Assessing the Carbon Budget of Almond Trees and Developing a 3-D Computer Simulation Model of Almond Tree Architectural Growth and Dry Matter Partitioning

Project No.: **11-PREC1-DeJong**

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Objectives:

This project has two major objectives. The first is to review available research data and collect new data on almond (and related species) tree growth; biomass productivity; dry matter partitioning; and carbon and nitrogen assimilation, utilization and distribution.

The second and longer term objective is to develop a comprehensive, functional-structural tree model of almond tree architectural development, growth, and carbon partitioning/source-sink interactions within the tree. This model will simulate growth and physiological responses to light distribution within the canopy and daily temperature changes as well as responses to user imposed pruning practices.

Interpretive Summary:

Objective one: A review of available literature on tree growth; dry matter partitioning and biomass productivity of almond trees over multiple years indicated that there is not enough published data to make reliable estimates of the amount of carbon contained in the standing biomass of mature almond orchards at this time. However in the past several years it has become standard practice to engage professional tree removal companies to remove almond orchards at the end of their productive life. Since these companies haul and weigh the chippings subsequent to the removal of an orchard, reasonable estimates of orchard standing biomass are available from these operations. However tree size and density vary greatly among orchards so it is necessary to develop a way to estimate the standing biomass in an individual orchard in a relatively simple manner. We have begun working with orchard removal companies to obtain data on the amount of biomass removed from several orchards that have recently been cleared. To develop a simple method for estimating standing biomass in existing orchards we are in the process of surveying specific orchards prior to removal to determine the average tree trunk cross sectional area (TCSA) per acre. We then plan to develop a mathematical relationship between TCSA/acre and the amount of biomass removed in the clearing process. We cannot determine how robust this relationship will be until we collect data from at least 20 removed orchards that represent a broad range of standing biomass per acre.

Objective two: Almond tree growth and yield is dependent on a complex set of interactions involving the plant genotype, the physiological and developmental processes that occur within the tree, the interaction of these processes with the environment that the tree grows in, and responses to horticultural manipulation of the tree by the grower. Understanding carbon budget, growth and yield responses of perennial crops like almond are even more complex than most crops because the effects of all these factors are carried out over multiple years.

Recent advances in computer technology have made it possible to develop functional-structural plant models that simultaneously simulate whole plant photosynthesis, tree architectural growth and carbon partitioning within the structure of the tree, and display tree structural development in three dimensions on a computer screen. The most advanced of these types of models is the L-Peach model. One objective of this project is to convert the L-Peach model to an L-Almond model.

The first step for conversion of L-Peach to an L-Almond model was to develop statistical models to describe patterns of buds that occur along Nonpareil almond shoots of different lengths. Development of these statistical shoot bud fate models for Nonpareil are now complete. The second step was to begin converting the L-Peach model into an L-Almond model by inserting leaf photosynthetic characteristics of almond trees and the statistical models of almond shoots into the L-Peach model. New almond shoot models have been inserted into the L-Almond model and we are now attempting to validate the architectural aspects of simulated trees with pictures of actual orchard trees of various ages.

While waiting on the almond shoot bud fate models, in 2011 we completed research to incorporate water transport within the tree structures generated by the L-Peach model so that hourly values for water potential can be calculated each hour for every node within the structure of the simulated trees. The hourly water potential values calculated by the model now interact with the physiological functioning of the trees so that tree growth and yield responses to irrigation scheduling can now also be simulated by the model. These advances have also now been incorporated in the L-Almond model. We have also recently upgraded the simulation of annual carbohydrate storage in woody tissues so that the tree growth and development can be simulated over multiple years, and the critical period of carbohydrate limitation between bloom and when there is sufficient new leaf area to support both vegetative and fruit growth in the spring can be realistically simulated. The primary work on the model that remains is validation of both the quantitative and visual outputs of the model. This is mainly being done by comparing model outputs with data and pictures previously collected in Dr. Lampinen's laboratory.

A corollary effort associated with this project has been the analysis of data from Regional Variety Trials and the spur dynamics study carried out by Dr. Lampinen's laboratory from 2001 to 2007, in order to develop data on long-term spur behaviour that can be used in the L-Almond model. This research has resulted in three publications and provided valuable insights into the fruit production behaviour of almond tree spurs that are useful for general understanding of almond tree productive behaviour as well as for developing the L-Almond model.

Materials and Methods:

Assembling Data on Whole Tree Biomass

Several biomass companies have been contacted to obtain standing biomass data at the time of orchard removal. We have begun to compile data on locations of removed orchards, age of orchards at the time of removal, spacing of the trees and cultivars. While we were doing this data compilation we realized that we needed to develop a surveying method that would allow us to relate biomass removal data with average tree size prior to tree removal. Since tree trunk cross sectional area (TCSA) is a common method to estimate tree size used in horticulture as well as forestry we have begun testing a linear plot sampling method to quickly determine the mean TCSA/acre of specific orchards slated for removal, prior to their actual removal. We have begun the process of collecting and analyzing those data but it is too early to report results since we will need data from at least 20 orchards representing a broad range of TCSA and biomass per acre to test this relationship. We believe that this approach will provide good estimates of standing biomass of mature almond orchards and will be useful for estimating the amount of carbon stored in trees in virtually any California almond orchard.

Development of an L-Almond Model

The second objective (developing a model of almond tree growth) began with statistically analyzing the structural patterns of various sizes of almond shoots using Hidden Semi-Markov Chain (HSMC) analysis techniques (Guedon et al. 2001). This work began in 2010 in a commercial 4-year-old almond orchard located near Sutter. This orchard had three cultivars ('Nonpareil', 'Aldrich', and 'Winters') exhibiting different tree architectures. Trees in the orchard were minimally pruned after the first year after planting, when the main scaffolds were chosen, so that trees developed their own architecture.

To characterize the branching patterns of the proleptic shoots, evaluations were executed after the second year of a shoot's growth, when lateral proleptic shoots develop. Five size categories of 2-year-old proleptic shoots in the tree canopies were selected: 'Long' shoots (more than 1 meter); 'Medium–Long' shoots (between 60 cm and 100 cm); 'Medium' shoots (between 20 cm and 60 cm); 'Medium–Short' shoots (between 5 cm and 20 cm); and 'Short' shoots (less than 5 cm). Before bloom in February, 2010, one shoot in each shoot category was randomly selected in each quadrant of 10 trees, totaling 40 shoots.

Lateral branching of the shoots was evaluated by describing each lateral type at every node from the tip to the base of the shoot. Four lateral production types could be described at each node: blind node or lack of an axillary meristem, spur, proleptic shoot, or sylleptic shoot.

For the branching pattern analysis, lateral production types at each node along the shoot were organized in the same direction as data were collected (i.e. from the tip to the base of the shoot). This succession of lateral types along the shoot was represented as a discrete sequence of data indexed by the node rank. The sequences were analyzed using V-Plants software (http://www-sop.inria.fr/virtualplants).

From the global models for each cultivar, specific parameters for the shoots from each shoot size category were extracted. To do this, the most probable state sequence of each observed sequence was estimated using the global hidden semi-Markov chain of each cultivar. This new sequence corresponded to the optimal segmentation according to homogenous zones of the observed sequence. Subsequently, the most probable state sequences, along with observed sequences, were separated according to shoot size category in which the shoot originally assigned. Finally, the segmentation of each shoot was used to obtain the zone occurrence along the shoot, as well as the zone lengths, for each shoot size category.

These data were analyzed collaboratively with colleagues at the INRA centre in Montpellier, France. These shoot models were then inserted into the L-Almond (Allen et al. 2005; Lopez et al. 2008) simulation model along with previously collected leaf and fruit growth characteristics to develop the L-Almond model.

Field studies that were initiated last year to evaluate the influence of water stress, cultivar (genotype) and severity of pruning on the structure of different size categories of almond shoots through HSMC analysis were also completed in 2011. These studies will be used as the basis for developing more robust sub-models of almond trees growing under different pruning practices and irrigation management strategies. Collection of data on the influence of water stress on shoot growth characteristics of Nonpareil trees was initiated in an ongoing field experiment of Dr. Lampinen (USDA-Pacific Area-Wide Pest Management Program for Methyl Bromide Alternatives-Almonds & Stone Fruits).

Associated Studies

A corollary effort associated with this project has been the analysis of data from the Regional Variety trials sponsored by the Almond Board (1993-2005) and from the spur dynamics study carried out by Dr. Lampinen’s laboratory from 2001 to 2007, in order to develop an understanding of factors controlling bearing and long-term spur behaviour needed for developing and validating the L-Almond model. We published one research paper from this effort in 2010 and two more in 2011. We are working on one additional paper concerning factors that influence fruit set at the spur and tree level.

Results and Discussion:

Developing a database on standing biomass in almond

Since relatively little published data are available on whole tree biomass accumulation in almond trees we have worked with professional orchard removal companies to obtain data from them on the weight of chippings they obtain subsequent to the removal of an orchard. While this has been more difficult than anticipated we have made good progress on this objective. Data from 61 removed orchards representing 2034 acres indicated that orchard standing biomass varies greatly among orchards. In this set of removed orchards the amount of dry biomass removed varied from 4 to 63 dry tons per acre with the mean and median dry tons per acre removed being 27.7 and 26.3, respectively.

In light of this large variation in orchard standing biomass we began surveying orchards to estimate orchard mean TCSA prior to orchard removal and we plan to correlate mean TCSA/acre values with standing biomass data collected upon orchard removal. If necessary, we will use missing tree data from aerial photography to make adjustments to the TCSA data to improve the estimation of standing tree biomass for specific orchards. This involves cooperative work between an orchard removal company (GF Ag Services LLC. Ripon), an enterprise specializing in remote sensing data (Newfields, Sacramento) and UC researchers. We anticipate having preliminary results from this effort by December, 2012.

Development of the L-Almond Model

The L-Peach model has been successfully converted to an L-Almond model. Physiological functions describing the behavior of almond fruits and leaves needed to make this conversion came mainly from the DeJong laboratory (Grossman and DeJong 1994, Esparza et al 1999, Esparza et al 2001). Statistical shoot models for describing the architecture and bud fates of Nonpareil, Winters and Aldridge shoots were developed. Examples of the bud fate hidden semi-Markov chain models developed are provided in **Figures 1-3**. The example models of medium proleptic and epicormic shoots clearly indicate the structural differences between shoots of the Nonpareil, Winters and Aldridge cultivars. Differences among cultivars were mainly confined to the mid-sections of the shoots while the basal and tip sections of the shoots of all three cultivars were very similar.

At present only the Nonpareil shoot models have been inserted into the L-Almond model in the place of statistical models describing peach shoots. Eventually, after the Nonpareil version of L-Almond has been satisfactorily validated, it will be relatively easy to adjust the model to simulate the growth of the Winters and Aldridge cultivars.

The L-Almond model is now capable of making reasonable simulations of architectural tree growth and cumulative biomass during the first four years after planting. **Figures 4** and **5** show the comparison of simulated trees with pictures of orchard trees during the first two years of growth. Initial runs of the model indicated that additional work was necessary on the over-wintering storage and spring mobilization of carbohydrate in the stems and roots. Preliminary adjustments have been made on the model but future data collection on this aspect of the physiology of almond will be necessary to insure that modeled behavior is accurate.

Currently, simulations beyond four years are difficult because the model keeps track of every plant part at the node level and when the simulated tree gets large the simulations get bogged down because of physical limitations in computer hardware. We are currently working on how to deal with this problem. We are also working to validate simulation results for the early years.

Interestingly, this modeling effort has identified an underappreciated, critical period during fruit growth and development that may be a major determinate of final yield. This is the period of fruit drop after pollination but before shell hardening. While this fruit drop has been a concern to growers for many years, the cause of this fruit drop has not been clear. The model indicates that this fruit drop is likely caused by a lack of carbohydrates available to support fruit growth during a critical period when vegetative and reproductive growth transitions from dependency on stored carbohydrates to current photosynthates. Additional field research is necessary to confirm this but the model can be used to pinpoint critical periods that must be studied.

Associated Studies

The corollary efforts associated with this project were based on an analysis of data from the Regional Variety trials sponsored by the Almond Board (1993-2005) and from the spur dynamics study carried out by Dr. Lampinen's laboratory from 2001 to 2007. These have resulted in three significant publications.

1. The first provides an understanding of the relationship between spring temperatures and the timing of hull-spit.

Fruit development in almond is influenced by early Spring temperatures in California
S. Tombesi, R. Scalia, J. Connell, B. Lampinen and T.M. DeJong
Journal of Horticultural Science and Biotechnology (2010) 85:317-322.

Abstract: The period from full bloom (FB) to fruit maturity for individual cultivars of peach, nectarine, plum, and prune is influenced by daily temperatures between the start of FB and 30 d after FB (DAFB). Typically, warm springs accelerate fruit development. Almond is closely-related to peach, but the date of fruit maturity is not always closely related to the date of harvest. Normally the date of “hull-split” (HS) signals the beginning of fruit maturity. The aim of this study was to determine if the length of the period between FB and HS in several important Californian almond cultivars was related to temperatures shortly after the start of FB. Data on the dates of FB and HS from three locations in the Central Valleys of California (North, Central, and South) were analyzed over 8 years to determine the effect of spring temperatures on the duration of fruit development. Data on 28 cultivars were evaluated, but only the results for 12 of the most important cultivars are reported here. The length of the period of fruit development from FB to HS was negatively correlated with the accumulation of degree-days between FB and 90 DAFB (mean R2 = 0.51 ± 0.3), with generally poorer correlations with degree-days to 30 or 50 DAFB (mean R2 = 0.31 ± 0.02 and 0.36 ± 0.3, respectively). These results suggest that temperatures in the first 90 DAFB are the primary factor influencing the time of nut maturity in almond cultivars in California.

Data from this paper have been used to develop a web-based model to help growers predict hull-split in their orchards by late May of each year.
See: Hull-split Prediction Model at http://fruitsandnuts.ucdavis.edu/Weather Services/

2. The second publication provides insight into the factors that influence individual spur productivity and mortality in almond tree canopies.

Spur behaviour in almond trees: relationships between previous year's spur leaf area, fruit bearing and mortality
Bruce D. Lampinen, Sergio Tombesi, Samuel Metcalf and Theodore M. DeJong
Tree Physiology (2011) 31: 700-706

Abstract: In mature almond (Prunus dulcis) orchards the majority of crop is borne on spurs (short, proleptic shoots) that can live for several years and can produce from one to five fruit. Previous research has led to the hypothesis that spur longevity is related to spur light exposure, cropping and age. However, limited quantitative data are available to substantiate these hypotheses. The objective of this study was to determine spur characteristics that were most highly correlated with spur productivity and longevity in mature, bearing almond trees. We particularly focused on characteristics related to the spur light environment and spur crop load. Previous year spur leaf area was strongly related to spur viability and flowering; the greater the leaf area in the previous year, the higher the probability of spur survival into the next year and the higher the probability for the spur to bear one or more flowers. Previous year bearing also appeared to influence viability and return bloom, especially in spurs with low leaf area. These results suggest that spur source-sink balance is basic to the life cycle of almond spurs. Furthermore, the results are consistent with the hypothesis that spurs are semi-autonomous organs with respect to carbohydrate balance for much of the growing season. The models developed from this work will provide the basis for developing a functional-structural almond crop model that simulates cropping at the spur level. Finally, this information provides general thresholds for maintaining spur viability and productivity that will be useful for developing and evaluating tree training systems and orchard management practices.

3. The third publication increases understanding of the potential for almond orchards to yield large crops in two successive years.

Relationships between spur- and orchard-level fruit bearing in almond (Prunus dulcis)
Sergio Tombesi, Bruce D. Lampinen, Samuel Metcalf and Theodore M. DeJong
Tree Physiology (2012) 31:1413-1421

Abstract: Almond is often considered to be a moderately alternate-bearing species but historical yield data typically do not exhibit clear patterns of alternate bearing at the orchard level, while research has indicated that spurs (the main fruit bearing unit in almond trees) rarely produce fruit in two subsequent years. The objective of the present work was to analyze the bearing behavior of almond trees at both the orchard level and the individual spur level over multiple years to explain this apparent paradox. The 10-

year yield patterns of three almond cultivars grown at three different sites within California were analyzed for tendencies of alternate bearing at the orchard level. At the individual spur level, data on spur viability, and number of flowers and fruits per spur were collected on 2400 individually tagged spurs that were observed over 6 years to characterize bearing at that level. At the orchard level one cultivar (Nonpareil) did exhibit a tendency for alternate bearing at one site (Kern) but other cultivars and sites did not. The orchard and the individual trees in which the spur population study was conducted showed tendencies for alternate bearing but the spur population did not. Only a relatively small percentage of the total tagged spur population bore fruit in any given year and therefore while individual fruiting spurs exhibited a high level of non-bearing after fruiting the previous year the spurs that did produce fruit in any year generally did not constitute enough of the total spur population to exhibit alternate bearing at the whole population level. Our results suggest that annual bearing fluctuations in almond are probably mainly due to year-to-year variations of parameters affecting fruit set and that high rates of fruit set in a given year may involve a larger-than-normal percentage of a spur population in fruit bearing. This would limit the size of the spur population available for flowering in the subsequent year and could cause alternate year bearing. However, from historical records, this would appear to be the exception rather than a normal circumstance. Therefore, almond should not be considered to be a strictly alternate-bearing species.

Acknowledgements:

We want to formally recognize the super collaboration of Drs. Evelyne Costes and Yann Guedan of UMR DAP INRA / AgroM / CIRAD / IRD Equipe Architecture et Fonctionnement des Espèces Fruitières, Montpellier, France, in helping to develop the Hidden Semi-Markov Chain models of the almond shoots.

References:

Allen, M.T., Prusinkiewicz, P., DeJong, T.M. (2005) Using L-systems for modeling source-sink interactions, architecture and physiology of growing trees: the L-PEACH model. *New Phytologist* 166, 869-880.

Allen, M.T., Prusinkiewicz, P., Favreau, R.R., DeJong, TM. (2007) L-Peach, an L-system-based model for simulating architecture, carbohydrate source-sink interactions and physiological responses of growing trees. In ‘Functional-structural plant modeling in crop production’ (Eds. J Vos, LFM. de Visser, PC. Struick, JB Evers)

Esparza, G., DeJong, TM., and Grossman, Y.L. (1999) Modifying PEACH to model the vegetative and reproductive growth of almonds. *Acta Hort.* 499, 91-98.

Esparza G., DeJong T.M., Weinbaum S.A. (2001) Effects of irrigation deprivation during the harvest period on nonstructural carbohydrate and nitrogen contents of dormant, mature almond trees. *Tree Physiology* 21, 1081-1086,

Esparza G., DeJong T.M., Weinbaum S.A., I. Klein. (2001) Effects of irrigation deprivation during the harvest period on yield determinants in mature almond trees. *Tree Physiology* 21, 1071-1079,

Guédon, Y., Barthélémy, D., Caraglio, Y., Costes, E. (2001) Pattern analysis in branching and axillary flowering sequences. *Journal of Theoretical Biology.* 212, 481-520.

Grossman, YL., and DeJong, TM. (1994) PEACH: A simulation model of reproductive and vegetative growth of peach trees. *Tree Physiology* 14, 329-345.

Lopez, G., Favreau, R.R., Smith, C., Costes, E., Prusinkiewicz, P. and DeJong, T.M. (2008) Integrating simulation of architectural development and source-sink behaviour of peach trees by incorporating Markov chain and physiological organ function sub-models into L-PEACH. *Functional Plant Biology* 35, 761-771.

Smith, C., Costes, E., Favreau, R., Lopez, G. and DeJong T. (2008) Improving the architecture of simulated trees in L-PEACH by integrating Markov chains and responses to pruning. *Acta Hort.* 803:201-208.

Tombesi, S., Scalia, R., Connell, J. Lampinen, B. and DeJong, T.M. 2010. Fruit development in almond is influenced by early Spring temperatures in California. *Journal of Horticultural Science & Biotechnology* 85:317–322Lampinen, B.D., Tombesi, S., Metcalf, S.G., and DeJong, T.M. 2011. Spur behaviour in almond trees: relationships between previous year leaf area, fruit bearing and mortality. *Tree Physiology* 31:700-706

Tombesi, S., Lampinen, B.D., Metcalf, S. and DeJong, T.M. 2011. Relationships between spur - and orchard-level fruit bearing in almond (*Prunus dulcis*). *Tree Physiology* 31: 1413–1421

Figures:

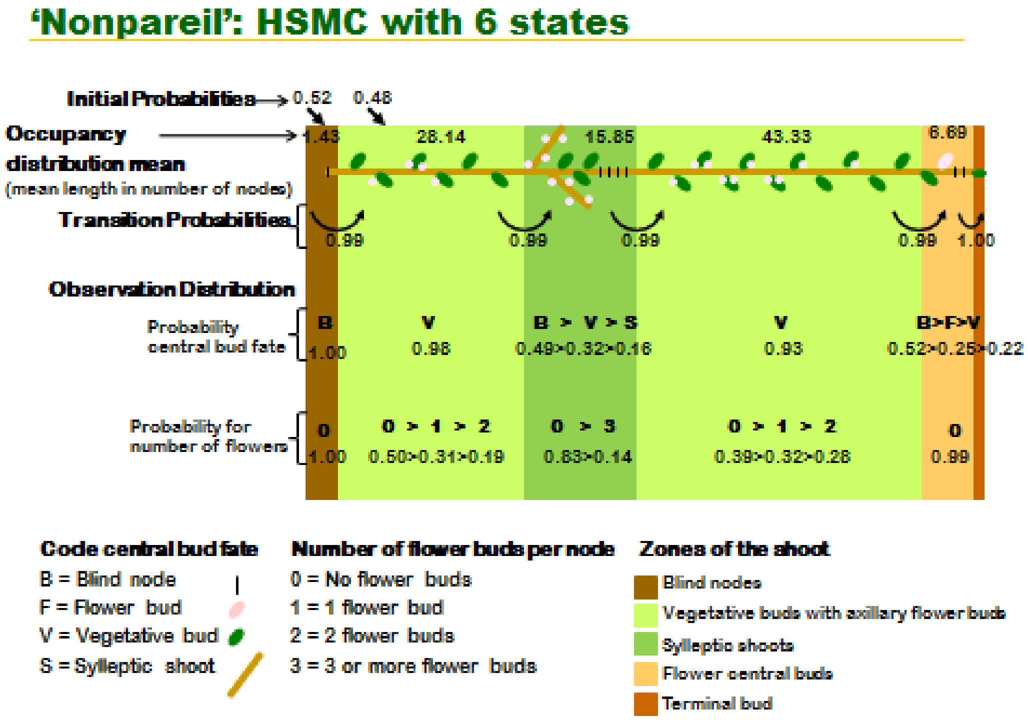
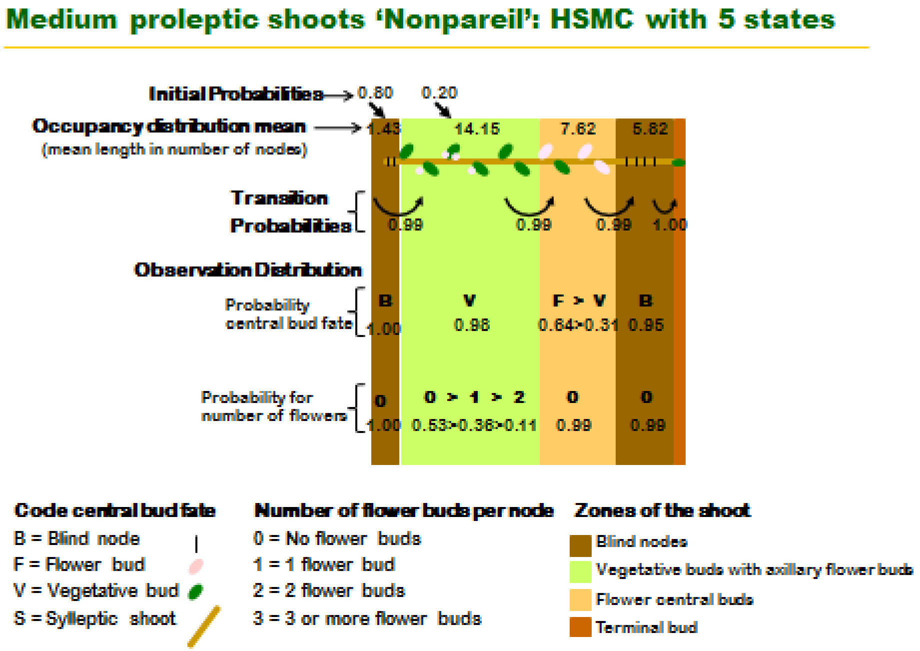


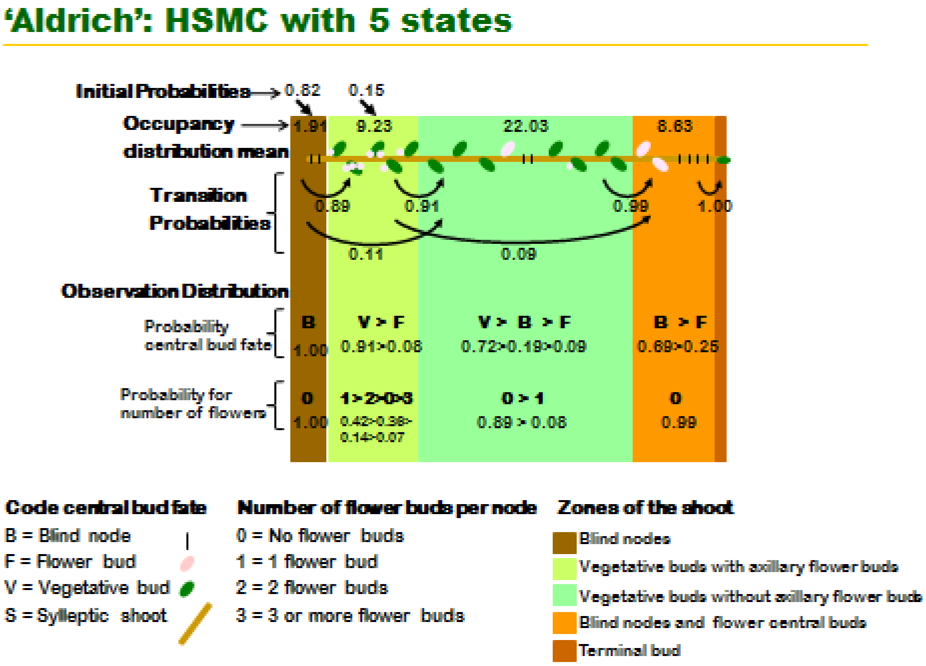
Figure 1. Schematic representation of the hidden semi-Markov chain for the **long proleptic shoots** of 'Nonpareil' with the four sets of estimated parameters. The mean length of the different zones of the shoots is represented by each segment. The observations for the central bud fate are: Blind node (B), Floral central bud (F), Vegetative bud (V), or Sylleptic shoot (S). The observations for number of flower buds per node are: no flower bud(0), 1 flower bud (1), 2 flower buds (2), and 3 or more flower buds (3)

(a)



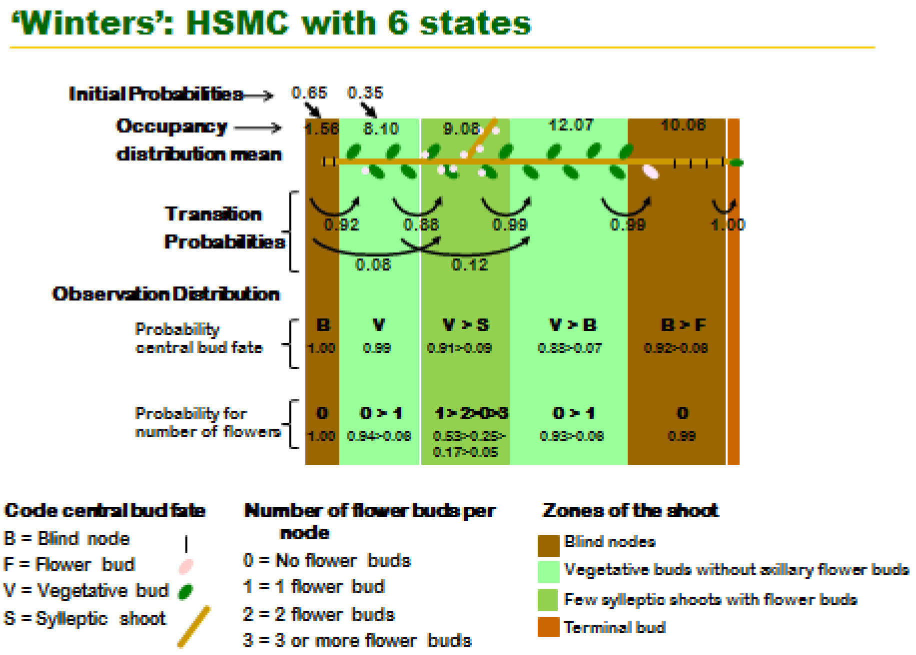
Mean total node number: 29

(b)



Mean total node number: 41

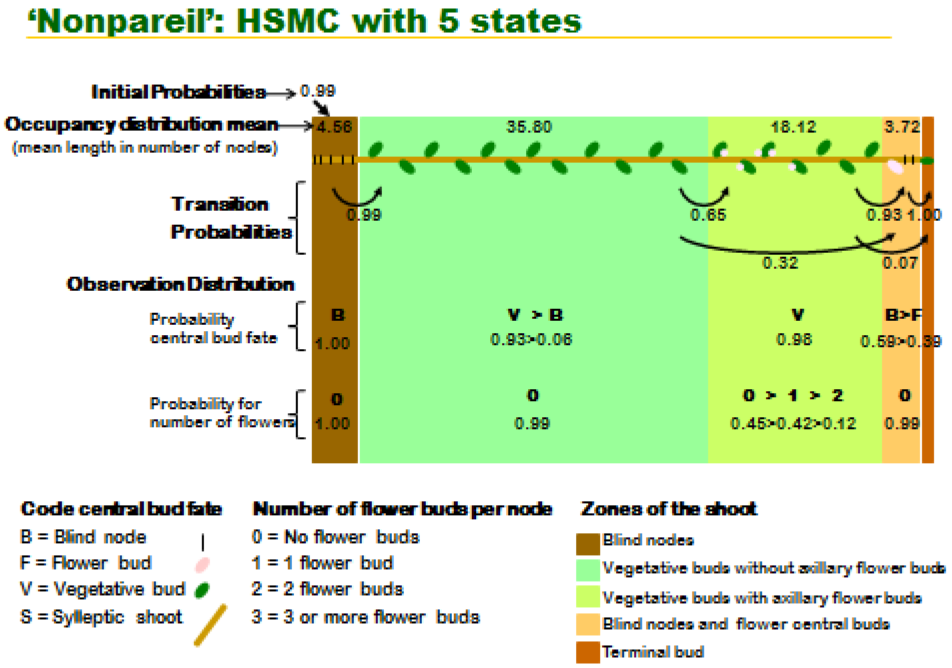
(c)



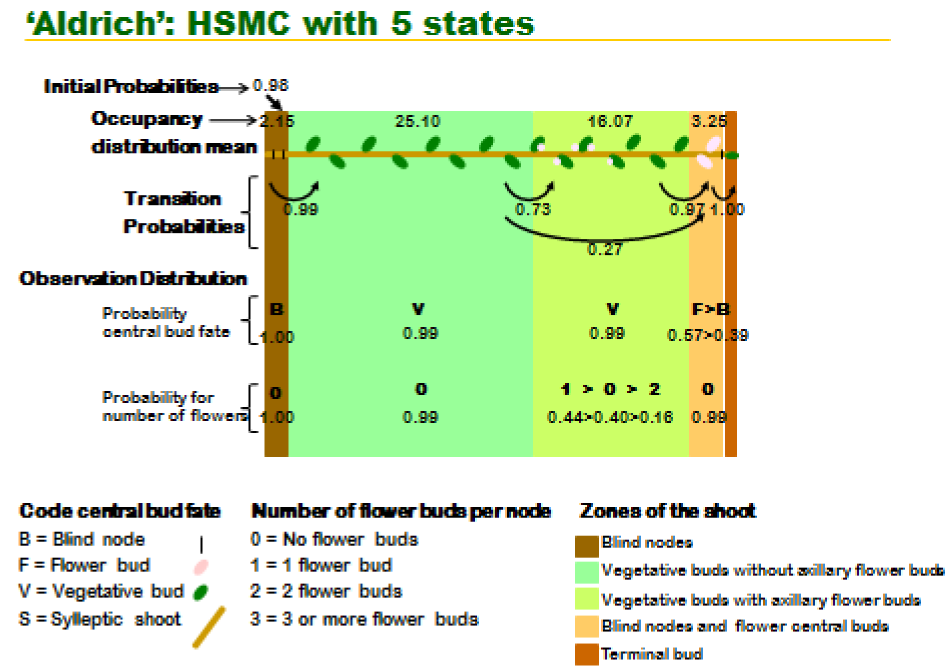
Mean total node number: 40

Figure 2. Schematic representation of the estimated model for the **medium proleptic shoots** of 'Nonpareil'(a), 'Aldrich'(b), and 'Winters'(c) with the main values of the observation distributions for the central bud fate and the number of flower bud per node variables.

(a)


'Nonpareil': HSMC with 5 states
Initial Probabilities
0.99
Occupancy distribution mean
(mean length in number of nodes)
4.56
35.80
18.12
3.72
Transition Probabilities
0.99
0.65
0.93
1.00
0.32
0.07
Observation Distribution
Probability central bud fate
B
1.00
V > B
0.93>0.06
V
0.98
B>F
0.59>0.39
Probability for number of flowers
0
1.00
0
0.99
0 > 1 > 2
0.45>0.42>0.12
0
0.99
Code central bud fate
B = Blind node
F = Flower bud
V = Vegetative bud
S = Sylleptic shoot
Number of flower buds per node
0 = No flower buds
1 = 1 flower bud
2 = 2 flower buds
3 = 3 or more flower buds
Zones of the shoot
Blind nodes
Vegetative buds without axillary flower buds
Vegetative buds with axillary flower buds
Blind nodes and flower central buds
Terminal bud

(b)


'Aldrich': HSMC with 5 states
Initial Probabilities
0.98
Occupancy distribution mean
2.15
25.10
16.07
3.25
Transition Probabilities
0.99
0.73
0.97
1.00
0.27
Observation Distribution
Probability central bud fate
B
1.00
V
0.99
V
0.99
F>B
0.57>0.39
Probability for number of flowers
0
1.00
0
0.99
1 > 0 > 2
0.44>0.40>0.16
0
0.99
Code central bud fate
B = Blind node
F = Flower bud
V = Vegetative bud
S = Sylleptic shoot
Number of flower buds per node
0 = No flower buds
1 = 1 flower bud
2 = 2 flower buds
3 = 3 or more flower buds
Zones of the shoot
Blind nodes
Vegetative buds without axillary flower buds
Vegetative buds with axillary flower buds
Blind nodes and flower central buds
Terminal bud

(c)

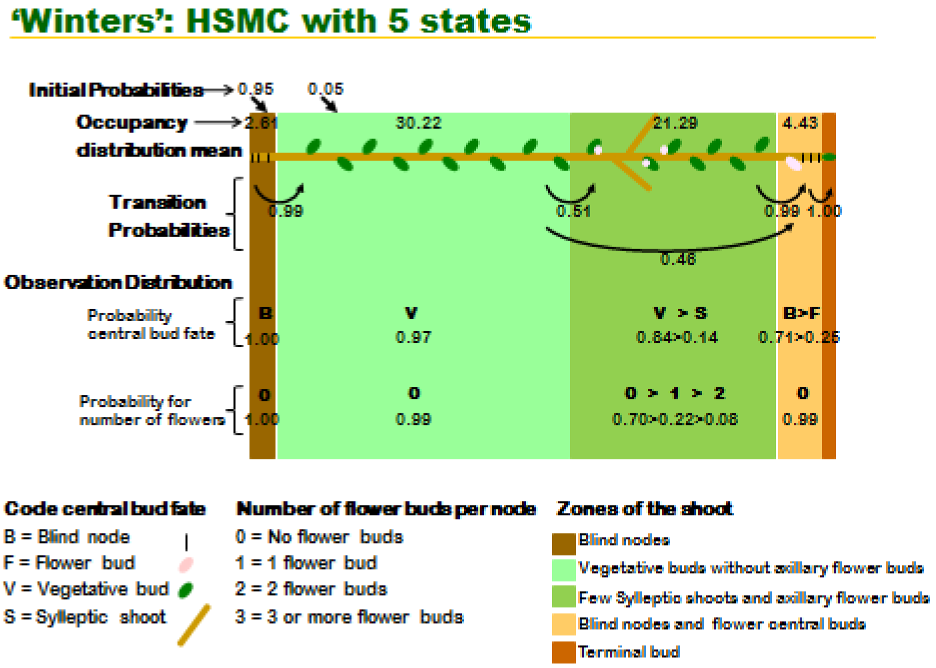


Figure 3. Schematic representation of the estimated model for **epicormic shoots** of 'Nonpareil'(a), 'Aldrich'(b), and 'Winters'(c) with the main values of the observation distributions for the central bud fate and the number of flower bud per node variables.

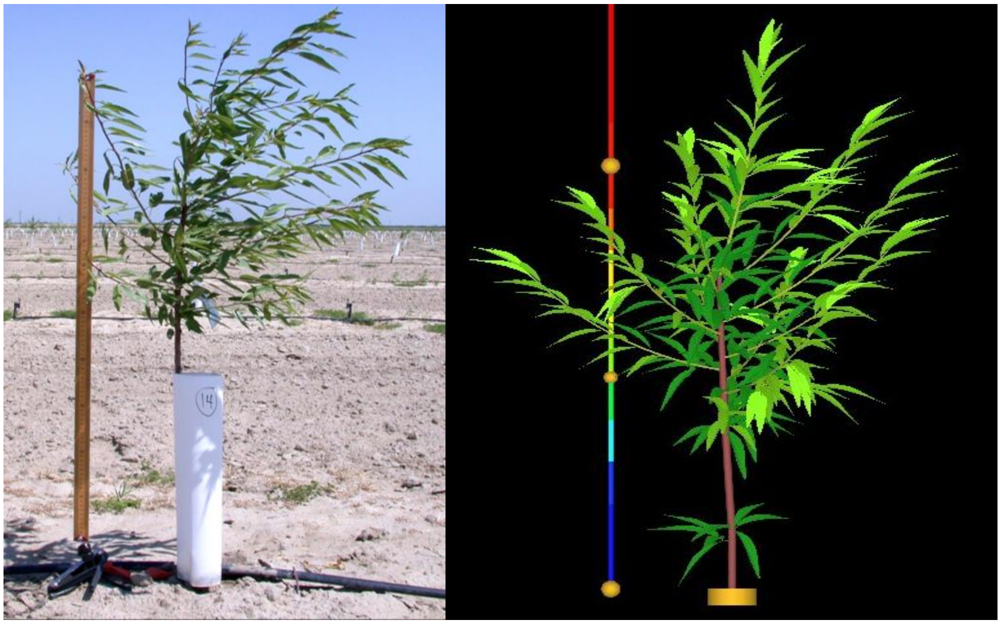


Figure 4. Comparison of the growth and architecture of a field-grown Nonpareil almond tree in April of the first year after planting and a tree of the same age simulated with the L-Almond model.

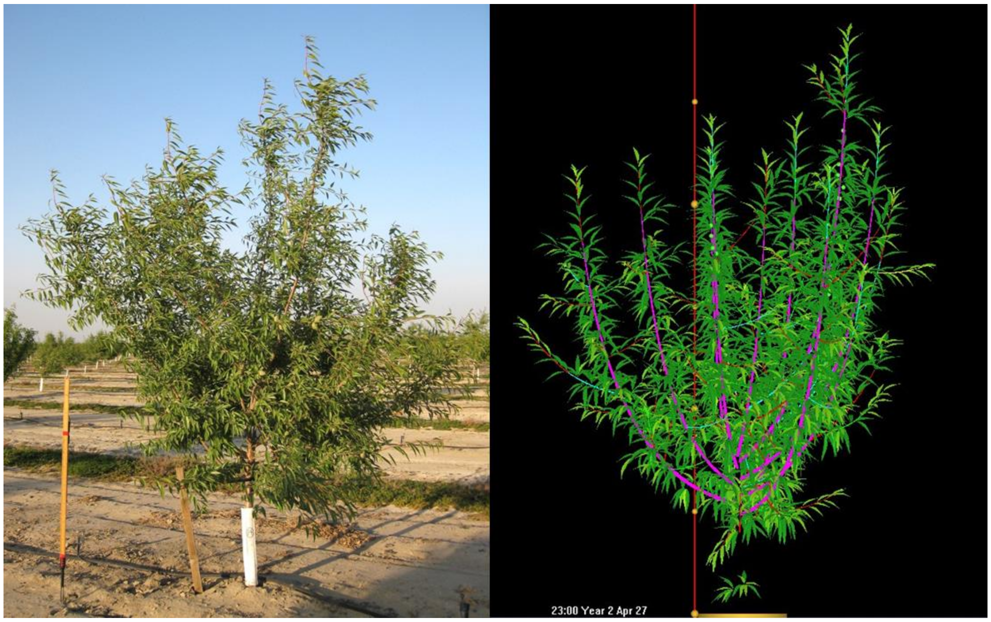


Figure 5. Comparison of the growth and architecture of a field-grown Nonpareil almond tree in April of the second year after planting and a tree of the same age simulated with the L-Almond model.