

The understanding of carbohydrate budgets in fruit trees made easy: what we know and ideas about what we need to know

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Abstract

For the past 30 years research in my laboratory has been largely concerned with understanding various aspects of carbohydrate assimilation and distribution in fruit trees. It is increasingly my belief that carbohydrate supply is the simpler side of the carbohydrate budget issue and under normal environmental conditions tree carbohydrate supply is simply a function canopy light interception. Understanding factors that dictate carbohydrate partitioning are more difficult to quantify but are conceptually also quite simple to understand since carbohydrate partitioning does not direct the growth of the tree but is the result of the growth and development of the organs that make up the tree. Quantifying carbohydrate partitioning in trees over time simply requires accurate estimations of seasonal organ growth potentials. Conceptually this is quite simple, but is complex in practice. To do this we chose to develop detailed models of seasonal organ growth and integrate them into a functional-structural tree growth model. This led to the development of submodels for fruit growth, leaf growth, shoot growth, root growth and carbohydrate storage capacity. With this approach even regulation of long-term carbohydrate storage in trees is much easier to understand than previously thought. In this paper I also outline what I believe could be interesting avenues for future research.

Keywords: leaf nitrogen, fruit growth, modeling, photosynthate, shoot growth, plant architecture, carbohydrate storage, carbohydrate mobilization

INTRODUCTION

When I began my career in fruit tree physiology my primary research experience was in environmental plant physiology and in trying to understand how plants partition resources to optimize canopy photosynthesis. During this early period, like many environmental physiologists, I relied on leaf gas exchange analysis to seek answers to multiple questions (DeJong, 1982, 1983, 1986; DeJong and Doyle, 1984) but the primary question that intrigued me was how trees managed to optimally distribute leaf nitrogen along gradients of leaf light exposure within their canopies (DeJong and Doyle, 1985). While I was pursuing answers to this question I became increasingly aware that, while questions about how trees optimize canopy photosynthesis were intriguing, the fact was that, in most cases trees are well adapted to do that, and they do it very efficiently. Therefore I became convinced that, from a horticultural and orchard management point of view, it would be much more fruitful for me to focus my career on trying to understand how trees manage to distribute the photosynthates they obtain and potentially improve that, rather than to try to improve upon tree canopy photosynthesis. This was based on the ecological premise that, in their natural setting, plants have been selected to optimize their traits for survival, and the job of horticulturists and crop physiologists is to determine what traits plants have that, either can be better provided for in their cultivated setting or, that can be changed so they are optimized for managed cropping. Since it is hard to imagine situations in which optimal plant photosynthesis would not be advantageous in both natural and managed plant growth conditions and there is actually very little evidence in the literature that natural plant photosynthetic mechanisms have ever been significantly improved upon (Evans, 1997), I chose to focus most of the remainder of my career on studying the distribution of



photosynthates in trees rather than studying the photosynthetic process itself. However, there is one aspect of the understanding of canopy photosynthesis that we discovered that I think is worth mentioning. The remainder of this paper will first describe the work on canopy photosynthesis and then focus on the research related to understanding how photosynthates are distributed within trees. Since I believe that the key to science is asking the right questions, I will also point out intriguing questions that I believe are worthwhile for future generations of tree crop physiologists and developmental biologists to pursue.

DISTRIBUTION OF LEAF NITROGEN FOR OPTIMAL PHOTOSYNTHESIS

In 1979, Mooney and Gulmon predicted that carbon gain for a whole plant would be maximized when leaf N is distributed such that the leaves in the micro-environments receiving the greatest amount of light would have the highest leaf N. In 1985 we demonstrated that leaf N per unit leaf area in peach trees conformed to this prediction but N concentration in leaves did not (DeJong and Doyle, 1985). This raised questions about how trees achieved this “optimal” distribution of leaf N. Subsequent research revealed that most likely, leaf light exposure triggers differences in leaf thickness (specific leaf area) and that N distribution in the canopy follows differences in specific leaf area (DeJong et al., 1989; Rosati et al., 1999, 2000). Follow up studies related to these phenomena led to confirmation that dense plant and tree canopies are so well adapted to distributing their leaf photosynthetic capacity along canopy leaf light gradients that whole canopy photosynthesis per day under non-stress conditions can be estimated from simply measuring canopy light interception over a day and the maximum leaf photosynthetic rate of well-exposed leaves (Rosati et al., 2001, 2002). This is based on the fact that individual leaf photosynthetic capacity of peach trees tends to be very well distributed along gradients of integrated daily leaf light exposure and that individual leaf angles with respect to the sun’s rays tend to be adjusted to partition light among leaves in the canopy in such a way that, on average, the maximum photosynthetic capacity of each leaf matches the maximum light exposure of that leaf so that collectively, leaves tend to make near-optimal use of available light (Rosati and DeJong, 2003).

MODELING THE DISTRIBUTION AND USE OF PHOTOSYNTHATES IN FRUIT TREES

When I began work on trying to understand how fruit trees distribute and use the photosynthates that they assimilate, nearly all mechanistic crop modeling efforts at the time focused on annual crops. Carbon partitioning in those models was deterministic using partitioning coefficients based on sequential harvests of whole plants to determine the amount of carbon allocated to specific organs over time (Jones et al., 2003; Brisson et al., 2003; Wang et al., 2002). It was clear that this approach would not work for long-lived trees. However, it was increasingly recognized that carbohydrate partitioning at the whole plant level is primarily driven by growth and development of individual organs (White, 1979; Watson and Casper, 1984; Weinstein and Yanai, 1994). We used this concept to develop the PEACH model (Grossman and DeJong, 1994) and later DeJong (1999) outlined four principle steps for applying this concept to logically understand carbon partitioning in peach (and other fruit) trees. Later a fifth principle was added as we developed the functional-structural virtual L-PEACH model (Allen et al., 2005, 2007; Prusinkiewicz et al., 2007; Lopez et al., 2008; DaSilva et al., 2011, 2014) that included context specific carbohydrate distribution from, and to, specific organs within the architectural framework of a tree.

The five principles for understanding carbohydrate distribution in trees (and plants in general) are: 1) a tree is a collection of semiautonomous organs and each organ has a genetically determined, organ-specific development pattern and growth potential; 2) the genetic potential of an organ is activated or deactivated by organ-specific, endogenous and/or environmental signals; 3) after organ growth is activated, current environmental conditions and genetic growth potential interact to determine conditional organ growth and metabolic capacity; 4) realized organ growth is a consequence of conditional organ growth and metabolic capacity, resource availability (assimilate and nutrient supply) and inter-organ competition for those resources; 5) inter-organ competition for CHOs is a function of

location relative to sources and sinks of CHOs, transport resistances, organ sink efficiency and organ microenvironment. The rationale for these principles is presented in DeJong (1999) and DeJong and Moing (2008). Upon examining these principles for understanding carbon partitioning it is apparent that the tree does not actively allocate its carbohydrate to the various organs in the tree but carbohydrate distribution within the tree is governed by the development and growth potentials/metabolic activity of the individual organs of the tree. Furthermore, phenological patterns of organ development and growth are the principle determinants of carbon partitioning in trees over a growing season. An important corollary to this is understanding that potential organ growth is dependent on organ development during a specific growth increment but organ development can proceed even if actual organ growth is less than potential growth as long as a minimum threshold of growth is achieved.

Since whole tree growth and carbohydrate distribution within a tree in both the PEACH and L-PEACH models were based on these principles much of my subsequent research focused on understanding and quantification of factors controlling or influencing the growth and metabolic activity of various organs in fruit trees. Most of my work was focused on peach trees but some work was also done on apple, plum, walnut and almond. References to the majority of my published research are available at <http://www.plantsciences.ucdavis.edu/PlantSciencesFaculty/dejong/research.html>.

FRUIT GROWTH STUDIES

The single most important breakthrough that allowed us to pursue an organ-centric approach to carbohydrate partitioning was that organ growth potentials during any period during the growing season could be quantitatively approximated in peach trees by manipulating crop loads and using relative growth rate analysis to describe patterns of organ growth under conditions in which it was reasonable to assume the organs of interest were growing at, or near their potential for a given set of environmental conditions (Grossman and DeJong, 1995a, b, c). This initially allowed us to focus on quantifying the sink potential of individual fruit (Pavel and DeJong, 1993; Grossman and DeJong, 1995a, b) and later vegetative organs (Grossman and DeJong, 1995c). With regard to fruit, relative growth rate analysis also provided a new understanding of the basis for the double sigmoid curve in stone fruit and a relatively direct means of estimating fruit respiration per increment of growth (DeJong and Goudriaan, 1989). It also allowed determining: when fruit growth tended to be more source limited than sink limited (Grossman and DeJong, 1995a), periods during which source limitations were due to overall tree carbohydrate supply or transport/competition limitations (DeJong and Grossman, 1995), how freely carbohydrates moved from one part of the tree to another (Marsal et al., 2003) and how tree water stress and nitrogen status affect fruit size (Berman and DeJong, 1996; Saenz et al., 1997). This research also led to a practical understanding of peach fruit growth responses to fruit thinning (Grossman and DeJong, 1995a) and the importance of early thinning to optimize fruit size and yields (DeJong, 2012). It also led to a better understanding of importance of early spring temperatures in determining the date of fruit maturity (Lopez and DeJong, 2007) and why warm springs tend to be associated with smaller fruit size at harvest (Lopez et al., 2011).

There are many interesting questions that remain to be addressed regarding the five principles outlined above and their ramifications for maximizing yields of acceptable size fruit in fruit trees. It is well known that tree crop load and mean fruit size are inversely related such that as crop loads increase mean fruit size decreases (Cain and Mehlenbacher, 1956). The challenge for fruit growers is to thin fruit to crop loads that will optimize both crop load and final fruit size to meet market demand and thus high economic returns. The more that is known about these interactions the better growers can make these types of management decisions. While researchers usually focus their analyses on mean fruit size, both growers and researchers recognize that, regardless of the mean fruit size on a tree, individual fruit sizes vary greatly (Basile et al., 2007). One potentially important avenue of future research could be directed toward understanding how crop load, pruning, thinning and environment affect the range of fruit sizes on individual trees. Another avenue of future

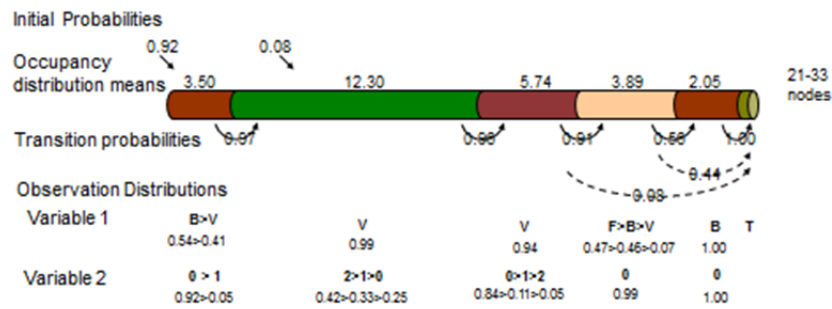
research that could be important for both fruit breeders and growers is that a cultivar's genetically determined "maximum fruit growth potential" (related to the first principle listed above) could have significant impacts on the tree crop load/fruit size relationship. The factors governing carbohydrate distribution outlined above lead to the hypothesis that cultivars with inherently larger fruit size potential should be able to produce greater crops of a specific fruit size than cultivars with inherently less fruit size potential even though the desired fruit size is within the range of fruit sizes attainable by both cultivars. In other words, are the economic yield potentials of cultivars dependent on their genetically determined maximum fruit size potentials? The rationale for this hypothesis is that the collective fruit sink strength on a tree during a specific period should be a function of the total fruit number and the collective individual fruit growth potential during that period (Grossman and DeJong, 1994). Having a high collective fruit sink strength should lead to a greater relative proportion of total available carbohydrates going to the fruit. This concept needs to be tested in field experiments.

SHOOT GROWTH AND ARCHITECTURE

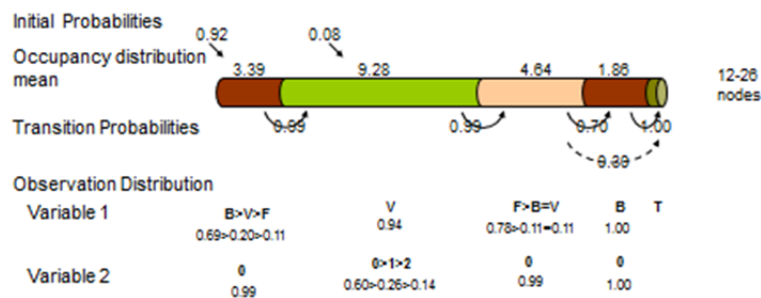
Since our crop modeling efforts were based on understanding the development and growth behaviors of individual organs many studies were also focused on vegetative development and growth. Studies focused on interactions between fruit and shoot growth (DeJong et al., 1987; Grossman and DeJong, 1995c; Berman and DeJong, 2003), developing relative growth rate functions for characterizing shoot carbohydrate demands over the season (Grossman and DeJong, 1995b) and understanding factors that control shoot growth rates, especially water relations and temperature (Berman and DeJong, 1997a, b; Basile et al., 2003; Solari et al., 2006). In 1997 Berman and DeJong reported that, on a daily basis, the period of maximum shoot extension growth occurred in late afternoon when temperatures were high and stem water potentials were recovering from their midday low point. In subsequent research, Solari and DeJong (2006) showed that shoot extension growth could be manipulated by pressurizing the roots of peach trees and interestingly most of the stem extension growth response occurred within seconds of changes in pressure applied to roots that caused changes in stem water potential. These studies may provide a hint to the broader question of why midday stem water potential is often indicative of plant water stress and vegetative growth in the field (Basile et al., 2003; Shackel et al., 1997). One hypothesis based on our shoot extension growth studies is that midday stem potentials may be related to the rate of recovery of plant water potential after midday minimums, and the rate of recovery from the midday minimum water potential is related to the dynamics of cell turgor pressure that stimulates extension growth. This is an hypothesis that requires testing both in the field and the laboratory but, if correct, it would provide greater understanding of midday stem water potential measurements and their value as indicators of plant water status.

When we began developing the virtual plant, functional-structural L-Peach model (Allen et al., 2005) we had to begin paying more attention to tree and shoot architecture. As a result we began to recognize growth behaviors of different types of shoots (proleptic, syleptic and epicormic), the importance of various shoot types in understanding overall vegetative shoot growth, and fruit bearing potentials of different shoot types (Gordon et al., 2006a, b; Gordon and DeJong, 2007; Pernice et al., 2006; Spann et al., 2008a). Knowledge of this also had many practical implications for tree canopy management and pruning strategies (DeJong et al., 2012). In order to capture details of the structures of different types of shoots to simulate shoot architecture, growth and fruit bearing we developed statistical models of different shoot types (Figure 1; Smith et al., 2008; DeJong et al., 2012; Négrón et al., 2013, 2014). This led to the discovery of some very interesting questions regarding factors that control the length and/or number of nodes of different shoot types and well as the bud fate patterns found on shoots of different lengths.

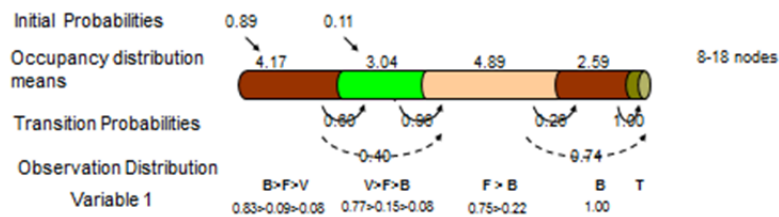
Long shoot: 5 states + terminal bud



Medium shoot: 4 states + Terminal bud



Short shoot: 4 states + terminal bud



Spur: 3 states + terminal bud

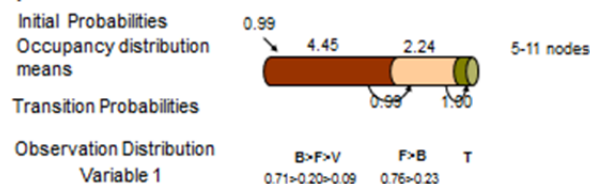


Figure 1. Hidden semi-Markov chain statistical structural analysis of 40 long, medium, short and spur proleptic shoots on pruned 'Summer Fire' nectarine trees. Variable 1 indicates the probability of the fate of central axillary buds, including Blind (B), Vegetative (V) or Floral (F) and variable indicates the relative abundance of each bud fate type. The analysis indicates that structural differences among shoots mainly occurred in mid-shoot zones (states). There was consistently a high probability of the "blind node zone" at the base of the shoot (>0.90) and then having a "lateral flower bud zone" and another "blind node zone" at the distal end of the shoots. The mid-shoots zones were dominated by a zone or zones with lateral vegetative buds that could be flanked by floral buds. The transitions between the zones were quite predictable (see transition probabilities). (variable 2 indicates the fate of lateral buds associated to the central bud; 0, 1, or 2 flower buds).

The first interesting observation was that, of all the proleptic shoots we analyzed in peach trees (shoots growing from lateral or terminal over-wintered dormant vegetative buds), the number of nodes along the shoot never exceeded thirty-four (Figure 1; DeJong et al., 2012). We know that the first 10-12 of those nodes were preformed in the proleptic bud (Gordon et al., 2006a). When additional nodes were added in addition to preformed nodes it is referred to as “free” (Kramer and Kozlowski, 1979) or “neoformed” growth (Spann et al., 2008a). Since new node development in peach trees occurs at a rate of one every 2-4 days (Davidson, DaSilva and DeJong, unpublished) and in California, proleptic shoot growth begins in mid-March, this means that virtually all proleptic shoot growth ceases in peach trees by mid-June (DeJong et al., 1987). Free or indeterminate growth in trees is generally thought to stop in response to environmental cues (Kramer and Kozlowski, 1979) but since changes in day-length are minimal and patterns of daily temperature are fairly regular during this period it seems unlikely that environmental factors cause this growth cessation in the absence of other environmental stresses. We have virtually no understanding of what factors determine the cessation of proleptic shoot growth in peach trees. This is a very interesting and important question that deserves more research. A correlated question is the development of a more complete understanding of the factors that cause the cessation of growth of epicormic shoots (water shoots). These are indeterminate shoots that are initiated from preventitious meristems after loss of a branch or a heavy pruning cut into >2-year-old branches (Fink, 1983; Wilson and Kelty, 1994; Gordon et al., 2006b). Epicormic shoots can have as many as ninety nodes and seem to grow until environmental conditions are not conducive for shoot growth (Négrón et al., 2013). However temperature, light or water stress thresholds for ceasing epicormic shoot growth are not well defined. Additional information on these thresholds could be important for managing vegetative vigor of peach and other fruit tree species. It would also be very worthwhile to determine if it is possible to suppress the expression of genes that control the initiation of epicormic shoots and thus more efficiently manage excessive vegetative growth in fruit orchards.

Another interesting developmental phenomenon became apparent when modeling the bud fate patterns along proleptic peach and almond shoots of differing lengths (Smith et al., 2008; Négrón et al., 2013). Lateral bud fate patterns along the shoots of different length categories (numbers of nodes) showed similar patterns near the base and terminal end of the shoots (Figure 1). The base of all shoots began with a zone containing predominately blind (no lateral buds) nodes followed by a zone that contained mixtures of predominately lateral vegetative and flower buds. Proleptic shoots of all length categories terminated with a zone with nodes with central flower buds followed by a zone with predominately blind nodes and a terminal vegetative bud. The number of nodes in these terminal zones averaged between 6 and 8 nodes. Since growth of all of these proleptic shoots was initiated at approximately the same time after budbreak and nodes on all shoots appear at 2-4 day intervals, the time of termination of growth of these shoots of different lengths occurred at different times after budbreak and the middle of June. Thus the bud fate composition along the terminal third of shoots appears to have been largely predetermined and not responsive to environmental cues since the prevailing environmental conditions during the development of the last several nodes of short, medium and long shoots would have been different during the different times of growth cessation. This is an interesting phenomenon that requires much more research to more fully document and understand.

CARBOHYDRATE STORAGE AND MOBILIZATION

Long-term carbohydrate storage plays an essential role in allowing temperate deciduous fruit trees to reactivate growth after winter dormancy (Oliveira and Priestley, 1988; Tromp, 1983). In spite of the importance of stored carbohydrates, there is little common understanding of the mechanisms that control carbohydrate storage and mobilization. Is carbohydrate storage a low-priority, passive process that accumulates only when C is in excess and indicates the status of the tree's C balance (Oliveira and Priestley, 1988; Kozlowski et al., 1991; Dickson, 1991; Körner, 2003)? Or, is tree carbohydrate storage a high-priority, active process (Cannell and Dewar, 1994; Silpi et al., 2007; Chantuma et al.,

2009) that accumulates at the expense of competing sinks, as suggested by Sala et al. (2012)? It is known that virtually all of the carbohydrates stored in a tree after leaf fall and the onset of dormancy and subsequently mobilized in winter or spring are stored in radial and axial xylem and phloem parenchyma (Dickson, 1991; Oliveira and Priestley, 1988). Based on the described principles governing the distribution of carbohydrates in trees I believe that long-term carbohydrate storage and mobilization in trees is fairly straightforward. Xylem and phloem axial and radial parenchyma cells function as the carbohydrate storage organelles. The collective storage sink in trees is a function the amount of annual growth of xylem and phloem each year, the density and relative size of parenchyma cells in active xylem and phloem tissue, how many years these parenchyma cells remain active and the relative change in storage activity of the parenchyma cells over time (DaSilva et al., 2014). It is fairly well accepted that xylem tissue is more important than phloem for long-term storage because, while the concentration of carbohydrates can be higher in phloem, the proportional mass of sapwood in trees is much greater than active phloem tissue (Kozlowski, 1992; Oliveira and Priestley, 1988). While this concept of storage is quite easy to understand it raises numerous interesting researchable questions such as: what environmental factors influence the density and size of parenchyma cells in xylem? What is the longevity and annual change in storage activity of sapwood with age and what is their sensitivity to environmental stresses? Is it possible to select for trees that have greater densities of parenchyma cells in their wood and would this lead to greater potential fruit set and yields in early maturing fruit tree cultivars because of the availability of more mobilizable carbohydrates early in the spring? How much do cultivars/species vary in their carbohydrate storage capacity and is this related to the length of their fruit development period?

There are also numerous very interesting questions about factors involved in triggering mobilization of carbohydrates from woody storage sinks. While the mobilization of stored carbohydrates after winter dormancy has been the focus of many investigations (Oliveira and Priestley, 1988) some species like pistachio (Nzima et al., 1997; Spann et al., 2008b) and macadamia (Stephenson et al., 1989a, b) appear to store carbohydrates in woody tissues during early summer and mobilize them in the same growing season to support final stages of fruit growth. The extent that this is done in other temperate deciduous fruit tree species is not well documented. A very interesting question regarding spring carbohydrate mobilization from storage involves signaling mechanisms. Spring budbreak in the branches of trees is thought to be triggered by exposure to winter chilling and subsequent exposure to warm temperatures (Kozlowski et al., 1991). However, some species such as kiwifruit, grapes and walnuts develop significant amounts of root pressure caused by the loading of stored carbohydrates into xylem vessels from adjacent xylem parenchyma cells (Wegner, 2014) prior to budbreak (Ryugo, 1988). The signals involved in timing this process are unknown and interesting because the roots are not thought to experience true dormancy (Kramer and Kozlowski, 1979). There is also no efficient mechanism to transfer hormones from the top of the tree to the roots prior to bud-break because the phloem is non-functional during the winter in temperate deciduous trees (Evert, 1963).

CONCLUSION

In addition to doing research I have been involved in teaching several classes at the undergraduate and graduate levels. I believe that my teaching activities have had a significant, positive effect on my research. The need to deliver a cohesive message about how plants function to students encouraged me to develop my own integrated understanding of tree growth and development processes. My involvement in developing an integrated, organ-based, functional-structural, virtual model for simulating fruit tree carbohydrate assimilation, transport and distribution along with architectural development and growth facilitated further development of that integrated understanding and forced me to expand my research focus into areas in which I lacked personal expertise. I am grateful to all my scientific colleagues who have been part of this research experience including; students,

visiting scientists, post-docs, academic staff and faculty collaborators. They have been invaluable in providing ideas, expertise, skills and energy to all the research I have been involved in. I realize that some of the interpretations and concepts developed in my research may be incorrect and I look forward to seeing the next generation of fruit tree researchers correct or build upon them.

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