Ecophysiological Limits to Yield of Peach Production Systems

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Abstract
   Over the past thirty years, along with students and colleagues, I have conducted research on numerous aspects of peach trees and peach orchard systems in order to better understand how trees grow and produce a crop. This understanding has helped identify key ecophysiological limitations to tree growth and crop yield potential in various orchard systems. While it is clear that one of the primary limitations to increasing yield is photosynthetic capacity, no one has ever succeeded in enhancing constitutive leaf photosynthetic capacity in fruit trees and the only thing that can be practically done to maximize photosynthesis at the orchard level is to optimize light capture and provide adequate water and nutrients. Therefore it is important to understand how photosynthates are used and the ecophysiological limitations to their optimal utilization in order to identify key limitations to tree growth and cropping potential that can be affected by crop breeding or orchard management.
   We have approached these problems by developing a functional-structural peach tree model that has served as a guide to focus research on specific details about tree, fruit and root growth and respiration as well as the dynamics of long term carbohydrates (CHO) storage and mobilization. Collectively the crop modeling has identified key "bottlenecks" that limit the cropping potential of peach trees.
   These "bottlenecks" include factors such as: tree anatomical and architectural characteristics, the dynamics of fruit growth, carbohydrate storage and carbohydrate mobilization and transport; to name a few. These factors are discussed in the context of identifying opportunities for future research that can reduce the effect of these "bottlenecks" and improve cropping potential.

INTRODUCTION

   Ultimately crop productivity is dependent on the efficiency of photosynthesis or the accumulation of dry matter and the allocation of photosynthates or dry matter to economic end-products (Cooper, 1976). Using an economic analogy, this can be thought of as a problem of understanding supply and demand. Supply of photosynthates or dry matter on the one hand and their allocation to fulfill demands for photosynthates on the other.
   Early research into fruit tree photosynthesis often focused on the question of whether photosynthesis is primarily driven by the presence of crop or crop load (Avery, 1975; Chalmers et al., 1975; Crews et al., 1975; Hansen, 1970) and there is evidence that crop can have effects on leaf stomatal conductance (DeJong, 1986, 1987). However most of these studies are largely irrelevant to the question of understanding the ecophysiological limits to yield in peach trees because in order to have yield, fruit must be present, and so leaf photosynthetic behavior in the absence of fruit does not matter. There is little debate about the fact that photosynthesis in the presence of fruit is mainly driven by light energy and can be affected by prevailing environmental conditions such as temperature and ambient CO_2 concentrations as well as the water and nutrient status of the tree. Therefore this paper will first focus on environmental and constitutive factors that influence photosynthesis. Then the demand side of the equation will be explored and the factors controlling the allocation of photosynthates or dry matter will be discussed. Both the supply and demand sides of the equation will be discussed in the context of what plant breeders or growers can do to enhance cultivars and management practices to optimize economic yields.
   In the case of peach and most fleshy fruit crops it is important to point out the difference between economic yield and total yield. There is a well-known relationship

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between fruit size (and quality) and crop load. Invariably, fruit size is inversely related to crop load (Cain and Mehlenbacher, 1956) and the economics of peach crop marketing are such that maximizing yield is much less important than optimizing yield of fruit of adequate size and quality to meet the demands of the consumer. So for the purposes of this paper the primary objective is to determine what factors affect the fruit size/crop load relationship with the objective of determining what can be done to change the fundamental relationship toward achieving more yield at a given fruit size or greater fruit size at a given yield. In other words the objective of this paper is to explore what can be done to change the fundamental relationship between the fruit size vs. crop load relationship shown in Figure 1. For the purposes of this discussion we will consider that the trees are not stressed by lack of water, nutrients or pest control measures.

The Supply Side
Like virtually all other temperate deciduous tree fruit species, peach leaves exhibit the classic characteristics of leaves having the C3 biosynthetic pathway of photosynthesis (Brown, 1994). Maximal reported rates of leaf CO_2 assimilation are around 20-22 μmoles m^{-2} s^{-1} (DeJong et al., 1989) while many researchers have reported lower values (Flore and Lakso, 1989). Leaf carboxylation efficiency appears to saturate well beyond intercellular CO_2 concentrations of 300 μL L^{-1} (DeJong, 1983; Rosati et al., 1999) and estimated intercellular CO_2 concentrations under normal conditions have been reported to be between 180 and 250 μL L^{-1} (DeJong, 1983, 1986a). Individual leaf CO_2 assimilation appears to approach light saturation at 700-1,000 μmoles m^{-2} s^{-1} depending on the leaf position in the canopy (DeJong, 1983; Kappel and Flore, 1983; Rosati et al., 1999). Leaf mass per unit area and leaf nitrogen concentration are nonlinearly related to absorbed photosynthetically active radiation (PAR), and there is a weak linear relationship between leaf nitrogen concentration per unit mass and absorbed PAR (Walcroft et al., 2002) but a strong relationship between leaf nitrogen per unit leaf area (DeJong, 1983; DeJong and Doyle, 1985; DeJong et al., 1989). The leaf Ribulose bisphosphate carboxylase content increases with the amount of nitrogen applied to young trees (Nii et al., 1997). In the canopy, spatial variability in photosynthetic capacity results from acclimation to varying absorbed PAR as the crown develops; acclimation being driven principally by changes in leaf mass per unit area rather than the amount or partitioning of leaf nitrogen (Rosati et al., 2000; Walcroft et al., 2002).

The leaf photosynthesis apparatus of peach appears to be fairly insensitive to changes in temperature between 20 and 32°C but can be substantially inhibited by temperatures above and below this range (Crews et al., 1975; Girona et al., 1993).

Although it is widely accepted that leaf age strongly affects the photosynthetic capacity of individual leaves of most species (Flore and Lakso, 1989), there is very little data available specifically for peach. Peach tree canopies grow quite rapidly and peach leaf CO_2 assimilation capacity is strongly influenced by internal canopy shading (DeJong et al., 1989; DeJong and Doyle, 1985; LeRoux et al., 2001; Marini and Marini, 1983; Rosati et al., 1999). Therefore it is difficult to separate leaf age effects from changes in leaf light exposure in natural growing, field canopies. It is apparent that leaves in the most exposed parts of the tree canopies tend to maintain relatively constant photosynthetic capacities in the absence of major stress during the middle part of the growing season from May to September (in the northern hemisphere) (DeJong, 1986).

There have been dramatic changes in peach genetic characteristics through domestication and breeding over the past couple of centuries. However, crop improvement efforts in peach have primarily focused on fruit quality traits and timing of fruit maturity. The resulting changes have apparently had little effect on leaf photosynthetic characteristics of peach (Quilot et al., 2004) although there appears to be substantial variability in the related *Prunus* species that are primarily related to tree canopy density and distribution of leaf nitrogen (DeJong, 1983; Rieger and Duemmel, 1992).

Although individual leaf photosynthesis rates can vary dramatically within a peach tree canopy due to long and short term effects of differences in light exposure, daily photosynthesis of individual leaves in a peach tree canopy at specific temperatures, humidity and

atmospheric CO_2 concentrations is linearly related to daily light interception (Rosati et al., 2002). This means that daily canopy photosynthesis of peach trees is essentially a function of daily canopy light interception when the trees are well managed with adequate nutrients and water. Thus, as has been documented for other tree crops, ultimately maximum potential yield should be a function of canopy light interception (Lampinen et al., 2012).

Thus the primary things that a grower can do to influence the supply side of the equation are to optimize water and nutrient supply as well as canopy light interception. Canopy light interception can be adjusted by tree planting density and pruning. However with peach production, especially production for the fresh market, economic yield is not only a function of crop biomass but fruit quality is vitally important; and tree nutrition, water status, density and within-tree light distribution and crop load can all have strong effects on fruit quality. To more fully understand this requires an understanding of what factors are involved in regulating the demand side of the equation.

The Demand Side

Although there have been many studies about what happens to photosynthates in leaves after they are assimilated as well as their transport out of leaves and their assimilation into fruit or other sinks in peach trees (DeJong and Moing, 2008) for the objective of this paper it is only necessary to focus on photosynthate or dry matter partitioning at the whole plant level. Over the past couple of decades the concept that carbohydrate partitioning at the whole plant level is primarily driven by growth and development of individual organs has become widely accepted (Gifford and Evans, 1981; Ho, 1988; Lacointe, 2000; Marcelis, 1994; Watson and Casper, 1984; Weinstein and Yanai, 1994). Grossman and DeJong (1994b) and Allen et al. (2005) used this concept in the development of the PEACH and L-PEACH models, respectively, and DeJong (1999) outlined four principle steps for applying this concept to logically understand carbon partitioning in peach (and other fruit) trees.

The first principle is that *a tree is a collection of semiautonomous organs and each organ has a genetically determined, organ-specific development pattern and growth potential*. Although much emphasis is often placed on considering plants as highly integrated organisms, the concept of semi-autonomy among organs is widely recognized (Harper, 1980; Sprugel et al., 1991; Watson and Casper, 1984; White, 1979). Indeed, the primary morphological features that distinguish one species or cultivar (in the case of peach) from another are at the organ or sub-organ level (i.e., fruit or leaf shape and size, floral characteristics, etc.), not at the whole plant level. Furthermore, although variation exists, the developmental patterns and growth rates of individual organs under specific environmental conditions are generally predictable and have been modeled. Models have been developed for the growth of peach fruit (DeJong and Goudriaan, 1989; Genard and Huguet, 1996; Genard and Souty, 1996; Grossman and DeJong, 1995b; Pavel and DeJong, 1993), shoots and branches (Costes et al., 1993; Genard et al., 1998; Grossman and DeJong, 1995a; Lescourret et al., 1998) and roots (Bidel et al., 2000). Although tree pruning and training can drastically alter the shape of peach trees, they generally have very little effect on individual organ characteristics other than those explained by changes in the local micro-environment of the organs or changes in the availability of carbohydrates due to the proximity of other sinks.

The fact that there appears to be some level of branch autonomy (Sprugel et al., 1991) in peach trees further reinforces this first principle. Branch autonomy tends to functionally isolate some sinks from sources of carbohydrates. When sinks are manipulated through pruning or fruit thinning to create an apparent abundance of photosynthate in one part of the tree and an under-supply somewhere else, the carbon does not freely move to the location of greatest demand. When one scaffold of Y-shaped peach trees was defruited the remaining fruit on the fruited scaffold benefited very little from the carbon that should have been available for fruit growth from the defruited scaffold (Marsal et al., 2003). Interestingly, scaffold diameter growth appeared to be one of the sinks that benefited most from the removal of fruit while root growth was only marginally affected. There is much to

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be learned about the movement of carbohydrates within the context of the whole tree. The role of branch autonomy in the early spring, when much of the carbon used for growth is mobilized from storage in the root, trunk and major branches and is presumably transported in the xylem, is still poorly understood.

Carbon partitioning at the branch level has been studied in peach explicitly with radioactive tracer studies (Corelli Grappadelli et al., 1996) and by manipulating leaf number and fruit load in isolated branches (Genard et al., 1998). Implicit conclusions about carbon partitioning within shoots have also been drawn from fruit thinning studies to determine optimal fruit positioning for fruit size (Marini and Sowers, 1994; Spencer and Couvillon, 1975). These studies support the idea that fruit are strong sinks for carbon within shoots but their influence on where recently fixed carbon goes varies substantially within the local context of the stem unit.

The second principle is that *the genetic potential of an organ is activated or deactivated by organ-specific, endogenous and/or environmental signals.* The semi-autonomous nature of individual organs can be demonstrated by the fact that individual organs on a tree can be experimentally activated by manipulating factors that stimulate the growth of specific organs independently from processes occurring in organs elsewhere on the tree. For instance, exposing individual buds on a branch to rest-breaking treatments can induce budbreak in those buds while similar buds on other parts of the tree remain inactive (Chandler, 1942). Similarly, grafting multiple cultivars with differing chilling requirements onto one trunk will not influence the inherent chilling exposure required for activation by the branch of each specific cultivar. Also, removing the apical meristem on a shoot will promote the activation of growth of lateral buds on the remaining part of the shoot while buds on other shoots are unaffected (Harris, 1983). Although the exact mechanism of the environment and/or endogenous signals that activate growth are not fully understood, the primary site of activation is clearly at the organ or sub-organ level. This is certainly one area where hormones play key roles in influencing carbon partitioning at the whole tree level, as suggested by data on hormone concentration in xylem sap (Sorce et al., 2002).

The third principle is that *after an organ is activated, current environmental conditions and genetic growth potential interact to determine conditional organ growth capacity.* Although often overlooked, ambient temperature is probably the single most important environmental factor influencing organ growth. The importance of temperature is related to the strong dependence of respiration on temperature. All real plant organ growth is dependent on metabolic activity and enzyme function, and these processes are linked to respiration. Plant respiration generally has a temperature response quotient (Q_{10}) of about 2 (doubles for every 10°C increase in temperature between 5 and 35°C, Amthor, 1989) and peach is no exception (Grossman and DeJong, 1994a; Pavel and DeJong, 1993). Therefore, conditional growth capacity of any organ is highly dependent on ambient temperature. The conditional growth capacity of peach fruits growing under near-optimal field conditions has been modeled for several peach cultivars using relative growth rate functions (Berman et al., 1998; DeJong and Goudriaan, 1989; Grossman and DeJong, 1995a; Pavel and DeJong, 1993). That other environmental factors such as water status can also have a substantial effect on organ growth is well-documented (Bradford and Hsiao, 1982). Extension growth of peach shoots has been successfully modeled by considering temperature and dynamic changes in shoot water status (Basile et al., 2003; Berman and DeJong, 1997a). Although peach fruit growth is quite sensitive to water stress it is important to distinguish between growth in fresh vs. dry matter since the former is much more sensitive than the latter (Berman and DeJong, 1997b; Girona et al., 2004). Nutrient availability also can strongly influence conditional organ growth capacity because certain nutrients are required as constituents for the growing organs. Accordingly, Saenz et al. (1997) have demonstrated that N-availability can influence developmental patterns of peach fruit.

The fourth principle is that *realized organ growth is a consequence of conditional organ growth capacity, resource availability (assimilate and nutrient supply) and inter-organ competition for those resources.* When conditional growth capacity of an organ is set, organ growth should proceed at a rate equal to the conditional growth capacity as long

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as transport is not limited and enough resources (carbohydrates) are available to support that organ's growth and the growth of all other competing organs. However, if the tree does not have enough carbohydrate to support the conditional growth capacity of all organs or carbohydrate transport within the tree is limited, then the growth of an individual organ will be a function of its ability to compete for available carbohydrates with other organs. Since flowering and pollination are not major problems in the more productive peach growing regions, most peach cultivars set very heavy fruit loads. Therefore lack of available assimilates and inter-fruit competition for carbohydrates is generally the primary factor limiting realized fruit growth in mature peach trees and fruit thinning is essential to manage this competition (Cain and Mehlenbacher, 1956; Costa and Vizzoto, 2000; DeJong and Grossman, 1995; Dorsey and McMunn, 1928; Grossman and DeJong, 1995b; Johnson and Handley, 1989; Pavel and DeJong, 1993b). Certainly there are some limitations to carbo-hydrate transport within the tree (DeJong and Grossman, 1995; Marsal et al., 2003) but these are difficult to quantify specifically. There is substantial evidence that peach fruit growth can compete effectively for carbohydrates with shoot, trunk and root growth when the crop loads are high and all fruit are considered as a collective sink (Grossman and DeJong, 1995a; Marsal et al., 2003; Proebsting, 1958). But there is some evidence to the contrary when pruning systems stimulate excess vegetative shoot growth (Grossman and DeJong, 1998). There is also clear documentation of the capacity of individual fruit organs to compete with each other and/or vegetative sinks at the local branch level (Genard et al., 1998). To complicate things further the competitive ability of fruit for carbohydrates appears to vary with the stage of fruit development (DeJong and Grossman, 1995).

A final principle is that *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.* Practical experience indicates that the distribution of sinks and sources for carbohydrates is important in peach trees since fruit found in clusters rarely attain similar sizes as fruits that are well distributed within a tree canopy. Indeed, the importance of fruit distribution has been documented by Marsal et al. (2003) and transport resistances between carbohydrate sources and sinks are affected by both fruit distribution and period during the growing season (DeJong and Grossman, 1995). Organ sink efficiency is likely governed by an organ's ability to unload carbohydrates from the phloem stream but this is quite difficult to quantify. Considering the fruit sink, phloem unloading is clearly a function of movement and complex conversions of specific sugars within the fruit (Genard and Souty, 1996; Genard et al., 2003). At the whole fruit level, organ sink efficiency is related to the intrinsic potential relative growth rate of the fruit of a specific genotype (Grossman and DeJong, 1995a; Berman et al., 1998). Differences in microenvironment within plant canopies, except for light, are often neglected in annual crops but since peach trees are quite large, organ microenvironment can have significant effects on organ development and growth. It is generally known that fruit in the lower parts of peach tree canopies mature later than in the top of the tree and Basile et al. (2007) documented significant differences in both fruit development and growth rates in different levels of peach tree canopies.

Upon examining these principles for understanding carbon partitioning it becomes apparent that phenological patterns of organ growth are the principle determinants of carbon partitioning in peach trees. When experiments are conducted involving different crop load treatments or some other treatment that dramatically favors the growth of one type of organ over others, biomass data collected at the end of the season appears to indicate that some organs are in direct competition with others (Chalmers and Van den Ende, 1975; Proebsting, 1958). However when seasonal patterns of growth are analyzed, it is apparent that direct competition between different organ types is often limited by temporal separation of growth activities (Berman and DeJong, 2003; DeJong et al., 1987; Miller and Walsh, 1988; Rufat and DeJong, 2001; Basile et al., 2007). Generally, in late maturing peach cultivars, shoot and root growth is the dominant sink shortly after bud break in the spring. This period is followed by a peak of fruit growth and then there is a resurgence of root growth (Ben Mimoun and DeJong, 2006) and shoot diameter growth after harvest

(Berman and DeJong, 2003; Grossman and DeJong, 1995a). It is interesting that breeding efforts to create cultivars with early fruit ripening times has apparently interfered with the natural temporal separation of dominant sink activities in peach trees. The dominant period of fruit growth of early maturing peach cultivars often coincides directly with the early peak of shoot growth. This has increased the competition between fruit and shoot growth, resulting in decreased yield potential (DeJong et al., 1987; Grossman and DeJong, 1995a). There is also some evidence that selection for early maturing cultivars has involved selection for decreases in the total fruit growth potential and dry matter content and these factors also account for differences in economic yield potential between early and late maturing cultivars (Berman et al., 1998).

The selection for early maturing fruit has also increased the competition for carbohydrates between organs within the fruit such that seed development corresponds with the period of flesh enlargement (Pavel and DeJong, 1993a) as well as increasing the individual fruit relative growth rates so that the tree cannot support as many fruits at one time (Grossman and DeJong, 1995a, 1995b).

Since economic peach yields are ultimately dependent on fruit development and growth (or fruit sink behavior) it is essential that we understand the factors involved in controlling these processes. DeJong and Goudriaan (1989) modeled peach fruit growth as a relative growth rate (RGR) function and demonstrated that using this type of analysis resulted in similar shapes of curves for both early and late maturing cultivars. They also demonstrated how two characteristics of the RGR curves (the initial slope and the asymptote) determine if the curve of fresh or dry mass accumulation exhibits a single or double sigmoid pattern. However the utility of fruit RGR analysis became more apparent when using it to understand limitations to peach fruit growth and develop models of peach crop production.

Since fruit RGR's are linearly related to fruit growth respiration rates they can be used to estimate the total carbohydrate cost of a growing fruit over specific intervals of time during development (DeJong and Goudriaan, 1989). This was very useful for development of a crop production model for peach trees (DeJong et al., 1990; Grossman and DeJong 1994; Allen et al., 2005; Lopez et al., 2008; DaSilva et al., 2011).

Logically peach fruit growth is limited both by the potential of the fruit to grow (sink) or the availability of resources (source) during specific intervals. However it is not possible to ascertain which is most limiting by comparing mass accumulation curves or fruit absolute growth rates. Comparison of fruit relative growth rate data from trees with little crop and with large crops has been used to indicate that primary periods of fruit growth limitation due to source limitation occur in the early and late stages of growth and growth during the middle period is largely sink limited (Pavel and DeJong, 1993a; Grossman and DeJong, 1995a). The primary effect of crop load on individual fruit size is a function of the amount of time fruit growth is source-limited compared to sink-limited. Furthermore, source-limitations to individual fruit growth can be a function of either lack total resources available in the tree to support fruit growth or transport/competition limitations imposed by transport resistances or competition from other sinks. DeJong and Grossman (1995) used RGR analysis to show that transport/competition limitations are prominent during early phases of fruit growth but overall resource supply is more important later. Subsequently, using similar techniques, Marsal et al. (2003) documented that patterns of fruit thinning within a tree had substantial influence on transport/competition limitations to fruit growth. Fruit RGR analysis to determine if peach fruit size reductions associated with nitrogen deficiency were caused by increased source or sink limitations yielded the rather surprising result that fruit RGR's of N deficient trees were similar to N sufficient trees during the course of the fruit growth and the most important factor causing decreased fruit size in N deficient trees appeared to be a shortening of the fruit development period (Saenz et al., 1997).

Probably the most practical application of fruit relative growth rate analysis is in using it to understand fruit growth and crop yield responses to fruit thinning. Fruit RGR's can be used to quantify the growth potential of fruit of a given cultivar for any interval throughout the fruit development period because mass accumulation is expressed per

existing mass at the beginning of the interval and the elapsed time during the interval. Thus the potential RGR for an interval is equivalent to the potential "interest rate" compounded on the mass at the beginning of an interval. Growth is compounded based on the potential RGR, the mass at the beginning of the interval and the ability of the tree to supply the resources to achieve the potential RGR. If the potential RGR is not achieved, the actual growth is less than the potential and both the potential and actual growth for every subsequent interval is less than it would have been because the growth for each subsequent interval is based on the mass at the beginning of that interval (Grossman and DeJong, 1995b). This means that any potential fruit growth that is not achieved early in the season cannot be made up later. Thus final fruit size is not only a function of crop load near harvest but also on crop load throughout the season.

This behavior of fruit growth has been verified with whole-tree, fruit thinning experiments of early and late maturing peaches in California (Grossman and DeJong, 1995b), crop modeling studies (DeJong et al., 2000; Grossman and DeJong, 2005; Lopez et al., 2008) and commercial orchard thinning trials. Commercial fruit thinning trials showed that thinning earlier than was previously recommended for commercial clingstone peach orchards in California resulted in either larger fruit sizes at similar crop loads or similar fruit sizes at higher crop loads, or both larger fruit sizes at higher crop loads without any significant increases in fruit defects such as split-pits (DeJong et al., 1992).

If global climate change brings an increase in temperatures one of the most pronounced effects of these increased temperatures will likely to be on shortening the fruit development period and a tendency for reduced fruit size of individual peach cultivars.

Reductions in fruit size resulting from warm springs can also be explained by relative growth rate analyses (Lopez et al., 2009). The length of the fruit development period for a given cultivar in a specific year is a function of the general genetically determined pattern of growth for the cultivar and the temperatures experienced in the field during the first 30 days after bloom (Ben Mimoun and DeJong, 1999; Marra et al., 2002). Temperature dependence of the length of the fruit development period has been successfully quantified by calculating the cumulative Growing Degree Hours during the first 30 days after full bloom (GDH30) for several Californian peach cultivars over numerous growing seasons (Ben Mimoun and DeJong, 1999; Day et al., 2008). Additional research has shown that most of the temperature dependent differences in the time between full bloom and the date of fruit maturity among years for a specific cultivar can be accounted for by differences in the time between full bloom and reference date (pit hardening + 10 days) (Lopez and DeJong, 2007). The same and subsequent research (Lopez et al., 2007; Lopez and DeJong, 2009) documented that in years when early spring temperatures were high (GDH30 >7000) there was a strong tendency for fruit sizes to be small while fruit sizes tended to be large in years when GDH30 <6000. The explanation for these trends in fruit size responses among years have been explained by running fruit RGR models for springs with high and low spring temperatures (Lopez et al., 2011). These analyses indicate that, in springs with high early temperatures, not only is the total fruit development period of a given cultivar shortened, but the daily carbohydrate requirements for fruit growth are much higher, earlier in the season. As previous fruit RGR analysis has shown, carbon deficits early in the season that result in reductions in fruit size relative to the potential, cannot be made up later in the season and final fruit sizes tend to be small. Furthermore it is likely that the some of the carbon deficits that limit fruit growth early in the season may be due to transport limitations rather than general supply limitations (DeJong and Grossman, 1995) since much of the carbon supplying fruit growth early in the season is from storage rather than current photosynthesis. If this is the case a grower is limited in what can be done to mitigate against smaller fruit sizes linked to high early spring temperatures. Appreciation of the relationship between spring temperatures 30 days after bloom is particularly important for growers of peaches in warm subtropical regions that often experience small fruit sizes since, in situations with high spring temperatures, early fruit thinning would be essential and if early fruit growth is limited by transport resistances it may not be possible to entirely compensate for small fruit sizes by early thinning.

The relationship between high temperatures 30 days after bloom and the total length of the fruit development period and fruit size is also important for peach tree breeders to recognize since it can explain year to year variations in the harvest dates and fruit size of new selections being evaluated. Furthermore it could be used to normalize date of fruit maturity data among years. It could also provide information that may make it possible to explain differences in cultivar performance in different climates.

What Can Be Done to Improve the Physiological Efficiency of Peach Production Systems?

Since, for the purpose of this discussion, it was assumed that water, nutrients and pests are not limiting factors, those factors will not be considered in this discussion of improving the physiological efficiency of peach orchards. Also since there has been virtually no success in trying to manipulate basic biochemical and physiological processes in fruit trees to increase photosynthetic efficiencies after more than fifty years of research this approach will also not be discussed. The primary means of improving the light harvesting efficiency of peach orchards is to select pruning systems and planting densities that harvest approximately 80% of the light incident to an orchard and distribute that light as evenly as possible within the tree canopies. This has been the subject of much research over the past several decades and unfortunately the V-shaped trellis systems that tend to be the most efficient in terms of light capture are also among the most expensive systems to install and maintain. Thus, systems that are the most physiologically efficient may not be the most economically efficient.

So what can be done regarding improving the physiological efficiency of peach orchards relative to distribution and use of photosynthates toward improving the fruit size vs. crop load relationship in Figure 1? Given that fruit growth rates are governed by a relative growth rate function the most obvious and critical thing for existing orchards is to reduce excessive crop loads as early as possible. Any incremental loss in fruit growth potential cannot be made up for later in the growing season. Recent advances in mechanical flower thinning have proven to be helpful in this regard (Miller et al., 2011) and the results of that research can be explained by the concept of fruit relative growth rates. In the absence of mechanical thinning options it is advisable to thin the fruit down to desired crop loads as soon as is economically feasible (DeJong et al., 1992).

In the longer term, one thing that should be tried is to select for genotypes that have intrinsically large fruit size potentials. Fruit tree breeders are often not concerned about fruit size potentials above a certain modest potential size because the market only requires modest sized fruit and it is assumed that crop yield goals can be achieved by leaving more fruit on the tree. However, our modeling research with fruit relative growth rates indicate that fruit of genotypes with intrinsically larger fruit sizes may actually be capable of higher crops of modest sized fruit because the sink efficiency of individual fruit with large fruit size potential should be higher than the sink efficiency of individual fruit with modest fruit size potential.

This concept needs to be tested by doing crop load vs fruit size studies with cultivars of contrasting intrinsic fruit size potentials.

A second potential avenue of research to pursue would be to breed for early maturing cultivars that have a greater potential to store more carbohydrates in their woody tissues over the winter period. Grossman and DeJong (1995b) showed that both early and late maturing peach cultivars were capable of committing the same amount of carbohydrates to fruit growth during the first couple of months of fruit growth even though the early maturing cultivar did not put any carbohydrates into fruit growth for two fewer months in the previous season.

If early maturing cultivars could be bred to store an amount of carbohydrate equivalent to the additional amount that the later maturing fruit put into fruit growth by maturing fruit later in the season, then the yields of early maturing cultivars could be substantially increased. More research needs to be conducted concerning factors controlling annual carbohydrate storage and mobilization in peach trees.

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Another factor that limits the efficiency of distribution and use of photosynthesis within a tree is that all the fruit on a tree consisting of one scion genotype develop and mature their fruit synchronously.

This means that the tree must meet the carbohydrate demands of all the fruit at the same time and the carbohydrate supply to all other components of the tree may suffer during the final stages of fruit growth. Correspondingly, early maturing cultivars spend much of the growing season producing excessive vegetative growth that must be later removed through pruning. A third potential means of enhancing the efficiency of the distribution and use of photosynthates in peach orchards could be to develop bi-cultivar trees and distribute them in alternating patterns in an orchard. If bi-cultivar, V-shaped trees were developed such that one scaffold of the tree was an early maturing cultivar and the other scaffold was a late maturing cultivar then the trees could be oriented in the orchard such that all scaffolds of one cultivar are oriented toward one row middle and all the scaffolds of the other cultivar are oriented toward the other row middle. Theoretically such bi-cultivar trees may be capable of greater combined yields of comparable sized fruit than a combination of individual trees of the same cultivars grown in an equivalent orchard space because the carbohydrate demands of the fruit with different development and growth patterns would be more evenly distributed throughout the growing season. Although there would likely be limited movement of carbohydrates from one side of the tree to the other in support of fruit growth (Marsal et al., 2003) carbohydrate supply to other parts of the tree should be more uniform and this may ultimately favor less vegetative growth and more collective fruit growth. Although such orchards may not be practically feasible on a large scale, never-theless such experiments would be instructive for developing further understanding about peach tree functioning at an orchard level.

A final and more practical means of increasing the efficiency of distribution and use of photosynthates is the use of vigor-controlling rootstocks. In many areas of the world, especially in California, growing conditions are such that peach trees produce excessive vegetative growth and regularly require extensive pruning. With the development of several size-controlling peach rootstocks that are now available (Tombesi et al., 2012; Rieghard et al., 2008) it is now possible to select peach rootstocks that provide a range of vigor control.

One of the primary growth responses to these rootstocks is the production of many fewer epicormic shoots (water sprouts) (Weibel et al., 2003; Basile et al., 2003; Pernice et al., 2006) that generally represent wasted energy. Trees grown on these rootstocks generally require less summer and dormant season pruning while maintaining similar yields to trees on vigorous rootstocks (DeJong et al., 2013). Thus, they have higher harvest to dry matter growth increments. Ultimately, planting trees on these rootstocks with appropriate training systems and tree densities, so that total orchard light interception is the same or greater than orchards planted with vigorous rootstocks, should be more physiologically efficient and provide opportunities for growers to reduce management costs associated with reduced tree heights.

Literature Cited

Allen, M.T., DeJong, T.M. and Prusinkiewicz, P. 2002. Using L-systems to model carbon transport and partitioning in developing peach trees. Acta Hort. 584:29-35.

Amthor, J.S. 1989. Respiration and Crop Productivity. Springer-Verlag. New York.

Avery, D.J. 1975. Effects of fruits on photosynthetic efficiency. p. 110-112. In: H.C. Pereira (ed.), Climate and the Orchard. Res. Rev. Common W. Bur. Hort. Planta. Crops. No. 5.

Basile, B., Marsal, J. and DeJong, T.M. 2003. Daily shoot extension growth of peach trees growing on rootstocks that reduce scion growth is related to daily dynamics of stem water potential. Tree Physiology 23:695-704.

Basile, B., Bryla, D.R., Salsman, M.L., Marsal, J., Cirillo, C., Johnson, R.S. and DeJong, T.M. 2007. Growth patterns and morphology of fine roots of size-controlling and invigorating peach rootstocks. Tree Physiology 27:231-241.

Ben Mimoun, M. and DeJong, T.M. 2006. Effect of fruit crop load on peach root growth. Acta Hort. 713:169-175.

Ben Mimoun, M. and DeJong, T.M. 1999. Using the relation between growing degree hours and harvest date to estimate run-times for PEACH: a tree growth and yield simulation model. Acta Hort. 499:107-114.

Berman, M.E. and DeJong, T.M. 1997a. Crop load and water stress effects on daily stem growth in peach (*Prunus persica*). Tree Physiology 17:467-472.

Berman, M.E. and DeJong, T.M. 1997b. Diurnal patterns of stem extension growth in peach (*Prunus persica*): Temperature and fluctuations in water status determine growth rate. Physiologia Plantarum 100:361-370.

Berman, M.E. and DeJong, T.M. 2003. Seasonal patterns of vegetative growth and competition with reproductive sinks in peach (*Prunus persica*). Journal of Horticultural Science & Biotechnology 78:303-309.

Berman, M.E., Rosati, A., Pace, L., Grossman, Y. and DeJong, T.M. 1998. Using simulation modeling to estimate the relationship between data of fruit maturity and yield potential in peach. Fruit Varieties Journal 52:229-235.

Bidel, L.P.R., Pages, L., Rivère, L.M., Pelloux, G. and Lorendeau, J.Y. 2000. Mass Flow Dyn I: A carbon transport and partitioning model for root system architecture. Annals of Botany 85:869-886.

Bradford, K.J. and Hsiao, T.C. 1982. Physiological responses to moderate water stress. p. 263-324. In: O.L. Lange, P.S. Nobel, C.B. Osmond and H. Ziegler (eds.), Physiological Plant Ecology II. Water Relations and Carbon Assimilation. Springer Verlag, Berlin.

Brown, R.H. 1994. The conservative nature of crop photosynthesis and the implications of carbon fixation pathways. p. 211-219. In: K.J. Boote, J.M. Bennett, T.R. Sinclair and G.M. Paulsen (eds.), Physiology and Determination of Crop Yield. American Society of Agronomy, Inc., Madison, W.I.

Cain, J.C. and Mehlenbacher, R.J. 1956. Effects of nitrogen and pruning on trunk growth in peaches. Proceedings of American Society for Horticultural Science 67:139-143.

Chalmers, D.J. and Van den Ende, B. 1975. Productivity of peach trees: Factors affecting dry-weight distribution during tree growth. Annals of Botany 39:423-432.

Chalmers, D.J., Canterford, R.L., Jerie, P.H., Jones, T.R. and Ugalde, T.D. 1975. Photosynthesis in relation to growth and distribution of fruit in peach trees. Australian Journal of Plant Physiology 2:635-645.

Chandler, W.H. 1942. Deciduous Orchards. Lea and Febiger, Philadelphia.

Cooper, J.P. 1981. Physiological constraints to varietal improvement. Phil. Trans. R. Soc. Lond. 292:431-440.

Corelli-Grappadelli, L., Ravaglia, G. and Assirelli, A. 1996. Shoot type and light exposure influence carbon partitioning in peach cv. Elegant Lady. Journal of Horticultural Science 71:533-543.

Costa, G. and Vizzotto, G. 2000. Fruit thinning of peach trees. Plant Growth Regulation 31:113-119.

Costes, E., Lanri, P.E., Guédon, Y. and De Reffye, P. 1993. Modelling growth of peach trees using the renewal theory. Acta Hort. 349:253-258.

Crews, C.E., Williams, S.L. and Vines, H.M. 1975. Characteristics of photosynthesis in peach leaves. Planta 126:97-104.

Da Silva, D., Favreau, R., Auzmendi, I. and DeJong, T. 2011. Linking water stress effects on carbon partitioning by introducing a xylem circuit into L-PEACH. Annals of Botany 108:1135-1145.

Day K., Lopez, G. and DeJong, T. 2008. Using growing degree hours accumulated thirty days after bloom to predict peach and nectarine harvest date. Acta Hort. 803:163-166.

DeJong, T.M. 1983. CO_2 assimilation characteristics of five *Prunus* tree fruit species. Journal of the American Society for Horticultural Science 108:303-307.

DeJong, T.M. 1986. Effects of reproductive and vegetative sink activity on leaf conductance and water potential in *Prunus persica* (L.) Batsch. Scientia Hort. 29:131-137.

DeJong, T.M. 1987. Fruit effects on photosynthesis in *Prunus persica*. Physiologia Plantarum 66:149-153.

DeJong, T.M. 1999. Developmental and environmental control of dry-matter partitioning in peach. HortScience 34:1037-1040.

DeJong, T.M. 2012. Fruit Growth and development as it relates to crop load, thinning and climate change. Acta Hort. 962:233-238.

DeJong, T.M., Grace, L., Almehdi, A., Johnson, R.S. and Day, K.R. 2013. Performance and Physiology of the Controller™ Series of Peach Rootstocks. Acta Hort. 1058:523-529.

DeJong, T.M., Andris, H., Beede, R., Day, K., Johnson, R.S., Olson, W., Ramos, D., Yeager, J. and Yoshikawa, F. 1992. Feasibility of increasing cling peach yields by early thinning. Annual Research Reports of the California Cling Peach Advisory Board, 9 p.

DeJong, T.M. and Goudriaan, J. 1989. Modeling peach fruit growth and carbohydrate requirements: reevaluation of the double sigmoid growth pattern. Journal of the American Society for Horticultural Science 114:800-804.

DeJong, T.M. and Doyle, J.F. 1985. Seasonal relationships between leaf nitrogen content (photosynthetic capacity) and leaf canopy light exposure in peach (*Prunus persica*). Plant, Cell and Environment 8:701-706.

DeJong, T.M., Doyle, J.F. and Day, K.R. 1987. Seasonal patterns of reproductive and vegetative sink activity in early and late maturing peach (*Prunus persica*) cultivars. Physiologa Plantarum 71:83-88.

DeJong, T.M., Day, K.R. and Johnson, R.S. 1989. Partitioning of leaf nitrogen with respect to within canopy light exposure and nitrogen availability in peach (*Prunus persica*). Trees: Structure and Function 3:89-95.

DeJong, T.M. and Grossman, Y.L. 1995. Quantifying sink and source limitations on dry matter partitioning to fruit growth in peach trees. Physiologia Plantarum 95:437-443.

DeJong, T.M. and Moing, A. 2008. Carbon assimilation, partitioning and budget modelling. p. 224-263. In: D.R. Layne and D. Bassi (eds.), The Peach: Botany, Production and Uses. CAB International, Oxfordshire, UK.

Dorsey, M.J. and McMunn, R.L. 1928. The third report on the Illinois thinning investigations. Proceedings of American Society for Horticultural Science 25:269-276.

Flore, J.A. and Lakso, A.N. 1989. Environmental and physiological regulation of photosynthesis in fruit crops. Horticultural Reviews 11:111-157.

Genard, M. and Souty, M. 1996. Modeling the peach sugar contents in relation to fruit growth. Journal of American Society for Horticultural Science 121:1122-1131.

Genard, M. and Huguet, J.G. 1996. Modeling the response of peach fruit growth to water stress. Tree Physiology 16:407-415.

Genard, M., Lescourret, F., Ben Mimoun, M., Besset, M.J. and Bussi, C. 1998. A simulation model of growth at the shoot-bearing fruit level. II. Test and effect of source and sink factors in the case of peach. European Journal of Agronomy 9:189-202.

Genard, M., Lescourret, F., Gomez, L. and Habib, R. 2003. Changes in fruit sugar concentrations in response to assimilate supply, metabolism and dilution: a modeling approach applied to peach fruit. Tree Physiology 23:373-385.

Gifford, R.M. and Evans, L.T. 1981. Photosynthesis, carbon partitioning and yield. Annual Review of Plant Physiology 32:485-509.

Girona, J., Mata, M., Goldhamer, D.A., Johnson, R.S. and DeJong, T.M. 1993. Patterns of soil and tree water status and leaf functioning during regulated deficit irrigation scheduling in peach. Journal of the American Society for Horticultural Science 118:580-586.

Girona, J., Marsal, J., Mata, M., Arbones, A. and DeJong, T.M. 2004. A comparison of the combined effect of water stress and crop load on fruit growth during different phenological stages in young peach trees. J. Hort. Sci. & Biotech. 79:308-315.

Grossman, Y.L. and DeJong, T.M. 1994a. Carbohydrate requirements for dark respiration by peach vegetative organs. Tree Physiology 14:37-48.

Grossman, Y.L. and DeJong, T.M. 1994b. PEACH: A simulation model of reproductive and vegetative growth in peach trees. Tree Physiology 14:329-345.

Grossman, Y.L. and DeJong, T.M. 1995a. Maximum fruit growth potential and seasonal patterns of resource dynamics during peach growth. Annals of Botany 75:553-560.

Grossman, Y.L. and DeJong, T.M. 1995b. Maximum fruit growth potential following resource limitation during peach growth. Annals of Botany 75:561-567.

Grossman, Y.L. and DeJong, T.M. 1995c. Maximum vegetative growth potential and seasonal patterns of resource dynamics during peach growth. Annals of Botany 76:473-482.

Grossman, Y.L. and DeJong, T.M. 1998. Training and pruning system effects on vegetative growth potential, light interception, and cropping efficiency in peach trees. Journal of American Society for Horticultural Science 123:1058-1064.

Hansen, P. 1970. 14C studies on apple trees. VI. Influence of the fruit on the photosynthesis of the leaves, and the relative photosynthetic yields of fruits and leaves. Physiologia Plantarum 23:805-810.

Harper, J.L. 1980. Plant demography and ecological theory. Oikos 35:244-253.

Ho, L.C. 1988. Metabolism and compartmentation of imported sugars in sink organs in relation to sink strength. Annual Review of Plant Physiology 39:355-378.

Johnson, R.S. and Handley, D.F. 1989. Thinning response of early, mid-, and late-season peaches. Journal of American Society of Horticultural Science 11:852-855.

Jordan, M.O. and Habib, R. 1996. Mobilizable carbon reserves in young peach trees as evidenced by trunk girdling experiments. Journal of Experimental Botany 47:79-87.

Lacointe, A. 2000. Carbon allocation among tree organs: a review of basic processes and representation in functional-structural models. Annual Forestry of Science 57:521-534.

Lampinen, B.D., Udompetaikul, V., Browne, G.T., Metcalf, S.G., Stewart, W.L., Contador, L., Negron, C. and Upadhyaya, S.K. 2012. A mobile platform for measuring canopy photosynthetically active radiation interception in orchard systems. Hortechnology 22:237-244.

LeRoux, X., Walcroft, A.S., Daudet, F.A., Sinoquet, H., Chaves, M.M., Rodrigues, A. and Osorio, L. 2001. Photosynthetic light acclimation in peach leaves: importance of changes in mass: area ratio, nitrogen concentration, and leaf nitrogen partitioning. Tree Physiology 21:377-386.

Lescourret, F., Ben Mimoun, M. and Genard, M. 1998. A simulation model of growth at the shoot-bearing fruit level I. Description and parameterization for peach. European Journal of Agronomy 9:173-188.

Lopez, G., Favreau, R.R., Smith, C., Costes, E., Prusinkiewicz, P. and DeJong, T.M. 2008. Integrating simulation of architectural development and source-sink behaviour of peach trees by incorporating Markov chains and physiological organ function sub-models into L-PEACH. Func. Plant Biol. 35:761-771.

Lopez, G. and DeJong, T.M. 2007. Spring temperatures have a major effect on early stages of peach fruit growth. J. Hort. Sci. and Biotech. 82:507-512.

Lopez, G., Day, K.R. and DeJong, T.M. 2011. Why do early high spring temperatures reduce peach fruit size and yield at harvest? Acta Hort. 903:1055-1062.

Marra, F.P., Inglese, P., DeJong, T.M. and Johnson, R.S. 2002. Thermal time requirement and harvest time forecast for peach cultivars with different fruit development periods. Acta Hort. 592:523-529.

Marcelis, L.F.M. 1994. A simulation model for dry matter partitioning in cucumber. Annals of Botany 74:43-52.

Marini, R.P. and Marini, M.C. 1983. Seasonal changes in specific leaf weight, net photo-synthesis, and chlorophyll content of peach leaves as affected by light penetration and canopy position. Journal of American Society of Horticultural Science 108:600-605.

Marini, R.P. and Sowers, D. 1994. Peach fruit weight is influenced by crop density and fruiting shoot length but not position on the shoot. Journal of American Society of Horticultural Science 119:180-184.

Marsal, J., Basile, B., Solari, L. and DeJong, T.M. 2003. Influence of branch autonomy on fruit, scaffold, trunk and root growth during Stage III of peach fruit development. Tree Physiology 23:313-323.

Miller, A.N. and Walsh, C.S. 1988. Growth and seasonal partitioning of dry matter in eight-year-old 'Loring peach trees'. Journal of American Society for Horticultural Science 113:309-314.

Miller, S.S., Schupp, J.R., Baugher, T.A. and Wolford, S.D. 2011. Performance of mechanical thinners for bloom or green fruit thinning of peaches. HortScience 46:43-51.

Nii, N., Yamaguchi, K. and Nishimura, M. 1997. Changes in carbohydrate and ribulose bisphosphate carboxylase-oxygenase contents in peach leaves after applications of different amounts of nitrogen fertilizer. Journal of the Japanese Society for Horticultural Science 66:505-511.

Pavel, E.W. and DeJong, T.M. 1993a. Relative growth rate and its relationship to compositional changes of non-structural carbohydrates in the mesocarp of developing peach fruits. Journal of American Society for Horticultural Science 118:503-508.

Pavel, E.W. and DeJong, T.M. 1993b. Seasonal CO_2 exchange patterns of developing peach (*Prunus persica*) fruits in response to temperature, light and CO_2 concentration. Physiologia Plantarum 88:322-330.

Pavel, E.W. and DeJong, T.M. 1993c. Estimating the photosynthetic contribution of developing peach (*Prunus persica*) fruits to their growth and maintenance carbohydrate requirements. Physiologia Plantarum 88:331-338.

Pernice, F., Solari, L. and DeJong, T.M. 2006. Comparison of growth potentials of epicormic shoots of nectarine trees grown on size-controlling and vigorous rootstocks. J. Hort. Sci. and Biotechnology 81:211-218.

Proebsting, E.L. 1958. A quantitative evaluation of the effect of fruiting on growth of 'Elberta' peach trees. Proceedings of the American Society of Horticultural Science 71: 103-109.

Quilot, B., Génard, M. and Kervella, J. 2004. Leaf light saturated photosynthesis for wild and cultivated peach genotypes and their hybrids: a simple mathematical modeling analysis. Journal of Horticultural Science and Biotechnology 79:546-553.

Reighard, G.L. and Loreti, F. 2008. Rootstock development. p. 193-220. In: D.R. Layne and D. Bassi (eds.), The Peach: Botany, Production and Uses. CAB International, Oxfordshire, UK.

Rieger, M. and Duemmel, M.J. 1992. Comparison of drought resistance among *Prunus* species from divergent habitats. Tree Physiology 11:369-380.

Rosati, A., Esparza, G., DeJong, T.M. and Pearcy, R.W. 1999. Influence of canopy light environment and nitrogen availability on leaf photosynthetic characteristics and photosynthetic nitrogen-use efficiency of field-grown nectarine trees. Tree Physiology 19: 173-180.

Rosati, A., DeJong, T.M. and Esparza, G. 2002. Physiological basis for light use efficiency models. Acta Hort. 584:89-94.

Rosati, A., Day, K.R. and DeJong, T.M. 2000. Distribution of leaf mass per unit area and leaf nitrogen concentration determine partitioning of leaf nitrogen within tree canopies. Tree Physiology 20:271-276.

Rufat, J. and DeJong, T.M. 2001. Estimating seasonal nitrogen dynamics in peach trees in response to nitrogen availability. Tree Physiology 21:1133-1140.

Saenz, J.L., DeJong, T.M. and Weinbaum, S.A. 1997. Nitrogen stimulated increases in peach yields are associated with extended fruit development period and increased fruit sink capacity. Journal of the American Society for Horticultural Science 122:772-777.

Sorce, C., Massai, R., Picciarelli, P. and Lorenzi, R. 2002. Hormonal relationships in xylem sap of grafted and ungrafted *Prunus* rootstocks. Scientia Hort. 93:333-342.

Spencer, S. and Couvillon, G.A. 1975. The relationship of node position to bloom date, fruit size and endosperm development of the peach, *Prunus persica* (L.) Batsch cv. 'Sullivan's Elberta'. Journal of American Society of Horticultural Science 100:242-244.

Sprugel, D.G., Hinkley, T.M. and Schaap, W. 1991. The theory and practice of branch autonomy. Annual Review of the Ecology System 22:309-334.

Tombesi, S., Marsal, J., Basile, B., Weibel, A., Solari, L., Johnson, S., Day, K. and DeJong, T.M. 2012. Peach Tree Vigor is a Function of Rootstock Xylem Anatomy and Hydraulic Conductance. Acta Hort. 932:483-489.

Walcroft, A., Le Roux, X., Diaz-Espejo, A., Dones, N. and Sinoquet, H. 2002. Effects of crown development on leaf irradiance, leaf morphology and photosynthetic capacity in a peach tree. Tree Physiology 13:929-938.

Watson, M.A. and Casper, B.B. 1984. Morphogenetic constraints on patterns of carbon distribution in plants. Annual Review of the Ecology System 15:233-250.

Weibel, A., Johnson, R.S. and DeJong, T.M. 2003. Comparative vegetative growth responses of two peach cultivars grown on size-controlling versus standard rootstocks. J. Amer. Soc. Hort. Sci. 128:463-471.

Weinstein, D.A. and Yanai, R.D. 1994. Integrating the effects of simultaneous multiple stresses on plants using the simulation model TREGRO. Journal of Environmental Quality 23:418-428.

White, J. 1979. The plant as a metapopulation. Annual Review of Ecology and Systematics 10:109-145.
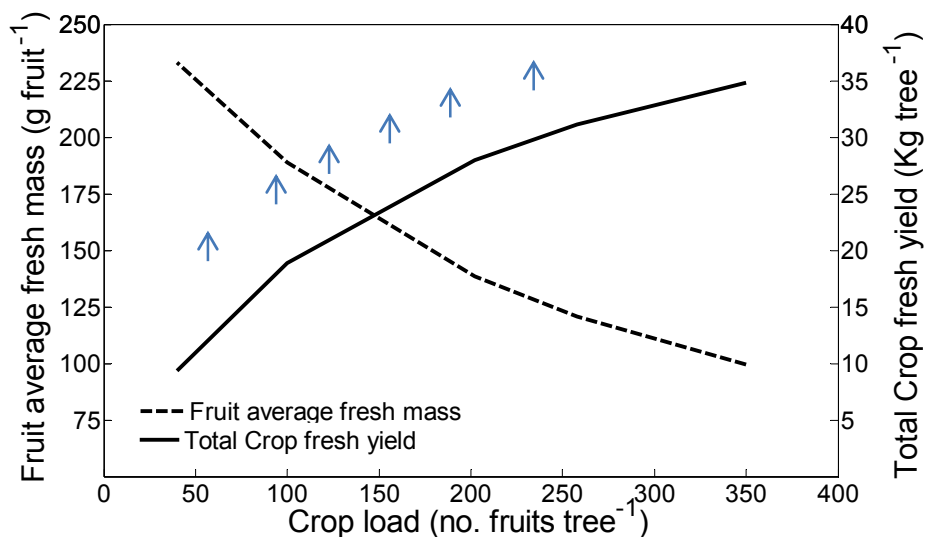
Figures

Fig. 1. The relationships between crop load and average fruit mass and total crop fresh yield as generated by the L-Peach model (Lopez et al., 2008). The focus of this paper is to discuss what can be done to increase crop yields while maintaining or increasing fruit size as indicated by the arrows.