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Running head: Simulating architectural growth and source-sink behaviour in peach trees

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 this work we incorporated Markovian models into L-PEACH in order to improve the architecture of 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 behavior and responses to management practices visually similar to trees in commercial orchards. The new architectural model along with a number of improvements in the carbohydrate partitioning algorithms derived from the model evaluation significantly improved 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), a mechanistic computer model, was developed to understand the functional carbon economy of peach trees, understand how fruit trees function in the field environment, and predict tree growth and crop yield responses of commercial peach trees. Although PEACH was able to simulate 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 modeled individually within an architectural model of canopy development. L-systems (Lindenmayer 1968; Prusinkiewicz and Lindemayer 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.* 2007b).

L-PEACH had thus been designed as a functional-structural plant model that simulates growth and carbon source-sink relationships within the architectural framework of a plant (Allen *et al.* 2005). However, substantial improvements of the model were needed to increase the realism of the simulated trees, as 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 previously used to simulate development of fruiting apple trees by incorporating a Markovian model into L-systems-based architectural tree models (Renton *et al.* 2006; Costes *et al.* this issue). The objectives of the present study were to improve the architectural development of simulated trees in L-PEACH by using Markovian models, evaluate the physiological characteristics of simulated trees within the new architectural model, and 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 mobilization, and maintenance respiration of peach trees during three consecutive years.

L-PEACH description

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

L-PEACH is written in the L+C plant modelling language (Karwowski and Prusinkiewicz 2003; Prusinkiewicz *et al.* 2007a) and implemented using the L-system-based modelling software L-studio (Prusinkiewicz 2004a). 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 sub-models 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 sub-models that allow simulating 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, three-dimensional depictions of the simulated tree can be defined graphically using the L-studio (4.0) software (Figure 1) while quantitative data generated during a simulation are automatically transferred to MATLAB (version 7.0, release 14) to perform data analysis and display 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 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 integrate all the architectural elements of the plant, while the Markovian models define the succession of shoots along an axis and the branching pattern of the shoots. We selected the strategy developed in MAppleT (Costes *et al.*, this issue) to insert Markovian models into L-PEACH.

In the L-system formalism, a plant is treated as a collection of semi-autonomous modules (Prusinkiewicz 2004b). 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. Regarding axillary buds, each phytomer has a central axillary bud, which 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 axillary buds, within a specific phytomer and along the parent shoot, are modelled according to bivariate statistical models estimated for three shoot types characterizing 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, while 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, the median zones being progressively skipped when the shoot length decreases (Table 1 and Fournier *et al*., 1998).

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 through 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 categorized 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. In spite of this similarity, the shoots differ in the number of zones and the number of vegetative and flower buds (Table 1). These vegetative buds may become active in the same season (sylleptic shoots), in the next growing season (proleptic shoots) or remain dormant. Regarding terminal bud fate, 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.*, this issue). 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 by either 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 realized length will be reduced (Costes *et al.* 2007). The 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 fall, and start and end of leaf abscission. These parameters can be easily specified by the user, and thus 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 thirty functions describing relationships between specific 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 were 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 in order to simulate different organ behavior or parameterize

specific simulations. The parameters used to determine the functional characteristics of sources and sinks are based in concepts of carbohydrate partitioning from literature. However, when quantitative detail on the functionality of a given source-sink component was unavailable, the functionality of the component was determined from simulated experiments *in silico* (Table 2).

Leaves

Leaves are programmed to perform net photosynthesis (Pn) and assimilate carbohydrates into the tree. The amount of Pn by the leaf over a day is the product of three functions:

$$Pn = f_a(\text{Leaf light exposure}) \cdot f_b(\text{Leaf carbohydrate storage}) \cdot f_c(\text{Leaf area}) \quad (1)$$

Function f_a captures the relation between the rate of assimilation and the incoming light. Carbon assimilation is simulated in time steps of a 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 (1994b). Function f_b (sigmoid function), which was previously characterized 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) 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) by using a sigmoid function (f_d):

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

where SLW denotes the specific leaf weight (the presented model uses the simplifying 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. Part of these carbohydrates remains 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 1994b) (Table 2).

Stem segments

Stem segments (internodes) act as conduits for carbohydrate transport within the tree. They 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 (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:

$$\text{stem length} = \max \text{stem length} \cdot f_d \left(\frac{\text{stem carbohydrate available for elongation}}{\max \text{stem length} \cdot \pi \cdot r_i^2 \cdot \rho_{stem} \cdot CRG_{stem}} \right) \quad (3)$$

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 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 can not exceed a user-specified value (Table 2). At floral bud break, carbohydrate from the storage is mobilized 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 carbohydrate 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 (1994b) (Table 2).

Fruits

Flower buds set fruit shortly after the bloom date. However, some of these fruits drop during the growing season. Fruit abscission may 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 the 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 1994b). 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 realized fruit growth over time. Fruit maintenance respiration rates were also programmed using data obtained previously (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 1994a). 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 mobilization 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, DeJong unpublished 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 1994b) (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 sub-circuits 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.* 2007b). Roots are treated as one large single module. Each sub-circuit has components (sources of electromotive force in series with resistances) that represent primary growth (elongation growth), secondary growth (girth growth), storage, and maintenance respiration (Figure 2). Parameters of these components capture plant module's physiological potential to utilize 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 1994b). The physiological potential of storage sinks to take up carbohydrates is estimated by assigning a storage capacity as a percent 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.* 2007b).

Because of the complexity of the interactions of all the components of the model, we developed tools for displaying and analyzing quantitative outputs and tracking the behaviour of individual modules. To this end, we incorporated into L-PEACH subroutines for generating data files that are subsequently analyzed and visualized 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 that make it possible to simulate management operations typically conducted in the field including: pruning, budding, fruit thinning, and harvesting.

Pruning is performed by directly manipulating the tree displayed on the screen with the LPFG plant modeling program (Prusinkiewicz *et al.* 2007a). Tree responses to pruning are modelled using the concepts of apical dominance (Wilson 2000) and reiteration (Hallé *et al.*, 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 (about May, Table 2) and 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 performed 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.* 2007a). The automated fruit thinning option is based in the proximity of fruits to one another, and attempts to simulate commercial fruit thinning practices. The fruiting shoots are scanned from the base to distal end, and if two or more peaches are separated by less than a specified number of stem segments, the more distal fruits of are removed. Thus the fruit than 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 the future versions of the model we plan to also include the effects of early spring temperatures on harvest date (BenMimoun 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, with the parameters presented in Table 2. Weather data was obtained from CIMIS (California Irrigation Management Information System, Davis, CA station). The simulated trees were either left unpruned or were trained to a perpendicular V system, following procedures described by DeJong *et al.* (1994) and simulated as interactive pruning cuts in winter.

Tree architecture

In the first growing season, prior to budding, a simulated tree had a single, very-long shoot that was cut before reaching its final length (Figure 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 prior to sale. Prior to the beginning of the second year, the trunk of pruned trees was cut to half a meter (Figure 3A). 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 (Figure 3A). 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 thus were less vigorous than their parent shoots. The first crop of fruit was produced on shoots formed in the previous (first) year (Figure 3B).

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 (Figure 3A). The selected branches received heading cuts, and thus 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 (Figure 3A). During the third growing season, unpruned trees produced a large crop causing a significant reduction in tree vigour compared with pruned trees (Figure 3B).

Source-sink behaviour of simulated tree

The complexity of L-PEACH makes it difficult to analyze 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 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 the components of a tree. However, in spite of these limitations, L-PEACH is a potential tool to integrate and evaluate source-sink relationships in peach trees and elucidate seasonal organ and whole-tree behaviour at higher levels of organization. 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 Figure 4A,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 to the differences in photosynthesis (Figure 4C). This phenomenon may be explained by an increase in the amount of carbohydrates mobilized from the leaf storage compartment in cloudy days. This is consistent with the observation by Wardlaw (1990) that carbohydrate reserves built up within the leaf may be mobilized and exported when current photosynthesis is decreased. The amount of carbohydrate assimilated by individual leaves was 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 (2) was also successful in reproducing peach leaf expansion over time (Figure 4B, 4D): leaf maturity was achieved about 25 days after vegetative break, consistent with observations by Steinberg *et al.* 1990. However, we recognize that our modelling approach could be improved using more detailed numerical methods (Seleznyova 2007).

Simulated seasonal patterns of tree daily carbohydrate assimilation increased with increases in total leaf biomass (Figure 5). Between 33% and 50% of the tree carbohydrate assimilation was used for tree maintenance respiration (Figure 5), indicating the importance of respiratory cost in the carbohydrate 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 (Figure 5, Figure 6A). When tree daily maintenance respiration reached its maximum rates, it accounted for a relatively constant amount of carbohydrate usage (Figure 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 (Figure 6B). Assuming that fruits were harvested before reaching the constant amount of carbohydrate usage (Figure 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 (Figure 7) (Loescher *et al.* 1990; Jordan and Habib 1996). The seasonal dynamics of reserves in the stem segments was 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 mobilization 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 correct model behaviour.

Simulated tree carbon assimilation provided sufficient carbohydrate to support organ growth (Figure 8). During the three years of simulation, most biomass was accumulated in the stem segments, and root weight was about one-third of total stem segment biomass (Grossman and DeJong 1994a). The fruits also accumulated a significant amount of assimilates while the leaves had lower amounts of standing biomass. The simulated patterns of organ growth also reflected the interaction with the tree architecture and the different components of the models (Figure 8). The reduction in total leaf and stem segment weights after the growing season was a consequence of leaf abscission and winter pruning, respectively. The seasonal patterns of simulated root weight reflected that the tree carbohydrate 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 Figure 8). The substantial reduction in fruit competition after fruit thinning allowed optimization on average fruit carbohydrate mass at harvest (~33 g $fruit^{-1}$) (Figure 8).

Conclusion

The use of the hidden semi-Markov chain concepts for modelling branching structures in L-PEACH was successful at reproducing trees that were similar to peach trees observed in orchards. The new architectural model along with a number of improvements in the carbohydrate partitioning algorithms significantly improved 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 previous three-dimensional 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.

Although L-PEACH is still in the early stages of development, it is a useful tool for simultaneously modelling tree architectural growth and carbohydrate source-sink relationships in peach trees. More quantitative validation of the model at the whole plant and individual organ levels is needed to increase the accuracy of simulated trees. Since much of the available data from previous experiments and literature are not suitable for quantitatively validating L-PEACH, there is a need to collect additional quantitative data for this purpose. L-PEACH can be used for identifying the relevant outputs of the model to be measured, developing new quantitative hypotheses and guiding experimental research. This will result in a greater understanding on the environmental physiology of peach trees, which is the overarching objective of the peach modelling project.

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Table 1. **Types of shoots and 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.**

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

Abbreviations: B = Blind buds, V = Vegetative buds, AF = Axillary flowers and F = Floral buds.

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

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 leaf abscission	288 (day of year)	User-defined
End leaf abscission	319 (day of year)	User-defined
Leaf		
f_a	f_a = [18.9 · leaf PAR exposure] -55	Rosati *et al.* 2002
max leaf area	40 (cm^2)	Steinberg *et al.* (1990)
Specific leaf weight (SLW)	0.004 (g dw cm^{-2})	Marini and Marini (1983)
CRG_{leaf}	1.463 (g CHO g^{-1} dw)	Penning de Vries *et al.* (1989)
Maintenance respiration	3.5 (mmol CO_2 g^{-1} dw s^{-1})	Grossman and DeJong (1994b)
Stem segment		
r_i	0.1 (cm)	User-defined
max stem length	2.7 (cm)	User-defined
ρ_{stem}	0.54 (g dw cm^{-3})	Grossman (1993)
CRG_{stem}	1.14 (g CHO g^{-1} dw)	Grossman (1993)
Storage ratio	20 (% of total stem mass)	User-defined
Storage mobilization period	60 (days after bloom)	User-defined
Maintenance respiration	0.8 (mmol CO_2 g^{-1} dw s^{-1})	Grossman and DeJong (1994b)
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 mobilization period	60 (days)	User-defined
Maintenance respiration	0.8 (mmol CO_2 g^{-1} dw s^{-1})	Grossman and DeJong (1994b)
Management practices		
Day of budding	136 (day of year)	Commercial practice
Fruit thinning date	130 (day of year)	Commercial practice
Fruit thinning space	4 (number of stem segments)	Commercial practice
Harvest day	240 (day of year)	Mid-late maturing cultivar

Abbreviations: CHO = carbohydrates, dw = dry weight, PAR = photosynthetically active radiation, CRG_{leaf} = carbohydrate requirements for leaf growth, CRG_{stem} = carbohydrate requirements for stem growth.

Figures

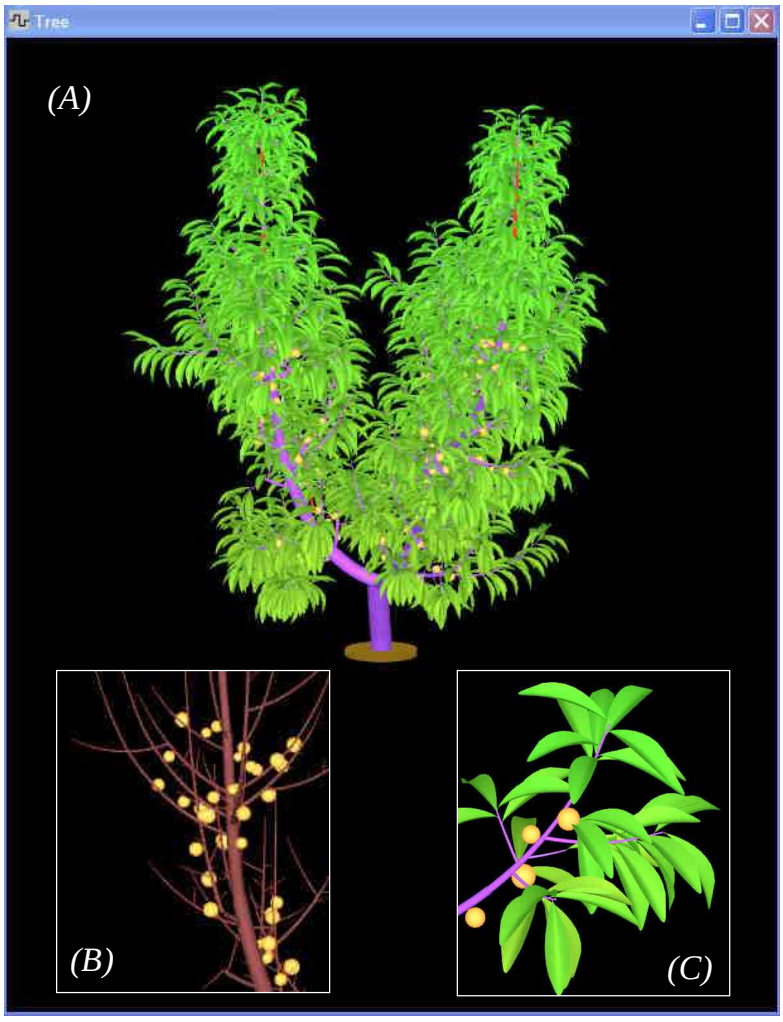

Fig 1. L-studio output showing the potential of L-PEACH to simulate three-dimensional structure of mature peach trees (A), and intra-canopy variability among organs of the same type in response to localized source-sink behaviors (B, C). L-studio also allows modifications in the property that is visualized by the stem's colors, *i.e.*, movement of carbohydrates through the tree (A,C) (see Allen *et al.* 2005 for further details on carbohydrate fluxes and colors), or a bark-like color (B). In Figure 1B, leaves were removed to increase visibility of fruit.

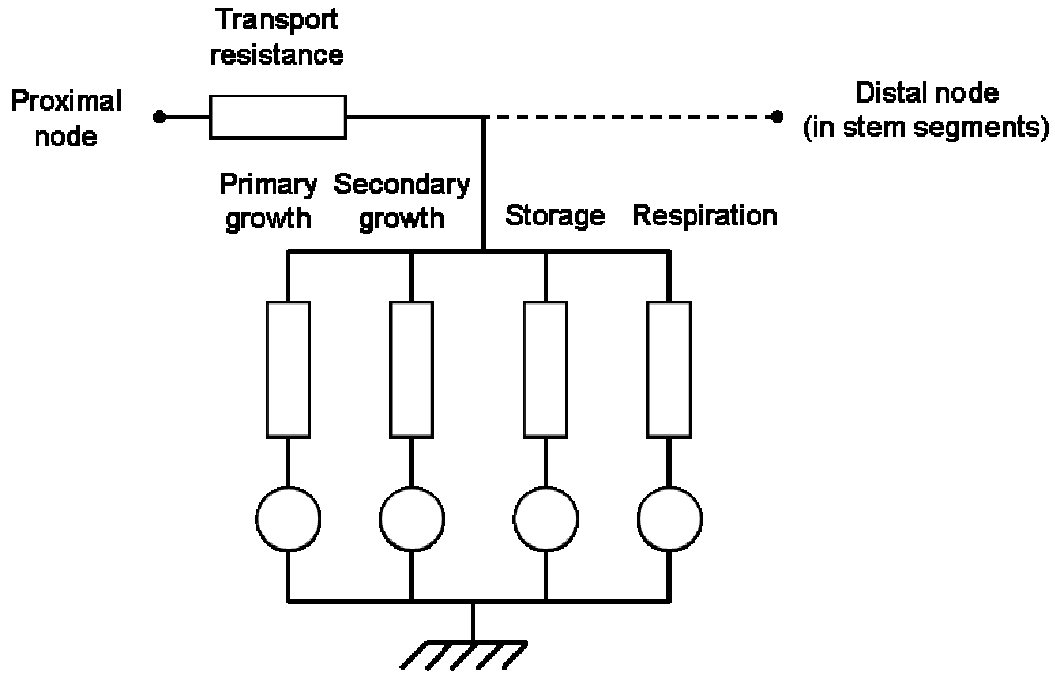

Fig 2. Schematic representation of any individual module within the tree branching network. Rectangles denote resistances; circles denote sources of electromotive force.

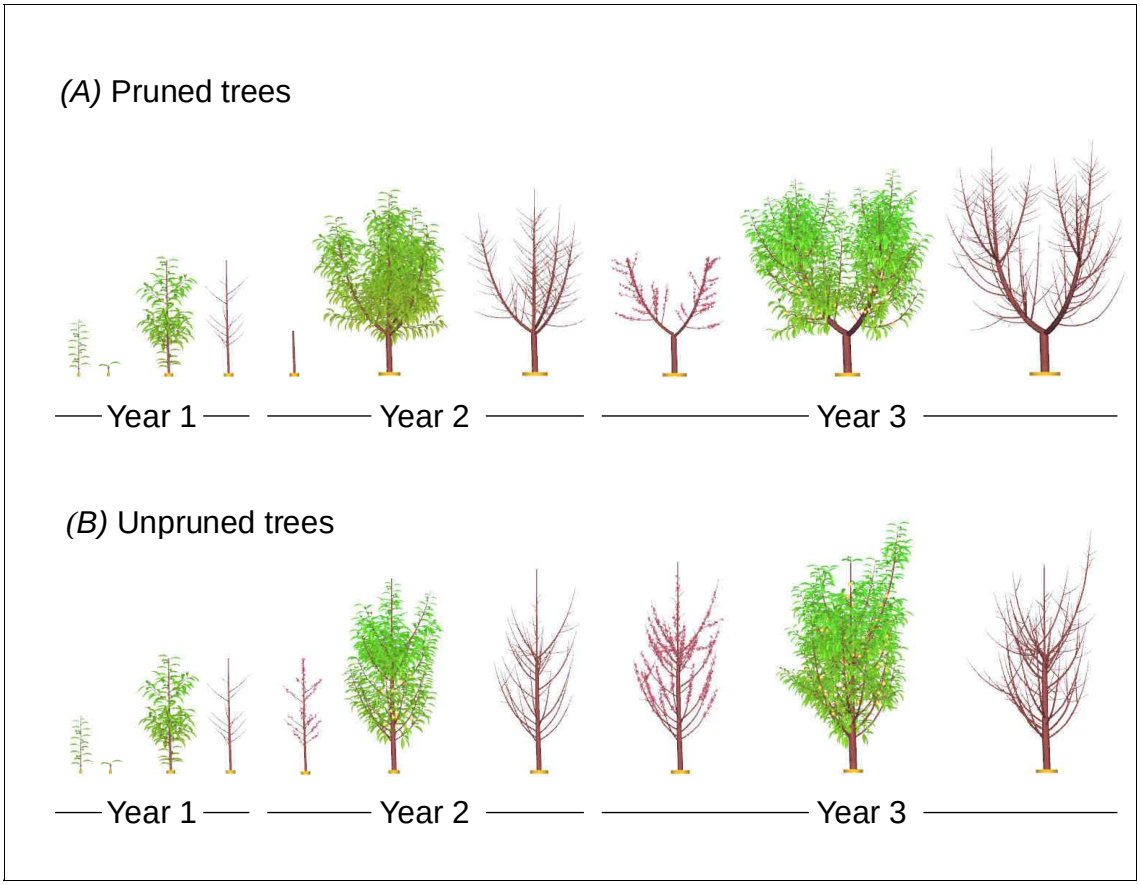

Fig 3. Model output showing three-dimensional depiction of a pruned peach tree (A) and an unpruned peach tree (B) over three years of growth. The pruned tree was trained to a perpendicular V system by means of pruning cuts in winter. The final tree height was about 3.0 m.

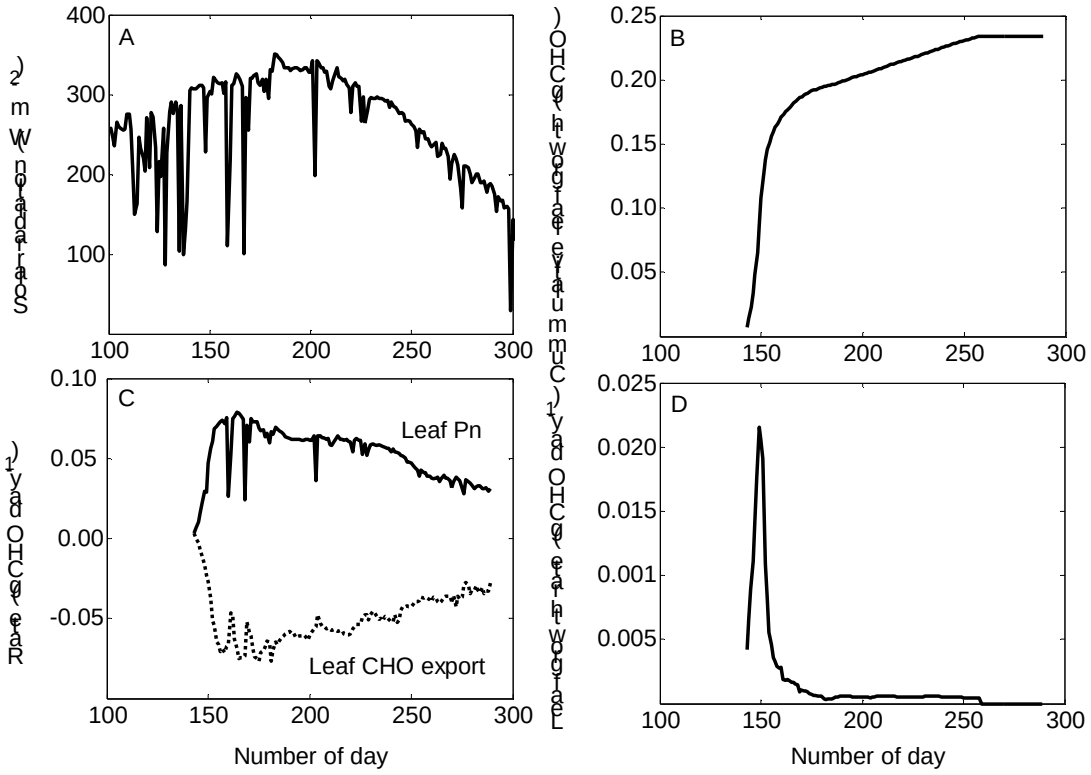

Fig 4. Seasonal patterns of solar radiation (A), individual leaf growth (B), leaf photosynthesis and leaf carbohydrate export (C), and individual leaf growth rate (D). Simulated data represent an individual leaf during the first year of tree growth. Abbreviations: Pn = photosynthesis, and CHO = carbohydrates.

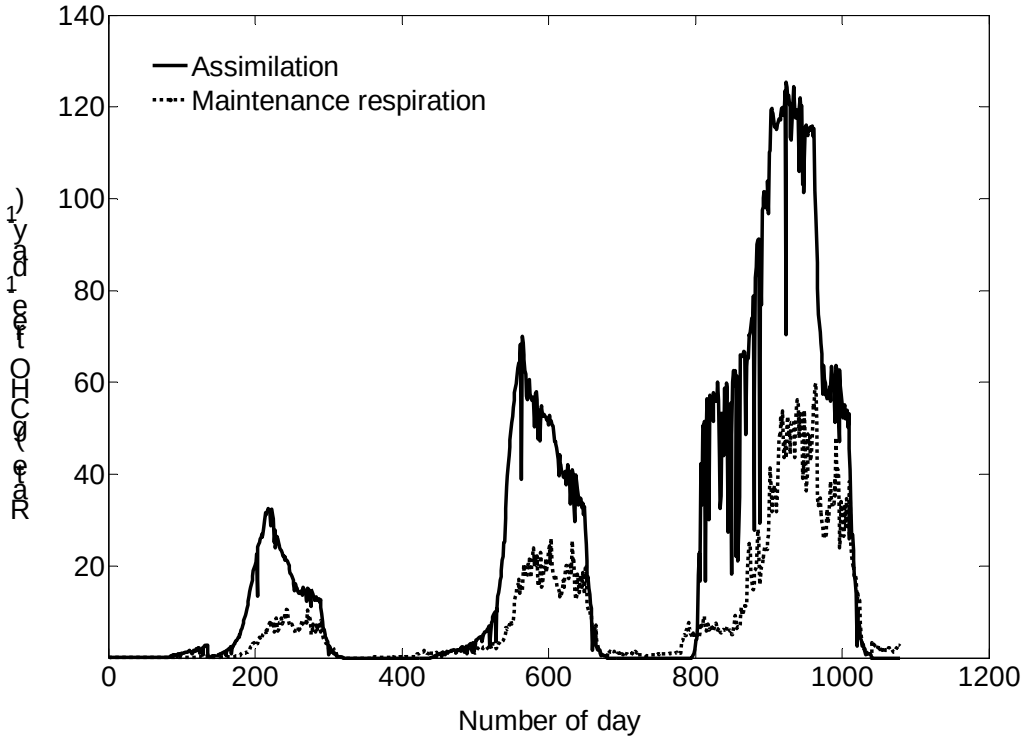

Fig 5. Simulated seasonal patterns of daily carbohydrate assimilation and maintenance respiration during three consecutive years of peach tree growth. The simulated tree was trained to a perpendicular V system. In the third year, crop load was 100 fruits tree^{-1}. Abbreviations: CHO = carbohydrates.

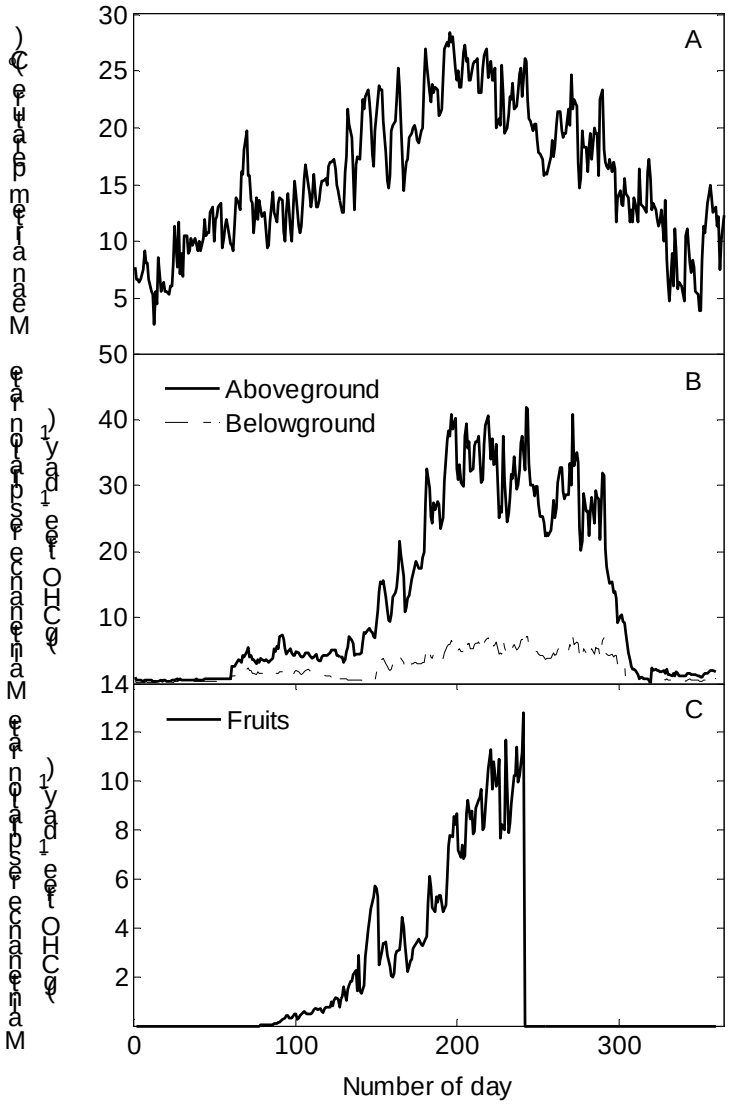

Fig 6. Seasonal patterns of daily air temperature (A), aboveground and belowground maintenance respiration (B), and total fruit maintenance respiration (C) during the third year of growth of peach trees trained to a perpendicular V system. Crop load was 100 fruits tree^{-1}. Abbreviations: CHO = carbohydrates.

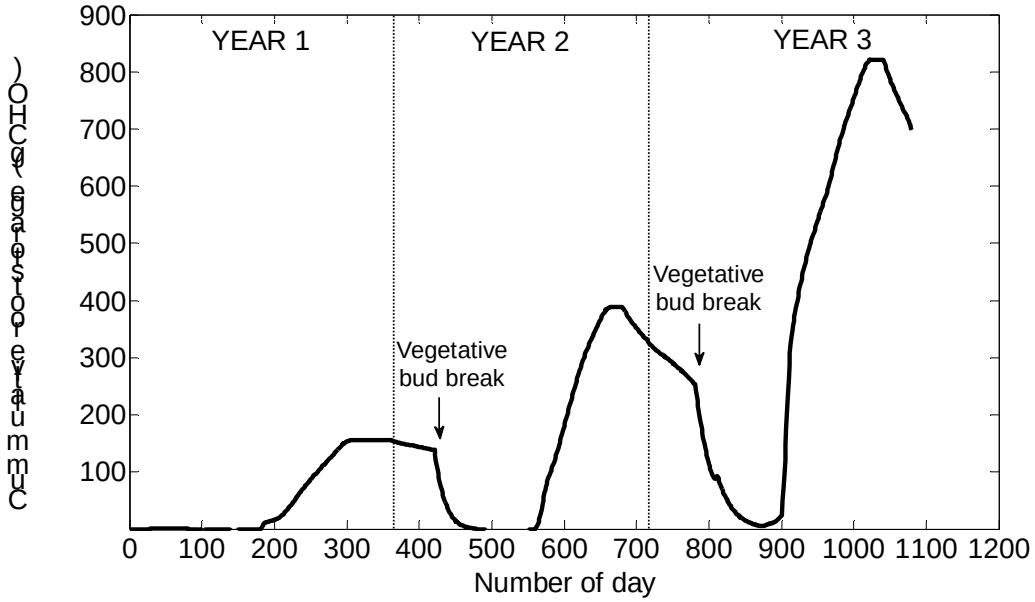

Fig 7. Seasonal variations of total carbohydrate reserves in the root during three consecutive years of peach tree growth. The simulated tree was trained to a perpendicular V system. In the third year, crop load was 100 fruits tree^{-1}. Abbreviations: CHO = carbohydrates.

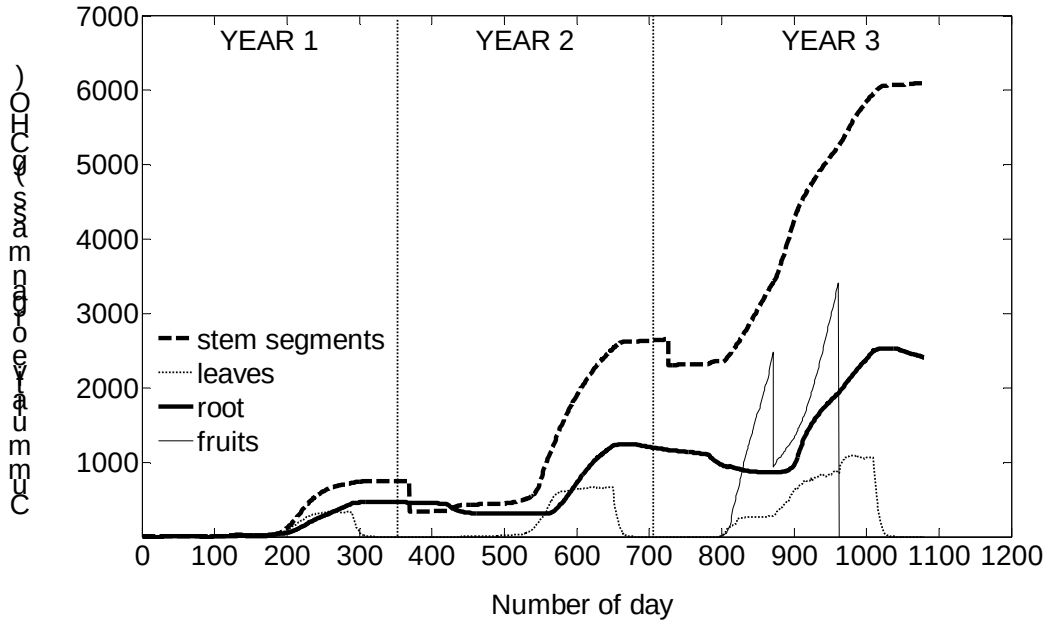

Fig 8. Organ mass during three consecutive years for simulated peach trees trained to a perpendicular V system. Sudden drops in cumulative mass of stems and fruits were due to pruning, fruit thinning and fruit harvest. In the third year, crop load after fruit thinning was 100 fruits tree^{-1}. Abbreviations: CHO = carbohydrates.