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

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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, functionalstructural 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.

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

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 should be available from these

operations. We have begun 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 subproject.

Objective two: 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. 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 functionalstructural 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 that is being developed to simulate peach tree growth and development. The long-term objective of this project is to continue the development of the L-Peach model and convert it to an L-Almond model. During the past year we continued to collect data needed to convert the current L-Peach model into L-Almond as well as continued 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. In addition, we completed an analysis of the influence of spring temperatures after bloom on almond fruit development rate so that the almond model can be adjusted to the weather patterns of specific years. We also began to analyze spur dynamics data previously collected by the Lampinen laboratory so that spur productivity and mortality sub-models can be developed for almond trees. This will be important for converting the L-Peach model to an L-Almond model because most peach fruit are borne on one-year-old shoots whereas most almond fruit are born on spurs.

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. Dr. Lampinen's laboratory has measured the total canopy light interception of some orchards just prior to removal to be able to calibrate the biomass estimates with ground cover estimates. We began the process of collecting and analyzing those data but it is too early to report results. 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 California almond orchards

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.

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 continued in 2009-2010. These studied 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). Data on shoot growth (rates of node initiation and shoot length growth), shoot structural characteristics and tree water potential are being collected bi-weekly during the growing season. 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. An additional field study was initiated in a young orchard near Davis to study the effects of severity of winter pruning on the structure of shoots that grow in the subsequent year.

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 a tree throughout daily cycles of growth. We are currently working on modeling the linkages between stem water potential and physiological and growth responses of the organs located at each node. 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.

A corollary to this project was undertaken to determine the effect of spring temperatures subsequent to bloom on the length of the fruit development period between full bloom and the initiation of hull-split. Previous research with peach, nectarine, plum and prune indicate that temperatures (growing degree-hour accumulation) during the first 30 days after bloom are critical for determining the length of time between full bloom and harvest maturity (Ben Mimoun and DeJong, 1999, Day et al. 2008, DeBuse et al. 2010). In an attempt to determine if similar relationships apply to almond, we initiated a study based on data from the Regional Almond Variety Trials to determine if the period from full bloom to1% hull-split could be predicted from growing degree hours accumulated 30 days after bloom.

A second subproject was undertaken to develop more complete understanding of factors that influence the behavior of individual almond spurs within canopies of Nonpareil almond trees. For this study we analyzed "spur dynamics" data previously collected by Dr. Lampinen's laboratory. In the spur dynamics study individual spur behavior was monitored on 48 trees in a 150 acre orchard that was planted in 1996. Tree spacing was 24 ft. between and 20 ft. within rows. Cultivar composition was 50% 'Nonpareil' with 25% 'Monterey' and 25% 'Wood Colony' as pollenizers (rows of Nonpareil trees planted with alternating rows of the pollenizers cultivars). The orchard was divided into four equal-sized replicate blocks and fifty spurs were tagged on twelve 'Nonpareil' trees within each of the four blocks. A total of 2,400 spurs were tagged with aluminium tags in late March and early April 2001. Twelve spurs were selected on each of the North-East and North-West quadrants of individual trees and 13 spurs were selected on each of the South-East and South-West quadrants of the same trees. Tagged spurs were located at positions ranging from shaded (near the trunk) to exposed (on the periphery) portions of the canopy at a height of \sim 6-10 ft.

The dynamics of annual growth, flowering, fruitfulness, and spur mortality were quantified using annual assessments of tagged spurs. In July 2001 the numbers of fruit and leaves per tagged spur were counted and relative leaf sizes were noted. In addition, a similar spur from a nearby location (but not so near as to be a direct influence on the tagged spur) with a similar light exposure was sampled for leaf area and leaf specific weight analysis. Leaf area was assessed by taking digital photographs of all of the leaves on each spur. Leaves were then dried and weighed. Leaf specific area (leaf area per unit dry weight) was calculated from leaf area and leaf dry weight measurements.

In July 2002, the numbers of flowers, fruit and leaves per tagged spur were counted and leaf sizes rated. Adjacent spurs were sampled for leaf area/dry weight analysis as in 2001. In July 2003, 2004, 2005 and 2006 the numbers of flowers, fruit and leaves per tagged spur were again counted. Leaf size was estimated from leaf length measurements by developing regression equations relating the length of the longest leaf on each spur with the leaf area of spurs (using an independent sample of 400 spurs from the range of locations within the canopy). Adjacent spurs were sampled again in July 2004, for leaf area/dry weight analysis from all 48 monitored trees. In July 2005, adjacent spurs were sampled from two trees per replication for a total of eight trees. In July 2006 and 2007, adjacent spurs were again sampled from all 48 monitored trees.

Specific leaf area was calculated as the spur leaf area divided the dry weight of leaves. The number of flowers produced on each tagged spur was counted in the spring of each year from 2002 through 2007.

To estimate the activity of a spur an Activity Index (AI) was calculated as the sum of the viability (0= dead; 1=alive) and the number of flowers produced in a year. Statistical analysis was carried using linear regression to test the effect of each variable on spur viability and flowering. Relative frequencies of living/dead spurs were calculated per leaf area interval of 5 cm². A χ^2 test was used to test the differences of frequencies where possible. P value was set at 0.001.

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. Data from peach can be used to fill in some of these gaps but it is also clear from the literature that almond and peach trees accumulate biomass at different rates (largely due to the pruning practices that are employed with each species).

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. To date we have not received data on enough removed orchards to make robust estimations of almond orchard standing biomass. We are still attempting to get more data from orchards that have been removed in the past two years.

Development of an L-Almond Model

To begin meeting the second objective of this project we began work to convert the existing L-Peach model into an L-Almond model. 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.

The first step for converting the L-Peach model to an L-Almond model 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. Last year's report contained results from preliminary attempts to develop HSMC models of bud fates of almond shoots. Field data were collected in 2009 and 2010 to expand these models to be representative of trees growing with different levels of mild water stress and pruning severity. We are also developing statistical shoot models for different growth types of almond ('Nonpareil', 'Winters' and 'Aldrich'). These field studies are ongoing and a large dataset on shoot growth dynamics is being developed to build robust statistical models of almond shoot growth. 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. However it is too early to report specific results of this research.

Attempts to improve the foundational software of the L-Peach/L-Almond simulation model (Allen et al. 2005; Lopez et al. 2008) have been very successful. This involved many theoretical calculations to successfully adapt the models to run on hourly timesteps and incorporate water transport within the modeled tree structures, and calculate daily courses of water potential at every node within the structure of simulated trees (**Figures 1 and 2**). This is the first model of its kind that has successfully modeled both carbon and water transport in a "virtual plant" and it opens up the possibility to explore simultaneous interactions between photosynthesis, individual organ growth, dry matter partitioning and plant water stress in ways that were never before possible. We are currently adjusting the inputs and verifying the outputs of these new modeling capabilities.

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.

Predicting Hullsplit

Initial attempts at establishing relationships between temperatures 30 days after full bloom and predicting the length of the fruit development period for 26 almond cultivars in a similar manner as for peach (Ben Mimoun and DeJong, 1999; Day et al., 2008) were only partially successful. But further analysis indicated that there was a strong relationship between the length of the period between full bloom and 1% hull-split and accumulated degree-days between full bloom and 90 days after full bloom for many cultivars (Tombesi et al 2010). Examples of these relationships for twelve Californian almond cultivars are shown in **Figures 3 and 4**.

These relationships indicate seasonal adjustments in the length of the fruit development period and can be used to adjust the L-Almond model according to the weather patterns of a specific year.

More importantly, these relationships can be used to help growers predict the date of 1% hull-split in May of any year. Based on the predicted date of 1% hull-split, harvest maturity can be predicted by using data from Connell et al. (2008) that provides the average time required for major cultivars to go from 1% to 100% hull-split. This information should be useful to growers and processors for planning their harvest and marketing season as early as late May in any given year. The UC Davis Fruit and Nut Research and Information Center website for predicting harvest of tree fruits is currently being updated to include a module that will enable growers to predict 1% hull-split from spring temperature data.

Modeling Spur Dynamics

Twenty-four hundred spurs were initially tagged in the spur dynamics study in 2001. During the first three seasons (i.e. until 2004) spurs died at the rate of about 9% per year. After 2004 this mortality rate increased to approximately 24% per year (Figure 5). Previous year leaf area (PYLA) of spurs was directly related to whether spurs remained alive and the number of flowers they bore in the following year (Figure 6). The probability that a spur bore flowers was also correlated with spur PYLA (Figure 7). The probability of flowering was over 80% for spurs with PYLA values over 48.5 cm². The same level of probability of survival after not bearing occurred with PYLA values >8.96 \textsf{cm}^2 . The probability of flowering in spurs that bore fruit in the previous year was so low that it could not be related to PYLA. The probability of different numbers of flowers occurring on a spur was significantly related to the spur PYLA (**Figure. 8**). For spurs with PYLA values less than 44.47 cm^2 , the probability of having two or less flowers was significantly greater than having three or more flowers per spur. Spurs with PYLA values higher than 44.47 cm^2 had a higher probability of having three or more flowers per spur than having less than two flowers.

These data provide clear insights into the morality and reproductive behaviour almond spurs. These data will provide valuable information for the development of the L-Almond model but they also provide insights into factors that determine the yield in almond trees. The lower spur mortality rate in the early years of the study corresponded with years just prior to canopy "closure" while the trees were still "filling their allotted space". After 2005 most trees had filled the alleyway and the trees reached near maximum light interception for this orchard. During this period approximately 25% of the spurs died in each year. This means that it would have been necessary to renew ~25% of its spur population each year in order to maintain a constant level of production. This study provides just an initial picture of the importance of maintaining spur health and spur renewal in mature bearing almond trees. We are continuing to further analyze the "spur dynamics" dataset to develop a clearer picture of the relationship between individual spur performance and orchard productivity.

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Figures:

Figure 1. Preliminary quantitative model outs depicting the rate of leaf expansion of five leaves on an almond shoot, the corresponding daily transpiration pattern of those leaves, and the daily pattern of xylem water potential of the stem bearing the leaves for a well-watered tree.

Figure 2. Preliminary quantitative model outs depicting the rate of leaf expansion of five leaves on an almond shoot, the corresponding daily transpiration pattern of those leaves, and the daily pattern of xylem water potential of the stem bearing the leaves for a tree that did not receive adequate water for several days.

Degree-days 90 dafb

Figure 3. The relationship between the number of days between full bloom and 1% hull-split and accumulated degree-days 90 days after full bloom for six almond cultivars. Regressions were based on data from Regional Variety Trials at Chico, Delta and Kern from 1997-2004.

Degree-days 90 dafb

Figure 4. The relationship between the number of days between full bloom and 1% hull-split and accumulated degree-days 90 days after full bloom for six almond cultivars. Regressions were based on data from Regional Variety Trials at Chico, Delta and Kern from 1997-2004.

Figure 5. Number of living, dead and retagged spurs for each year in the spur dynamics study. Percentages refer to number of spur dead in relation to the number of spurs alive in the previous year.

Figure 6. Probability estimation (%) of spur survival after bearing and not bearing fruit in the previous year in relation to spur previous year leaf area (PYLA, \textsf{cm}^2).

Figure 7. Probability estimation (%) of spur survival and flowering after not bearing in the previous year in relation with spur previous year leaf area (PYLA, cm²).

Figure 8. Probability estimation (%) of spur survival after bearing and probability of spur bearing less than 2 flowers and more than 3 flowers after not bearing in the previous year in relation with spur previous year leaf area (PYLA, cm²).