Using L-Systems to Model Carbon Transport and Partitioning in Developing Peach Trees

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Abstract

Previously, Grossman and DeJong developed the model "PEACH" to simulate the growth of peach trees based on the hypothesis that carbon partitioning within the tree is driven by competition among sinks. In these simulations, sinks were generalized compartments that included maintenance respiration, leaves, fruits, stems, branches, trunk, and roots. More recently, we have begun to use L-systems to extend these modeling efforts to explicitly include canopy architecture in the simulation of carbon partitioning and growth. This approach, in which various components of the canopy interact as semi-autonomous elements of a complex network, has provided a context for exploring the influence of canopy architecture on source-sink interactions within a growing tree canopy. Each internode of the shoot system is represented as a finite element of a resistor network, which functions to connect carbon sources and sinks into a simulated tree canopy. Carbon is loaded at the sources and unloaded at individual sinks.. At each sink, the sink potential is a function of the growth or storage potential of that sink. Carbon flow from sources to sinks is determined for each time step using the current values for each source and sink potential, combined with the resistances of each internode and the overall topology of the canopy. In this manner, carbon is partitioned and canopy growth occurs as a byproduct of the interaction between a large number of individual sources and sinks, rather than as the result of a whole-tree level set of allocation and growth rules.

INTRODUCTION

The partitioning of resources within a tree canopy, and the mechanisms that underlie this process, are topics of considerable theoretical and applied interest to physiologists concerned with tree growth and development. The modeling of carbon partitioning within plants has previously taken a variety of forms, ranging from the use of empirical partitioning coefficients to mechanistic approaches based on the hypothesis that competition among carbon sinks within a canopy drives the partitioning among those sinks. Previously, Grossman and DeJong (1994) developed the model "PEACH" to simulate the growth of peach trees based on this latter hypothesis. In these simulations, sinks were treated as generalized compartments that included maintenance respiration, leaves, fruits, stems, branches, trunk, and roots. Although this approach was successful in predicting carbon partitioning among these general compartments, it does not provide a platform for asking questions related to the interaction between carbon partitioning and canopy development and architecture. For example, the model can accurately predict the whole tree allocation of carbon to fruit growth, but it does not provide a way to explore the possible effect of an individual fruit's position within the canopy (i.e. its position relative to carbon sources, etc.) on fruit size and/or quality.

In an effort to establish a modeling platform for exploring the interactions among carbon partitioning, canopy architecture, and canopy growth, we have recently begun to use L-systems to extend our modeling efforts. L-systems was introduced by Aristid Lindenmayer in 1968 as a method for modeling the development of multicellular organisms, and was subsequently applied to the modeling of plants (Prusinkiewicz et al. 1997). L-systems treats plant bodies as collections of semi-autonomous parts (or modules) that follow user defined rules in their interactions with each other (by communication with immediate neighbor modules), or with the environment. Plant canopies can be represented as a branching structure composed of any number of these semi-autonomous modules, and the growth of the simulated canopy is the result of the instructions given to each of these individual parts played out over the time course of the simulation (Prusinkiewicz 1998). Although L-systems has previously received considerable attention within the fields of computer science and computer graphics, biologists have only recently begun to utilize L-systems as a tool for implementing spatially explicit, three dimensional models of plant development and growth.

Description of Modeling Methodology

Using an analogy to electronic circuits, each stem segment of the modeled tree is represented as a finite element of a resistor network, which functions to connect carbon sources (sites of carbohydrate generation – typically leaves) and sinks (sites of carbohydrate consumption, such as growing shoot tips, fruit, or roots) into a simulated tree canopy. Carbohydrate is loaded at the sources in such a way as to maintain a locally constant sugar concentration for the duration of one time step of the model, which represents one day of growth. The magnitude of a given leaf's "potential" is a function of its simulated daily exposure to light combined with its photosynthetic properties. At each sink, the sink potential is a function of the influx of carbohydrate from the previous time step combined with the rate of unloading from that sink. Carbohydrate flow from sources to sinks is determined for each time step using the current values for each source and sink potential, combined with the resistances of each stem segment and the overall topology of the canopy. At the end of each computational cycle, the potential at each sink is updated, and growth of the sink is calculated as a function of its carbohydrate accumulation for that time step. In this manner, carbohydrate is partitioned and canopy growth occurs as a byproduct of the interaction between a large number of individual sources and sinks, rather than as the result of a whole-tree level set of allocation and growth rules.

The architectural growth of the canopy is simultaneously simulated based on a set of biological concepts that govern the developmental fates of the individual elements, or "metamers" that comprise the tree. For example, if a shoot apex acquires sufficient carbohydrate (as a result of the source/sink interactions described above) it might "grow" by replacing itself with a new shoot segment (with its own new shoot apex). This type of rule could be written in the following way (where the arrow signifies the replacement of the element on the left with the element(s) on the right):

Apex → New Shoot segment + New Apex

As the simulation proceeds, the canopy develops as the result of a series of such growth rules, with different rules applying to different structural elements of the canopy (leaf, stem segement, shoot apex, etc.). Additionally, certain rules might be invoked only if given environmental or developental conditions are met. This type of modeling not only permits the ability to model organ growth individually in the context of canopy location, but it also provides a visual, three dimensional display of the growth processes as they are simulated (Figures 1, 2, and 3).

With the general framework of the model established, it is developing into a potentially effective tool for exploring the hypothesis that carbon partitioning is driven by competition among sinks. One of the advantages this approach is that it demands an integration of our understanding of various structure/function relationships within a tree, with the model providing a framework for exploring potential interactions among processes that are often studied in isolation of one another. Some future goals of this research include:

A more detailed integration of light capture into the determination of leaf source strength, which will provide for a more thorough treatment of the interplay between light capture and tree architecture. The current method for calculating light interception by leaves is a good first approximation (see Figures 2 and 3), but does not provide for the consideration of factors such as leaf angle, light quality, or scattering of light within the canopy.

The inclusion of root functionality into the model. Currently, roots act as a carbon sink, but do not provide any useful service to the plant. The inclusion of rules that model resource capture by the roots, and the distribution of these resources (i.e. water and nutrients) to the shoot system will allow us to use the model as a tool to explore questions related to the functional and structural balance between roots and shoots.

The inclusion of more mechanistic developmental rules that govern interactions among modules, particularly those interactions that determine the developmental fate of an individual module. These processes would include such things as: branching patterns, bud break, flowering, etc. Currently, the developmental rules used by the model are very simple and deterministic, but these will be replaced by developmental rules based instead on interactions among neighboring modules. Processes such as correlative inhibition, apical dominance, and apical control would then govern the fate of individual buds within the simulated tree canopy.

Parameterization of the model using data from field experiments. Work to this point has focused on the development of a general infrastructure, which can then be modified to allow for the modeling of specific trees under various simulated environmental and/or horticultural regimes.

Although this modeling effort using L-systems to model growth and dry matter partitioning in fruit trees is still in its infancy, the work to date clearly documents the potential for using this approach to develop highly sophisticated, graphically based, simulation models that will be useful for integrating many complex factors that govern fruit quality parameters as well as tree and fruit growth. It is envisioned that these models will not only be valuable as research tools but their three-dimensional graphical nature will also make them ideal for educational purposes.

Literature Cited

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Figures

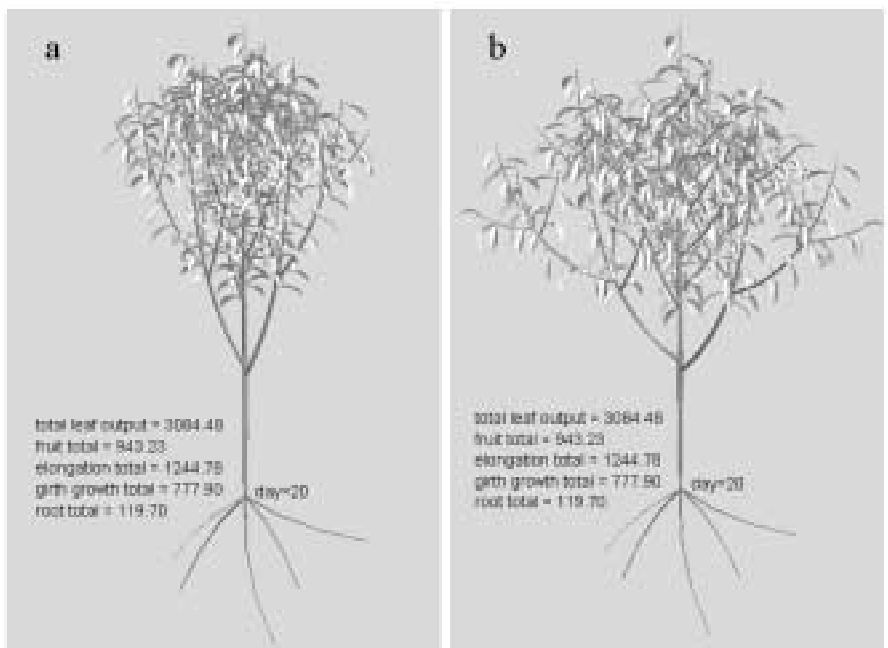

Fig. 1. This is a simple example of how a small modification of a growth rule can affect canopy morphology. This image shows two canopies that differ only in the angle specified for the growth of new branches (35 degrees in Fig. 1a, 60 degrees in Fig 1b). Modifying the branching angle is just one of the myriad ways that the model developer can affect the form of the tree canopy that will "grow" during the simulation.

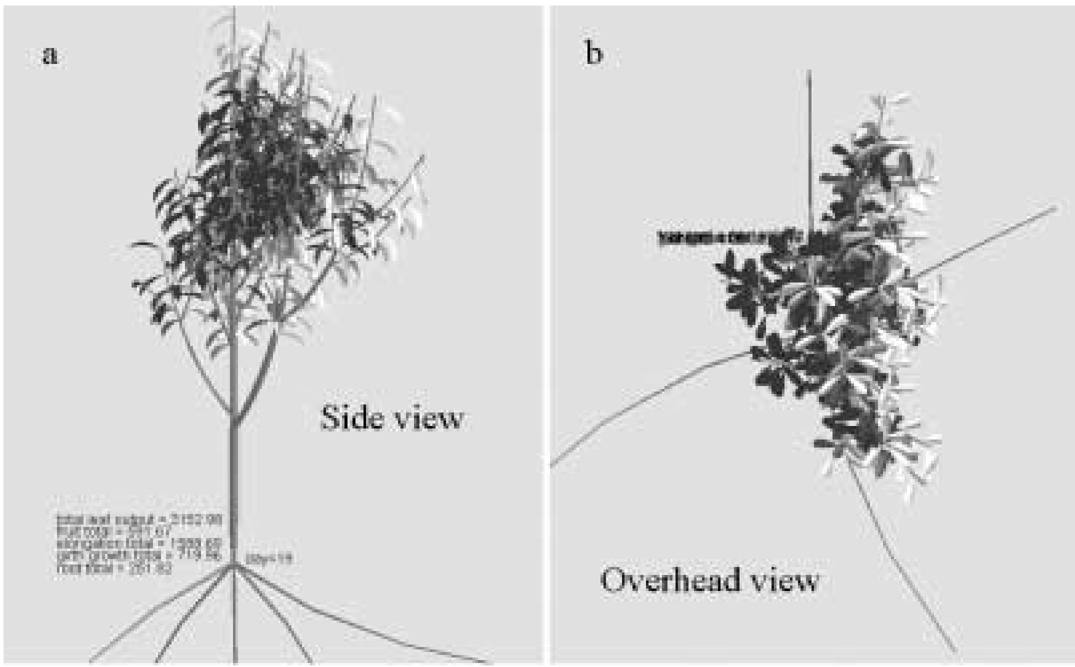

Fig. 2. In the simulation shown in Figure 1, light was assumed to be uniform throughout the canopy, and thus each leaf within the canopy is an equivalently strong source of carbohydrate. However, it is also possible to base a leaf's source strength on its photosynthetic activity, which for now is simplified to mean its access to light. The images above are side (Fig. 2a) and overhead (Fig. 2b) views of a simulated canopy that was grown with the light source directly to the right of the tree. In the images above, the relative brightness of the leaves indicate their exposure to light - bright leaves have the most exposure, with black leaves being completely shaded and medium gray leaves having intermediate exposure. The consequences of this light regime after a few simulated seasons of growth are shown in the images above - the right side of the canopy develops more vigorously.

Fig. 3. In addition to the effect of this light regime on the growth of the shoot system (as shown in Figure 2), an effect can also be observed on fruit growth. This image is a close up view of the same canopy seen in Figure 2, and the effect of light source direction on fruit size at different places in the canopy is visible. Fruits growing on the left side of the tree, farther away from strong carbohydrate sources, do not grow as large as those growing on the right side.