

Simulation of tree growth for three almond cultivars with contrasting architecture with the L-ALMOND model

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Abstract

The L-PEACH and L-ALMOND models use L-systems to simulate the architectural development and carbohydrate dynamics (assimilation, transport, distribution, storage and remobilization) of growing peach and almond trees, respectively. The models were able to successfully simulate tree growth and development and produce realistic estimates of tree size, structure and productivity over several years after planting, but always only for a specific cultivar. We here show how L-ALMOND can be adapted to simulate the architectural growth of three cultivars ('Nonpareil', 'Aldrich', and 'Winters') differing in tree architecture after three steps for each cultivar: i) inclusion of specific shoot architectures for six types of shoots (watersprouts, long, medium-long, medium, medium-short, and small shoots). Branching patterns and flowering occurrence for each type of shoot were previously assessed by developing hidden semi-Markov statistical models based on field research. Spur morphology was the same. Very different patterns emerged of sylleptic shoot production from lateral meristems on watersprouts, long, and medium-long shoots. 'Aldrich' and 'Winters' produced many more sylleptic shoots than 'Nonpareil'. No sylleptic shoot growth appeared from medium, medium-short, and small shoots in any cultivar; ii) definition of the type of shoot derived from a sylleptic shoot. In 'Aldrich' and 'Winters' most sylleptic shoots were spurs and short shoots, respectively, while in 'Nonpareil' their length varied widely (spurs, small, medium-short, and medium shoots); and iii) adjustment of a parameter to modify shoot bending to simulate differences in growth habit observed in the field. 'Aldrich' was more erect than 'Winters' and 'Nonpareil'. After modifications, L-ALMOND 3-dimensional tree simulations were similar to actual pictures of field trees, demonstrating how different shoot architectures result in different tree architectures over time, and especially the role that sylleptic shoot production plays in determining final tree architecture in almond.

Keywords: functional-structural plant model, L-PEACH model, *Prunus dulcis*, shoot architecture, tree growth

INTRODUCTION

Fruit tree architecture has multiple implications for tree management and fruit production (Costes et al., 2006). A model-assisted analysis of canopy architectural development is therefore valuable for understanding fruit tree functionality. Functional-structural plant models (FSPMs) have been developed to simulate the architectural growth and development of important fruit trees such as apple (MAppleT; Costes et al., 2008), peach (L-Peach; Lopez et al., 2008, 2010), and almond (L-ALMOND; DeJong et al., 2017). Models have produced realistic tree architectures (Lopez et al., 2016) making possible the integration of relevant physiological processes within the modeled architecture such as light distribution in the canopy (Lopez et al., 2008), supply/demand concepts of carbon allocation (Allen et al., 2005), carbon reserve dynamics (Lopez et al., 2008; Da Silva et al., 2014), movement of water within the tree (Da Silva et al., 2011), and hydraulic resistances between different parts of the tree (Da Silva et al., 2015). The modeled tree architectural framework also allowed the incorporation of concepts related with apical dominance and reiteration to



simulate tree responses to pruning (Lopez et al., 2008). The realistic architecture of the tree, responses to pruning, drought and size-controlling rootstock can be observed in some demonstrative simulations at <http://dx.doi.org/10.5281/zenodo.47228>.

In FSPMs such as MAppleT, L-Peach and L-ALMOND tree architecture relies on statistically-based Hidden semi-Markov Chain models of bud fates on different types of shoots (Costes et al., 2006) obtained from field observations for a given cultivar. In the case of L-ALMOND, the model was originally developed for 'Nonpareil' because it is the most widely grown almond cultivar in California. However, tree architecture can be substantially different among almond cultivars and almonds are minimally pruned (if at all), making it difficult to understand if differences in tree functionality and production between cultivars could be explained by differences in tree architecture per se. The first objective of this presentation was to simulate the architectural growth of three almond cultivars ('Nonpareil', 'Aldrich', and 'Winters') that have different tree architectures by incorporating available models of shoot structure for each cultivar (Negron et al., 2013) into the L-ALMOND model (DeJong et al., 2017). A secondary goal was to document all the changes necessary to simulate different cultivars to facilitate the use of L-ALMOND as a template for modeling other temperate deciduous tree crop species.

METHODS

Modelling tree architecture with L-ALMOND

L-ALMOND was developed from a previous peach model (L-PEACH) that simultaneously simulates the architectural development and carbohydrate dynamics (assimilation, transport, distribution, storage and remobilization) of growing peach trees (Lopez et al., 2008). In L-PEACH and in L-ALMOND the modelled tree is described as a branching network of phytomers. L-ALMOND uses L-systems to simulate all the architectural elements of the plant. Each phytomer consists of an internode with a specified initial length and a node that has a leaf and different types of buds (vegetative or floral). Vegetative buds produce new phytomers (shoots) and floral buds produce flowers. Flower buds remain dormant in the season in which they are generated and set fruit in the next season shortly after the bloom date. Buds can be terminal or axillary. Terminal buds are located at the end of a shoot and are always vegetative. Each phytomer has a central axillary bud that can be blind (failing to produce phytomers or flowers), floral or vegetative. Vegetative buds could be accompanied with zero to three 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. 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 organization 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 states (zones) that can differ in their axillary bud fates. 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 fates of the central bud and the lateral buds within each zone, respectively.

L-ALMOND is initiated with a stem segment that has a leaf, a vegetative terminal bud, a vegetative axillary bud and an axillary latent bud. Simulations begin with 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 determined by the bivariate model outlined above. Shoot types are categorized by their length into seven categories (watersprouts, long, medium-long, medium, medium-short, and small shoots). Another important feature of the model is that axillary 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 fates, the potential

length of the new shoots is based on the concept that succeeding shoots have less vigor 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 when carbohydrates are limited and when they are produced late in the season (Costes et al., 2007). The architectural model is governed by calendar time. 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.

Modifications in L-ALMOND to simulate different cultivars

To simulate the architecture of different almond cultivars with L-ALMOND, the following modifications were necessary. First was the inclusion into L-ALMOND of specific shoot architecture for seven types of shoots based on their length (watersprouts, long, medium-long, medium, medium-short, and small shoots) for each cultivar. The branching patterns and flowering occurrence for each type of shoot for each cultivar were extracted from hidden semi-Markov statistical models developed by Negron et al. (2013). To facilitate the incorporation of the models into L-ALMOND a window in the L-ALMOND graphical user interface (GUI) was developed so the model operator can easily implement the files with shoot architecture information (Figure 1). These files need a specific format with information related to the number of states (zones) 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. An example of the code format required for a given shoot file is presented in Figure 2. Secondly, the definition of probabilities for sylleptic shoot production from lateral meristems on watersprouts, long, and medium-long shoots was also required. The probabilities were adjusted until sylleptic production was similar to that observed in the field (Negron et al., 2013) generating a specific sylleptic transition matrix for each cultivar (Table 1). These specific transition matrices were then implemented in L-ALMOND using the L+C plant modeling language (Prusinkiewicz et al., 2007a) (code not shown) and they can be individually called from the GUI using the cultivar option (Figure 3). Third was the modification of branch bending to simulate difference between cultivars observed in the field. This was performed by modifying the strength of the tropism vector of the modelled tree, a parameter that can modify shoot bending (Karwowski and Lane, 2006). This parameter can be easily modified using the GUI (Figure 3). The selected value for 'Aldrich' was 0.050. The selected value for 'Winters' and 'Nonpareil' was 0.025 (Figure 3).

Table 1. Transition matrix for the sylleptic production from a proleptic lateral bud for watersprouts, long and long-medium shoots for three almond cultivars. There are no sylleptic productions from medium, medium-short and small shoots.

	Long	Long-medium	Medium	Medium-short	Small	Spurs
Nonpareil						
Watersprouts	-	-	0.5	0.5	-	-
Long	-	-	0.1	0.64	0.26	-
Long-medium	-	-		0.49	0.51	-
Winters						
Watersprouts	-	-	-	-	1	-
Long	-	-	-	-	1	-
Long-medium	-	-	-	-	1	-
Aldrich						
Watersprouts	-	-	-	-	-	1
Long	-	-	-	-	-	1
Long-medium	-	-	-	-	-	1

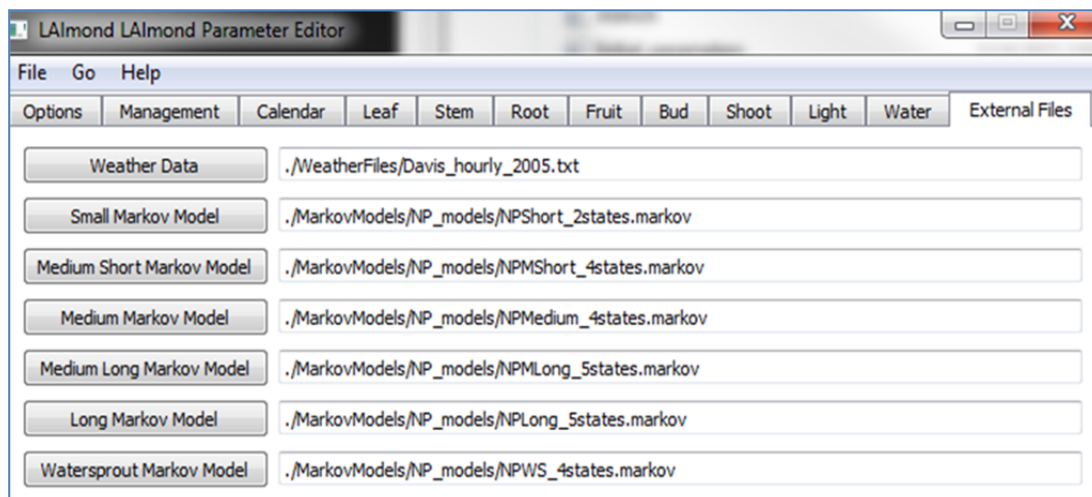


Figure 1. Graphical user interface developed to facilitate the incorporation of different types of shoots into L-ALMOND. The current view shows the specific selection for 'Nonpareil'.

```

HIDDEN_SEMI-MARKOV_CHAIN
//Definition of the number of states (zones)
6 STATES

//Initial probabilities for each zone at the base of the shoot
INITIAL_PROBABILITIES
0.974 0.026 0 0 0 0

//Transition probabilities between zones
TRANSITION_PROBABILITIES
0 0.944 0.03 0.026 0 0
0 0 0.66 0.34 0 0
0 0 0 1 0 0
0 0 0 0 1 0
0 0 0 0 0 1
0 0 0 0 0 1

// Occupancy distributions representing the length of each zone
STATE 0 OCCUPANCY_DISTRIBUTION
NEGATIVE_BINOMIAL INF_BOUND:1 PARAMETER:0.720799 PROBABILITY:
:0.111186

STATE 1 OCCUPANCY_DISTRIBUTION
NEGATIVE_BINOMIAL INF_BOUND:1 PARAMETER:8.39374 PROBABILITY:
0.345421

STATE 2 OCCUPANCY_DISTRIBUTION
NEGATIVE_BINOMIAL INF_BOUND:1 PARAMETER:18.21 PROBABILITY:
0.445435

STATE 3 OCCUPANCY_DISTRIBUTION
NEGATIVE_BINOMIAL INF_BOUND:1 PARAMETER:2.7624 PROBABILITY:
0.148599

STATE 4 OCCUPANCY_DISTRIBUTION
NEGATIVE_BINOMIAL INF_BOUND:1 PARAMETER:1.38767 PROBABILITY:
0.144615

//Definition of the observation distributions
2 OUTPUT_PROCESSES

//Central bud (o=blind; 1 = floral; 2 = vegetative
//3 = sylleptic, 4 = terminal)
OUTPUT_PROCESS 1:NONPARAMETRIC

STATE 0 OBSERVATION_DISTRIBUTION
OUTPUT 0:0.184
OUTPUT 1:0.034
OUTPUT 2:0.782

STATE 1 OBSERVATION_DISTRIBUTION
OUTPUT 0:0.003
OUTPUT 1:0.002
OUTPUT 2:0.993
OUTPUT 3:0.002

STATE 2 OBSERVATION_DISTRIBUTION
OUTPUT 0:0.493
OUTPUT 1:0.070
OUTPUT 2:0.436
OUTPUT 3:0.001

STATE 3 OBSERVATION_DISTRIBUTION
OUTPUT 0:0.066
OUTPUT 1:0.002
OUTPUT 2:0.926
OUTPUT 3:0.006

STATE 4 OBSERVATION_DISTRIBUTION
OUTPUT 0:0.602
OUTPUT 1:0.300
OUTPUT 2:0.098
OUTPUT 3:0

STATE 5 OBSERVATION_DISTRIBUTION
OUTPUT 4:1

//Lateral buds (0 = 0 flowers, 1 = one flower,
//2 = two flowers, 3 = three flowers)
OUTPUT_PROCESS 2:NONPARAMETRIC

STATE 0 OBSERVATION_DISTRIBUTION
OUTPUT 0:1

STATE 1 OBSERVATION_DISTRIBUTION
OUTPUT 0:0.209
OUTPUT 1:0.496
OUTPUT 2:0.290
OUTPUT 3:0.005

STATE 2 OBSERVATION_DISTRIBUTION
OUTPUT 0:1
OUTPUT 1:0
OUTPUT 2:0
OUTPUT 3:0

STATE 3 OBSERVATION_DISTRIBUTION
OUTPUT 0:0.653
OUTPUT 1:0.247
OUTPUT 2:0.096
OUTPUT 3:0.004

STATE 4 OBSERVATION_DISTRIBUTION
OUTPUT 0:1
OUTPUT 1:0
OUTPUT 2:0
OUTPUT 3:0

STATE 5 OBSERVATION_DISTRIBUTION
OUTPUT 4:1

```

Figure 2. Example of code required in the L-ALMOND model to incorporate information about shoot architecture. The example represent a long-medium shoot for 'Nonpareil'.

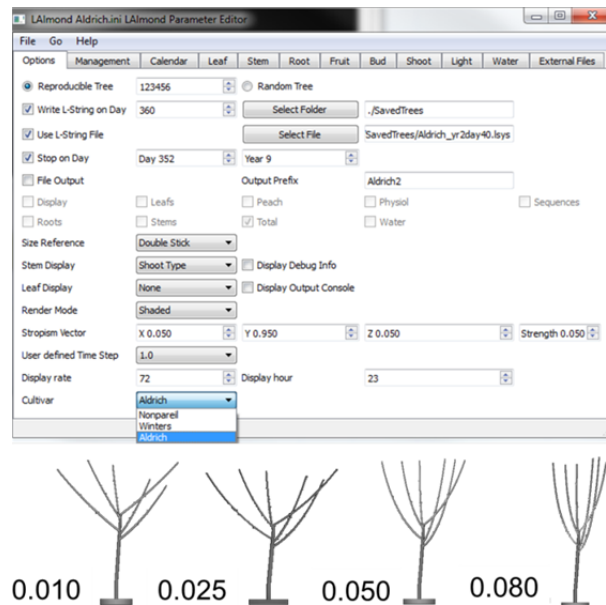


Figure 3. Graphical use interface (GUI) of the L-ALMOND model (top). Using the options from the GUI it is possible to select the cultivar and the effect of the strength of the tropism vector in tree bending. The strength was modified to 0.010, 0.025, 0.050, and 0.080 and the consequences can be observed in the bottom part of the figure.

Model performance

The L-ALMOND model did a reasonable job of simulating the architectural tree growth of the three cultivars (Figure 4). Major differences and similarities among almond cultivars observed in the field (Negron et al., 2013) can be visually observed in the simulations (Figure 4). The first similarity among cultivars is that all of them share the same type of shoots (watersprouts, long, medium-long, medium, medium-short, short shoots, and spurs) (Negron et al., 2013). However, each of the shoot types (except spurs) have different shoot architectures as demonstrated by statistically-based Hidden semi-Markov Chain models of shoot architecture (Negron et al., 2013). Another important difference between almond cultivars was related to syllepsis (lateral buds that are activated in the current season) and the type of shoots generated during sylleptic growth. This behavior was very different among the three cultivars. 'Aldrich' and 'Winters' produced many sylleptic shoots while the number of sylleptics observed in 'Nonpareil' was much less (Figure 4). Simulations did not produce sylleptic shoot growth from medium, medium-short, and small shoots in any cultivar. In 'Aldrich' and 'Winters' most sylleptic shoots were spurs and short shoots, respectively. Sylleptic shoots in 'Nonpareil' were more variable in terms of their length (spurs, small, medium-short, and medium shoots). An example of the sylleptic production for long shoots can be observed in Figure 4. At the whole tree level the main differences among cultivars was related with branch bending. Bending was lower in 'Aldrich' than in 'Winters' and 'Nonpareil' as can be observed in Figure 4. However, these differences have not been quantified with field measurements.

DISCUSSION

The new version of the L-ALMOND model is able to simulate the architecture of different almond cultivars. Before starting a simulation with L-ALMOND, it is now possible to select one of the three available cultivars ('Nonpareil', 'Aldrich', and 'Winters') in the GUI (Figure 3). L-ALMOND offers the flexibility of incorporating other cultivars if information of shoot architecture like the data presented in Figure 2 are available. Since L-PEACH and L-ALMOND share the same code structure we have realized that it will be useful to generate a

generic L-TREE model where specific functions for organ functionality and plant architecture can be called from a GUI as was done in L-ALMOND to implement different transition matrices for the sylleptic shoot production (Table 1). Since the underlying concepts within L-PEACH and L-ALMOND are generic for all fruit crops, the existence of a generic L-TREE model could facilitate the study of water and carbon transport within trees of other cultivars and species that have received less attention.

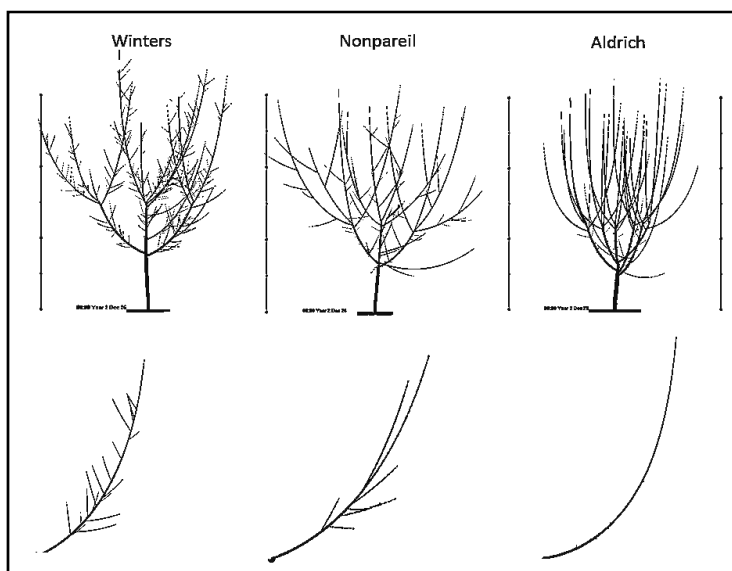


Figure 4. Simulation of whole tree architecture and a long shoot for three almond cultivars using the L-ALMOND model. Trees are three years old.

L-PEACH and L-ALMOND were mainly conceived as tools to guide experimental research by helping to identify or develop quantitative hypotheses that can be answered with new research. During the simulation of different cultivars with the L-ALMOND model it became evident that sylleptic shoots plays a significant role in almond tree architecture. However, the causative genetic differences responsible for sylleptic shoot production between almond cultivars have not been studied and it is therefore not known which genes control syllepsis in almond. Identification of genes responsible for syllepsis in almond may be useful for generating unique L-ALMOND models for different cultivars based on genetic changes governing syllepsis. This approach has been already used to simulate the architecture of inflorescences (Prusinkiewicz et al., 2007b) but has not been accomplished for studying the architecture of fruit trees.

Now that a version of the L-ALMOND is able to simulate the architecture it is possible to perform multiple virtual experiments to have a better understanding of the variability in yield determinants and their interaction with environmental variables. One example would be to simulate different pruning strategies and their effects on the production of different shoot types to determine long term potential effects on nut production based on the resulting tree architectures. Most pruning experiments are currently conducted in the field and with relatively little appreciation for the quantitative effects of pruning treatments on tree architecture in relation to tree yield. Tree models such L-ALMOND afford the opportunity test these relationships in silico and use the results to guide more nuanced approaches to studying these relationships in the field.

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