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# Linking Carbon Economy and Architectural Development of Peach Trees by Integrating Markovian Models into L-PEACH

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## Introduction

Linking tree architectural development and carbon partitioning during a growing season has been identified as a weak point in functional-structural plant models (LeRoux *et al.*, 2001). In the L-PEACH model (Allen *et al.*, 2005), carbon partitioning was used to drive organ growth, but the organs and shoot types were not accurately distributed within the tree. Our goal was to propose a solution for linking statistically-based models of architectural development with a physiologically-based model of carbohydrate partitioning in peach trees. The approach was to integrate Markovian models representing the tree's topology, that is, the connectivity of the tree's entities (Guédon *et al.*, 2001 and Renton *et al.*, 2006), into the L-PEACH model.

## Simulating Peach Tree Topology with Markovian Models

In peach trees, each node can lack a bud (blind node) or can have a central bud that can be blind, floral or vegetative. Vegetative central buds can have zero, one or two lateral floral buds (Costes *et al.*, 1999). Axillary buds are organized along a shoot into successive zones. Within each zone the bud fates are homogeneous and between zones they strongly differ. For example, in one zone there may be dormant vegetative buds mixed with short lateral shoots, while in another zone, axillary flowers mixed with sylleptic shoots. To represent these branching patterns, bivariate hidden semi-Markov chains (HSMCs) were parameterized from observations (Costes *et al.*, 1999). The first variable represented the central bud fate and the second variable represented the number of additional floral buds. Models were developed for different shoot types. Three shoot types with decreasing vigor were considered: very vigorous (or water sprouts), vigorous (or mixed shoots) and moderate. Short shoots (spurs of low vigor) were assumed not to branch. HSMCs corresponding to the categories of branched shoots mainly differed by the number of zones: basal and distal zones were common to all shoot types while the median zones disappeared when moving from the most to the least vigorous shoot types.

## Linking Carbon Availability and Growth

In the L-system simulation, the tree was started in the first spring with a very vigorous shoot. Then, a shoot category was attributed to each bud depending on its position within the tree. Each attributed category was assumed to represent the maximum growth that can develop from each bud. Axillary bud fates were determined by HSMCs. Terminal bud categories had decreasing length potentials as the tree developed, based on observations of tree ontogeny that have been carried out on different species (Gatsuk *et al.*, 1980 and Nozeran *et al.*, 1984). As previously done in an apple tree model (Smith *et al.*, 2007), the changes in shoot category with years were modeled with transition probability matrices of simple Markov chains.

To link tree growth to carbon economy, we first assumed that a given amount of carbon is required to build up each new metamer. If the tree has a sufficient amount of carbon the shoots grow to their full size; but, if there is a carbon deficit, the shoots are reduced in length. When the rate of growth is significantly slower than a target rate of growth, buds produced by the metamer are downgraded. For example, a central vegetative bud with two lateral floral buds may have the floral buds removed. Since the rate of growth only slows when there is a carbon deficit, this ties the local shoot architecture to carbon availability. If the rate of growth remains slow for several consecutive metamers in a zone, the remaining metamers in that zone are skipped. A limit is also placed on the potential length of shoots based on how late in the growing season the shoot starts growing. A shoot that begins growth at spring bud break may reach its full size; but, a shoot that begins growth later in the season, as may happen with sylleptic shoots or in response to summer pruning, will have its size limited. This is imposed by reducing the bounds of the Markovian sequences (*e.g.*, a medium shoot at bud break may be 16–35 metamers, but later in the season it will only be 12–25 metamers). If the bounds are reduced by a large amount, the shoot category may be downgraded (*e.g.*, a moderately vigorous shoot may be downgraded to a low vigor shoot).

### Simulation Results and Interpretation

Using HSMCs for determining axillary bud fates and Markov chains for terminal bud fates, we simulated a series of trees which displayed different lateral branching along the one-year-old trunks (Figure 1).

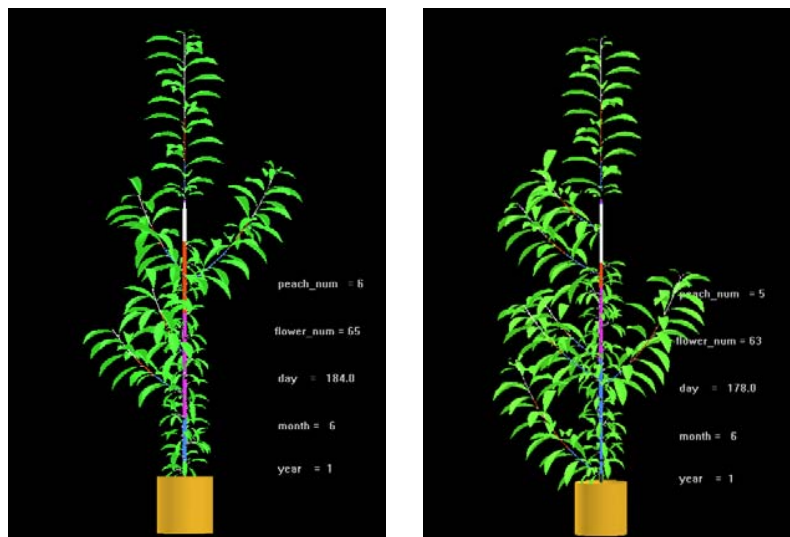


Fig. 1. Two stochastic simulations of growth and lateral branching on trunks of peach trees. Colors represent the successive branching zones along the shoots. The simulated time span is 1.5 years.

The dependence between the current charge of the last internode developed and the potential of the shoot to develop new organs, allowed linkage of tree organogenetic potential to carbon availability. Thus the length of a developed shoot depended on both its initial category and the carbon available during its growth period. One of the most obvious results obtained concerned the median zones (particularly, the zones of sylleptic and floral axillary shoots) which varied greatly depending on the carbon threshold of the growing zones along the shoot (Figure 2). A higher carbon threshold for continuing into some zones led to a progressive reduction in the organogenetic activity in both the main shoot growth and in lateral shoots. Both the number of internodes along the main shoots and the number of lateral shoots decreased as the thresholds increased. The most extreme case resulted in such a decrease in the main shoot growth that branching did not occur (Figure 2, right). The reduction of the current shoot length due to carbon limitation also impacted the subsequent year of growth.

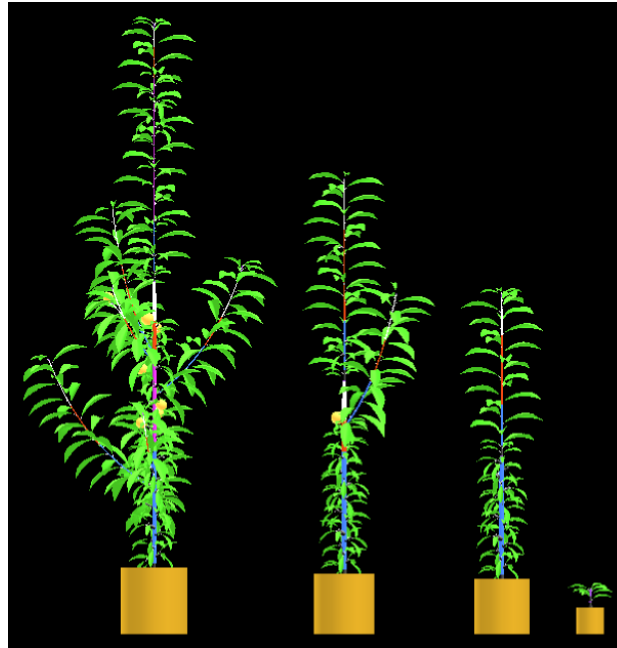


Fig. 2. Reduction in growth and lateral branching along a peach tree trunk depending on the carbon threshold required to build successive zones. The tree on the left is the normal case (all zones are developed). In the right most tree, the carbon thresholds for each zone were twice those of tree on the left. The simulated time span is for 1.5 years.

### Conclusion

The integration of Markovian models for representing the tree topology in terms of shoot categories provides a new version of L-PEACH with the capability to tune the architectural development of whole trees according to carbon economy. This constitutes a step forward the integration of interactions between the bud organogenetic potential and carbon partitioning since the previous version of L-PEACH only tuned the organ development. Moreover, this model provides a new tool to further investigate the interactions between tree ontogenetic gradients and growing conditions. However, as was noted, the mechanism of skipping branching zones when carbon is in short supply is hypothetical; the values chosen for the thresholds are thus speculative. Further research must be done to establish experimental support for this mechanism and quantify the carbon thresholds.

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