Improving the Architecture of Simulated Trees in L-PEACH by Integrating Markov Chains and Responses to Pruning

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Abstract

A tree's architectural development can be described using statistically-based models. Here, we demonstrate the integration of an architecture described with hidden semi-Markov chains (HSMC) with L-PEACH, a carbon partitioning model for simulating developing peach trees. In previous studies, it was shown that in peach trees, several axillary buds can be found at each node, organised as a central bud, which can be blind, floral, vegetative (bud formed) with or without one or two lateral flower buds or latent (bud not fully formed). Axillary buds were also shown to be organised along a shoot into successive zones. Within each zone, the bud fates were fairly homogeneous, but between zones, they differed strongly. To represent these architectural patterns, bivariate HSMCs that were previously parameterised for unpruned trees in France were adapted to model pruned trees in California. From different models that have been previously estimated depending on shoot categories (as defined by the number of metamers), we considered limitations on the shoot sizes to be related to carbon availability and physiological factors. We also modelled responses to pruning and included algorithms for automatically handling some pruning and fruit thinning cases. This work demonstrates that HSMC concepts for describing tree architecture can be used to model pruning responses to simulate peach trees visually similar to those found in orchards.

INTRODUCTION

Our goal was to link architectural growth and carbon partitioning during the growth season: this has been identified a weakness in previous carbon-based models (Le Roux et al., 2001). An approach for integrating statistically-based models of architectural development with physiologically based models of carbon partitioning in trees is presented. The approach was to insert Markovian models representing a tree's branching patterns (Costes et al., 1999) into L-PEACH, an L-system model of carbon partitioning (Allen et al., 2005). It has been previously demonstrated that Markov model representations of architecture can be well-integrated in L-system models of fruiting trees (Renton et al., 2006) and combined with other modelling principles to simulate tree form over several years of development (Smith et al., 2007). As the architecture of peach trees in orchards is also directed by pruning practices (Marini, 2002), we also included responses to pruning in L-PEACH.

SIMULATING PEACH TREE TOPOLOGY WITH MARKOV CHAINS

Peach trees have nodes with several buds. In this simulation each node may be blind or have a central bud, which may be floral or vegetatively active in the same season (sylleptic) or the following season (proleptic) or remain latent. A central vegetative bud can also have up to two lateral floral buds. The buds' fates are organised along each shoot in zones (Fournier et al., 1998). Within each zone, the potential vegetative bud fates (whether they become blind, vegetative or floral) are homogeneous but between zones they strongly differ. For example, one zone may have mixed vegetative and blind buds and another may have mostly floral buds. To represent these branching patterns, bivariate hidden semi-Markov chains (HSMCs) have been parameterised. The first variable represented the central bud fate, whether the bud will be blind, vegetative or floral, and the second variable represented the number of lateral floral buds. We assumed that at each metamer, there are at most two floral buds. Models have been developed for different shoot types. Four shoot types with decreasing vigour were modelled with HSMC: extremely vigorous shoots (water sprouts), shoots of high or moderate vigour and low vigour shoots. HSMC models corresponding to the categories of branched shoots mainly differed by the length and number of zones (Costes et al., 1999): basal and distal zones are common to all shoot types, while the median zones disappear when moving from the most to the least vigorous shoots. On extremely vigourous shoots (water sprouts) the buds in the median zone break shortly after they have formed (Génard et al., 1994).

The HSMCs used in L-PEACH are similar in their structure, i.e. in the number and order of the zones, as those developed in a previous study of peach under conditions and training practices common in France (Costes et al., 1999). However several HSMC parameters were adapted to represent common Californian cultivars. These adaptations concerned the observation probabilities of flowers and the length of the median zones where sylleptic shoots may develop. In addition, an extremely vigorous shoot category was added with many long sylleptic lateral shoots and almost no floral buds associated with the vegetative central buds. The three HSMCs used in L-PEACH are illustrated in Figure 1. Spurs (very low vigour) were assumed not to branch and are modelled as a short sequence of blind nodes.

Other models (Renton et al., 2006; Smith et al., 2007) have used tree age as a selection criterion for shoot categories. However, age was not an appropriate criterion when the terminal portions of shoots or branches were pruned in a simulation. Shoots that appeared after a terminal portion of a shoot or branch was pruned grew with vigour comparable to the part that was removed, thus reiterating the cut branch (Ishii et al., 2007). In contrast, if is the simulation did not involve pruning, the vigour of new shoots was reduced compared to the parent shoot. Thus in a few years, an unpruned tree produces mostly spurs and only a small number of moderately vigorous shoots. We thus conserved age as a criterion for selection of the category of new shoots when the parent shoots are unpruned, moving progressively from vigorous shoots to low vigour shoots. In contrast, new shoots were in the same shoot category as the parent shoot when the parent shoots were pruned.

RESPONSES TO PRUNING

We modelled responses to pruning based on the concept of apical dominance (Wilson, 2000). When a cut is made, the fates of the buds between the cut and the next branching point are reassigned. If vegetative buds are present, the distal buds (the number that break corresponds to the width of the shoot) are assigned the same shoot category as the cut shoot and the rest remain latent. This follows the idea that the distal buds are no longer under apical dominance, and so they break; but, the distal buds also now have a strong dominance effect on more proximal buds, and so they are suppressed. If there are no preformed vegetative buds present, then the distal latent buds become active vegetative buds that develop into water sprouts (extremely vigorous). If the cut is made during the vegetative season, the distal buds break immediately with their newly assigned shoot categories; otherwise, they break, with the new categories, at the same time as the rest of the dormant buds begin growing in the following spring. The response to pruning is illustrated in Figure 2.

LINKING CARBON AVAILABILITY AND GROWTH

In each daily simulation step of the model, daily incident global solar radiation and daily max-min temperatures were used as environmental drivers to compute daily photosynthesis by individual leaves, organ maintenance respiration and organ development rates, respectively. The carbohydrate produced from photosynthesis were distributed and used or stored in the plant according by algorithms governing source-sink interactions described elsewhere (Allen et al., 2007).

In L-PEACH, a tree starts as a single bud that produces a very vigorous shoot. Then, a shoot category is attributed to each bud depending on its position within the tree. Each category represents the maximum growth that can develop from each bud. Axillary bud fates are normally determined by HSMCs but may change in reaction to pruning. Bud categories have decreasing length potentials as the tree develops, based on observations of tree ontogeny that have been carried out on different species (Gatsuk et al., 1980; Nozeran, 1984); a succeeding terminal shoot has less vigour than its mother shoot.

The architecture of the tree is primarily determined by the Markovian models. When there is sufficient carbon available, the shoots and buds are formed as they are described by the sequences extracted from the models. But, when there is insufficient carbon, three mechanisms can be involved in reducing the architecture. First, a given amount of carbon is assumed to be required to build up each new metamer. A new metamer is only added when the supporting stem has accumulated at least the minimum amount of carbon for the new metamer. If the tree has a sufficient amount of carbon the shoots will grow to their full size; but, if there is a carbon deficit, the shoots will be reduced in length.

Second, when the rate of growth is significantly slower than the target rate of growth, as can happen when there are low amounts of carbon available, buds produced by the metamer are downgraded. For example, flower buds that would normally be produced lateral to a central vegetative bud are removed and only the central vegetative bud is produced in that zone. If the rate of growth remains slow for several consecutive metamers in a zone, the remaining metamers in that zone are skipped.

Third, a limit is 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 budbreak may reach its full size; but, a shoot begins growth later in the season, as may happen with sylleptic shoots or in response to summer pruning, will have its size limited. This limitation results from limiting the bounds of the Markov sequences (e.g., a medium shoot at budbreak has a potential of 16–35 metamers, but later in the season that potential may be reduced to 12–25 metamers), and 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 vigour shoot).

MANUAL AND INTERACTIVE PRUNING AND FRUIT THINNING

L-PEACH now includes both manual and automated pruning and fruit thinning. For manual pruning and thinning, we have introduced a three-step process that is designed to minimise user errors in pruning. First, the user presses a button to enter the pruning mode. Second, the user selects the shoots and fruits to be removed. Third, the user can commit the selection, at which point the selected parts of the structure are deleted. Alternatively the user can undo the selection, preventing the deletion of accidentally selected parts.

Automated fruit thinning is based on the proximity of fruits. A pass from the base of the tree to the distal ends is done and whenever two peaches separated by less than four metamers (approximately ten centimetres) are found (that distance can be adjusted as a parameter of the model) the distal most fruit is removed. This simulates a common, fruit thinning method used in the field (Costa and Vizzotto, 2000; Ingles et al., 2001). The effect of the automated fruit thinning is shown in Figure 3.

Automated pruning algorithms simulating topping and hedging are also included. These algorithms are based directly on those for simulating topiaries with L-systems (Prusinkiewicz et al., 1994). This is done by defining a boundary, usually by a plane or a polyhedron, and then removing all the stems that fall on the outside of the boundary. Topping is the removal of the stems above a plane parallel to the ground, and hedging is the removal of the stems on a particular side of a plane perpendicular to the ground. It is also possible to use automated pruning to limit the tree to a particular volume, such as a cylinder or sphere.

SIMULATION RESULTS AND INTERPRETATION

To test the realism of the architecture produced from this new L-PEACH, we simulated several trees and applied standard pruning practices. A simulated tree, pruned following a V-shaped training system is shown in Figure 4. The first panel shows a new trunk, with many sylleptic shoots. In the next panel the tree has been pruned back to stimulate growth of new water sprouts. In the two subsequent years, the inside branches were removed, fruiting branches grew and the distal shoots were cut again to stimulate more water sprouts. All the pruning was done in the dormant seasons. In Figure 5, the same tree, in the spring of its third year, is shown beside a picture of a real tree, pruned in the same V-shaped manner. It can be seen in this juxtaposition that the simulated tree has a similar architecture. There is a similar pair of major axes that come from the water sprouts, and medium and small shoots appear in similar places and flowers also appear in similar places. Topping applied to the same tree is shown in Figure 6.

CONCLUSION

Generally, the use of the HSMC concept to model branching structures in L-PEACH was very successful at reproducing trees that were visually similar to pruned peach trees observed in orchards. Several training systems have been simulated with a high fidelity. It was also shown by Lopez et al. (2008), that the introduction of architecture, along with a number of improvements to the carbon partitioning algorithms, has demonstrably improved the simulation results related to carbon allocation and physiology (e.g., the fruit sizes, photosynthesis, carbon storage, and organ respiration).

The improved architecture and pruning tools now allow L-PEACH to be used as a tool for experimentation and teaching. Future in silico explorations may include examinations of how experimental pruning methods may affect fruit production, or how architectures are affected by crop load. Educational uses may include interactive lessons on common training and fruit thinning practices.

There are some weaknesses in the current statistical descriptions of architecture used in L-PEACH that need to be addressed in future research. First, there is a paucity of data required to build comprehensive statistical HSMC descriptions of architecture for the peach trees of California. The parameters of the Markov chains currently used in L-PEACH were chosen from observations of shoots from pruned trees growing in California. A thorough analysis of their architecture is needed to increase the accuracy of the simulated trees; however it is clear that use of HSMC concepts is an efficient means for modelling tree architecture. Ongoing research is being conducted to develop more representative HSMC descriptions for Californian peach trees and when this is complete we will attempt to validate an updated L-Peach model with quantitative biomass data collected on field grown trees.

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Figures

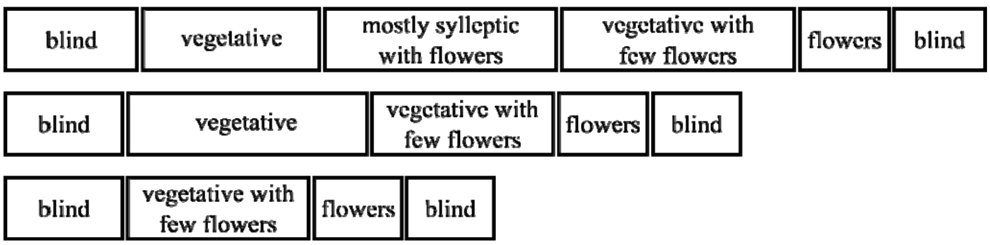

Fig. 1. Illustrations of three of the HSMCs used in L-PEACH, (Top) for the extremely vigorous shoots, (Middle) the highly and moderately vigorous shoots and (Bottom) the low vigour shoots. The very low vigour shoots (spurs) are not shown. All the HSMCs show similarities in their structure; they all start with a blind zone and end with a floral and blind zone. The extremely vigorous shoots are exceptional by having more zones of vegetative buds of various distributions. The highly and moderately vigorous shoots only differ by the length of the zones. The moderate and low vigour shoots are nearly identical, except for the deletion of one zone in the low vigour shoots.

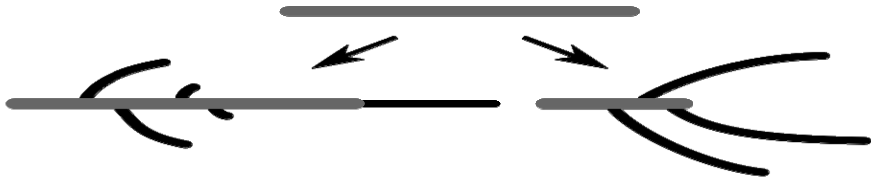

Fig. 2. An illustration of the pruning response. A shoot (top, in grey), if not pruned produces a terminal succession and a number of small, lateral shoots in the subsequent year (bottom left, new growth in black); however, if pruned, a number of vigorous lateral shoots grow near the distal end in the subsequent year (bottom right, new growth in black).

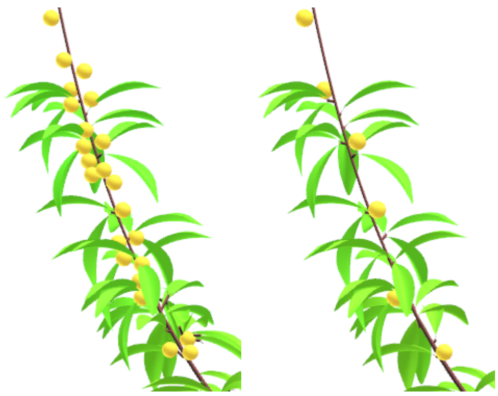

Fig. 3. (Left) Prior to thinning, a shoot has many, crowded fruit. (Right) The automated fruit thinning algorithm was applied, and now the fruit are all at least separated by four metamers. In both images, some shoots were removed for visibility.

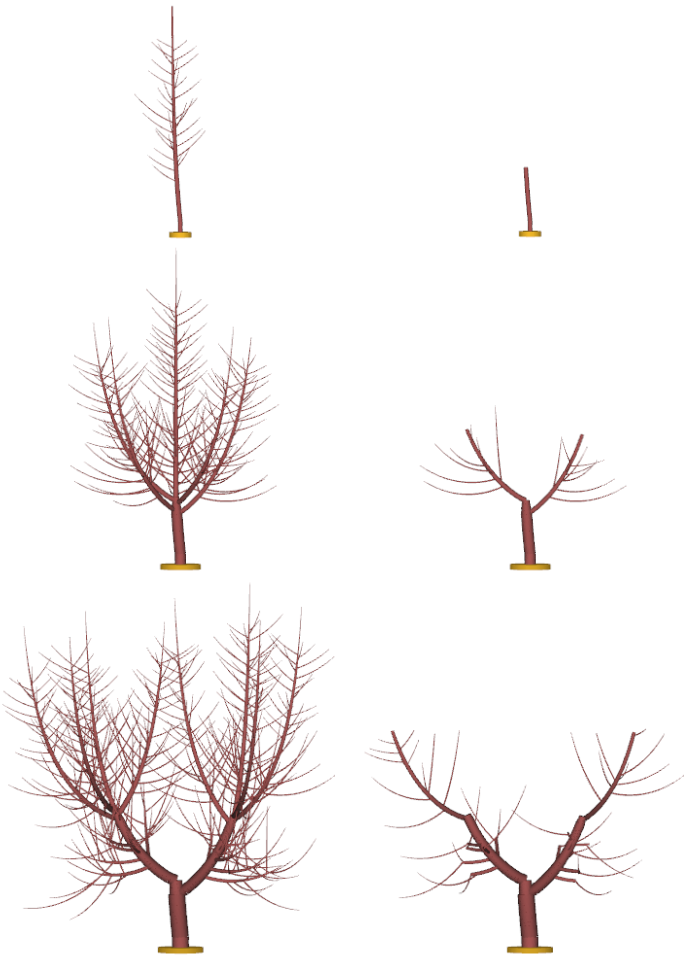

Fig. 4. A peach tree over four years of growth, shown at the end of each year, shown before (left column) and after winter pruning (right column). (Top Left) At the end of the first year, the trunk has grown with a large number of sylleptic shoots. (Top Right) The trunk was cut to half a metre. (Middle Left) By the end of the second year many water sprouts have grown. (Middle Right) Two water sprouts were selected as the main axes for the V-shaped training system. (Bottom Left) Water sprouts have grown from the ends of the main branches and medium-sized branches have grown. (Bottom Right) Most of the branches were pruned away.

Fig. 5. The L-PEACH simulation can be used to simulate trees similar to trees found in the orchard.

Fig. 6. An example of automated topping. All the stems above a selected height were cut away from the tree on the left to produce the tree on the right. This process is analogous to topping with a machine.