



Review

Opportunities and challenges in fruit tree and orchard modelling

T.M. DeJong

Department of Plant Sciences, UC Davis, Davis, USA

Summary

Over the past 30 years there has been a virtual explosion in technology associated with data collection, analytical techniques and computational science. Scientists interested in fruit tree genetics, growth, physiology and management have unprecedented opportunities for using computer-based technologies to study and develop an integrated understanding of how trees function and can be optimally managed to meet the goals of growers in rapidly changing economic and climate contexts. Field and remote sensing and data transfer technology has made it possible to gather real-time data more quickly than ever before and there are a growing number of private enterprises who are collecting tree or orchard specific data but also a lack of creative ideas about how these data can be optimally used. Similarly, genotype-specific genetic data can be obtained for a fraction of the time and cost of a decade ago but the application of this genetic information to solve practical fruit production issues is still largely illusive. Determining optimal genotypes requires identifying optimal phenotypes, and optimizing phenotypes for specific environments requires dynamic and integrated understanding of how trees grow and respond to changing environments and management practices. The key to developing this understanding is computer modelling. From my perspective, modelling is best used to develop an integrated understanding of specific processes or phenomena and then applications of the derived models/understanding can be applied to address practical problems; rather than starting with a specific applied goal and trying to build a model primarily based on empirically-derived relationships without a fundamental, mechanistic understanding of the system. This is especially important with fruit trees since they are relatively large, long-lived, and their behavior is governed by multi-year phenomena; thus they are not as amenable to short-term empirical studies as annual crops. In this manuscript I will provide examples of how building a comprehensive model of fruit tree growth, architecture and physiology has led to model applications but will mostly focus on interesting opportunities for future modelling research.

Keywords

carbon partitioning, fruit growth, shoot growth, root growth, carbohydrate storage, tree architecture, functional-structural modelling

Significance of this study

What is already known on this subject?

- This paper outlines a talk that was presented at an ISHS symposium and is a brief summary of my thinking regarding challenges and opportunities for using computer simulation modelling to understand fruit tree development, growth and productivity.

What are the new findings?

- This paper does not really present new findings but presents a synthesis of numerous aspects of fruit tree simulation modelling and how complex issues regarding integrated tree growth and physiology can be approached and understood through the process of computer modelling.

What is the expected impact on horticulture?

- The goal of this paper is to promote the idea that understanding the complexity of fruit tree growth and productivity can be effectively approached through computer simulation modelling and this endeavor presents great opportunities for advancing horticultural understanding of tree crops.

Introduction

When I began my career as a fruit tree physiologist my prior research experience was in environmental plant physiology so I began by studying leaf and 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, from a horticultural and orchard management point of view, it would be much more fruitful for me to focus 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, trees have been selected to optimize their traits for survival, and the job of horticulturists and crop physiologists is to determine the traits that plants have, and how they can be either better provided for in their cultivated setting, or 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 growth conditions and there is very little evidence that natural plant photosynthetic mechanisms have ever been significantly improved upon (Evans, 1997), I began to focus on studying the distribution of photosynthates in trees rather than studying the photosynthetic process itself. This led me into crop and computer simulation modeling. I will briefly describe some of the modelling activities that I have been involved in, but 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 modelers, physiologists and developmental biologists to pursue.

Modelling the distribution and use of photosynthates

At the time when I became interested in crop modelling, most mechanistic crop modelling efforts were focused on annual crops. Carbon partitioning in those models was deterministic, using partitioning coefficients based on empirical data from 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. At the same time, 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). This concept was applied to distribute carbohydrates in the PEACH model, using four principal steps for understanding carbon partitioning in peach (and other fruit) trees (Grossman and DeJong, 1994). Subsequently a fifth principle was added as the functional-structural virtual L-PEACH model was developed (Allen et al., 2005, 2007; Prusinkiewicz et al., 2007; Lopez et al., 2008; Da Silva 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; and 5) inter-organ competition for carbohydrates (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 has been presented in DeJong (1999) and DeJong and Moing (2008). These principles assume 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 principal determinants of carbon partitioning in trees over a growing season and environmental influences on organ phenology are the primary ways that the environment influences carbon partitioning within a tree. An important corollary to this is the 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 developing sub-models of factors controlling or influencing the growth and metabolic activity of the various organs in fruit trees.

Fruit growth studies

An organ-centric approach to carbohydrate partitioning was possible because organ growth potentials for any period during the growing season can 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 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 focusing on modeling the sink potential of individual fruit (Pavel and DeJong, 1993; Grossman and DeJong, 1995a, b) and later of vegetative organs (Grossman and DeJong, 1995c). 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 modelling fruit respiration requirements per increment of growth (DeJong and Goudriaan, 1989). It also allowed estimating when fruit growth tended to be more source-limited than sink-limited (Pavel and DeJong, 1993; 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 modelling peach potential fruit growth and yield responses to date of fruit maturity (Berman et al., 1998) and fruit thinning (Grossman and DeJong, 1995a); and indicated 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); why warm springs tend to be associated with smaller fruit size at harvest (Lopez et al., 2011); and the development of a decision support tool to predict annual harvest timing of several orchard crops (http://fruitsandnuts.ucdavis.edu/Weather_Services/Harvest_Prediction_About_Growing_Degree_Hours/).

Fruit size within fruit tree canopies is also highly variable (Basile et al., 2007) and this is also accompanied by large variations in fruit quality. While the L-PEACH model is able to capture some of the potential drivers of differences in fruit size within tree canopies (Allen et al., 2005) the group of Drs. Génard and Lescourret have led the way in attempting to model factors that lead to differences in fruit quality within peach trees (Génard and Bruchou, 1992; Génard and Huguet, 1996; Génard and Lescourret, 2004; Génard and Souty, 1996; Lescourret et al., 2011; Mirás-Avalos, 2011). There would appear to be excellent opportunities to incorporate their research into a functional-structural tree model that explicitly links fruit quality parameters with tree architecture.

Shoot growth and architecture

Since our crop modelling efforts were based on 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 environmental 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 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 provided some of the basis for coupling shoot growth rates with plant water status in the later versions of the L-PEACH model (Da Silva et al., 2011).

When we began developing the L-PEACH model (Allen et al., 2005), we had to pay 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., 2008). Knowledge of this 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 (Smith et al., 2008; DeJong et al., 2012; Negron et al., 2013, 2014). This led to some very interesting questions regarding factors that control the length and/or number of nodes of different shoot types, as well as the bud fate patterns found on shoots of different lengths.

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 (DeJong et al., 2012). We know that the first 10–12 of those nodes were pre-formed in the proleptic buds (Gordon et al., 2006a). Since new node development in peach trees occurs at a rate of one every 2–4 days (Davidson et al., 2015) and, in California, proleptic shoot growth begins in mid-March, 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 (Kozłowski et al., 1991) 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. Thus, proleptic shoot growth in peach trees appears to be determinate. There is also need for more complete understanding of the factors that cause the initiation and cessation of growth of epicormic shoots (water shoots). These are indeterminate shoots that are initiated from pre-ventitious 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 in peach and seem to grow until environmental conditions are not conducive for shoot growth (Negron et al., 2013). However, temperature, light or water stress thresholds for ceasing epicormic shoot growth are not well defined. In addition to the modelling changes these issues present, 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 shoot growth behavior question involves the time between the addition of two successive leaves, i.e., the phyllochron. In annual crops the phyllochron has been assumed to be primarily governed by the accumulation of thermal time and day length (Fleisher et al., 2006; Cousens et al., 1992; Kirby, 1995). However research on field grown peach trees indicates that the phyllochron of shoots increases seasonally in ways unrelated to patterns of temperature or radiation (Davidson et al., 2015). Furthermore, both shoot type and carbon availability appears to affect the phyllochron (Davidson et al., 2017). Accurately modelling the phyllochron of fruit trees remains a challenge and it is interesting that things as fundamental as the factors that govern the addition of new leaves are still relatively unknown.

Another intriguing developmental phenomenon became apparent when modeling the bud fate patterns along proleptic peach and almond shoots of differing lengths (Smith et al., 2008; Negron et al., 2013). Lateral bud fate patterns along peach shoots of different length categories (numbers of nodes) showed similar patterns near the base and terminal end of the shoots. 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 most shoots appear at 2–4 day intervals, the time of termination of growth of these shoots of different lengths occurred at different times. 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. The statistically based Hidden semi-Markov Chain models used to describe bud fate patterns along shoots are a very useful tool for analyzing these patterns, but ultimately it should be a goal of tree modelers to develop more mechanistic models that predict these patterns, rather than using statistical models to describe bud fate outcomes. There is some evidence that rates of metamer elongation are correlated with bud fates at specific nodes (Kervella et al., 1995) but that research was carried out on a fairly uniform shoot population growing on young, potted peach trees and more robust mechanistic models of this behavior in field-grown, mature fruit trees still await development.

The genetic traits governing fruit tree architecture and shoot characteristics are just beginning to be explored for fruit trees (Segura et al., 2006, 2007, 2008) and this type of research is sure to lead to the ability to link traits modelled by functional-structural fruit tree models with genetic traits. As this type of research expands, the power of fruit tree modelling will be more fully realized since many of the functional and structural behaviors of fruit tree models clearly demonstrate phenotypic traits that correspond with genetic traits.

Root growth and development

While the L-PEACH model did not explicitly simulate root development, growth or architecture, some aspects of growth in size and function were incorporated into late versions of the model that simulated water uptake from the soil, transport through the tree, and water potentials in various organs of the tree (Da Silva et al., 2011). Functional-structural models of root growth and function have been available for several years (Bidel et al., 2000; Dunbabin et al., 2013; Pagès et al., 1996) but as far as I am aware no functional-structural tree model has incorporated both above- and below-ground architectural growth and physiological functioning. This is a very interesting modelling challenge that could be used to test whether current understanding of balances between above- and below-ground behavior of fruit trees is robust enough to provide realistic simulations.

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). A common problem among many plant models has been the lack of attention paid to mechanistic modelling of carbohydrate storage and mobilization (LeRoux et al., 2001). This is probably because carbohydrate storage is often viewed as being 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; Kozłowski et al., 1991; Dickson, 1991). An alternative view is that tree carbohydrate storage is a high-priority, active process (Cannell and Dewar, 1994; Silpi et al., 2007). 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). Thus the collective storage sink in trees can be modelled as a function of 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 (Da Silva et al., 2014). While this concept of storage is quite easy to understand, it raises numerous interesting structural modelling 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?

There are also very interesting challenges regarding modelling mobilization and transport of carbohydrates from storage sinks and their transport up a leafless tree prior to budburst. An interesting phenological modelling 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 (Kozłowski, 1992). However, while there has been much recent modelling activity with regard to tree phenology (Luedeling and Brown, 2011; Pope et al., 2014), there have been limited attempts to incorporate seasonal phenological models of dormancy and bud-break into comprehensive tree crop models. Such research is urgently needed to help understand potential effects of climate change on tree crop productivity (Atkinson et al., 2013). Additionally, 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 Kozłowski, 1979) and there are no efficient mechanisms to transfer growth regulators 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). Similarly, mechanistic modelling of the movement of remobilized carbohydrates up a tree is also problematic since there is limited transpiration prior to bud-break.

Thoughts about usefulness of modelling

I have been involved in teaching a graduate class on research perspectives in horticulture for nearly thirty years. One of the papers that we have students read in this class is titled "Accountability, Philosophy and Plant Physiology" by J.B. Passioura (1979). In discussing the responsibilities of plant physiologists Passioura asserts that for the bulk of plant physiology "...attempts to be directly useful are futile, and the plant physiologist's responsibility is much more subtle...". I would argue the same is true for most tree crop modelling. While we often assert that our comprehensive models will be directly useful to orchardists, they are usually much too complex to be directly useful. That has certainly been the case for our L-PEACH model. Nevertheless, I assert that developing models has great value.

Passioura (1979) also asserted that the plant sciences are divided into camps of scientists interested in either the community/whole plant or molecular levels of organization with less interest in middle levels of organization such as organs, tissues and cells, or the connections/interactions between them. I believe that tree crop modelling helps to address this problem. It provides a platform for integrating knowledge about form and function at numerous levels of organization and provides a way to test whether prevailing ideas about how all the parts fit together and function are sufficient to build a functional plant model. Models help identify where information and understanding are lacking. I strongly believe that the key to doing interesting research is to ask the "right" questions. Once one begins doing dynamic, mechanistic modelling it becomes clear that opportunities for doing innovative research are almost limitless. This is very important for young researchers who are often searching for interesting and important problems to work on.

Some modellers assert that a quote attributed to Einstein, "Everything should be made as simple as possible, but not simpler", pertains to crop modelling and thus believe that the simplest models are best. I don't ascribe to this principle for comprehensive tree models. Trees are complex by nature and modellers should embrace that complexity and include as much of that complexity in their models as is functionally feasible. The type of modelling discussed here must not be confused with developing models to directly aid in decision support for orchard management. Decision support models should be made as simple as possible to make them practically useful for growers and thus do not need the complexity required to simulate multiple aspects of tree development and growth. However, the process of developing comprehensive integrated tree crop models can lead to simpler sub-models that can be directly useful in developing decision support tools such as developed by Lakso and Robinson (2014), Lopez and DeJong (2007), and Lopez et al. (2011).

Tree crop simulation models can also be great educational tools. Models that visually simulate tree growth and productivity in response to environmental or management inputs excite students of all ages. I believe that a long-term goal of the tree modelling community should be to embrace complexity and develop comprehensive simulation models that integrate as many processes, at as many levels of organization as possible. To quote P. Prusinkiewicz (2004), “Computational plant models or ‘virtual plants’ are increasingly seen as a useful tool for comprehending complex relationships between gene function, plant physiology, plant development, and the resulting plant form”.

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Address of author:

T.M. DeJong

Department of Plant Sciences, UC Davis, One Shields Ave., Davis, CA 95616, USA