised by their length (number of stem segments in the shoot) as small (5), medium-small (7–17), medium (16–35), long (36–56) and very long (59–87). The succession of zones within shoots is presented in Table 1. Small shoots are assumed to have five blind nodes. The remaining shoots have different lengths, but they all

start with a blind zone and end with a floral and blind zone. Despite this similarity, shoots differ in the number of zones and the number of vegetative and flower buds (Table 1). These vegetative buds can become active in the same season (sylleptic shoots), in the next growing season (proleptic shoots) or remain dormant. With regard to terminal bud fate, the potential length of the new shoots is based on the concept that succeeding shoots have less vigour than their parent shoot (Durand *et al.* 2005). This is modelled by a transition matrix representing a first-order Markov chain, as proposed in MAppleT (Costes *et al.* 2008). In addition, potential shoot length is reduced for shoots produced late in the season (Costes *et al.* 2007). Once the type of shoot is determined either by the Markov chain for terminal buds or the HSMCs for axillary buds, if there is no carbohydrate limitation the shoot will grow to its full size. If there is a carbohydrate limitation, the realised length will be reduced (Costes *et al.*

2007). Flower buds remain dormant in the season in which they have been generated and set fruit in the next season shortly after the bloom date.

The architectural model is governed by calendar time (Table 2). The time parameters include dates of floral bud break, vegetative bud break, full bloom, initiation of bud dormancy in the late summer or autumn, and the start and end of leaf abscission. These parameters can be easily specified by the user and provide flexibility for simulating experiments that are conducted for model evaluation. We anticipate that future versions of the model could include environmentally and physiologically induced differences in the calendar parameters.

Functional characteristics of source and sinks

The original model (Allen *et al.* 2005) contained more than 30 functions describing relationships between specific

Table 2.   Parameters used to determine architectural development, physiological functionality of source and sinks, and management practices in the L-PEACH model

CH_2O, carbohydrates; CRG_{leaf}, carbohydrate requirements for leaf growth; CRG_{stem}, carbohydrate requirements for stem growth. Day of year pertains to the northern hemisphere

Parameter	Value (unit)	Origin
Architectural development		
Floral bud break	60 (day of year)	User-defined
Full bloom	72 (day of year)	User-defined
Vegetative bud break	78 (day of year)	User-defined
Bud dormancy	257 (day of year)	User-defined
Start of leaf abscission	288 (day of year)	User-defined
End of leaf abscission	319 (day of year)	User-defined
Leaf		
f_a	$f_a = [18.9 \times$ leaf PAR exposure$] - 55$	Rosati *et al.* (2002)
Maximum leaf area	40 (cm^2)	Steinberg *et al.* (1990)
Specific leaf weight	0.004 (g DW cm^{-2})	Marini and Marini (1983)
CRG_{leaf}	1.463 (g CH_2O g^{-1} DW)	Penning de Vries *et al.* (1989)
Maintenance respiration	3.5 (mmol CO_2 g^{-1} DW s^{-1})	Grossman and DeJong (1994*b*)
Stem segment		
r_i	0.1 (cm)	User-defined
Maximum stem length	2.7 (cm)	User-defined
ρ_{stem}	0.54 (g DW cm^{-3})	Grossman (1993)
CRG_{stem}	1.14 (g CH_2O g^{-1} DW)	Grossman (1993)
Storage ratio	20 (% of total stem mass)	User-defined
Storage mobilisation period	60 (days after bloom)	User-defined
Maintenance respiration	0.8 (mmol CO_2 g^{-1} DW s^{-1})	Grossman and DeJong (1994*b*)
Fruit		
Fruit abscission	80 (% of total flowers)	User-defined
Fruit abscission period	60 (days after bloom)	User-defined
Maintenance respiration	0.63 (mmol CO_2 g^{-1} DW s^{-1})	DeJong and Goudriaan (1989)
Root		
Storage ratio	30 (% of total root mass)	User-defined
Storage mobilisation period	60 (days)	User-defined
Maintenance respiration	0.8 (mmol CO_2 g^{-1} DW s^{-1})	Grossman and DeJong (1994*b*)
Management practices		
Day of budding	136 (day of year)	Commercial practice
Fruit thinning date	130 (day of year)	Commercial practice
Fruit thinning space	4 (no. stem segments)	Commercial practice
Harvest day	240 (day of year)	Mid-late maturing cultivar

variables in the model, and was not calibrated to specific units of carbon. The model is now calibrated to a basic 'currency' equivalent to grams of carbohydrate, and many of the original functions have been simplified by using common sigmoidal functions to model functions with similar shapes, with scaling parameters for calibrating these functions to specific components. These parameters can be easily modified by the user to simulate different organ behaviour or parameterise specific simulations. The parameters used to determine the functional characteristics of sources and sinks are based on concepts of carbohydrate partitioning from the literature. However, when quantitative parameter values of a given source–sink component were unavailable, the functional values for the component were estimated using *in silico* simulation experiments to find values that yielded reasonable results (Table 2).

Leaves

Leaves are programmed to perform net photosynthesis (Pn) and to assimilate carbohydrates into the tree assuming that water and nutrients are not limiting. The amount of Pn by the leaf over a day is the product of three functions:

$$Pn = f_a \text{ (leaf light exposure)}$$
$$\times f_b \text{ (leaf carbohydrate storage)} \times f_c \text{ (leaf area)}, \quad (1)$$

where f_a captures the relationship between the rate of assimilation and the incoming light. Carbon assimilation is simulated in time steps of 1 day, and is calculated as a linear function of accumulated light exposure of a leaf during a day (Table 2). Interactions between tree architecture and light environment are taken into account by using a model of light attenuation through the canopy as described by Grossman and DeJong (1994*b*). Function f_b (sigmoid function), which was previously characterised by Allen *et al*. (2005), describes the feedback inhibition of leaf photosynthesis as a function of the existing amount of carbohydrates in the leaf (Neales and Incoll 1968; Foyer 1988). Function f_c relates the amount of carbohydrate assimilation to the leaf area. Leaf area is not constant and is programmed to reach a maximum value (Table 2) that is dependent on the amount of carbohydrate available for leaf growth during a specific leaf growth period. Leaf area is calculated by placing an upper limit on the total accumulated amount of carbohydrate (g) using a sigmoid function (f_d):

$$\text{leaf area} = \text{max leaf area}$$
$$\times f_d \left(\frac{\text{leaf carbohydrate mass}}{\text{max leaf area} \times \text{SLW} \times \text{CRG}_{leaf}} \right), \quad (2)$$

where SLW denotes the specific leaf weight (the present model uses the simplified assumption that the SLW is constant in time and throughout the canopy) and CRG_{leaf} is the carbohydrate requirement for leaf growth (Table 2). According to the f_d function, as a leaf approaches its final size ($f_d \sim 1$) it accumulates carbohydrates at a decreasing rate, even if the carbohydrate concentration at the point where the leaf is attached is high.

The carbohydrates gained by the leaf through photosynthesis are first stored in the leaf. Some of these carbohydrates remain in the leaf, simulating starch accumulation. The remainder is used by the leaf for its growth or is exported to other parts of the tree. From the time of leaf emergence to the time at which the leaf reaches its final size, the gained carbohydrates are used primarily to build the young leaf. Afterwards, the leaf is a net source of carbohydrates, which are exported from the leaf. Carbohydrates assimilated by the leaf are also used for leaf maintenance respiration, which has been programmed to respond to temperature using previously determined leaf-specific respiration rates (Grossman and DeJong 1994*b*) (Table 2).

Stem segments

Stem segments (internodes) act as conduits for carbohydrate transport within the tree and require significant amounts of carbohydrates for elongation growth, girth growth, storage and maintenance respiration. Stem segments have been programmed to reach their maximum lengths following similar procedures described for leaf area expansion (eqn 2). In this case, we considered that a stem segment has the shape of a cylinder and that stem elongation occurs before secondary (girth) growth:

$$\text{stem length} = \text{max stem length}$$
$$\times f_d \left(\frac{\text{stem carbohydrate available forelongation}}{\text{max stem length} \times \pi \times r_i^2 \times \rho_{stem} \times \text{CRG}_{stem}} \right), \quad (3)$$

where r_i is the initial radius of the segment, ρ_{stem} is the stem density and CRG_{stem} is the carbohydrate requirement for stem growth (Table 2). Once the maximum length is achieved, girth growth is simulated using the pipe model (Shinozaki *et al*. 1964). For most of the growing season the stem segments act as sinks competing for carbon with other growing organs. The ratio of storage carbohydrate to structural carbohydrate (the sum of primary and secondary growth) in a given segment cannot exceed a user-specified value (Table 2). At floral bud break, carbohydrate from the storage is mobilised for a user-defined period of time (Table 2) and exported to other parts of the tree to support initial leaf and fruit growth before current carbohydrates from photosynthesis can support total tree carbohydrate demand. Stem segment maintenance respiration is calculated using specific respiration rates for branches determined by Grossman and DeJong 1994*b*) (Table 2).

Fruits

Flower buds set fruit shortly after the bloom date. However, some of these fruits drop during the growing season. Fruit abscission might vary according to weather and local growing conditions. To cover these types of scenarios, several parameters can be adjusted by the user. These parameters include the fraction of the fruit that abort and the period of time over which fruit abscission can occur (Table 2). Fruit growth is programmed following seasonal relative growth rates, as a function of accumulated degree days after full bloom. Different peach cultivars can be modelled using growth rate functions obtained from field experiments (DeJong and Goudriaan 1989; Grossman and DeJong 1994*b*). The relative growth rate functions provide the growth potential of fruit for each time interval and interact with the amount of carbohydrates available for fruit growth over specific intervals to generate realised fruit growth over time. Fruit maintenance respiration

rates were programmed using previously obtained data (DeJong and Goudriaan 1989) (Table 2).

Root

Similar to the stem segment modules, the root can act both as a sink or a source during the growing season. Root growth is programmed as a function of root weight and above biomass weight, according to data obtained from field experiments (Grossman and DeJong 1994*a*). Root carbohydrate storage varies significantly during the year according to concepts described by Loescher *et al*. (1990). Specifically, root reserves are depleted at floral bud break for a user-defined storage mobilisation period (Table 2). The amount of carbohydrates available for initial reproductive and vegetative development is a defined percentage of the total root weight. This percentage can be modified by the user, with data on root starch concentrations in winter (Lopez *et al*. 2007; T. M. DeJong, unpubl. data) suggesting values between 10 and 30% of the total root mass. Once current photosynthates are available for reproductive and vegetative organ growth and maintenance, root reserves are replenished until leaf abscission. Root maintenance respiration rates were programmed using respiration coefficients from PEACH (Grossman and DeJong 1994*b*) (Table 2).

Carbohydrate assimilation, transport and partitioning algorithm

For the purpose of carbohydrate assimilation, transport and partitioning within the modelled tree, the tree branching network described in the tree architecture section is abstracted into a dynamically reconfigured, non-linear and non-stationary electric circuit. Its subcircuits represent individual stem segments or plant organs (buds, flowers, fruits and leaves), connected into a network with transport resistances (Allen *et al*. 2005; Prusinkiewicz *et al*. 2007*b*). Roots are treated as one large single module. Each subcircuit has components (sources of electromotive force in series with resistances) that represent primary growth (elongation growth), secondary growth (girth growth), storage and maintenance respiration (Fig. 2). Parameters of these components capture the plant module's physiological

Fig. 2. Schematic representation of any individual module within the tree-branching network. Rectangles denote resistances; circles denote sources of electromotive force.

potential to utilise carbohydrates for growth, respiration or storage. Physiological potentials for growth and growth respiration are primarily based on defined relative growth rate functions for each organ, while maintenance respiration is estimated from temperature and empirically derived relationships (Grossman and DeJong 1994*b*). The physiological potential of storage sinks to take up carbohydrates is estimated by assigning a storage capacity as a percentage of dry weight to each module capable of storage. In each simulation step, the electric circuit is used to calculate the amount of carbohydrate exchanged between all the elements of the electric circuit. The circuit is then updated to reflect the resulting changes, and the next simulation step proceeds. A numerical method implemented using L-systems was developed to iteratively solve the equations for carbohydrate flow and allocation (Prusinkiewicz *et al*. 2007*b*).

Because of the complexity of the interactions of all components of the model, we developed tools for displaying and analysing quantitative outputs and for tracking the behaviour of individual modules. To this end, we incorporated into L-PEACH subroutines for generating data files that are subsequently analysed and visualised using MATLAB (version 7.0, release 14). This has allowed for systematic analysis and debugging of many aspects of the model.

Simulation of commercial practices

In the current version of L-PEACH we included modules in the model that make it possible to simulate management operations typically conducted in the field, including pruning, budding, fruit thinning and harvesting.

Pruning is carried out by directly manipulating the tree displayed on the screen with the LPFG plant modelling program (Prusinkiewicz *et al*. 2007*a*). Tree responses to pruning are modelled using the concepts of apical dominance (Wilson 2000) and reiteration (Hallé 1978). When a pruning cut is made, the fates of the buds between the cut and the next branching point are reassigned. Following reiteration concepts, we assumed that, if axillary vegetative buds are present, the distal buds are assigned to the same shoot category as the shoot that has been removed. Following the apical control concept (Wilson 2000), we also assumed that only a few axillary buds become active, while the rest remain latent. This follows the idea that the distal buds are no longer under apical dominance, but as they emerge they have a dominance effect on the more proximal buds. The number of activated buds is determined by the stem segment circumference below the pruning cut. If only axillary latent buds are present, then the distal latent buds become active and develop very-long shoots (Pernice *et al*. 2006). In any case, if the pruning cut is made during the growing season, the distal buds become active immediately. If pruning is done during the dormant period, the distal buds become active at vegetative bud break.

To increase the realism of the model while simulating commercial fruit tree growth, vegetative propagation of the tree by budding can be simulated by pruning a simulated young seedling tree back to a few centimetres above the ground, and growing a new tree from the new shoot that grew in response to the hard pruning cut. As budding is usually carried out in the spring (around May; Table 2) and the potential length of
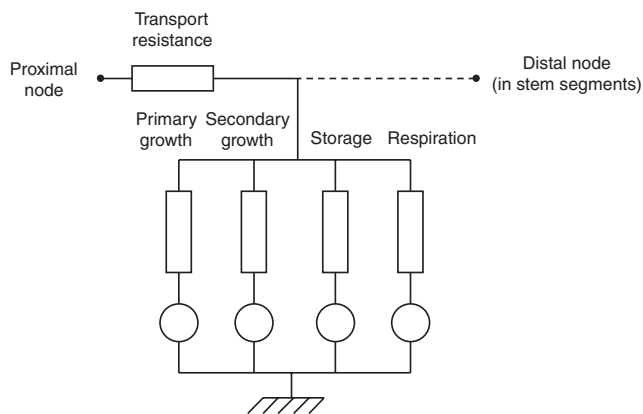
shoots is based on how late in the growing season the shoot starts to grow, a budded tree has a final size limitation dependent on the 'budding' date.

Fruit thinning can be carried out either manually or automatically. For manual fruit thinning the user can select the fruits to be removed by directly manipulating the displayed tree (Prusinkiewicz *et al.* 2007*a*). The automated fruit thinning option is based on the proximity of the fruits to one another, and attempts to simulate commercial fruit thinning practices. The fruiting shoots are scanned from the base to the distal end, and if two or more peaches are separated by less than a specified number of stem segments, the more distal fruits are removed. Thus, the fruit that remain after thinning can be automatically spaced to a specified minimum number of internodes between fruit.

Harvest date is a user-defined parameter (Table 2). Taking into account that fruit growers classify peach cultivars based on harvest date, the harvesting parameter is an important component of simulating different peach cultivars. In future versions of the model we also plan to include the effects of early spring temperatures on harvest date (Ben Mimoun and DeJong 1999).

Evaluation of the new architectural model and its subsequent effects on source–sink behaviour of simulated peach trees

Evaluation of the model was carried out by simulating peach tree development during three consecutive years using the

parameters presented in Table 2. Weather data were obtained from the California Irrigation Management Information System (CIMIS), Davis, CA station. The simulated trees were either left unpruned or were trained to a perpendicular V system following the procedures described by DeJong *et al.* (1994) and simulated as interactive pruning cuts in winter.

Tree architecture

In the first growing season, before budding, a simulated tree had a single, very-long shoot that was cut before reaching its final length (Fig. 3; Table 1). After budding, a very-long shoot emerged and grew in the direction of the main axis, while axillary vegetative shoots grew sylleptically (Genard *et al.* 1994). The resulting simulated trees were similar to those found in a fruit tree nursery just before sale. Prior to the beginning of the second year, the trunk of the pruned trees was cut to half a metre (Fig. 3*A*). This cut prompted a reiteration response, resulting in the production of new very-long shoots below the cut after bud break. This new shoot growth compensated for the perturbed equilibrium between the shoot and the root after the pruning cut (Genard *et al.* 1998; Pernice *et al.* 2006). The sylleptic shoot growth behaviour within the new very-long shoots was similar to that of the first growing season (Fig. 3*A*). This response is the key to eventually developing the strong, open structure of commercial peach trees. In contrast, in unpruned trees new shoots grew mainly from the terminal buds and were less vigorous than their parent
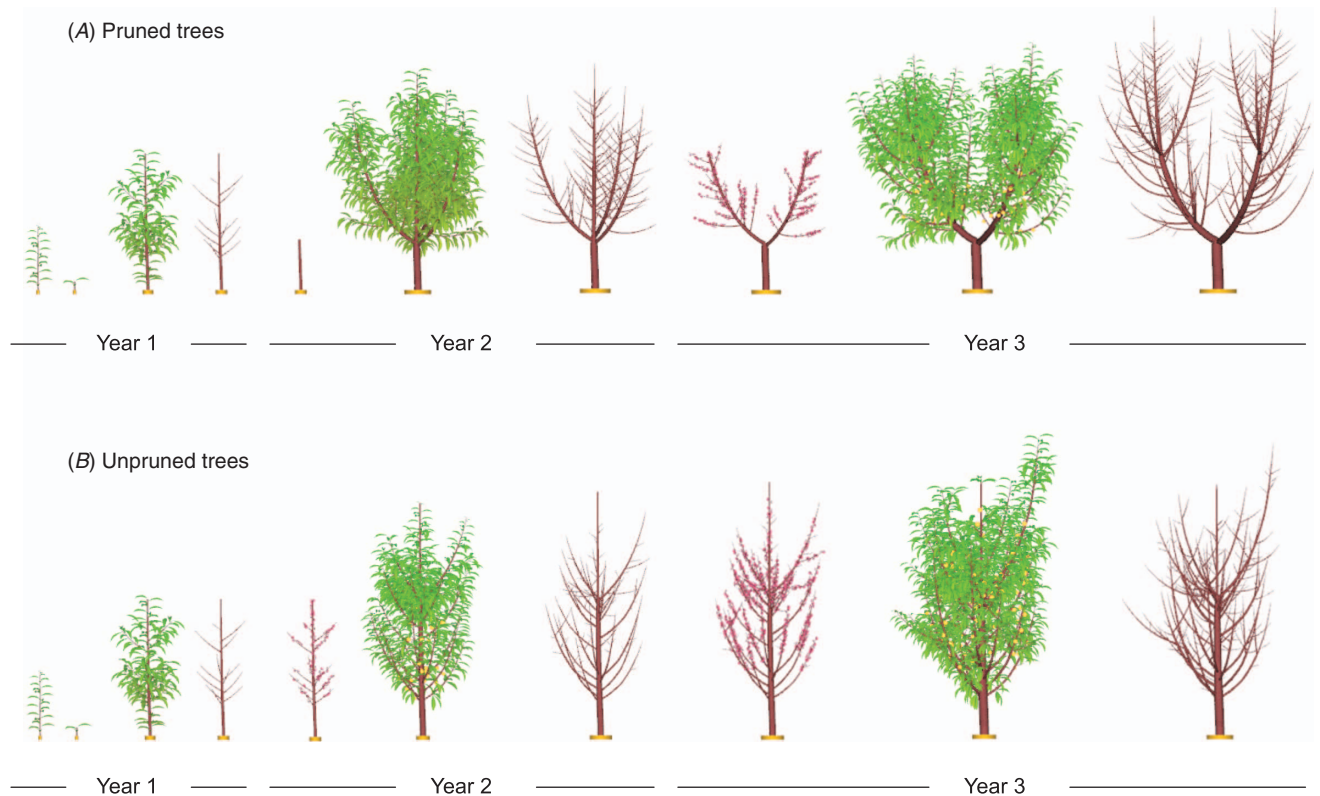

Fig. 3. Model output showing 3D depiction of (*A*) a pruned peach tree and (*B*) an unpruned peach tree over 3 years of growth. The pruned tree was trained to a perpendicular V system by pruning cuts in winter. The final tree height was ~3.0 m.

shoots. The first crop of fruit was produced on shoots formed in the previous (first) year (Fig. 3*B*).

At the beginning of the third year, two branches oriented in the same vertical plane were selected for developing the main scaffolds of the V-shaped training system (Fig. 3*A*). The selected branches received heading cuts and very-long shoots grew again from their terminal ends after vegetative bud break. Sylleptic shoots that were formed during the previous year on the previously established main scaffolds remained unpruned. These shoots produced flowers, fruits and proleptic shoot growth after bud break (Fig. 3*A*). During the third growing season, unpruned trees produced a large crop, causing a significant reduction in tree vigour compared with pruned trees (Fig. 3*B*).

Source–sink behaviour of the simulated tree

The complexity of L-PEACH makes it difficult to analyse the relationships between individual components of the model. For instance, the direction and quantity of carbon flux through a stem segment at any given time step depends on the sink demands and source supplies above, below and within this segment, and it is difficult to predict these values *a priori*. For the same reason, quantitative verification of all of the individual components of the model is difficult, and it would be virtually impossible to design a field experiment to independently evaluate the physiological characteristics of all of the components of a tree. However, despite these limitations, L-PEACH is a potential tool to integrate and evaluate source–sink relationships in peach trees and to elucidate seasonal organ and whole-tree behaviour at higher levels of organisation. For demonstration purposes

some quantitative outputs are presented here to illustrate simulated results related to carbon allocation, such as carbohydrate assimilation, maintenance respiration, reserve dynamics and organ growth.

As illustrated in Fig. 4*A*, *C*, L-PEACH effectively models variations in net photosynthesis as a consequence of variable weather conditions. The model is sensitive to cloudy days, although differences in the leaf export rate are reduced compared with differences in photosynthesis (Fig. 4*C*). This phenomenon might be explained by an increase in the amount of carbohydrates mobilised from the leaf storage compartment on cloudy days. This is consistent with the observation by Wardlaw (1990) that carbohydrate reserves built up within the leaf might be mobilised and exported when current photosynthesis is decreased. The amount of carbohydrate assimilated by individual leaves is also a function of the physiological state of the leaves. Our basic approach for dynamically modelling leaf growth as a function of available resources and potential leaf size (eqn 2) was also successful in reproducing peach leaf expansion over time (Fig. 4*B*, *D*): leaf maturity was achieved ~25 days after vegetative break, consistent with observations by Steinberg *et al.* (1990). However, we recognise that our leaf growth submodel could be improved by a more detailed analysis of peach leaf growth and by using more numerical methods to describe the growth (Seleznyova 2007).

Simulated seasonal patterns of tree daily carbohydrate assimilation increased with increases in total leaf biomass (Fig. 5). Between 33 and 50% of the tree carbohydrate assimilation was used for tree maintenance respiration (Fig. 5), indicating the importance of respiratory cost in the carbohydrate
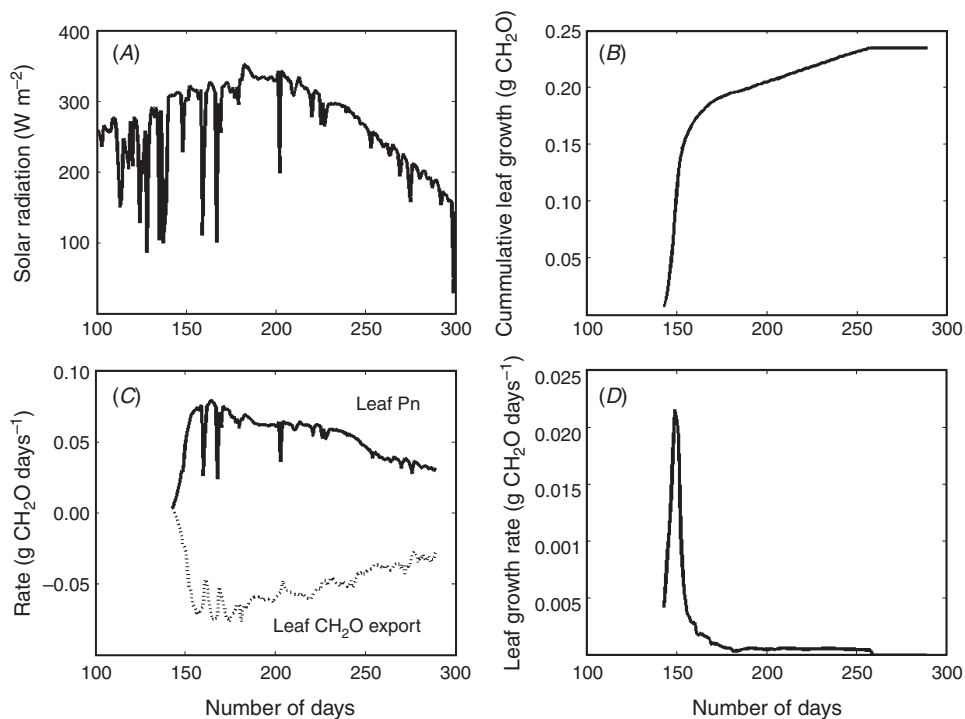

Fig. 4.   Seasonal patterns of (*A*) solar radiation, (*B*) individual leaf growth, (*C*) leaf photosynthesis and leaf carbohydrate export and (*D*) individual leaf growth rate. Simulated data represent an individual leaf during the first year of tree growth. Pn, photosynthesis; CH₂O, carbohydrates.

balance of the tree (Grossman and DeJong 1994b; Vivin et al. 2002). Simulated tree daily maintenance respiration increased with increases in temperature and whole-tree biomass (Figs 5 and 6A). When tree daily maintenance respiration reached its
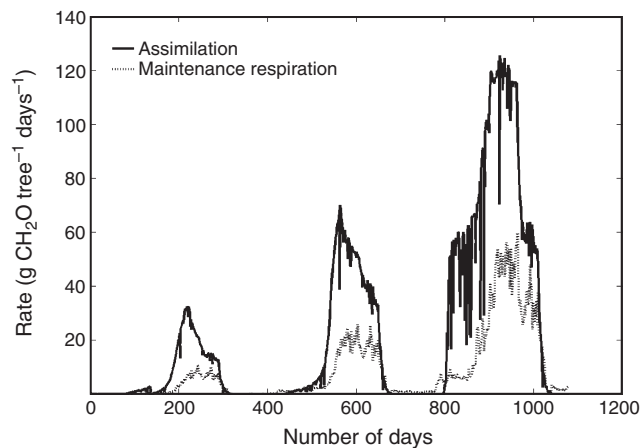

Fig. 5. Simulated seasonal patterns of daily carbohydrate assimilation and maintenance respiration during three consecutive years of peach tree growth. The simulated tree was trained to a perpendicular V system. In the third year the crop load was 100 fruits per tree. CH_2O, carbohydrates.
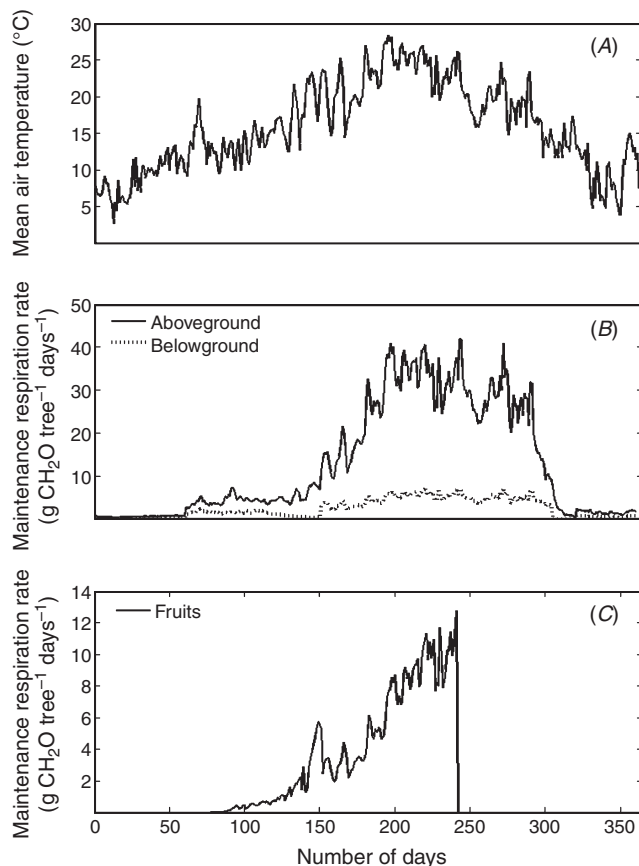
Fig. 6. Seasonal patterns of (A) daily air temperature, (B) aboveground and belowground maintenance respiration and (C) total fruit maintenance respiration during the third year of growth of peach trees trained to a perpendicular V system. The crop load was 100 fruits per tree. CH_2O, carbohydrates.

maximum rates, it accounted for a relatively constant amount of carbohydrate usage (Fig. 5) (Grossman and DeJong 1994b). Similar behaviour to that reported for total tree maintenance respiration was observed for both the above- and below-ground structural organs (Fig. 6B). Assuming that fruits were harvested before reaching a constant amount of carbohydrate usage (Fig. 6C); the shape and magnitude of simulated fruit respiration curves were consistent with the results of DeJong and Walton (1989) for late-maturing peach trees.

Part of the carbohydrates assimilated by the tree during the growing season was stored in the root and stem segments. Root carbohydrate reserves were subsequently used for maintenance respiration during the winter season and to support early tree growth after bud break (Fig. 7) (Loescher et al. 1990; Jordan and Habib 1996). The seasonal dynamics of reserves in the stem segments were not as clear as the dynamics observed in the root. This was because the root supplied carbohydrates to the stem segments before bud break and because part of the carbohydrates stored in the stem segments were removed after winter pruning (results not shown). More refinement is needed to quantify carbohydrate storage and mobilisation functioning in the model, but modelling stem and root storage as explicit sinks and sources for specified periods of time, as suggested by Cannell and Dewar (1994), appears to yield generally reasonable model behaviour.

Simulated tree carbon assimilation provided sufficient carbohydrates to support organ growth (Fig. 8). During the 3 years of simulation, most of the biomass (in carbohydrate equivalents) was accumulated in the stem segments. The roots accumulated approximately one-third as much biomass as the stem segments (Grossman and DeJong 1994a). The fruits also accumulated a significant amount of assimilates, while the leaves had lower amounts of biomass. The simulated patterns of organ growth also reflected the interaction with tree architecture and the different components of the models (Fig. 8). The reductions in total leaf and stem segment carbohydrate equivalents in biomass after the growing season were a consequence of leaf abscission and winter pruning, respectively. The seasonal patterns of simulated root biomass showed that the tree carbohydrate
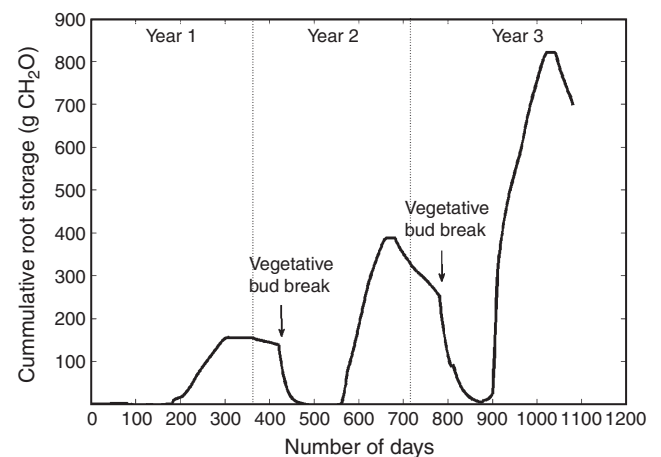

Fig. 7. Seasonal variations in total carbohydrate reserves in the root during three consecutive years of peach tree growth. The simulated tree was trained to a perpendicular V system. In the third year the crop load was 100 fruits per tree. CH_2O, carbohydrates.
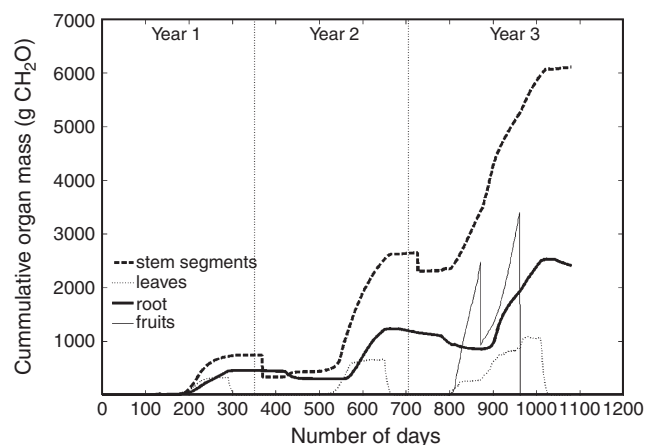
Fig. 8. Organ mass during three consecutive years for simulated peach trees trained to a perpendicular V system. Sudden drops in the cumulative mass of stems and fruits were the result of pruning, fruit thinning and fruit harvest. In the third year the crop load after fruit thinning was 100 fruits per tree. CH_2O, carbohydrates.

balance was source limited at the beginning of the growing season. Total fruit carbohydrate mass per tree decreased with a reduction in the number of fruits per tree after fruit thinning (day 870 in Fig. 8). The substantial reduction in fruit competition after fruit thinning allowed optimisation on average fruit carbohydrate mass at harvest (~33 g fruit^{-1}) (Fig. 8).

Conclusions

The use of hidden semi-Markov chain concepts for modelling branching structures in L-PEACH successfully reproduced trees that were similar to the peach trees observed in orchards. The new architectural model along with several improvements in the carbohydrate-partitioning algorithms significantly improved the results related to carbon allocation, such as organ growth, carbohydrate assimilation, reserve dynamics and maintenance respiration. The model results were in general agreement with observations of peach trees growing under field conditions.

The current L-PEACH model substantially improved on the previous 3D depictions of peach trees presented by Allen *et al*. (2005, 2007). The realism of the new architecture and the pruning responses can help understand the general practices that should be followed for training systems designed to obtain specific tree shapes. Users can observe how the natural growth habit of the tree is modified by pruning, how the tree responds to different types of pruning cuts, including improper cuts, without dramatic commercial consequences. These features allow L-PEACH to be used as a tool for teaching, including interactive lessons on common training practices.

L-PEACH is still in the early stages of development, but it is already a useful tool for simultaneously modelling tree architectural growth and carbohydrate source–sink relationships in peach trees. L-PEACH can also be used to guide experimental research by helping to identify or develop quantitative hypotheses of potential yield-limiting processes that can be measured in the field. The current model assumes that the water and nutrient resources required for normal growth are not limiting and additional model development is underway to

address these limitations. Similarly, the Markov chain shoot submodel data currently used in the model needs to be quantified for pruned trees growing under commercial conditions. More quantitative validation of the model at the whole plant and individual organ levels is needed to evaluate the accuracy of simulated trees. As much of the available data from previous experiments and from the literature are not suitable for quantitatively validating L-PEACH, additional quantitative data need to be collected for this purpose. As there are hundreds of peach cultivars grown commercially and each tree is heavily managed (especially pruning) over multiple years, the overall goal of this project is to develop a general model of peach tree physiology and architectural growth and development that can be adjusted for specific cultivars, management practices and growth environments to simulate what can be expected to happen in the field under specified conditions. It is unlikely that L-PEACH will ever be completely validated for a specific peach tree. We are continuing to test simulated predictions of tree behaviour under specified conditions as field validation data become available. Although far from complete, this new L-PEACH model provides an example of how architectural growth, carbohydrate assimilation and partitioning, and organ growth can be combined to simulate tree growth and physiology and provide integrated understanding of the environmental physiology of peach trees.

Acknowledgements

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