FRUIT TREE MODELS: SCOPE AND LIMITATIONS

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INTRODUCTION

Models are used extensively in research, in the social sciences [e.g. economics] as well as in the physical, chemical and biological sciences. As a preliminary definition one could think of a model as an attempt to describe a certain process or system through the use of a simplified representation, preferably a quantitative mathematical expression, that focuses on a relatively few key variables that control the process or system.

The predecessors of the currently available agricultural crop models may be found in two areas:
A) Climate based models. These were originally designed to correlate [and predict] a specific biological phenomenon with climate data, mostly temperature data. Models using cumulative heat or chilling units to predict spring growth and phenology, to predict fruit ripening dates or to predict the satisfaction of chilling requirement in perennial dormancy and their more sophisticated descendents belong to this category (Ben Mechlia and Carroll, 1989; Bustan et al., 1996; Erez et al., 1990; Fuchigami and Nee, 1987; Hall and McPherson, 1997; Reuther, 1973; Salinger et al., 1993). Modeling of vegetation and crop water use is driven by climatic variables (Allen et al., 1998). More recently these simplified models have often become sub models of more comprehensive plant or crop models discussed below.
B) Ecological systems. Models have been and are still major tools in the hands of ecologists in their efforts to identify and quantify the state variables which affect the ecosystem and the interactions of its components. Agrisystems have many features in common with ecosystems but they are much simplified, heavily managed, often limited in interactions amongst species and as such are outside the scope of ecologists. However, a recent broadening of views of the interactions of agrisystems with the surrounding environment has led to more common ground (Room et al., 1996).

The development of modern agricultural crop models was closely associated with the advent of computer programming and faster computers during the last decades of the 20th century that facilitated the many calculations needed in complex models. Annual crops such as sugar beet, potato, corn and cotton were modeled first. Fruit tree models were developed only later.

The purpose and orientation of the model may differ according to the researcher's interest – a variety of agricultural problems [including water use, predicting phenology or fruit ripening, predicting climate effects, evaluation stress responses and/or pest management] have been modeled (Boote, et al., 1996). However, in the present analysis we would like to emphasize carbon-based crop productivity models with a focus on fruit tree models.

As convincingly demonstrated by de Wit (1986), agricultural productivity depends primarily on the carbon assimilation and partitioning systems. Thus the backbone of crop models of this type involves modeling of plant photosynthesis, respiration and the allocation of the net photosynthate to the fruit or organs of interest. This includes, of course, annual crops as well as fruit tree crops.

Does the modeling of fruit tree crops differ from modeling of annual crops? The answer in a general sense is 'no', since the dry matter production and allocation systems are basically the same. Nevertheless, the complexity of the fruit tree differentiates fruit tree models from annual crop models. The perennial nature and specific characteristics of fruit tree crops as outlined below, turn the modeling of fruit tree productivity into a formidable task.

FEATURES OF FRUIT TREE MODELS

For modeling purposes, the fruit tree is a very complex organism. It is probably not by coincidence that sugar beet was among the first crop plants to be modeled. Sugar beet has just two major organs; a rosette type crown of leaves (source) and a storage root (sink) and is therefore relatively easy to model. Other annual crop plants (e.g. soybean, cotton) are more complex, having leaves, shoots, roots and reproductive structures, but the entire lifespan is a few months. Fruit trees are still more complex, however, having perennial trunk, branches and scaffold roots of several ages, in addition to a very large number of current year's vegetative and reproductive organs.

The perennial nature means that every year is dependent in several ways on the previous years of life. These permanent structures provide reserves of carbon and nutrients, but also carry effects from year to year. In deciduous fruit trees, for example, the number of flowers, and thus crop potential is determined the previous season and reflect stresses and carry-over status of tree physiology from prior years; sometimes patterns persist for several years. Developing multiple year models is very difficult as many of the important carry-over effects on growth or cropping are not well understood. Additionally, fruit trees are distinguished by discontinuous canopy structures, strong management via pruning and training, manipulation of crop levels, and the grafting onto rootstocks that give varying, but poorly understood, growth and cropping effects.

Evaluation of the biomass produced by the tree or orchard is one of the initial tasks of the modeler. This seems to be a rather straight-forward assignment with an annual crop plant that starts its development from seed [the biomass of which is negligible] and the dry matter of all its organs can be determined at harvest [although shedding of leaves and floral organs must be taken into account]. In a fruit tree, however, there is a perennial woody skeleton which not only grows and develops during the annual cycle, but also accumulates and exports carbohydrates and other reserve materials. This complicates the estimation of the net increase in biomass of a fruit tree during the annual cycle. As a consequence, calculation of the Harvest Index [= the fraction of dry matter allocated to the fruit or corresponding harvested organ] also becomes more difficult. The validation by growth analysis experiments is particularly difficult due to the amount of standing dry matter in the spring, the variations caused by previous years, and the limited number of large plants that can be harvested.

The focus in fruit tree culture is also somewhat different than in most annual crops. Yield, which is limited by, but roughly corresponds to dry matter production, [and is generally predetermined by the genetic make-up of the cultivar,] is the major parameter of success in field and garden crops. Quality considerations play a limited role. For several reasons fruit tree models focus on aspects of reproductive development not commonly included in models of field and garden crops. Generally only a small percentage of the flowers on a fruit tree will remain as fruit to harvest, so most flowers and young fruits must abscise. Optimizing the final size and especially quality of the crop depends on a quite precise regulation of the final fruit numbers. Consequently, fruit tree growers manipulate and attempt to control fruit numbers with chemical thinning sprays and/or hand thinning. This of course disrupts normal processes in crops that are essentially wild-type. Finally, the regulation of abscission in fruit trees, natural or artificially-induced, is an extremely complex process to model. Many current and carry-over physiological effects interact with grower management and highly variable weather during the spring bloom and fruit abscission period.

CARBON SUPPLY AND CONSUMPTION BUDGET

One option for provision of an overall, quantitative description of fruit trees' annual productivity is through equations of C supply and consumption.

$$Pn + Sto = Sr + Rr + Dr + Fn.w.r + Pr + Sto$$

Where:
Pn – photosynthate production
Sto – nonstructural C reserves
Sr – current year's shoot mass [including leaves and stem], multiplied by a respiratory quotient
Rr - current year's root mass, multiplied by a respiratory quotient
Dr - current year's drop of flowers and fruitlets, multiplied by a respiratory quotient
Fn.w.r - fruit number, multiplied by w, fruit weight, multiplied by a respiratory quotient
Pr – perennial organ mass, multiplied by a respiratory quotient

This expression is simple and yet detailed enough to indicate major parameters that need to be determined experimentally or compiled from existing data. The C supply consists of current year's photosynthesis + some C reserves which might be mobilized to support current year's growth activity, primarily in the spring, although they might be available also later, particularly under stress conditions. The reserves appear also in the right wing of the equation, since reserves are replenished during the year. The vegetative organs (shoots and roots) appear separately with their specific respiratory quotient. The dropped reproductive structures are treated separately. The yield expression contains fruit numbers and unit weight, since both are of significance in fruit tree crops. The bioenergetic cost of production of varying organs needs to be included to convert from fixed co_2 to dry matter and compare demands of different organs on the same energetic basis (Walton and DeJong, 1990; Bustan and Goldschmidt, 1998). This expression of bioenergetic costs is important for comparing species that are more carbohydrate based like most fruit trees (apples, citrus, peach) to crops that produce large amounts of energetically-expensive dry matter like lipids and proteins, for example avocado (Wolstenholme, 1986) or pistachio (Stevenson and Shackel, 1998).

DIFFERENCES BETWEEN FRUIT TREE SPECIES

In reference to the previous section, it might be worthwhile to consider the differences amongst fruit trees and identify the components of the equation that will be affected. First, the differentiation between deciduous and evergreens has important implications. Whereas in deciduous fruit trees the entire leaf population is replenished each year, in evergreens [avocado, citrus, date palm, mango, olive] this is not necessarily the case.

An additional difference between deciduous and evergreens concerns the role of the reserves. The reserves seem to play a critical role in deciduous trees supporting the emergence of the spring flush (Priestley, 1970; Loescher et al, 1990) but much less so in evergreens like citrus (Goldschmidt, 1999). There are also differences in the relative time of bloom amongst the deciduous species. Stone fruits (peaches, cherries, etc.) bloom almost immediately in the spring before a leaf canopy is produced. The flowering and initial fruit development therefore depends highly on reserve carbon. Apple and pear, however, bloom approximately one month after bud break when about 15-25% of the final leaf area is already established. Reserves in this case are primarily used to support initial growth until about bloom, and then begin to be replenished. Consequently, the role of reserves in fruit development may differ considerably with species.

The size of the root system (both structural and fine roots) and the cost of its growth and maintenance may also vary amongst species. The few studies done with fruit trees suggest that the properties of roots vary widely amongst species (Bouma et al., 2001). The grafting of fruiting selections onto a range of rootstocks of varying genetics adds complexity and uncertainty for modeling. Environmental and management factors may also affect root system size and requirements. For example, in arid climates trees in irrigated orchards, in particular drip irrigated and fertigated, do not need to search for water and minerals and their root system might be more restricted due to the concentrated resources supplied (Bravdo, 2000). Abscission of reproductive structures also varies greatly among fruit tree species. Mango, avocado, citrus, apple and peach for example produce a multitude of flowers and fruitlets, most of which (90%) eventually drop. These organs also have high respiratory rates (Bustan and Goldschmidt, 1998). The bioenergetic cost of fruit production also varies from one species to another. Fruits rich in fat [avocado, nuts, olive] have a higher bioenergetic cost. Subtle differences exist, of course, even among varieties of the same species.

Finally, all models depend on a database of growth, productivity and physiological measurements on which to base or validate model structure and assumptions. Unfortunately, due the historically low number of fruit crop physiologists and the range of different tree fruits, the databases are generally much thinner than for the major annual crops. Within tree fruits there are variations with apple and citrus having the best data while stone fruits being relatively weaker and tropical fruits having great gaps of critical knowledge.

EVALUATION OF TREE PHOTOSYNTHESIS

A central feature of crop models is the estimation of tree photosynthesis that provides the energy and carbon skeletons for biological productivity. There are a variety of approaches, primarily borrowed from earlier crop modeling, such as modifications of the annual crop growth model, SUCROS'86 (Grossman and DeJong, 1994). The light interception problem has also been addressed by separation of the total leaf area into sunlit and shaded components (Lescourret et al., 1998). Lloyd et al (1995) showed that whole tree gas exchange rates of macadamia and lychee trees could be accurately simulated by treating the tree surface as a hemisphere and calculating gas exchange characteristics separately for sunlit and shaded portions of the tree. This model has also been adopted for citrus (Syvertsen and Lloyd, 1994; Bustan et al., 1999).

A common approach is to estimate light penetration into the canopy from canopy structure leaf area and the Beer's law extinction function. The light intensity gradient is estimated, and then photosynthesis is calculated by leaf area at given levels of light. This is usually done at time intervals of minutes or hours and summed for daily totals. Due to the movement of the sun, radiation geometry and canopy form must be included in the calculations. For orchards with rows of discontinuous canopies and consequently significant lateral radiation fluxes, the role of diffuse light on canopy photosynthesis should be taken into account (Allen et al., 1974). This is especially true with thin vertical canopies typical of vineyards and some orchards where an entire side of the canopy may receive only diffuse radiation. This may be an important consideration in humid climates such as the Northeast US or northern Europe where 40% of the total summer radiation can be diffuse.

Another simpler approach is to use a "big leaf" model that estimates canopy photosynthesis as a daily canopy light response to daily intercepted radiation that is based on incident radiation, fractional interception as estimated by Beer's law, and exposed leaf photosynthesis (Charles-Edwards, 1982). This approach ignores the gradients of light and photosynthesis of differing leaf populations and varying radiation geometry over time, but is much simpler. It may however be adequately accurate for many models. Both approaches require photosynthesis data and canopy extinction coefficients, but the daily big leaf model uses only daily radiation data. Additionally, daily fractional light interception from direct measurements can be entered to further simplify the model. This approach has been used in a simplified apple dry matter production model (Lakso and Johnson, 1990; Lakso et al, 2001) and the values simulated were quite well validated with field canopy gas exchange measurements (Lakso, unpublished data).

A recent new approach to plant and crop that has become popular is a very concise programming language called “L-Systems” (Prusinkiewicz, 2004). Based on the simplified rules of how plants grow elucidated by the botanist Aristid Lindenmayer, the structure of plants is modeled graphically as other architectural models have done, except that L-Systems can superimpose an environment such as a radiation regime and can make individual plant elements respond appropriately. Thus it can calculate light interception and canopy photosynthesis as well as many other processes. Though not simple to learn, it appears to be very powerful, and in fruit research has been used initially to model a peach tree (Allen et al., 2002).

RESPIRATION COSTS

Estimates of respiration costs (maintenance respiration and growth respiration) are needed in any carbon-based crop model. Typically, respiration costs of organs are estimated with empirically-determined specific respiration rates/unit of organ tissue multiplied by the total amount of that type of organ. Responses to temperature are normally estimated by an exponential equation, often with a Q_{10} of 2. Maintenance and growth respiration are usually modeled separately, as feedbacks from the partitioning may vary between growth and maintenance. Maintenance respiration cannot be experimentally separated from growth respiration on growing tissues although several methods for distinguishing between maintenance and growth respiration have been developed (Amthor, 1989).

An additional complexity is that much of the limited data in the literature on respiration are short-term measurements on stratified samples that can lead to large errors if extrapolated over long periods. For example, published apple leaf respiration data is typically taken on exposed exterior leaves; but those leaves may have up to 5 times the respiration rate of interior shaded leaves (Lakso et al., 1999a). Bryla et al (1997) has found for citrus roots that respiration rates may adjust very markedly over time if held at constant temperatures. This effect was greatest for higher temperatures where factors other than temperature may become limiting. Similar results have been found in grapevine roots as well (D.Eissenstat and A. Lakso, unpublished data) suggesting that this response may be fairly general.

The specific patterns of fruit respiration have received detailed attention in different fruit crops (Jones, 1981; Walton and DeJong, 1990; Blanke and Whiley, 1995; Bustan, 1996), but most fruits have higher specific respiration early in development during cell division followed by lower rates as cells expand.

SOURCE – SINK RELATIONSHIPS AND PARTITIONING PRIORITIES

Using the supply – demand terminology, we can distinguish between two situations:

A] SUPPLY > DEMAND

Under such conditions each sink should receive its share according to its potential growth rate. Growth of sink organs is not limited by the availability of photosynthate, but by other resources or genetic potential. Excess carbohydrates may exert a feedback inhibition and, according to the hypothesis of Neales & Incoll (1968) reduce the photosynthetic activity of source leaves. Photosynthesis is reduced indeed in girdled, fruitless branches (Bustan, 1996). This feedback control is not easily determined with whole trees under field conditions as there may be alternate sinks, roots in particular. There is, nevertheless convincing evidence that this feedback control exists (Lakso et al., 1999b) and some fruit tree models have incorporated it into their models (Lescourret et al., 1998). Correspondingly, the tree may compensate for source limitation by increasing its photosynthetic rates (Layne and Flore, 1992).

B] SUPPLY < DEMAND

Under such conditions [source limitation] the plant must 'decide' how to partition the available photosynthate among its sinks. The situation is comparable to economic problems of resource allocation and is known as the ' partitioning priorities' problem.

All the modelers of plant productivity face this problem (Marcelis et al, 1998) but selection of the priority scheme is generally based on theoretical assumptions and only seldom on experimental evidence. Two kinds of partitioning modes may be envisaged:

1] A 'hierarchical' mode, assuming predetermined organ priorities (Gutierrez et al., 1985).

2] A 'proportional' mode, in which every organ gets a fixed portion of the photosynthate supply, according to its relative sink strength.

Most models have adopted some kind of hierarchical, sink ranking approach. Maintenance respiration is generally assumed to have the highest priority and reserves are believed to have the lowest priority. In their peach model Grossman and DeJong (1994) assume that having satisfied the top priority needs of maintenance respiration, then fruits, leaves, stems and branches have the same priority rank, followed by the trunk and finally the roots. Lakso et al (2001) used in their apple model the following priority ranking: shoots >> fruits > roots = structure. During the spring flush of vegetative growth, bloom and fruit set there seems to be a competition between the different, actively growing sink organs. In apple, early in the season, shoots appear to have higher priority than the reproductive organs under carbon-limiting low light conditions (Bepete and Lakso, 1998). Later, as shoots terminate growth, the partitioning shifts to fruits and other organs (Lakso et al., 2001).

The problem has been addressed experimentally by Bustan & Goldschmidt (1999) who examined fruit/root partitioning ratios using potted citrus trees and a simulation model. Young fruit [7d after petal fall] were inferior to roots in competition for photosynthate, whereas older fruit [30d after petal fall] proved to be strong, dominating sinks. The varying patterns of fruit development suggest that the fruit sink demands vary with different stages of development. The similarity of the results with citrus described above and observations on apple development suggest that young fruit in general may have lower sink strength. This could be a mechanism to induce the large abscission needed to avoid excessive cropping in any year and the resultant erratic cropping over many years. Additionally, if fruit inhibit root and shoot growth as often reported, too much fruiting may be detrimental to survival in resource limiting conditions where root or shoot growth is needed to obtain the limited resource (e.g. water, nutrients or light). The results of Bustan and Goldschmidt (1999) indicate that although the proportional mode of partitioning might be valid under certain circumstances, hierarchical partitioning mechanisms are necessary for the emergence and development of new plant organs.

REPRODUCTIVE DEVELOPMENT AND FRUIT GROWTH

Fruit development is an important research area which is not specific to fruit trees; the tomato has served as a model fruit in numerous studies. Nevertheless, fruit tree modelers have devoted considerable efforts to the reproductive processes which are in the core of crop development. The long chain of developmental stages may be divided into 3 major steps; flowering, fruit set (the cessation of fruit drop) and fruit enlargement (Goldschmidt & Monselise, 1977). The regulation of flowering is complex and may vary among and even within the same species. Although a threshold level of carbohydrates may be required for flower bud differentiation (Goldschmidt et al., 1985), other, probably hormonal factors play a critical role (Goldschmidt and Samach, 2004). Temperature determines the time and duration of spring anthesis but not flower formation per se. Thus, dry matter productivity models do not usually assume a dependence of flower formation on carbohydrate availability.

Fruit set is the second critical step in the fruiting process. Lack of set inevitably results in abscission of the young fruitlet. It may sometimes be useful to distinguish between ‘initial set’ which represents the fruit retained by the end of anthesis, after petal fall, and ‘final set’ representing the fruit remaining after the June drop (Goldschmidt and Monselise, 1977). Modeling of fruit set is not a simple task. Generalizations are almost impossible due to endless variations in pollination compatibility, parthenocarpic potential and hormonal effects. Furthermore, fruit set of most fruit species [temperate zone as well as subtropicals] occurs during late spring [April – May in the northern hemisphere], a period with extremely unstable weather. Cold spells as well as dry heat waves may severely interfere with the sensitive reproductive processes in cool, temperate zones and warmer, subtropical zones, respectively.

There are nevertheless indications that the level of carbohydrate availability for fruit growth is a major determinant of the extent of fruitlet abscission (Gomez Cadenas et al, 2000). Lakso et al (2001) developed a fruitlet abscission model based on observations (Bepete and Lakso, 1998) that abscission occurs if early fruit growth rate is not maintained above a critical level. In this model the supply of carbohydrates to the fruit in relation to the crop demand determines fruit growth rates. If these rates fall below critical levels for that stage of development, abscission occurs. This model gives realistic behavior in relation to several environmental and management factors suggesting that carbon balance is a critical factor in apple fruit abscission.

The fruit enlargement phase generally occurs in the mid and late season and is characterized by primarily cell expansion. This process is accessible to the modeling approach and has, indeed, been included in most fruit tree models. For once, fruit size is clearly and quantitatively dependent upon the availability of photosynthate, as demonstrated in girdling and fruit thinning experiments (DeJong and Grossman, 1995; Fishler et al., 1983; Goldschmidt, 1999) as well as foliar pest effects (Francesconi et al., 1996). It also appears that in some fruits such as apple, the demand and potential growth during the cell expansion phase is determined by cell numbers resulting from earlier growth by cell division, which may be limited by carbon supply as noted above (Goffinet et al., 1995). Therefore there may be early-season effects of carbon balance (fruit abscission and size potential) that are manifested for the entire season. In mango, final fruit size is closely correlated with the initial dry fruit mass, acquired during the stage of cell division (Lèchaudel, 2004). A well-known effect in apple production is that early thinning to a given crop level will give larger fruits than later thinning to the same crop level. This is supported by experimental evidence in peach (Grossman and DeJong, 1995).

Fruit size is one of the most important economically significant quality traits. Competition between the fruits fed by a given leaf area determines their final size; the inverse relationship between fruit no. and size is, however, curvilinear (Goldschmidt and Monselise, 1977; DeJong and Grossman, 1995). For modeling fruit growth demand can be estimated from curves of weight over time of fruit on lightly cropping trees, where there is no sink limitation. Extreme thinning and girdling combinations have resulted in huge fruit [e.g. a 705g grapefruit, vs. 330g for fruit at normal cropping levels; (Bustan et al., 1995; Goldschmidt, 1999), the further growth of which is probably limited by the cell number acquired during the early stage of fruit development, prior to the application of thinning and girdling treatments.

ROLE OF CLIMATE IN PRODUCTIVITY MODELS

Climate comprises the most important complex of environmental factors which affect every aspect of plant life. Temperature participates in the regulation of all biological processes. Solar irradiance provides the energy for photosynthesis and exerts photomorphogenetic effects. Thus, the rate of “Valencia” orange development and maturation varies greatly between locations with warmer or cooler climates (Reuther, 1973). The climatic variations cause a problem for comparisons between locations or between early and late varieties. The use of a time scale based on 'days after anthesis' or 'degree days' can help alleviate these difficulties (Grossman and DeJong, 1995; Lakso et al., 2001). Precise evaluation of temperature effects on plant performance only became possible when controlled environment facilities came into use and this happened with fruit trees later than with smaller plants.

A linear response to temperature has been assumed in most degree day and heat accumulation models. Although the predictions provided by such models are useful for practical purposes, the 'linearity' assumption is valid only in a narrow range of temperatures. Degree day models work well only under cooler conditions when temperature is the limiting factor. Similarly, the optimum temperature for growth of citrus fruits is about 23^{o}C; higher temperatures interfere with fruit enlargement (Bustan et al., 1996). Predictions based on average daily temperature may also be improved by hourly data processing whereby differences in the amplitude of day/night temperatures can be taken into account (Bustan et al., 1996).

The problem with this, as with many other aspects of modeling, is to find the compromise between accuracy and simplicity. Calibration of temperature effects shows that every process [photosynthesis, shoot growth, fruit growth etc.] has its specific temperature dependence curve; consequently, supply - demand balances and relative partitioning also change with temperature. In apple, temperatures about 20 ^{o}C are optimal for fruit set, while temperatures above 30 ^{o}C stimulate vegetative growth at the expense of fruit retention.

Furthermore, temperature responses may adjust over time as temperatures warm over the season due to physiological adaptation (Lange et al., 1974), or as developmental stages occur. Stages of fruit development may vary in their temperature sensitivity. For example, apple fruit during early cell division growth are quite sensitive to temperature, while later, in mid-season they are surprisingly insensitive (Warrington, et al., 1999). Varietal differences in patterns of fruit development need also to be taken into account.

PREREQUISITES FOR CONSTRUCTION OF A MODEL

Preparation of a fruit tree model, or another crop simulation model, cannot be undertaken unless some background knowledge of the system is available.

It might be said that in order to develop useful and robust models one must have:
*Reasonable conceptual understanding of the physiological processes involved
*Imaginative, quantitative thinking
*An extensive agricultural/biological database

It is extremely important to carefully define the goals of the model. Is the goal to integrate incomplete data to elucidate seasonal patterns of growth and production? Is the goal to estimate responses to specific treatments or environmental factors? Is the goal to provide a specific output for management purposes (prediction of optimal harvest, giving an action threshold for integrated pest management, specifying a concentration of a chemical thinning spray, etc.)? The goal will have an over-riding effect on the choice of model structure, complexity and development.

A basic decision that must be made before constructing the model is the time step that will be used. Due to the methods of estimating radiation penetration for estimation of tree photosynthesis, many models have adopted short time steps of minutes or hours. Maintenance respiration is also very sensitive to temperature. For this reason the model of Grossman and DeJong (1994) calculates temperature and maintenance respiration hourly. The difficulty with this is that we have very little comparable data on diurnal patterns of organ growth or gas exchange. Most growth data are at the day-to-week resolution. Multiple time scales can be used in a model, but this adds to the complexity. Using longer time steps such as daily or weekly can simplify the modeling process, but it may lose resolution that is desired. The choice should vary with the reasons for and the expectations of the modeling.

A critical set of decisions needed is how many processes and parameters to include in the model and which to ignore. Thus, Lescourret et al (1998) have included fruit carbon assimilation in their model, while others have considered it to be negligible. These are not easy choices as there have not been enough models on any fruit crop to do good sensitivity analyses. General guidance on many fundamental processes is available from other plant models. Finding the right balance of enough key processes to provide realistic behavior without being incomprehensible to the developer or user is a challenge (Fig 1).

One usually finds that much of the available data are not suitable for quantitative modeling and there is generally a need to collect new and additional quantitative data for the model. The question then arises what kind of experimental systems should be used. In physiological experiments the principle of reductionism is often applied; using leaf discs for studies of senescence etc. For crop modeling purposes, however, we must integrate processes and environment to obtain realistic estimates of process activities and cumulative quantities of key parameters (e.g. dry matter, leaf area, crop mass) over time. Data obtained with model systems may not be appropriate. Container-grown trees may not be equivalent to trees growing in the field and girdled branches may differ from whole trees. And yet, only container trees can be used in growth cabinets, and data obtained with girdled branches are sometimes in satisfactory agreement with field data. So, the conclusion, perhaps, is that one should be aware of the possible pitfalls and try to get as close as possible to reliable field data. In our experience the most useful data from model systems are those that help describe the general responses of fundamental processes such as light response curves of photosynthesis, temperature responses of respiration or fruit growth, or inherent patterns of fruit development. The variance from field response is primarily in the amplitude or timing of such processes (e.g. photosynthesis rates are different, but the light response curves are the same shape).

THE VALUES OF CROP MODELING

The general values of crop modeling are the same, regardless of the crop of interest. In some cases, however, the value of tree crop models of mature trees is relatively greater due to the lack of detailed growth analysis data so difficult to obtain in large mature trees.

One of the greatest values is simply the requirement for a systematic analysis of the key processes that regulate plant behavior. Key processes cannot be ignored (at least at the conceptual stage) even if they are difficult to experiment with, such as root physiology. The systematic review of the quantitative data and knowledge bases for a crop reveals strengths and weaknesses, and helps to focus experimental research efficiently on key gaps of knowledge.

Another major value of crop modeling is the integration of information over time that is not readily done with instantaneous measurements taken only at intervals. For example, we may have measurements of mid-day leaf photosynthesis under sunny conditions and night respiration of organs at 2-week intervals over a season. Without integration over time and over all leaves by modeling, it is not possible to estimate the total dry matter production, how much fixed carbon is respired versus accumulated, or the relative amounts of respiration amongst organs.

Probably the greatest value for more complex crop models is to examine patterns of plant behavior and responses to environment and/or treatments. Prediction of exact values of crop or fruit size are not the strength of crop models as there are so many factors not included in the models that may affect the amplitude of values. The identification of critical times in the crop development and the generation of quantitative hypotheses is especially important. For example, a simplified apple carbon balance model was able to identify two relatively brief periods of excessive demand in relation to carbon supply, 2-3 weeks after bloom and just before harvest (Lakso et al., 1999b). This information has helped focus research on these critical times.

Last, perhaps, is the more profound, general understanding which emerges from modeling. Whereas the horticulturist is usually concerned with problems of a specific cultivar or species, the modeling effort bring out the more general principles of plant behavior, emphasizing the unifying concepts rather than the numerous variations in manifestation of these principles.

LIMITATIONS

It is critical to understand the limitations of any crop model that is developed and used since they are necessarily gross simplifications of complex systems. As George E.P. Box Systems Science Professor reportedly said “All models are wrong. Some models are useful”. It is important to acknowledge the first statement for complex systems like fruit trees, but to strive for usefulness.

A difficult decision for any modeler is how simple or complex to make the model. There is a balance as models that are too simple are easy to understand, but ignore too many important factors. So their behavior is unrealistic and unreliable. However, models that include all the key processes generally behave realistically in more cases, but they become too difficult to understand and errors become difficult to elucidate. The ideal is to have key processes and principles drive the model, but in as simple a form as possible. As Einstein was reported to say "Make it as simple as possible, but no simpler".

A particular limitation for fruit tree crop models is the limited and incomplete database of good quantitative data for modeling. The best data and knowledge bases generally are for (1) phenology, (2) leaf photosynthesis (light and temperature responses), (3) shoot growth and leaf area development, and (4) fruit growth and respiration. Some of the major gaps are (1) root growth patterns, respiration, root turnover rates and its implications, (2) respiration rates in general – available data is almost all short term measurements; responses to temperature done in short term, not long-term, (3) the seasonal demands for carbon of different organs, and (4) detailed understanding of fruit abscission processes.

A unique aspect of fruit tree orchards that challenge modeling is the high level of management of canopies that may lead to very restricted canopy forms such as thin vertical walls or Y-shaped hedgerows, or mid-summer pruning. As discussed earlier, calculation of the interactions of the radiation and tree geometries is not trivial if there are unnatural canopy forms. One hybrid solution is to use a daily time step, "big leaf" model that estimates canopy photosynthesis by a whole-canopy light response to intercepted radiation (Charles-Edwards, 1982; Lakso and Johnson, 1990). The radiation interception can be modeled or can be an input based on field measurements of radiation interception by the modeled trees. Since there are relatively simple methods to estimate fractional radiation interception in orchards (Wünsche, et al., 1995), this may avoid a complex modeling step and allow concentration on other parameters.

Finally, a major limitation in the entire field of modeling is the difficulty in understanding other researchers' models. The complexity of the models themselves, the myriad of assumptions made, and the computer programming used often discourages even minimal understanding by those who were not involved in the model. Additionally, publication of crop models is difficult as scientific journals usually discourage the extensive length and discussion needed to fully explain the assumptions, characteristics and limitations of crop models. Consequently, there is much less understanding of other's work in this field than in most other fields. The difficulties in accessibility of the crop models to a broader audience have also led to the lack of implementation of models in horticultural management decisions. Hopefully, the worldwide web will allow much easier access to full descriptions of crop models and enhance their use.

This problem is also aggravated in tree fruit research by a lack of researchers with strong mathematical and programming skills. The researchers have inherent interest in modeling in the qualitative sense and have good experience with the fruit tree systems, but are discouraged or uneasy by the perceived requirement of strong math skills and knowledge of computer programming. Fortunately, some easy-to-use simulation software, such as the STELLA® software used in the current apple model can make modeling much more accessible.

We hope that the limitations can be overcome and that crop models of tree fruits will become an important part of the scientific study and the practical application of knowledge to further tree fruit agriculture.

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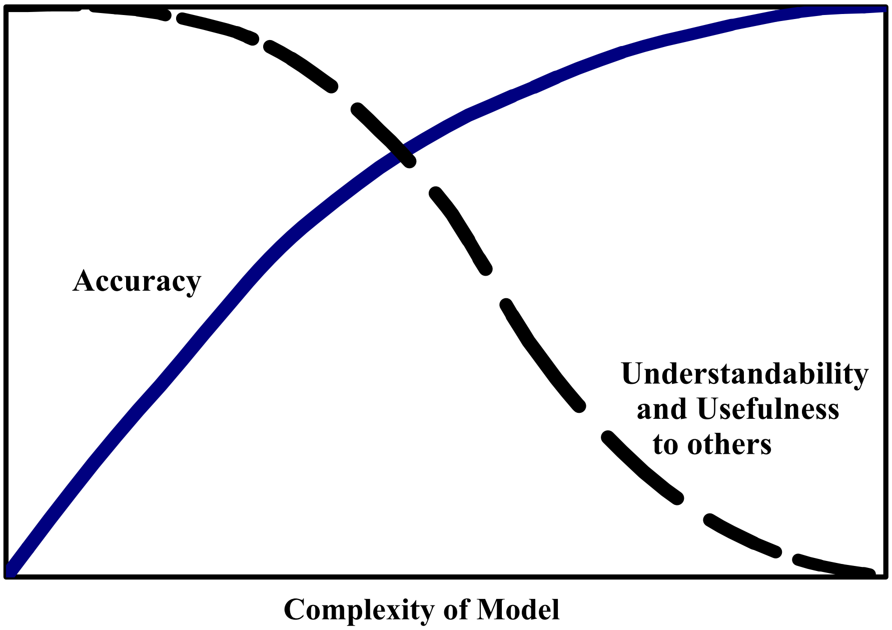

Fig. 1 General diagram indicating that as models increase in complexity from the most simple (e.g. single driving factor), the accuracy of predictions may increase, but the understandability of all the interactions and regulation of the model decreases. Finding an appropriate balance is a challenge with all models, but especially with crop models in natural environments.

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