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.: **08-STEWCROP4-DeJong**

Project Leader:
Ted M. DeJong
Department of Plant Sciences
UC Davis
Mail Station #2
One Shields Avenue
Davis, CA 95616
(530) 572-1843
tmdejong@ucdavis.edu

Project Cooperators and Personnel:
Johan Six, Plant Sciences Dept, UC Davis
Bruce Lampinen, Plant Sciences Dept, UC Davis
C. Negron, Plant Sciences Dept, UC Davis
(Graduate Student)

Objectives:

This project has two major objectives. The first is to review the available research data that has been collected in California 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 and growth, and carbon partitioning/source sink interactions within the plant. This model will simulate growth and physiological responses to light distribution within the canopy and daily temperature changes as well as respond to user imposed pruning practices.

Pertinent data from both of these objectives will be compiled and provided to Johan Six's laboratory for greenhouse gas modeling purposes.

Interpretive Summary:

The first objective of this proposal was to review the published literature on almond and a closely related species (peach) to gain insight into whole tree biomass accumulation rates as trees age. It was also important to know the relative proportions of that biomass that are found in roots compared to the tops of trees. Unfortunately relatively little published data are available on whole tree biomass accumulation in almond trees. However more data are available for peach. The data from both species were summarized, but it became clear that more data are needed for a clear assessment of the standing biomass accumulation that occurs in commercial almond orchards as trees age. Therefore we have begun to investigate ways to fill in this gap in available data. In 2009 we began to work with selected orchard removal companies and growers to try to retrieve data that may be in their records concerning orchard characteristics (acreage, age, cultivars, spacing) and tree biomass removed from specific almond orchards that have been pulled out in recent years. It is too early to report results on this new subproject.

A second way to develop information about the potential rate of biomass accumulation in almond orchards is to develop a dynamic simulation model of almond trees. The rate at which almond trees grow 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, and responses to horticultural manipulation of the tree by the grower. 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 simultaneously display tree structural development in three dimensions on a computer screen. The most advanced of these types of models is being developed to simulate peach tree growth and development and recent advances have successfully simulated responses to pruning and fruit thinning as well as environmental factors such as light and temperature. During the past year we began to collecting data to convert the current L-Peach model into L-Almond, as well as continue to improve the current basic modeling program so that irrigation can be an input variable and the growth and the physiology of the simulated tree can respond to tree water relations.

Materials and Methods:

Assembling Data on Whole Tree Biomass

The initial work on the first objective was to do a literature search for available quantitative data on whole-tree biomass of almond and peach trees. To do this we searched for and evaluated numerous published papers that reported data on whole tree biomass and summarized it into a common form. Initially we had anticipated also accessing unpublished data from previous UC researchers; however we discovered that all those data had been discarded. We also used the existing data to calculate the root-shoot biomass ratios of peach and almond trees to determine if, in the future, we can use above-ground biomass data to estimate whole tree biomass.

We are currently attempting to obtain data on standing biomass of recently removed (or those slated for removal) mature orchards by contacting orchard removal companies and accessing records concerning orchard characteristics (acreage, age, cultivars, spacing) and tree biomass removed.

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). A total of 40 shoots of each of four size categories (water shoots, long shoots, medium shoots, and short shoots (spurs) were sampled from 10, 4-yr-old Nonpareil almond trees. Bud fates of at each node along the shoots were recorded, beginning at the base of the shoot as well as recording the total number of nodes and the length of the shoots. These data were subsequently analyzed collaboratively with colleagues at the INRA Centre in Montpellier, France, using HSMC techniques to develop statistical models of almond shoots. These shoot models were then inserted into the L-Peach (Allen et al. 2005; Lopez et al. 2008) simulation model along with previously collected leaf and fruit growth characteristics to generate a prototype L-Almond model.

Additional field studies were initiated 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 to get a better understanding of the influence of these factors on the architecture and productivity of almond branches, and to be able to more accurately model shoot and tree growth behavior of almond trees. 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). Data on shoot growth (rates of node initiation and soot length growth), shoot structural characteristics and tree water potential are being collected bi-weekly. Data on genotypic differences in shoot growth and structural characteristics also are being collected in a commercial orchard containing Nonpareil, Winters, and Aldrich. These cultivars were chosen because of their contrasting growth habits.

We have also spent substantial effort improving the foundational software of the L-Peach/L-Almond simulation model (Allen et al. 2005; Lopez et al. 2008). The original models used daily steps to simulate physiology and growth but this significantly limited the ability to simulate detailed physiological responses to environmental factors such as temperature and plant water potential. Therefore we changed the model to function on hourly time steps and more recently have successfully improved the model so that it can estimate the water potential at every node in the trees throughout daily cycles of growth. We are currently working on modeling the linkages between node water potential and physiological and growth responses of the organs located at each node. It is too early to present the results of these updates but we are confident that what we have achieved in these areas is ground-breaking and will provide substantial new insights into the physiology, growth and productivity of almond and peach trees.

Results and Discussion:

Assembling Data on Whole Tree Biomass

The first objective of this proposal was to review the published literature on almond and a closely related species (peach) to gain some insight into whole tree biomass accumulation rates as trees age. It was also important to know the relative proportions of that biomass that are found in roots compared to the tops of trees. Unfortunately relatively little published data are available on whole tree biomass accumulation in almond trees however more data are available for peach. **Figure 1** summarizes the published biomass accumulation data for almond data reported in four different studies. Clearly there are large gaps in the data. However, data from peach (**Figure 2**) can be used to fill in some of these gaps, but it is also clear from these figures that almond and peach trees accumulate biomass at different rates (largely due to the pruning practices that are employed with each species).

Since the rate at which both almond and peach trees accumulate biomass is highly dependent on numerous factors such as growing conditions, cultivar, and management practices (such as pruning and crop load) it is not be possible to predict tree biomass based on tree age alone. However we were interested to know if there was a consistent relationship between root biomass and above-ground biomass. It appears that there is a relatively predictable relationship between root and shoot biomass regardless of large differences in total tree biomass (**Figure 3**) This relationship can be used to estimate total tree biomass from additional data collected on above-ground biomass. We are in the process of trying to access this type of more limited data.

Since the data on whole tree biomass of mature orchards is very limited we have begun to investigate ways to fill in this gap in available data. In 2009 we began to work with selected orchard removal companies to try to retrieve data that may be in their records concerning orchard characteristics (acreage, age, cultivars, spacing) and tree biomass removed from specific almond orchards that have been pulled out in the recent years. While some of the orchard removal companies have begun to share their data, it would be desirable to have more specific data on the orchards being removed. Therefore we have also begun to try to access grower information about orchards that have been removed or are currently slated for removal to increase the data set on standing biomass of mature orchards. It is too early to report results on this new subproject.

Development of an L-Almond Model

Crop growth and yield is dependent on a complex set of interactions involving the plant genotype, the physiological and developmental processes that occur within the crop plant, the interaction of these processes with the environment that the plant grows in, and responses to horticultural manipulation of the plant by the crop manager. Understanding carbon budgets and crop growth and yield responses of perennial crops like almond are more complex than most crops because the effects of all these factors are carried out over multiple years. Most experimental research concerning factors that influence these complex processes and the interactions between them has been limited to dealing with one, two or at most three, environmental and/or management factors at a time and then monitoring a limited set of plant responses at the tissue, organ, or whole plant level. While these experimental approaches have yielded substantial information about patterns of carbon allocation and crop responses to specific factors, many experiments have led to conflicting results and it has been very difficult to develop an integrated understanding of carbon budgets and crop growth and yield responses over multiple years in complex environments. Because of this lack of integrated understanding, research tends to be repeated in various forms over the years and true progress in some areas tends to stagnate until new experimental approaches are developed. Furthermore research tends to get concentrated on specific topics that are measurable with newly available equipment (like photosynthesis, stomatal conductance, water potential, etc.) while information on other important topics (like canopy development processes, canopy architecture, bud fates, carbohydrate storage, etc.) tends to be neglected.

Because perennial crop growth is so complex and dynamic over long periods of time there have been very few quantitative studies of tree growth dynamics and carbon budgets over time. The work that has been done in California has come mainly from the DeJong laboratory (Grossman and DeJong 1994, Esparza et al. 1999, Esparza et al. 2001, Rufat and DeJong 2001). However this research needed to be expanded to provide a more dynamic and accurate picture of tree growth and resource utilization dynamics at specific periods during the growing season.

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 simultaneously display tree structural development in three dimensions on a computer screen (Allen et al. 2005, 2007). The most advanced of these types of models has been developed to simulate peach tree growth and development and recent advances have successfully simulated responses to pruning and fruit thinning (Smith et al. 2008) as well as environmental factors such as light and temperature (Lopez et al. 2008). This project attempts to develop an almond tree model that would adapt all of the features of the L-Peach model to simulating almond tree growth, crop productivity and above- and belowground C allocation.

To begin meeting the second objective of this project we began work to convert the existing L-Peach model into an L-Almond model. The first step for doing this was to develop statistical hidden semi-Markov chain (HSMC) models to describe patterns of buds that occur along Nonpareil almond shoots of different lengths. This was done based on data collected from Nonpareil almond shoots collected prior to spring of 2008. **Figures 4 a-d** represent graphical depictions of the structure of four different size categories of shoots. Each shoot is made up of different zones that are classified according to the characteristics of the lateral buds in a zone. There are zones with high percentages of blind (B) nodes, or nodes with lateral vegetative (V) buds, syleptic shoots (S), or lateral floral (F) buds. Numbers associated with forward solid arrows indicate the statistical probabilities of transitioning from one zone to the next. Dashed arrows indicate the frequencies for skipping specific zones and reverse arrows indicate that sometimes there are reversions to previous zones. The first row of numbers associated with the letters B, V, S, F and T give the probabilities of their occurrence within each the zone. The probabilities of 0, 1, or 2 floral buds being associated with each node is given by the second row of numbers below each shoot diagram. In some cases lateral vegetative buds also have lateral floral buds associated with them. While quite complex, these figures indicate that the general structure of almond shoots is statistically predictable.

We believe that the construction of these statistical models of almond shoots may also be an excellent way to characterize the influence of genetic, environmental and management factors on almond tree growth. Thus as stated above, we have initiated field experiments to assess these effects. However it is too early to report on this research.

The HSMC statistical models described above were inserted into the L-Peach model in place of similar types of models that described peach shoot growth in order to begin converting the previously existing L-Peach model into an L-Almond model. After doing this and changing the model input parameters to describe the physiological and morphological characteristics of Nonpareil almond leaves and fruit we were able to run the first graphical simulations of an L-Almond model and compare the outcomes with photographs of young almond trees (**Figure 5**). Although these preliminary runs were quite promising, much more work needs to be done to quantitatively check the results. We will continue to refine this model in order to realistically simulate the architectural growth of the tree (including spur development) and the carbon budget associated with the crop as well as the vegetative growth of the tree. Eventually this will provide dynamic estimates of both carbon assimilation and use for tree and crop growth, and respiration as well as indicate how much carbon can be sequestered by a tree on an annual basis.

As mentioned above we have also spent substantial effort improving the foundational software of the L-Peach/L-Almond simulation model (Allen et al. 2005; Lopez et al. 2008). This involved a lot of theoretical calculations and we have successfully adapted the models to run on hourly time-steps, incorporated water transport within the modeled tree structures, and calculated daily courses of water potential at every node within the structure of simulated trees. We are currently adjusting the inputs and verifying the outputs of these new model capabilities so it is too early to present detailed results.

The development of this integrated dynamic simulation model of almond tree growth and productivity is well on its way and when completed will result in the most sophisticated environmental physiology-based model of a fruit or nut tree ever developed. We believe that it will provide new, unique insights into factors affecting the growth and yield of almond trees as well as provide the basis for estimating the carbon sequestered in the standing biomass of almond orchards.

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, MT., Prusinkiewicz, P., DeJong, TM. (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, MT., Prusinkiewicz, P., Favreau, RR., 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) pp. 1

Bi, G., Scagel, C. F. and Fuchigami, L. H. (2004) Effects of spring soil nitrogen application on nitrogen remobilization, uptake, and partitioning for new growth in almond nursery plants. . *Journal of Horticultural Science & Biotechnology* 79 (3) 431–436

Chalmers, D.J., and van den Ende, B. (1975) Productivity of peach trees: factors affecting dry-weight distribution during tree growth. *Ann. Bot.* 39:423-432.

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 auxiliary 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.

Inglese, P., Caruso, T. Gugliuzza, G. and Pace, L.S. (2001) The effect of crop load and rootstock on dry matter and carbohydrate partitioning in peach trees (Prunus [persica BATSCH). *Acta Hort*. 557:447-455.

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.

Miller, A.N. and Walsh, C.S. (1988) Growth and seasonal partitioning of dry matter in eight-year-old 'Loring' peach trees. *J. Am. Soc. Hort. Sci*. 113:309-314

Niederholzer, F.J.A., DeJong, T.M. Saenz, J.-L., Muraoka, T.T. and. Weinbaum S.A. (2001) Effectiveness of fall vs. spring soil fertilization of field-grown peach trees. *J. Am. Soc. Hort. Sci.* 125(5):644-648.

Sanchez, E.E., Weinbaum, S.A. and Johnson, R.S. (2006) Comparative movement of labeled nitrogen and zinc in 1-yr-old peach [Prunus persica (L.) Batsch] trees following late-season foliar application. *J. Hort. Sci. & Biotech.* 81:839-844.

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.

Solari, L.I., Johnson, S. and DeJong, T.M.. (2006) Hydraulic conductance characteristics of peach (*Prunus persica*) trees on different rootstocks are related to biomass production and distribution. *Tree Physiology* 26: 1343-1350.

Williamson, J.G. and Coston, D.C. (1989) The relationship among root growth, shoot growth, and fruit growth of peach. *J. Am. Soc. Hort. Sci.* 114:180-183

Zasoski, Weinbaum, Meyer, Edstrom, Rolston. (1994) Nitrogen efficiency in drip irrigated almonds. *Almond Research Final Report*.

Figures:

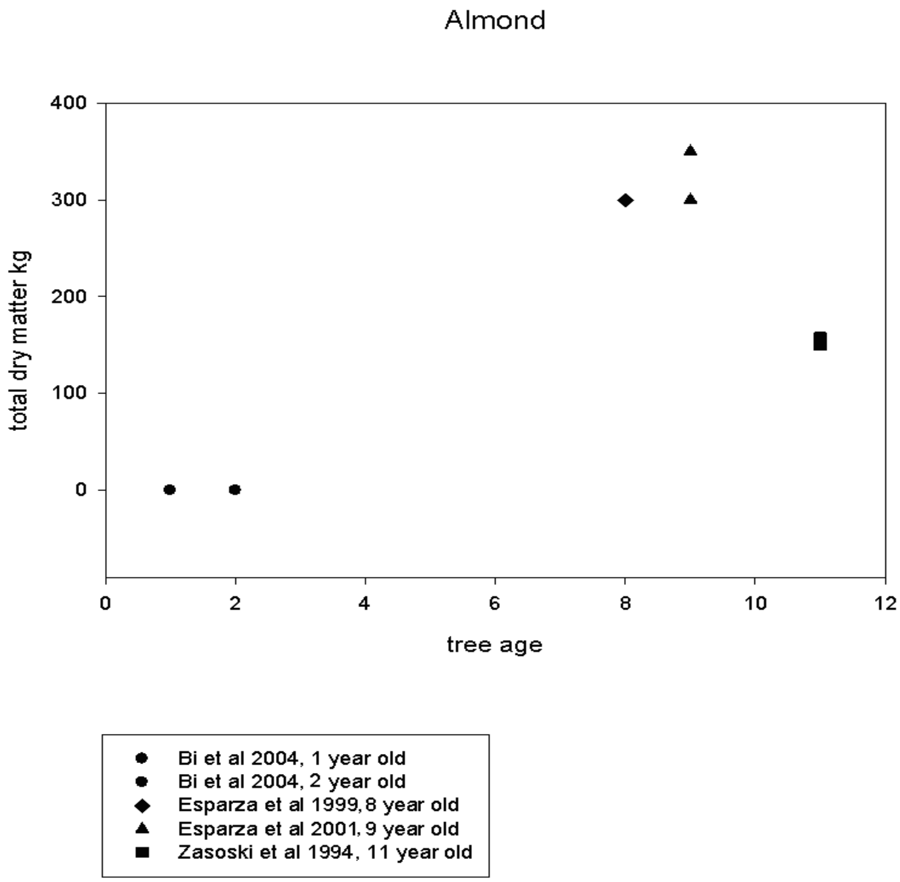

Figure 1. A summation of four published works on biomass accumulation for almond trees with tree age.

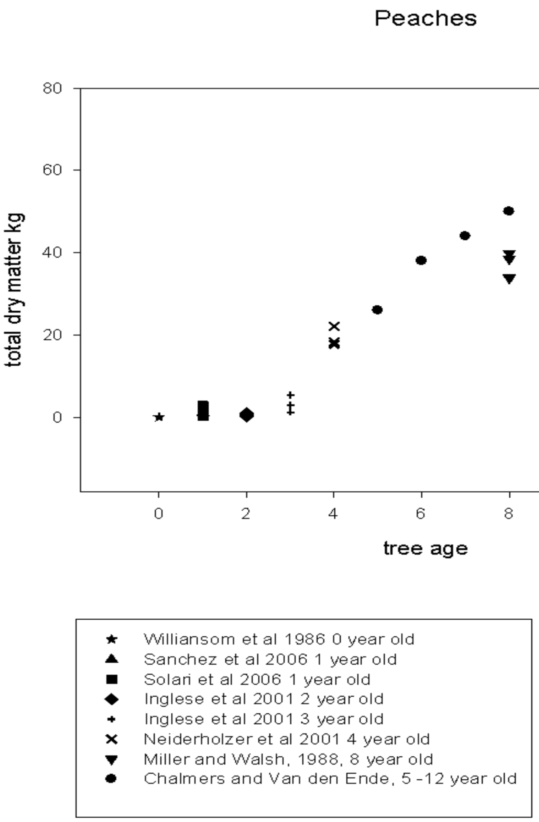

Figure 2. A summation of multiple published works on peach biomass accumulation with tree age.

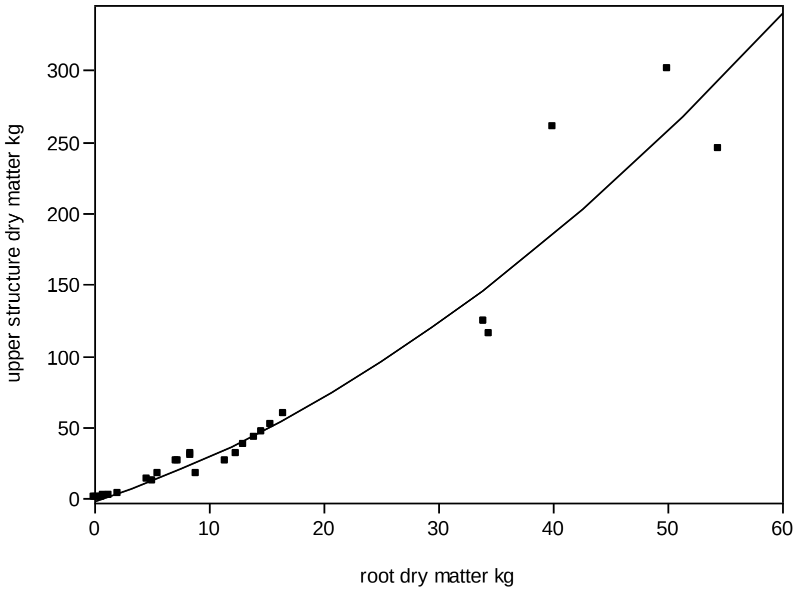

Figure 3. The curvilinear relationship between shoot and root biomass of almond and peach trees. (Data adapted from the studies cited in Figures 1 and 2.)

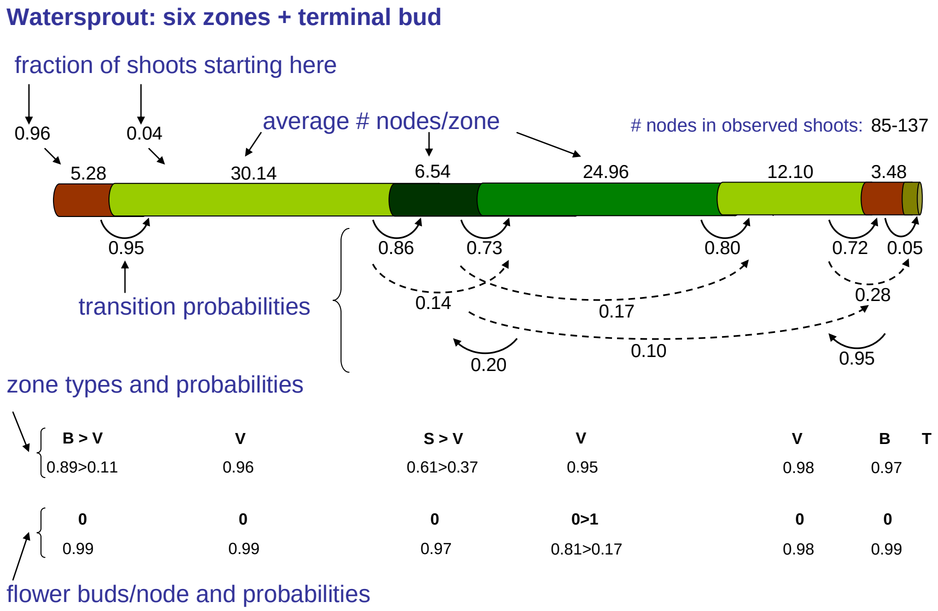

Figure 4a. Hidden Semi-Markov Chain (HSMC) model diagram of Nonpareil water sprout shoots. (See text for details)

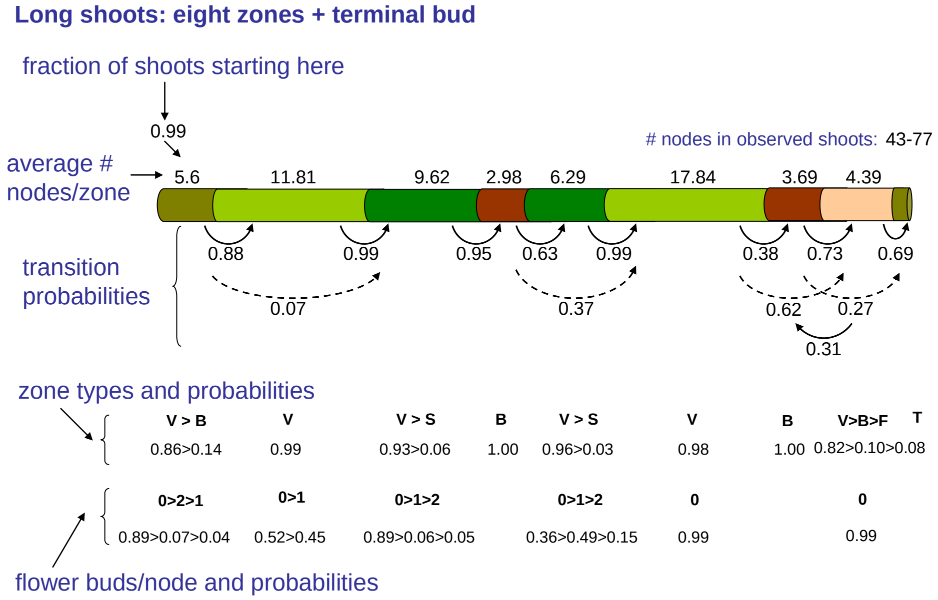

Figure 4b. HSMC model diagram of long (43-77 nodes) Nonpareil shoots. (See text for details)

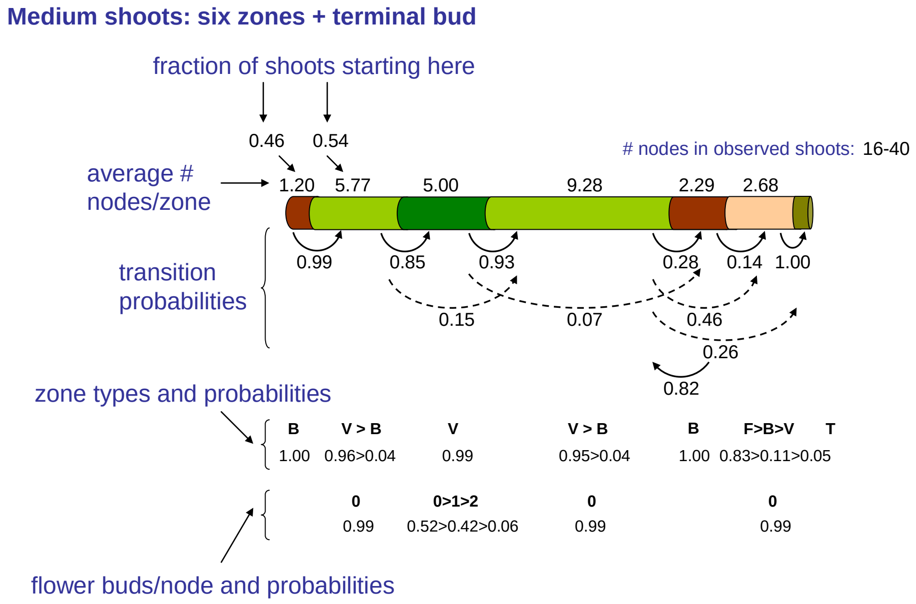

Figure 4c. HSMC model diagram of medium (16-40 nodes) Nonpareil shoots. (See text for details)

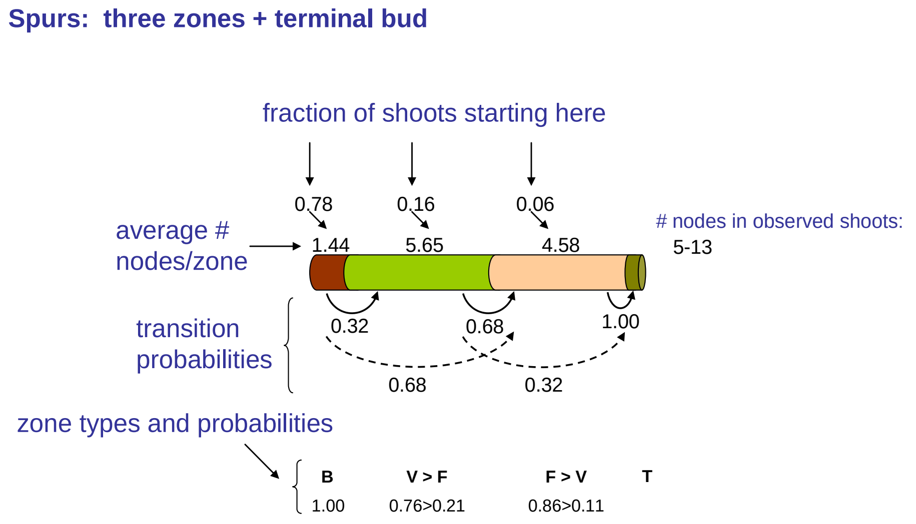

Figure 4d. HSMC model diagram of Nonpareil spur shoots (43-77 nodes). (See text for details)

Figure 5. A picture of a field grown tree compared to graphical output of a simulated tree generated by the preliminary L-Almond model.