

Avocado Tree Physiology – Understanding the Basis of Productivity

Continuing Project: Year 5 of 5

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The Project's Benefit to the California Industry

A grower's profit margin is the difference between the input costs to produce a marketable crop and the gross amount of money realized from the sale of the "output", or the production itself. Anything that affects one or both of these can make the difference between profit and loss. The management of the avocado tree under southern California conditions, which can experience rapid changes in temperature and relative humidity, provides a challenge under the best of conditions. Increasing market competition from other countries is pressuring the California grower to become increasingly ingenious in orchard management practices so that profits can be made, including changes in irrigation schedules and tree management strategies. For example, more growers are pruning older trees or considering high-density plantings. These canopy management strategies hinge on effective light management to increase fruit size and production. However, current strategies used to manage tree canopies and tree water status were poorly understood. This project has been examining, in detail, the response of avocado leaves to light, temperature, and changes in light and temperature by analyzing carbon assimilation (which fuels both tree and fruit growth) and changes in evaporative demand (which governs the amount of water the tree requires). The goal of this project was a better understanding of the tree's response to California's environmental stresses, which, in turn, has allowed us to develop a model of carbon assimilation in the canopy based upon the environmental conditions. The results of this research will provide a valuable framework for cultural management decisions and future research on the physiology of the avocado.

2005-06 Project Objectives

During this fiscal year we have focused on several areas in order to complete this project and to prepare for the field validation of a full canopy model. We focused on the following three aspects of the avocado tree:

Leaves

- [1] Light Intensity and Assimilation;
- [2] Parameters of Photorespiration (CO₂ Concentration and Assimilation);
- [3] Effects of High Temperature on Assimilation;
- [4] Effects of Leaf Developmental Age Upon Assimilation Production and Use;
- [5] Boundary Layers of Leaves.

Flushes and Branch Processes

- [1] Effect of New Flush Development upon Older Flushes;
- [2] Movement of Assimilate (Carbohydrate) between Flushes;

Canopy

- [1] Modeling Canopy Processes (Combining Our Measurements with Potential Models):
- [2] Validating Model with Canopy Measurements (Determination of Possible Problems).

Overall Project Summary

The goal of this research for the past 5 years has been to develop an understanding of how the 'Hass' avocado tree functions under varying environmental conditions such as temperature, water stress and differing light intensities and to provide the grower community with information to guide them in management decisions that are based on this knowledge. Much of this work has been conducted under controlled environmental conditions, allowing the researchers to discern the impact of varied individual conditions on 'Hass' avocado.

There are several outcomes from this research. Of particular note is a greater appreciation for the importance of leaf age and growth flush interactions, the role of photorespiration and temperature in changing the net leaf productivity, and the flow of air around the leaf and canopy for good mixing of the canopy's atmosphere. We have developed methods that allow us to measure these phenomena, including the physiological age of the leaf and flush, and have used these measurements to integrate a total systems approach to the whole tree. Summarized below are some of the key discoveries made during this research project.

Response to Temperature and Light

- The stomata, which are very sensitive to the water status of the tree, control assimilation almost completely. Since assimilation feeds directly into productivity, the behavior of the stomata will play a major role in tree productivity.
- High temperature (>85 F) inhibits assimilation and thus causes stomatal closure due to a rise in CO₂ within the tissue. However, that closure is slow and since transpiration continues, a large amount of water loss without assimilation occurs to the detriment of the tree.
- Avocado leaf stomata close quickly in response to decreasing light. This means that interior canopy leaves or those shaded by neighboring trees have very low productivity.

- Sudden increases in light (sunflecks) do not result in increased productivity of avocado leaves because the stomata are slow to open.

Significance of this area of research:

Gaining an understanding of how the leaf, which is the productivity factory of the tree, captures light for subsequent fruit and tree growth, is critical to the development of management strategies to optimize tree performance.

This research has documented that the stomatal behavior is the driving force behind productivity. This project has also demonstrated the impact of high temperature on ‘Hass’ leaf productivity and explains in part why some growers in warmer inland areas appear to have greater problems with fruit size and overall consistent tree performance.

The work carried out in this project regarding the response of ‘Hass’ leaves to varying light intensities lays the groundwork for further development of pruning/canopy management strategies. Canopy manipulation strategies need to take into account how the ‘Hass’ avocado leaf stomata responds to light. Since the stomata close quickly with decreasing light but are slow to open with increasing light, growers should manage trees to maximize the percentage of leaves exposed to full sunlight. Pruning strategies that rely on “windows” into the canopy, or on sunflecks permeating the canopy, are therefore not as effective as training trees to maximize leaf area exposed to full sun. These results have important implications for tree spacing and explain, in part, the umbrella shaped canopies of mature groves.

Leaf Area

- In order to accurately follow changes in leaf assimilation and productivity, one needs to be able to have a way to quantify physiological leaf age. We have described a “plastrochron index” that can be used to describe the physiological age of each leaf; this allows one to quantify the rate of shoot growth.
- The plastrochron index is based on an easily measured parameter, leaf area, or when a large number of leaves are used, leaf length alone.
- Development of an “easy-to-use” program for field measurement.

Significance of this area of research:

The development of a plastrochron index methodology allows one to “standardize” measurements based on leaf age—critical to reduce data variability and to understand how flush growth influences whole tree physiology.

The plastrochron index can be easily adopted by avocado researchers such as entomologists and pathologists to more accurately examine the interaction of pests and disease (avocado thrips, avocado root rot) to avocado tree growth. This system is also useful to plant physiologists that are looking at the impact of environmental stress, i.e. salinity, drought and flooding on tree growth, by providing them with the tools to more accurately quantify how the tree responds to stress.

Sap Flow

- An increased understanding of how water moves within branches, which in turn helps to describe the conductance of each leaf and how the plant responds to environmental stress.
- The research has demonstrated that conductance (stomatal opening) controls CO₂ flow into the leaf, thus influencing photosynthetic assimilation (productivity).
- The research has demonstrated that sap flow measurements are a valid approach, and in some ways, an improved method for measuring the water status of the tree since sap flow measures an integrative response of a total branch.

Significance of this area of research:

The work with sap flow measurements has provided the research community with the tools to examine more critically the manner in which ‘Hass’ avocado responds to environmental stress. This knowledge can be utilized in further research examining the influence of water or salinity stress on water movement within the tree. It also provides a novel way to compare different rootstocks to these stresses and to water relations.

Canopy Processes: Model Development

- The relationship between different growth flushes has been explored. The existing leaves on a branch show decreased photosynthesis leading to their abscission when the new flush is approximately half fully-developed.
- A simple model that predicts sap flow within the tree has been developed. This model of water use (sap flow) and productivity (carbon assimilation) is directly dependent upon air temperature, relative humidity and light intensity falling on the leaf.
- Sap flow represents the water movement to the leaves from the roots on an individual branch. This water flow brings nutrients from the soil and cools the leaf and is lost from the leaves through the evaporation of water.
- The rate of evaporation is directly proportional to the photosynthetic carbon assimilation or how “open” the stomata are; which is largely governed by the light intensity available to the leaf and the conductance of the stomata to atmospheric CO₂. The driving force for this evaporation is the vapor pressure of the atmosphere compared with the vapor pressure within the leaf.

Significance of this area of research:

The functioning of the model in the field is most important. This research has clearly shown that the measurement of a few, easily obtained environmental parameters, combined with previous measurements of leaves, predict the assimilation of carbon in the tree.

The field testing of the model began in the summer of 2006 and has shown that one can predict assimilation based upon the environment around the tree. The model will assist us to further understand the interaction between leaves of different ages.

This model, once validated in the upcoming year, can be utilized by any researcher studying avocado physiology and soil/pest interactions. For interested growers, this easy-to-use model based on parameters that they can measure in the field, will allow them to monitor tree performance.

2005-06 Research Summary

During the past five years we have been collecting data on a wide range of physiological processes of avocado trees to understand the fundamental development of efficient production within the leaf, based upon assimilation (A). These processes include light dependence (A vs I), responses to light flecks (high light intensity over a short time interval), internal CO₂ dependence (A vs C_i), response to varied temperatures, reactions to varied levels of relative humidity, and measurement of age of leaves/shoots. Much of the first portion of this past year's grant period was spent integrating this data into a coherent package. We have not altered the individual data sets but rather attempted to understand how they fit into a usable model (described below) and how to express the statistical scatter such that this variation can likewise fit into the model. This procedure is best described as a re-evaluation of the original observations in order to maximize the full use of them.

Leaf Area

Our development of the plastochron index to describe the physiological age of each leaf upon a branch has been previously described (see previous reports). Our goal is to simplify all measurements so that they can be easily taken in the field to calculate leaf age in a simple manner. This year we have developed a simplified spreadsheet with the associated calculations and diagrams, so that individuals not versed in the use of a spread sheet (as Excel) can make a few basic measurements and determine the age of the branch and each leaf.

By measuring the length and width of a leaf, leaf area can be approximated, which we have previously used as the measure of leaf's age¹. Those measurements are taken with a simple ruler but require some time to measure and record, not easily done in the field. Recently we have discovered a program that will simplify the measurements of the area of the leaf. It is a free program that has been developed under the umbrella of the US National Institute of Health², called Image J. This program can do many evaluations of graphical data but we have used it in a simplified mode, shown in Figure 1. In the field one can take an electronic photograph of the leaf, still attached to the tree, against a white paper on which has been scribed a scale. These pictures can be then returned to the laboratory where they can be easily evaluated after down-loading as either a bitmapped or a jpg image. This concept seemed to be a step forward, and indeed worked beautifully in a lab setting. However, when we tried to take this approach out to the field, we encountered difficulties, namely the overlapping of leaves on a branch interferes with the ability to obtain adequate photographs. Furthermore, it was not simple to orient leaves in tall trees for good photos. In fact, when there are a large number of branches each with many leaves on a major branch (50-100), the only manageable way to find a total leaf area of the branch is to measure individual leaf lengths and use a scaling factor with the square of the length to approximate area.

¹ As has been previously stated, it is the dry weight of the leaf that is most closely related to the age but that is impossible to obtain without destructive sampling. Under most conditions leaf area is an acceptable surrogate for the dry weight.

² We wish to acknowledge aid in determining this protocol. Dr. Grant Thorp passed the existence of the program to Mr. Reuben Hofshi, who in turn gave it to us. This program can be obtained from: <http://rsb.info.nih.gov/ij> .

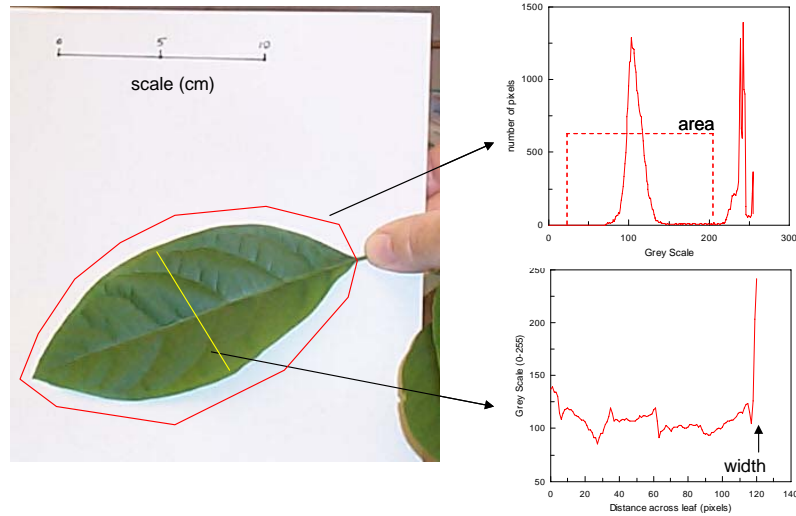


Figure 1. Measurement of Leaf Length and Area. The above diagram of how the program, Image J, can be used to extract linear dimensions or area of the leaf from an electronic photograph of the attached leaf. The photo can be used to measure an area (above right) or width (below right, width is used for convenience here). The idea is to allow easy collection of the data in the field with evaluation later in the laboratory. The use of a scale in the original photo allows for any difference in how the photo is taken.

Sap Flow

Sap flow, that is water flow through the xylem vessels, is the critical measurement of how water moves within branches, which in turn can aid in the description of total leaf conductance (a measurement of the opening of the stomata). It is this conductance which controls the CO₂ flow into the leaf, and therefore photosynthetic productivity or assimilation (Figure 2). Thus, we have devoted considerable time in understanding what exactly the monitors of sap flow measure. We now feel that we have an understanding of how to calibrate precisely those monitors and what is occurring with water flow in the avocado tree. While the fundamental processes are similar, some of our observations are not quite the same as has been described previously for other plants.

The instructions for the sap flow monitor state that flow is zero just before dawn (generally taken to be about 5AM). The flow at this time is therefore set to zero and the fundamental coefficient for heat flow within this particular branch is determined. We have found that this does not work for avocado. There is a small predawn water flow which confounds our zeroing process. We have found by careful examination of months of data taken on many trees that there is no flow of water from about 11PM to 2AM in the morning (Figure 3A). During this time interval we daily calculate our coefficient. We find that the coefficient usually does not vary by more than 0.002-0.004 out of a relative value of 1.0, which is less than a percent variation over the three weeks that we usually run a typical experiment. Under many conditions, this small correction is not very important to the large sap flow during the day.

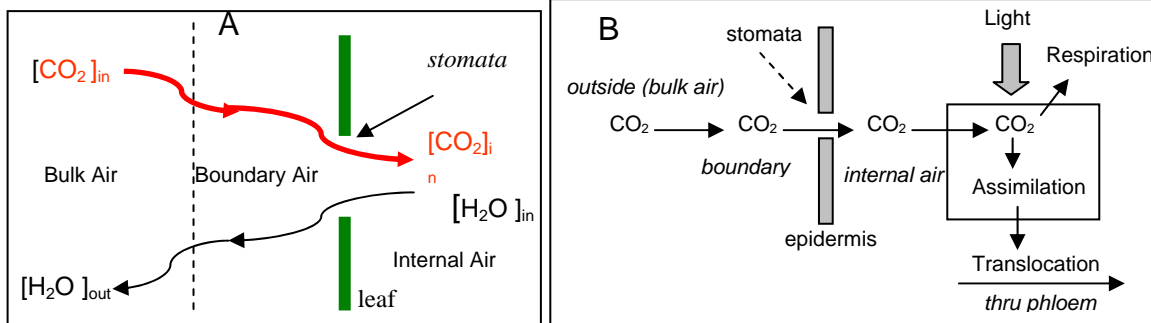


Figure 2. General Gas Flow and Nutrient Movements within Leaves. These diagrams have been used previously but show the linkage between water and CO_2 flow (A) as well of the fate of the assimilation products (B). See text for more details.

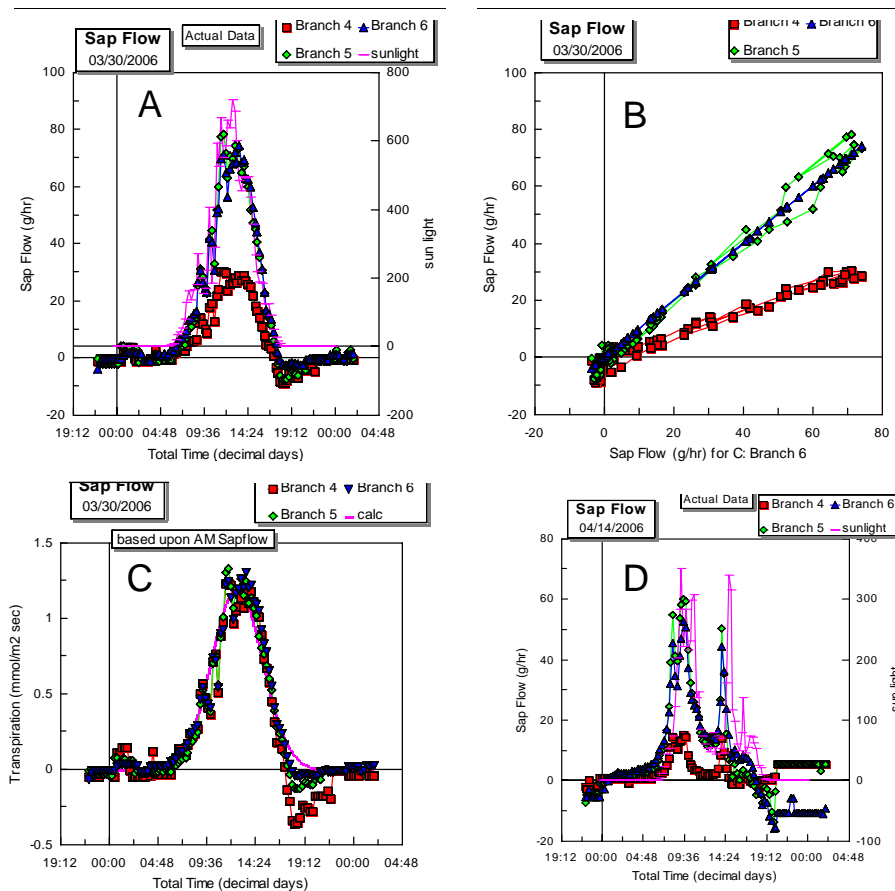


Figure 3. Daily Sap Flow from Three Similar Branches on a Single 'Bacon' Tree. A. Typical sap flow during a day, demonstrating difference between branches and how it varies with light intensity during the day. B. Relation of the sap flow in each of the other branches compared with that of branch 6, demonstrating the linear relationships between each branch's sap flows. C. The data from A converted into transpiration by using the leaf area on each branch. Here the calc values are values of light intensity (right axis). D. The demonstration of equivalence of the sap flow in each branch during a cloudy day. The flow matches again the light intensity.

However, in the late afternoon sap flow may be very low. When this occurs, we lose some precision in the measurement if that coefficient is not calculated each day.

Sap flow is dependent upon the total number of illuminated leaves and so the total water flow (in g/h) for each branch varies. However, if water flow at each time point for several branches on the same tree is plotted against the same time point for a single branch, we find that these branch plots are linearly related (Figure 3B). Hence, we only have to divide the water flow by the illuminated area to obtain the transpiration rate (Figure 3C), which are nearly identical for each branch. Even if cloud cover lowers the total illumination and the water flow declines, the flow in each branch tracks one another (Figure 3D).

However, what was a surprise was a negative flow of water occurring in some varieties just as the sun was setting, most easily seen in Figure 3A and D. ‘Hass’ avocado shows only a small amount of negative flow but ‘Bacon’ has a very pronounced afternoon negative flow. This negative flow occurs under conditions in which sap flow was very high during the mid-day. At this stage of our investigations we feel that the reverse flow of water is real and is not a zeroing artifact. What we believe is that near sunset the water within the roots and soil-root zone is nearly exhausted by the transpiration during the day. We have found earlier (see the reports of the work in Years 1 and 2) is that high transpiration during the morning leads to greatly depressed transpiration in the late afternoon; the stomata have been shown to close, even if illuminated during this time. This is due to a lowered water potential of the leaf and is called the “mid-day depression of assimilation”. Once the conductance is reduced to zero, little water is lost from the leaf. Evaporative demand is no longer present. In the late afternoon, the leaf’s water potential is low but now becomes higher than that of the depleted water potential around the root zone. This causes water to flow to the roots from the leaves and thus we observe a negative water flow. Of course, the water potential of the trunk or of the higher branches may influence this flow and thus we must study further the water relationship of the entire tree.

Last year we reported that ‘Hass’ on Duke 7 seemed to yield much “better” transpiration rate than ‘Hass’ on its own roots. Here “better” is defined as a higher sap flow. We have developed two methods to indicate which rootstock can continue flow into the afternoon. Figure 4 shows one method. Here we plot the sap flow from branches of two different trees against each other. The initial slope is the morning sap flow and its value represents the integrated transpiration from all of the illuminated leaves (dependent upon the total leaf area). Under conditions where the two trees behave similarly in the afternoon, that slope remains the same through the afternoon (Figure 4B). If there is an afternoon closure of the stomata and/or a problem with the water delivery system of the tree, a break in the slope occurs. Here the rooted tree maintains a lower but constant water flow; while the clonal tree increases its transpiration.

Another method (not shown) is to take the total water loss in the morning (sum of water loss from 8 to 10AM) and divide it into the total water loss in the afternoon (sum of water loss from 2 to 4PM). When the stomata close in the afternoon, this ratio will be much lower. This mirrors the daily performance of individual leaf conductance measurements that we reported in previous years. High morning conductance or sap flow gives rise to a much lower afternoon conductance or sap flow due to early stomata closure. We prefer to use the sap flow method at this point in our research since this method measures total branch water flow, not just single leaf conductance, and therefore a better estimation of whole tree performance. To show the

validity of sap flow measurements, we took the sap flow system out to the field (using an experimental field at ACW in Fallbrook)³. Here there were a block of 6 trees (3 ‘Hass’ rooted, and 3 ‘Hass’ on Duke 7); each tree had an individual sap flow monitor on a branch. We measured the length of each leaf on each branch and converted that length to area, which was used to convert sap flow (in g / hr) into a measure of integrated transpiration (moles H₂O evaporated /m²-leaf area second). The integrated transpiration is then divided by the leaf water deficit at that time interval⁴, which yields a calculated conductance (in stomata conductance units⁵), shown in Figure 5. This plot is a composite of daily calculated conductance for a single branch of 6 individual trees over 12 days. The results are remarkably consistent and show an increase in morning conductance followed by a closure in the afternoon. The scattered points, principally at night during the very early AM is due to a small amount of noise which is present in the sap flow and a very small vapor pressure deficit, due to lower air temperature and higher relative humidity in the night. For the most part, the conductance is virtually zero during the night. We plan to conduct further field tests at this site in the upcoming year to further validate these measurements under a range of tree varieties and soil conditions.

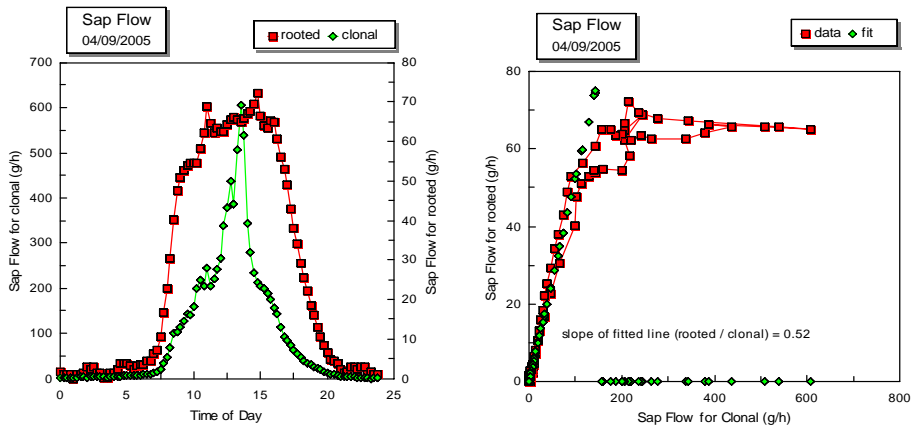


Figure 4. Sap Flow for ‘Hass’ Trees on Two Rootstock Types. **A** (left side of figure). Sap flow during the day for a Hass tree on its own roots (red squares, rooted) or a Hass tree on Duke 7 roots (green diamonds, clonal). Note the difference of sap flows: rooted with a maximum flow of 65 g/h (right side of A) compared with clonal with a maximum flow of 590 g/h (left side of A). This is due in part to a difference in leaf area (larger total area on clonal). **B** (right side of figure). The sap flows of both trees are compared with the x-axis being the clonal and the y-axis, the rooted. Note that both are linearly related (during the early morning) with a slope of 0.52. In fact, the clonal has nearly twice as many leaves as the rooted tree. The rooted trees reach maximum earlier in the morning and remains at a steady state during the day (shown by the leveling of this figure at about 65 g/h for the rooted).

³ The power was supplied by photocell array and the experiment lasted for three weeks.

⁴ The vapor pressure deficit is obtained by using the water vapor pressure at saturating conditions less the water vapor pressure at the air relative humidity. The saturated water vapor pressure is highly dependent upon air temperature. Both the air temperature and relative humidity were collected at the same time as the sap flow during the day.

⁵ The units are cm/sec, which is due to the methodology of the calculation and is of classical form. To obtain modern units (mmoles/m²sec) multiply these units by 400.

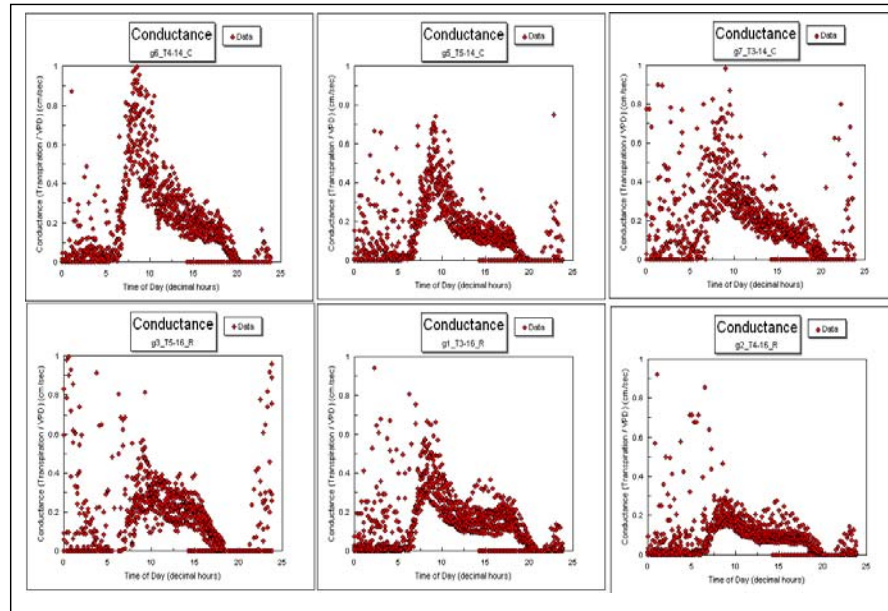


Figure 5. Comparison of the Calculated Conductance between Rooted and Clonal Rootstock in the Field. Sap flow (g/hr) converted by leaf area (m^2) into transpiration ($\text{mmol}/\text{m}^2 \text{ sec}$). Using VPD (mol/m^3) with relative humidity and air temperature, the transpiration is converted into conductance (m/sec). To obtain “standard” conductance, multiply these numbers by 250 to obtain conductance as $\text{mmol}/\text{m}^2 \text{ sec}$. These are total conductance, not those from LICOR measurements (which miss the boundary layer). Data are from six trees planted at a field plot at ACW, Fallbrook, spaced by 10 feet from 7/6 to 7/17/06.

The field data also shows that the rooted plants have a lower morning conductance (all are about 0.5 cm/sec at the maximum) and while the afternoon conductance is low, it continues longer during the afternoon, when compared with the clonal plants (the morning conductance varies from 0.7 to 0.9 cm/sec). This is similar to what we have observed under controlled environmental conditions.

Canopy Processes

In order to develop a more comprehensive model of the tree canopy, we must first understand the processes occurring in each leaf since the leaf is the fundamental production organ of the tree. The elemental processes in assimilation within the leaf (Figure 2) are the flow of CO_2 into the leaf, assimilation of the CO_2 into carbohydrates and other metabolites, movement of those compounds into storage (such as starch), respiration (to provide energy), and transport (translocation) to other growing parts of the plant including the fruit (actual productivity). All these processes depend upon light intensity, air temperature and relative humidity, and the water potential within the plant. The temperature at which these processes operate is the leaf temperature. Further, the magnitude of all these processes of assimilation depends upon the developmental age of the leaf.

Model of Leaf Productivity

A study of the canopy processes remains difficult since the avocado canopy is a complex and variable structure. While we have laid the foundation of understanding the smaller units that make up the canopy, more work is required to place them rationally into a canopy concept. The development of this model gives us scaffolding on which to place our measurements that allow insightful predictions of what should occur and what we should measure at a higher biological organizational level, e.g., the canopy. We began our investigations towards a model by using the sap flow through a large branch as a surrogate of the assimilation process (Figure 6). The sap flow represents water movement largely through the xylem vessels to the leaves on the branch.

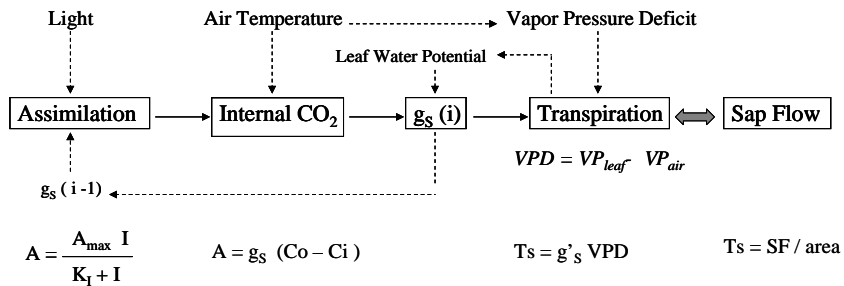


Figure 6. The Fundamental Diagram of the Model of Leaf Assimilation. The driving element is light intensity shown at the left of the diagram. This is used with the past conductance (that calculated during the last period of measured sap flow, 15 minutes). The relationship of the conductance and A-I light curve parameters are used to calculate assimilation. Assimilation is used with the relationship of the internal CO₂ (C_i) to generate the value of conductance for the current 15 minute period. That conductance is used to determine transpiration, together with the current level of vapor pressure deficit (VPD, difference between that inside the leaf and that outside). Transpiration and sap flow can be directly compared.

Water is lost from the leaf by transpiration in which the conductance of the stomata of the leaf represent the “valve” of the leaf and the lower vapor pressure of the atmosphere, when compared with the vapor pressure within the leaf, is the driving force of the movement (Figure 6). Typically the conductance varies from near zero in the dark and late at night (when the stomata are closed) to a high level in the morning before the total water loss induces a “strain” on the leaf by lowering its water potential, which in turn tends to close the stomata (see above). The photosynthetic assimilation is largely governed by the light intensity available to the leaf and the conductance of the stomata to CO₂ exchange.

Thus, our goal was to model the conductance of the leaf based upon only easily-measured environmental factors. Once we understood how the conductance varied during day, we could understand how the assimilation was varying and thus obtain a measure of the productivity of the tree. The testing of this conductance model uses sap flow which could be measured by our sap flow monitors. Once the sap flow can be monitored accurately, we will be able to test the validity of the conductance model of productivity.

Our model begins with the light falling on the leaf, or at this point the light intensity at the level of the top of the canopy (see Figure 3, the variation of the intensity of light tends to match the variation of the conductance). That can be measured via a wide range of light intensity monitors, sensitive to the photosynthetic active radiation (PAR, wavelengths from 400 to 700nm). At this stage we are not correcting for any light, either reflected by or transmitted through the leaf, as those processes represent small losses from the total amount of light which is absorbed by the leaf (about 5%, see earlier reports).

For the first approximation, the light intensity was converted into assimilation (see below) by a simple formula based upon two “constants” (A_{\max} and K_I , but see below), based upon our earlier findings (the “A vs I” curves). The assimilation was converted to conductance by assuming a constant amount of internal CO_2 within the leaf⁶. This conductance, after correction for movement of water vapor rather than for CO_2 , was used to calculate the transpiration based upon the vapor pressure deficit between the air and the leaf. These are all simple transformations and while they worked in part, they lead to a flattened daily-transpiration curve which did not match the sap flow.

There were two small changes in the model based upon our past work which improved the accuracy of our model. We found that the two “constants” (A_{\max} and K_I , described above) were not constant but depended upon the stomata conductance (see below); they increased in value with increasing conductance. We added that dependence to our model. Furthermore, the internal CO_2 , while largely constant, does vary somewhat with conductance. Again, this was a past finding from our research. We have added that to our model. Ultimately, the internal CO_2 concentration can be made to vary with temperature and that addition will allow us to model assimilation and transpiration at different temperatures.

The model is used to calculate ultimately the sap flow in terms of 15 minute intervals (the time used to take the sap flow and environment measurements). Initially we use a conductance that was calculated in the earlier time interval (15 minutes, earlier, given as $i-1$ in the diagram). The calculation in the current interval (i^{th} interval) is used to find the conductance for this interval. The driving element of the model is light intensity (see above). This is used with the past conductance (that calculated during the last period of measured sap flow) and the relation of the A vs I light curve parameters to calculate assimilation. This value of assimilation is used with the relationship of the internal CO_2 to generate the new value of conductance for the current interval. That conductance is used to determine transpiration, using the current level of vapor pressure deficit (difference between that inside the leaf and that outside). It is this transpiration that can be directly compared to the sap flow. As discussed above, the use of the vapor pressure deficit can convert the transpiration into a stomata conductance of the leaf. That calculated conductance compares very favorably with the measured conductance of an individual leaf.

The role of transpiration will be of importance to build into the model the gradual loss of water from the leaf during the day. It is hoped that our previous data on the relation between conductance and water potential will then be incorporated into this model. We should be able to predict mid-day depression due to an early closure of the stomata. Currently, the model does

⁶ We earlier found that the leaves tend to hold the internal CO_2 remarkably constant (ambient of 380 ppm, with an internal of about 280-290 ppm).

not predict this phenomenon very well. Also, we are finding problems with a good fit when the soil undergoes drying. We hope to be able to place the measured soil water potential into our model shortly. What a dry soil does to transpiration is lower it compared with our model calculations. In essence, it tends to lower the conductance. What it will do to the model is to lower the A vs I curves (Figure 7) and that lowering will then lower the calculated conductance. We will incorporate this factor into the model as we begin field validations studies in the upcoming year.

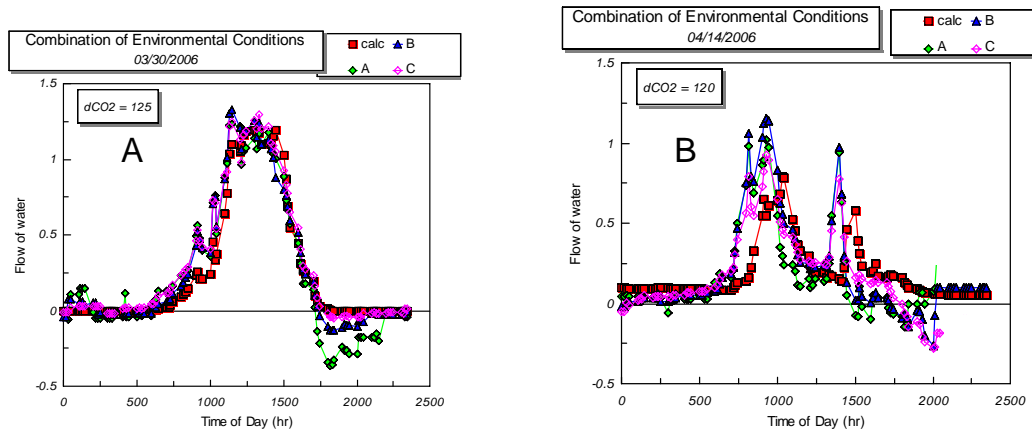


Figure 7. Comparison between the Model and the Actual Sap Flow. The sap flow is taken from Figure 3 and the model is calculated according to Figure 4. In A, the fit is quite good except for the later portion of the afternoon, in which a pronounced negative sap flow is observed (see text for a possible explanation). In B, there is a small lag of the model when compared to the sap flow data. The reason for this is not yet fully understood.

Dependence of Conductance upon Light Intensity and Assimilation

At the turn of the last century, many attempts were made to measure the relationship between the CO₂ gas exchange and light intensity but the technology of the day was limiting. Gas exchange could really only be measured by changes in gas pressure as the gas was used up or released. This limited the time scale of the experiments as well as the precision of the measurements. It was believed that CO₂ fixation linearly increased with light intensity until a limitation was reached at which point the CO₂ fixation no longer increased at all with increasing light intensity. This was expressed by Blackman in 1907 as the “operation of limiting factors”, in which the rate of photosynthesis depended one for one upon light intensity but reached a constant rate beyond a threshold limit of intensity⁷. Fixation seemed to be governed by one step.

Yet biological processes have proven to be not quite so “lock-step” but are more generally regulated so that the process is not governed by only one step. Rather, all steps are modulated to provide a maximum output until many are limited. This is true of light limitations of gas

⁷ For an interesting discussion of this, see the older Plant Physiology Textbooks such as Stiles and Cocking, 1967 edition of a largely intact 1948 version, p 171-173.

exchange. While most of the early researchers worried about the role of stomata on limiting gas exchange, algae and aquatic plants such as mosses were used to prevent any interference by stomata. It is now clear that under many conditions stomata limit gas exchange even in an excess of light. Thus, under many cases light is not ultimately limiting but rather other factors are interfering with gas exchange.

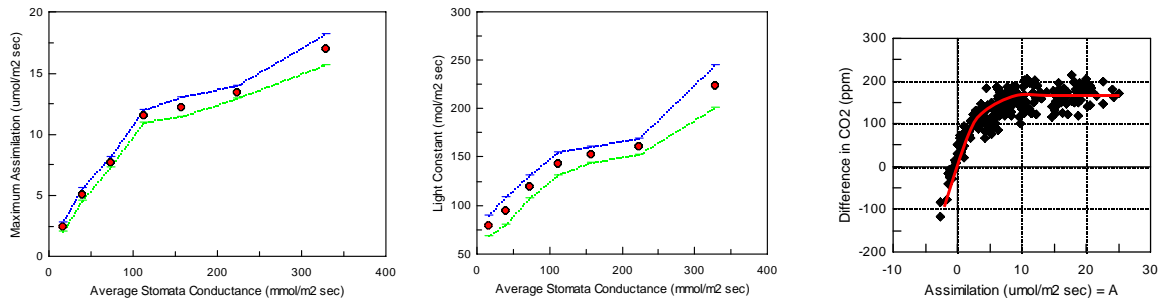


Figure 8. The Relations Used in the Model of Figure 6. A and B. (Left two plots) Parameters (maximum assimilation and Light Constant) describing the A-I curve. These plots have been shown previously in earlier reports and represent averages (with standard errors) over a small band of conductance. This technique smoothes the data and allows for a relationship to be found that can be used within a model. **C.** (Right-most plot) The dependence of internal CO₂ (difference is external less internal) upon the assimilation rate, as determined from a wide range of field data (from Xuan, Mickelbart and Arpaia).

Yet as we have noted, light intensity generally drives assimilation directly and as such, that dependence must be investigated (generating the A vs I plots). We obtained excellent light curves for assimilation for the ‘Hass’ avocado, but the light curves cannot be generated by increasing the intensity. For a fixed light intensity, the steady-state assimilation rate is balanced by the fixed conductance of the stomata (see our data in earlier reports). This is easily observed by plotting the assimilation rate measured under varied but stable environmental conditions⁸ — assimilation is directly related to conductance⁹.

Our determinations of A vs I relations are done in a short time scale. The concept is to prevent changes from happening to alter the A vs I dependence; in particular, a change in the stomata conductance. Yet, the conductance of the stomata is never uniform at the beginning of the experiment. Thus, if A vs I is determined by increasing the intensity, the stomata are unable to respond rapidly and therefore, almost immediately limit assimilation. While the gas exchange rate may increase with increasing intensity at first, the conductance limits much of the potential increase and the Blackman’s “operation of limiting factors” comes into play. Thus, a sequence

⁸ Field conditions are rarely truly stable. They are dynamic throughout the day. However, one must remember that they change over tens of minutes intervals and then somewhat slowly. The physiology of the plant can react to these changes since evolution has forced the plant to adapt to the environment. For example, stomata can open and close in tens of minutes, but not instantly or even within seconds.

⁹ We showed this in an earlier report in which a large number of independent measurements, taken largely under field conditions, were combined.

of light intensities can generate the correct observed assimilation rate only if the intensity decreases. Under these conditions, the conductance does not limit gas exchange at all.

This interference of light-driven assimilation affects two processes of the avocado productivity. One is the constancy of A_{\max} and K_i ; they do vary with conductance (Figure 8). The second is concerned with light or sun flecks. As the light intensity upon a leaf declines, the assimilation declines but the stomata begin to close (more slowly than the light intensity declines generally). Thus, the assimilation follows the light intensity. After tens of minutes in low light, the assimilation and conductance are balanced. When the light increases (a sun fleck falls on the leaf), the assimilation can rise but is limited immediately by the conductance. By the time the conductance rises (10-20 minutes) such that the assimilation can take advantage of the light, often other portions of the canopy shade the leaf. Thus, the leaf being intermittently illuminated does not operate efficiently. The sun flecks must be of duration of at least 15-30 minutes to allow for stomata conductance re-adjustment.

SUMMARY OF 2005-06 PROGRESS

We stand poised to demonstrate an assimilation model for the avocado tree. With environmental parameters which can be simply measured, we can predict the amount of carbon which flows into the productivity of the tree. With other measurements (as to size of the root and fruit mass) we can use the model to predict the efficiency of fruit production.

With the information outlined above (for more detail see previous progress reports), we are near the critical cap-stone of this work. We hope to take this information obtained under controlled conditions into the field. We expect similar results under field conditions and our initial field work (Figure 5) verifies this. However, in order to finalize recommendations to the grower community, we must corroborate and validate our previous findings. We expect this further work to give us insight into canopy management, tree density, tree architecture, and allow for further development and refinement of a model to predict phenological events for the avocado and to generate innovative practices to increase efficiencies of grove operations and orchard profits.