

BURLEIGH DODDS SERIES IN AGRICULTURAL SCIENCE

Achieving sustainable cultivation of temperate zone tree fruits and berries

Volume 1: Physiology, genetics and cultivation

Edited by Professor Gregory A. Lang, Michigan State University, USA

E-CHAPTER FROM THIS BOOK



Advances in understanding fruit tree growth

Ted DeJong, University of California-Davis, USA

- 1 Introduction
- 2 Factors that influence photosynthesis in fruit trees
- 3 Distribution and use of photosynthates
- 4 Fruit tree canopy architecture
- 5 Conclusion
- 6 Where to look for further information
- 7 References

1 Introduction

In a sense, a fruit tree can be viewed as a massive network of solar energy collectors. The individual solar collection plates (grana stacks) are located in chloroplasts, green microscopic structures within biological cells of the leaves. Each leaf contains thousands of chloroplasts that function as solar energy cells and the tree, in turn, has thousands of leaves. The solar energy cells (chloroplasts) only function if they are in aqueous solution, so leaves are specially designed to maintain the solar cells in a hydrated state inside the biological cells even though leaves are usually exposed to dry ambient conditions (Taiz et al., 2015). In this analogy, the woody framework of the tree can be viewed as providing the structure by which the tree is capable of exposing optimal numbers of solar cells to light energy. In addition to providing the structural framework for optimum light exposure, the wood and bark provide a vascular tissue for transporting water and nutrients to the leaves and chemical energy (photosynthates) from the solar cells (chloroplasts) in the leaves to other parts of the plant. The efficiency of a fruit tree as a solar energy collector network depends on its efficiency in capture and conversion of light energy into chemical energy (photosynthesis) and the subsequent transport, storage and utilization of that chemical energy for fruit production. This concept is supported by the fact that maximum yields of fruit and nut orchards, when optimally managed, have been shown to be directly related to the percentage of daily solar radiation intercepted (Lampinen et al., 2012; Palmer et al., 2002; Wünsche and Lakso, 2000).

<http://dx.doi.org/10.19103/AS.2018.0040.03>

© Burleigh Dodds Science Publishing Limited, 2019. All rights reserved.

Chapter taken from: Lang, G. A. (ed.), *Achieving sustainable cultivation of temperate zone tree fruits and berries Volume 1: Physiology, genetics and cultivation*, Burleigh Dodds Science Publishing, Cambridge, UK, 2019, (ISBN: 978 1 78676 208 5; www.bdspublishing.com)

Looking at the functioning of fruit trees from this perspective is useful for both scientific and practical horticultural reasons. Because of the importance of photosynthesis to the efficient functioning of plants as solar energy collectors, scientists have been intensively studying the process of photosynthesis for more than 100 years with the hope of increasing its efficiency. However, there is little evidence that scientists have been or will be able to increase this efficiency in crop plants in the near future (Horton, 2000). On the other hand, there is substantial evidence that fruit trees distribute their nutrient resources and photosynthetic competency, and adjust the angles of leaves in different parts of their canopy to optimize use of resources and sunlight as it passes through a tree canopy (Auzmendi et al., 2013; DeJong and Doyle, 1985; DeJong et al., 1989; Niinemets, 1995, 1997; Rosati et al., 1999, 2000, 2002).

So why should horticulturists be concerned about studying and understanding photosynthesis and the distribution of photosynthates in fruit trees? Trees have evolved to optimize these processes in the context of survival and reproduction in diverse natural environments. The horticulturist's goal is to optimize orchard conditions for enabling fruit trees to carry out photosynthesis and the efficient distribution and use of photosynthates towards obtaining economic yields in managed, agricultural systems. An orchard manager's concern is to optimize inputs that influence these processes to produce an economically valuable crop. This requires a basic understanding of the plant's fundamental processes and the factors that influence them.

1.1 Photosynthesis

Simply summarized, photosynthesis is the process by which energy from the sun is trapped in green pigments (chlorophyll), converted into chemical energy and used to convert carbon dioxide (CO_2) and water into simple carbohydrates that eventually become sugars ($[\text{CH}_2\text{O}]_n$) that can be distributed throughout the plant. Oxygen is given off in the process. The reverse process, whereby all plants and animals recover energy from these simple carbohydrates, is called respiration (Taiz et al., 2015).

The actual photosynthetic process is a complex set of reactions involving many of the nutrients green plants require. For example, nitrogen (N) is a constituent of photosynthetic enzymes and chlorophyll; phosphorus is important in the energy transfer process; magnesium is an essential part of the chlorophyll molecule; potassium, iron, manganese and other nutrients play important roles in specific photosynthetic reactions (Taiz et al., 2015). The carbohydrate products of photosynthesis are collectively called photosynthates. A principal product is glucose, a six-carbon sugar. It is transformed into other simple sugars, that is fructose, sucrose and sorbitol, a sugar alcohol. In most plants, sucrose is the predominant carbohydrate that is transported from the leaves to other parts of

the plant; however, in most Rosaceous fruit trees, sorbitol is the primary transported carbohydrate (Bieleski, 1982).

The CO₂ for photosynthesis must come from the air surrounding the leaf, and the water comes up from the soil through the plant's vascular system. CO₂, which makes up only about 0.040% of the earth's atmosphere (~400 ppm in air), diffuses through the stomata located in the lower epidermis of most fruit tree leaves. The stomata not only allow entry of CO₂ into the leaf, but also allow water vapour to escape from the leaf. Thus, to minimize water loss from the leaf (transpiration), the stomata have an active mechanism for controlling their opening to permit just enough CO₂ into the leaf to allow photosynthesis to continue without excessive loss of water (Taiz et al., 2015).

1.2 Interactions between photosynthesis and water use

During daylight hours when photosynthesis occurs, the tree loses (transpires) as much as 400 molecules of water for every molecule of CO₂ that is absorbed depending on the ambient temperature and humidity (Taiz et al., 2015). The water that is lost from the leaf is replenished by transport of water through the tree from the soil. If the soil around the tree is moist, water also evaporates into the air directly from the soil. The total quantity of water lost by the tree and the soil is called orchard evapotranspiration or crop evapotranspiration (ETc). Tree transpiration usually accounts for most crop water use. In recent years, because of increasing water scarcity in many agricultural growing areas, there has been increased research emphasis placed on developing plants with increased photosynthetic water use efficiency. However, again most of this research has had limited success because photosynthesis can only be carried out in aqueous solution within cells of leaves, and the laws of physics (diffusion) dictate the amount of water loss when stomata open to allow CO₂ to be taken up to supply the photosynthetic process (Taiz et al., 2015; Blum, 2009). The primary successes in increasing orchard water use efficiencies have been achieved by enhancing efficiencies of delivery systems used for orchard irrigation, changing to localized irrigation systems that more precisely deliver water to trees where they need it and scheduling irrigation so that it is delivered when they most need it (Blum, 2009; Auzmendi et al., 2011; Lopez et al., 2016; Marsal et al., 2016; Behboudian et al., 2011).

2 Factors that influence photosynthesis in fruit trees

2.1 Light

Since a fruit tree's primary function is to be a solar energy collector, light is the most important driver of photosynthesis. However, there is seemingly a flaw in this system since photosynthesis of an individual fruit tree leaf, as well

as leaves of most other crop plants, is light saturated at approximately one-third to one-half full sunlight if a leaf is exposed perpendicular to the sun's rays (Taiz et al., 2015; DeJong, 1983; Li and Lakso, 2004). However, only leaves on the outer surface of a tree canopy are ever exposed to direct sunlight for long periods and even those leaves are usually oriented vertically and often folded at the midrib. Thereby they only receive direct exposures for very short periods of the day as the orientation of the sun to the tree changes from east to west (DeJong and Doyle, 1985; Rosati et al., 1999). Each leaf, located in its zone of the tree canopy, has its own ever-changing light environment (DeJong and Doyle, 1985). Thus, light is shared among leaves in deciduous fruit tree canopies so that most leaves in a mature tree function most of the day on the steep, rather than the light saturated portion of the photosynthetic light response curve (Rosati et al., 2002). Light becomes limiting for photosynthesis along a gradient from the outer, exposed edge to the centre of the foliar canopy, and often this gradient is depicted as a continuous reduction of light intensity towards the interior of tree canopies (Robinson et al., 1991). However, much of the light intercepted by all leaves is in the form of sun flecks, and the reduction in light exposure of interior leaves is a function of the amount of time leaves are exposed to sun flecks as opposed to being in shade (DeJong and Doyle, 1985). Thus, interior leaves contribute less photosynthates to the local fruit bearing shoots to which they are attached, and those shoots develop less leaf area and are less productive than more exposed shoots. These shoots may eventually die if total light interception is below the threshold for shoot survival (Lampinen et al., 2011), reinforcing the importance of solar energy collection in a tree's economy.

2.2 Sink strength

In horticulture, much attention has been paid to the question of whether photosynthesis of fruit trees is strongly controlled by a tree's demands for carbohydrates, as opposed to environmental drivers of photosynthesis such as light (Neales and Incoll, 1968). Researchers have reported that photosynthesis can be substantially increased in the presence of high demand for carbohydrates by fruits in several fruit crops (Avery, 1975; Hansen, 1970; Maggs, 1963), and this led some researchers to assert that fruit demand for carbohydrates is a major factor controlling photosynthesis in fruit trees. However, other research has indicated that the effect of fruit on photosynthesis can be relatively minor (DeJong, 1986). Close analysis of much of the literature reporting strong effects of crop load on photosynthesis indicates that those effects are mainly present when there are factors such as dwarfing rootstocks (Palmer et al., 2005; Wünsche et al., 2000) or girdling (Ben Mimoun et al., 1996) that limit the flow of photosynthates to alternative sinks and cause a feed-back-mediated reduction

in carbohydrate movement from the leaves. While there may be a tendency for stomata to function less conservatively in controlling the ratio of CO₂ uptake to water loss in the presence of fruit (DeJong, 1986), there does not appear to be strong evidence for crop load being a primary regulator of photosynthesis in the absence of some 'artificial' mechanism that limits the capacity of alternative sinks to utilize photosynthates for growth. This corresponds with the concept that a tree species' success and survival in nature is expected to be associated with garnering as much carbohydrate resource as possible to grow and compete for space in addition to reproducing (Stephenson, 1981).

2.3 Temperature

Photosynthesis functions optimally at leaf temperatures between about 20°C and 30°C in many temperate deciduous fruit trees (Ro et al., 2001). While the temperature-based limits for temperate deciduous fruit trees are dictated most often by winter and spring cold events or lack of winter chill, rather than photosynthetic temperature optima, growing season temperatures can influence fruit quality and yield through effects on photosynthesis. Crops that have fruits with high sugar contents, such as many stone fruits, tend to be sweeter in climates where daytime maximum temperatures are greater than 30°C. Whereas many starch-accumulating fruit species do better in areas where temperatures rarely exceed 30°C. More research is needed to explore whether this is related to the photosynthetic process or downstream carbohydrate metabolism in these species. It is important to note that even in regions where maximum temperatures often exceed 30°C, these temperatures usually only occur for a relatively small part of a day (afternoon) in most regions where temperate deciduous crops are commercially grown.

All commercial fruit bearing species use what is known as C₃ photosynthesis (the first carbon compound assimilated in the photosynthetic process has three carbon atoms) (Taiz et al., 2015). Some plant scientists have suggested that the productivity of temperate deciduous fruit trees could be enhanced if they could be converted to the C₄ photosynthetic pathway found in some other plants, such as corn (*Zea mays*). This is highly unlikely, since C₄ photosynthesis would not be as efficient as C₃ photosynthesis in early spring when temperatures are relatively low (Taiz et al., 2015) and there is no competitive advantage of C₄ photosynthesis under the shady conditions (Pearcy and Ehleringer, 1984) that are common within the canopies of most fruit tree species.

3 Distribution and use of photosynthates

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; Lacoïnte, 2000; Marcelis, 1994; Watson and Casper, 1984; Weinstein and Yanai, 1994). Grossman and DeJong (1995b) used this concept in the development of the PEACH model and later DeJong (1999) outlined the following four principles for applying this concept to logically understand carbon partitioning in fruit trees.

3.1 The tree as a collection of semiautonomous organs

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 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. Models have been developed for the growth of fruit (DeJong and Goudriaan, 1989; Genard and Huguet, 1996; Genard and Souty, 1996; Grossman and DeJong, 1995b; Pavel and DeJong, 1993b; Lakso et al., 1995), shoots and branches (Costes et al., 1993, 2014; Costes and Guédon, 1996; Genard et al., 1998; Grossman and DeJong, 1995c; Lescourret et al., 1998; Johnson and Lakso, 1986) and roots (Bidel et al., 2000). Although tree pruning and training can drastically alter the shape of 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; Heerema et al., 2008) in fruit 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 were de-fruited, the remaining fruit on the fruited scaffold benefited very little from the carbon that should have been available for fruit growth from the de-fruited 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 be learned about the movement of carbohydrates within the context of the whole tree. The role of

branch autonomy in 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 being elucidated (Zwieniecki et al., 2015).

Carbon partitioning at the branch level has been studied 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.

3.2 Activation of an organ's genetic potential

The second principle is that the genetic potential of an organ is activated or deactivated by organ-specific, endogenous and/or environmental signals. The semiautonomous nature of individual organs is further 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 bud break 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 is 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 (Sorice et al., 2002).

3.3 Interaction of current environmental conditions and genetic growth potential

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. This

importance is related to the strong dependence of respiration on temperature. All irreversible 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 (respiration doubles for every 10°C increase in temperature between 5°C and 35°C, Amthor, 1989). Therefore, conditional growth capacity of any organ is highly dependent on ambient temperature. The conditional growth capacity of fruits growing under near-optimal field conditions has been modelled for several peach and apple cultivars using mathematical functions responsive to heat accumulation (Berman et al., 1998; DeJong and Goudriaan, 1989; Grossman and DeJong, 1995a; Lakso et al., 1999; Pavel and DeJong, 1993a; Reyes et al., 2016). 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 shoots has been successfully modelled by considering temperature and dynamic changes in shoot water status (Basile et al., 2003; Berman and DeJong, 1997a). Although fruit growth is generally 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., 1993). Nutrient availability also can strongly influence conditional organ growth capacity because certain nutrients are required as constituents for growing organs. Accordingly, Saenz et al. (1997) have demonstrated that limited N availability can increase developmental rates of peach fruit.

3.4 The nature of organ growth

The fourth principle is that actual organ growth is a consequence of conditional organ growth capacity, resource availability (assimilate and nutrient supply) and inter-organ competition for those resources. Inter-organ competition for carbohydrates is a function of location relative to sources and sinks of carbohydrates, transport resistances, organ sink efficiency and organ microenvironment. When conditional growth capacity of an organ is set, organ growth should proceed at a rate equal to the conditional growth capacity as long 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. When flowering and pollination occur under favourable conditions, many fruit tree cultivars set very heavy fruit loads. Therefore, lack of available assimilates and inter-fruit competition for carbohydrates are generally the primary factors that limit realized fruit growth in

these situations, 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; Goffinet et al., 1995). Certainly, there are some limitations to carbohydrate transport within trees (DeJong and Grossman, 1995; Marsal et al., 2003), but these are difficult to specifically quantify. There is substantial evidence that fruit growth of many species 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). Yet, there is some evidence to the contrary when pruning stimulates excessive 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). A further complication is that the ability of fruit to compete for carbohydrates appears to vary with the stage of fruit development (DeJong and Grossman, 1995) and location within a tree (Basile et al., 2007).

Upon examining these principles for carbon partitioning in fruit trees, it becomes apparent that phenological patterns of organ growth are the main determinants of carbon partitioning. When experiments are conducted involving different crop load treatments or some other treatment that dramatically favours the growth of one type of organ over others, biomass data collected at the end of the season appear 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 analysed, 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). Generally, in late-maturing fruit 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 (Pace, unpublished data) 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 have apparently interfered with the natural temporal separation of dominant sink activities in fruit trees. The dominant period of fruit growth of early-maturing peach cultivars often coincides directly with the early peak of shoot growth. This increased competition between fruit and shoot growth results 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 coincidental selection for decreases in the total fruit growth potential and dry matter content, and these factors account for some of the differences in yield potential between early- and late-maturing cultivars (Berman et al., 1998). Selection for early-maturing fruit has also increased

the competition for carbohydrates between sub-organs within the fruit such that seed and endocarp 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,b).

3.5 Carbohydrate storage

Where does 'allocation to storage' fit into this scheme of carbon partitioning? Long-term carbohydrate storage is essential for tree survival during adverse conditions (particularly winter for temperate deciduous crops) and subsequent productivity. However, there has been confusion about factors controlling storage reserves in trees (Epron et al., 2012). The prevailing view has been that trees store carbohydrate reserves during times of 'excess' photosynthate production (when current supply exceeds demands for growth and tissue metabolism), and deplete reserves when the potential rate of carbohydrate utilization exceeds the rate of current photosynthate production (Oliveira and Priestley, 1988; Kozłowski et al., 1991; Dickson, 1991). This has created the notion that carbohydrate storage occurs only when photosynthates are in excess of demand.

Some researchers have challenged this passive concept of carbohydrate storage arguing that storage reserves are extremely important and storage sinks should not be conceived of as passive reservoirs (Cannell and Dewar, 1994). They cited examples of control mechanisms for the use of carbohydrate reserves, and that storage sinks are refilled at the same time as the growth of other carbohydrate sinks (Weinstein et al., 1991). Indeed, careful evaluation of seasonal dynamics of reserve mobilization and accumulation that correspond to periods of shoot and fruit growth indicates that, although rates of reserve accumulation are generally lower when fruit growth rates are high, reserve accumulation still occurs during this period even though potential fruit growth rates are likely not at a maximum (Ryugo and Davis, 1959; Priestley, 1970). Similarly, although autumn appears to be the main period for accumulation of carbohydrate reserves in temperate deciduous trees, some reserves are accumulated while growth is still occurring during summer (Barbaroux and Bréda, 2002; Landhäusser and Lieffers, 2003; Wong et al., 2003). Wargo (1979) reported that substantial storage of carbohydrates preceded radial growth of *Acer saccharum* roots and even speculated that root storage of that species may have priority for transported carbohydrates over growth.

Da Silva et al. (2014) pointed out that long-term carbohydrate storage in trees is a function of the volume of xylem and phloem parenchyma tissue in the tree. Furthermore, the volume of xylem parenchyma greatly exceeds the volume of phloem parenchyma. Thus, the collective storage 'organ' of a tree

can be thought of as the woody parenchyma tissues of the tree. The storage capacity of that 'collective organ' is mainly comprised of the overall mass of xylem parenchyma, the maximum potential concentration of carbohydrates in the xylem parenchyma, the minimum amount of carbohydrates remaining in the xylem parenchyma after maximum mobilization and the relative change in storage activity with xylem ageing.

If tree carbohydrate storage capacity is determined primarily as wood is formed, and only current-year sapwood growth can be affected by environmental conditions in a given year, the overall ability for a tree to adjust its storage capacity in response to environmental conditions is very limited. However, this also opens up important questions for future research into the effects of growing conditions on development of carbohydrate storage capacity in trees, the dynamics of storage and mobilization over time and the transport of substances from tree's bottom to the top at different periods during the season (DeJong, 2016). While most carbohydrate transport is usually thought of as occurring in the phloem, it is clear that much of the upward transport of carbohydrate mobilized from xylem parenchyma in the spring occurs in the xylem (Bonhomme et al., 2010; Ameglio et al., 2002). Tixier et al. (2017) have proposed a novel concept for how carbohydrates stored in lower parts of a tree can be delivered to growing shoot tips in the xylem before there is little or no transpiration to facilitate xylem flow. In addition, while seasonal changes in stored carbohydrates have been known to occur for a long time (Kozłowski et al., 1991), recently it has been shown that diurnal and seasonal changes in temperature patterns cause dynamic changes in starch storage throughout dormancy and facilitate re-distribution of storage carbohydrates in response to changes in temperature (Zwieniecki et al., 2015; Sperling et al., 2017). It appears likely that the dynamics of carbohydrate storage in trees may influence tree phenology to a much greater extent than previously recognized.

4 Fruit tree canopy architecture

4.1 Tree architecture

In recent years, there have been major advances in the understanding of fruit tree architecture. While the growth characteristics of specific fruit tree species and cultivars have been generally recognized for many years, recent advances in statistically based analyses and descriptions of bud fate distributions and shoot and branch growth patterns of multiple species have revealed previously under-appreciated similarities and differences among growth characteristics of numerous fruit tree species (Durand et al., 2005; Costes et al., 2006). This has led to a greater understanding that trees are composed of repeating growth units with similarities in patterning of lateral vegetative and floral buds along their axes and that patterns at the shoot level lead to differences in fruit bearing

at the shoot level and overall tree architecture at the whole tree level (Costes et al., 2014).

These types of statistical analyses of tree architecture have been used to describe differences in growth and architectural development of different apple (Costes and Guedon, 2002; Costes et al., 2003) and almond (*Prunus dulcis*) cultivars (Negron et al., 2013), the influence of dwarfing apple rootstocks on scion growth and flowering (Costes and García-Villanueva, 2007; Seleznyova et al., 2003) and similarities and differences in bud fate structures among Rosaceous species (Costes et al., 2014). It also has been used in developing simulation models to demonstrate canopy growth dynamics in apple (Renton et al., 2006), sweet cherry (*Prunus avium*) (Lang et al., 2004), peach (Lopez et al., 2008; Lescourret et al., 2011) and almond (DeJong et al., 2017).

4.2 Architecture-informed pruning

In fruit crops, it is well recognized that there are two objectives with regard to optimizing the capture of solar energy to achieve maximum economic yields: (1) optimizing the total light interception by the canopy and (2) distributing the light within the canopy to obtain as many high-quality fruit as possible while nurturing high-quality fruiting spurs/shoots for the following year's crop. The increased understanding derived from shoot growth and tree architecture models has been valuable in developing canopy management strategies that optimize pruning procedures that work with the natural growth characteristics of trees to achieve these goals (Costes et al., 2006; Lauri, 2002). This has led to the development of 'centrifugal' pruning techniques involving 'spur extinction' in apples (Lauri et al., 2004, 2009; Tustin et al., 2011), and less intrusive training systems in stone fruits that adapt pruning practices to the natural growth characteristics of trees (Day et al., 2013; Lang, 2001). Recent research in nut crops, for which concerns about distribution of light within tree canopies to maintain quality are less than for fruit crops but have been traditionally pruned similarly to fruit crops, has led to the realization that the growth habits and architectures of some nut tree species naturally lend themselves to efficient capture of solar energy. Thus, high yields can be achieved without extensive pruning and training (Tombesi et al., 2011). In California, it is now recommended that young almond and walnut (*Juglans regia*) orchards be managed without traditional, annual pruning (Duncan, 2010; Lampinen et al., 2015).

5 Conclusion

While it is important to continually increase knowledge and understanding of fundamental aspects of the physiology of fruit trees and there is still much to be learned, it also is important to recognize that researchers have had very

little success in improving upon what aeons of natural selection has provided in terms of fundamental tree functioning. This should not be a surprise, since trees are solar energy collection systems that have been evolving these systems for millions of years. Most horticultural progress has been achieved through empirical research or using physiological knowledge and understanding to improve tree and orchard management practices, rather than improving physiological processes.

6 Where to look for further information

Research reports and articles on many of the subjects discussed in this chapter authored by the author of this chapter can be found at <http://dejong.ucdavis.edu/research-overview-publications/>.

Updates on fruit tree physiology can be obtained by following the publications from the International Society for Horticultural Science (<https://www.ishs.org/>) and the American Society for Horticultural Science (<https://www.ashs.org/>).

An interesting and very readable book focused on the structural growth of trees is *The Growing Tree* by Wilson (1970). Further information on detailed studies of fruit tree architecture has been reviewed by Costes et al. (2006).

Further information of the details of photosynthesis, physiology and growth of plants can be found in Taiz et al. (2015).

7 References

- Améglio, T., Bodet, C., Lacoïnte, A. and Cochard, H. (2002). Winter embolism, mechanisms of xylem hydraulic conductivity recovery and springtime growth patterns in walnut and peach trees. *Tree Physiology* 22:1211–20.
- Amthor, J. S. (1989). *Respiration and Crop Productivity*. Springer-Verlag, New York, NY.
- Auzmendi, I., Mata, M., Lopez, G., Girona, J. and Marsal, J. (2011). Intercepted radiation by apple canopy can be used as a basis for irrigation scheduling. *Agricultural Water Management* 98:886–92.
- Auzmendi, I., Marsal, J., Girona, J. and Lopez, G. (2013). Daily photosynthetic radiation use efficiency for apple and pear leaves: Seasonal changes and estimation of canopy net carbon exchange rate. *European Journal of Agronomy* 51:1–8.
- Avery, D. J. (1975). Effects of fruits on photosynthetic efficiency. In: *Climate and the Orchard*. H. C. Pereira, ed. Res. Rev. Common W. Bur. Hort. Planta. Crops. No. 5, pp. 110–12.
- Barbaroux, C. and Breda, N. 2002. Contrasting distribution and seasonal dynamics of carbohydrate reserves in stem wood of adult ring-porous sessile oak and diffuse-porous beech trees. *Tree Physiology* 22:1201–10.
- 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., Solari, L. I. and DeJong, T. M. (2007). Intra-canopy variability of fruit growth rate in peach trees grafted on rootstocks with different vigour-control capacity. *Journal of Horticultural Science and Biotechnology* 82:243–56.
- Behboudian, M. H., Marsal, J., Girona, J. and Lopez, G. (2011). Quality and yield responses of deciduous fruits to reduced irrigation. *Horticultural Reviews* 38:149–89.
- Ben Mimoun, M., Longuenesse, J.-J. and Genard, M. (1996). Pmax as related to leaf: Fruit ratio and fruit assimilate demand in peach. *Journal of Horticultural Science* 71:767–75.
- Berman, M. E. and DeJong, T. M. (1997a). Crop load and water stress effects on daily stem growth in peach (*Prunus persica*). *Tree Physiology* 17:467–72.
- 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* 100:361–70.
- 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 and Biotechnology* 78:303–9.
- 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* 52:229–35.
- Bidel, L. P. R., Pages, L., Rivière, L. M., Pelloux, G. and Lorendeau, J. Y. (2000). MassFlowDyn I: A carbon transport and partitioning model for root system architecture. *Annals of Botany* 85:869–86.
- Bielecki, R. L. (1982). Sugar alcohols. In: *Encyclopedia of Plant Physiology*, Volume 13A, Plant Carbohydrates I. Intracellular Carbohydrates. F. A. Loewus and W. Tanner, eds. Springer-Verlag, Berlin, pp. 158–92.
- Blum, A. (2009). Effective use of water (EUW) and not water-use efficiency (WUE) is the target of crop yield improvement under drought stress. *Field Crops Research* 112:119–23.
- Bonhomme, M., Peuch, M., Améglio, T., Rageau, R., Guillot, A., Decourteix, M., Alves, G., Sakr, S. and Lacoïnte, A. (2010). Carbohydrate uptake from xylem vessels and its distribution among stem tissues and buds in walnut (*Juglans regia* L.). *Tree Physiology* 30:89–102.
- Bradford, K. J. and Hsiao, T. C. (1982). Physiological responses to moderate water stress. In: *Physiological Plant Ecology II. Water Relations and Carbon Assimilation*. O. L. Lange, P. S. Nobel, C. B. Osmond and H. Ziegler, eds. Springer-Verlag, Berlin, pp. 263–324.
- 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* 67:139–43.
- Cannell, M. G. R. and Dewar, R. C. (1994). Carbon allocation in trees: A review of concepts for modeling. In: *Advances in Ecological Research*, volume 25. M. Begon and A. H. Fitter, eds. Academic Press, London, pp. 59–104.
- Chalmers, D. J. and Van den Ende, B. (1975). Productivity of peach trees: Factors affecting dry-weight distribution during tree growth. *Annals of Botany* 39:423–32.
- Chandler, W. H. (1942). *Deciduous Orchards*. Lea and Febiger, Philadelphia.
- Corelli-Grappadelli, L., Ravaglia, G. and Asirelli, A. (1996). Shoot type and light exposure influence carbon partitioning in peach cv. Elegant Lady. *Journal of Horticultural Science* 71:533–43.

- Costa, G. and Vizzoto, G. (2000). Fruit thinning of peach trees. *Plant Growth Regulation* 31:113-19.
- Costes, E. and García-Villanueva, E. (2007). Clarifying the effects of dwarfing rootstock on vegetative and reproductive growth during tree development: A study on apple trees. *Annals of Botany* 100:347-57.
- Costes, E. and Guédon, Y. (1996). Modeling the annual shoot structure of the apricot tree (cv Lambertin). in terms of axillary flowering and vegetative growth. *Acta Horticulturae* 416:21-8.
- Costes E. and Guédon, Y. (2002). Modelling branching patterns on 1-year-old trunks of six apple cultivars. *Annals of Botany* 89:513-24.
- Costes, E., Lanri, P. E., Guédon, Y. and de Reffye, P. (1993). Modelling growth of peach trees using the renewal theory. *Acta Horticulturae* 349:253-8.
- Costes, E., Sinoquet, H., Kelner, J. J. and Godin C. (2003). Exploring within-tree architectural development of two apple tree cultivars over 6 years. *Annals of Botany* 91:91-104.
- Costes, E., Lauri, P. E. and Regnard, J. L. (2006). Analyzing fruit tree architecture: Implications for tree management and fruit production. *Horticultural Reviews* 32:1-60.
- Costes, E., Crespel, L., Denoyes, B., Morel, P., Demene, M.-N., Lauri, P.-E. and Wenden, B. (2014). Budstructure, position and fate generate various branching patterns along shoots of closely related Rosaceae species: A review. *Frontiers in Plant Science* 5:Article 666, 11pp.
- Da Silva, D., Qin, L., DeBuse, C. and DeJong, T. M. (2014). Measuring and modelling seasonal patterns of carbohydrate storage and mobilization in the trunks and root crowns of peach trees. *Annals of Botany* 114:643-52.
- Day, K. R., Johnson R. S. and DeJong, T. M. (2013). Developing a pedestrian plum orchard: the role of tree form, density and height. *Acta Horticulturae* 985:175-80.
- DeJong, T. M. (1983). CO₂ assimilation characteristics of five *Prunus* tree fruit species. *Journal of the American Society for Horticultural Science* 108:303-7.
- DeJong, T. M. (1986). Fruit effects on photosynthesis in *Prunus persica*. *Physiologia Plantarum* 66:149-53.
- DeJong, T. M. (1999). Developmental and environmental control of dry-matter partitioning in peach. *HortScience* 34:1037-40.
- DeJong, T. M. (2016). Demystifying carbohydrate allocation to storage in fruit trees. *Acta Horticulturae* 1130:329-34.
- 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* 8:701-6.
- DeJong, T. M. and Goudriaan, J. (1989). Modeling peach fruit growth and carbohydrate requirements: reevaluation of the doublesigmoid growth pattern. *Journal of the American Society for Horticultural Science* 114:800-4.
- 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* 95:437-43.
- 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. *Physiology Plantarum* 71:83-8.

- 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* 3:89-95.
- DeJong, T. M., Da Silva, D., Negron, C., Cieslak, M. and Prusinkiewicz, P. (2017). The L-ALMOND model: a functional-structural virtual tree model of almond tree architectural growth, carbohydrate dynamics over multiple years. *Acta Horticulturae* 1160:43-9
- Dickson, R. E. (1991). Assimilate distribution and storage. In: *Physiology of Trees*. A. S. Raghavendra, ed. John Wiley & Sons, Inc., New York, pp. 51-85.
- Dorsey, M. J. and McMunn, R. L. (1928). The third report on the Illinois thinning investigations. *Proceedings of American Society for Horticultural Science* 25:269-76.
- Duncan, R. (2010). Pruning almond trees does not pay. <http://cestanislaus.ucanr.edu/files/111772.pdf> (Cooperative Extension web post).
- Durand, J.-B., Guédon, Y., Caraglio, Y and Costes, E. (2005). Analysis of the plant architecture via tree-structured statistical models: the hidden Markov tree models. *New Phytologist* 166:813-25.
- Epron, D., Nouvellon, Y. and Ryan, M. G. (2012). Introduction to the invited issue on carbon allocation of trees and forests. *Tree Physiology* 32:639-43.
- Genard, M. and Huguet, J. G. (1996). Modeling the response of peach fruit growth to water stress. *Tree Physiology* 16:407-15.
- Genard, M. and Souty, M. (1996). Modeling the peach sugar contents in relation to fruit growth. *Journal of American Society for Horticultural Science* 121:1122-31.
- 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.
- 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* 118:580-6.
- Goffinet, M. C., Robinson T. L. and Lakso A. N. (1995). A comparison of 'Empire' apple fruit size and anatomy in unthinned and hand-thinned trees. *Journal of Horticultural Science* 70:375-87.
- Grossman, Y. L. and DeJong, T. M. (1995a). Maximum fruit growth potential and seasonal patterns of resource dynamics during peach growth. *Annals of Botany* 75:553-60.
- Grossman, Y. L. and DeJong, T. M. (1995b). Maximum fruit growth potential following resource limitation during peach growth. *Annals of Botany* 75:561-7.
- Grossman, Y. L. and DeJong, T. M. (1995c). Maximum vegetative growth potential and seasonal patterns of resource dynamics during peach growth. *Annals of Botany* 76:473-82.
- 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* 123:1058-64.
- 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* 23:805-10.
- Harper, J. L. (1980). Plant demography and ecological theory. *Oikos* 35:244-53.

- Harris, R. W. (1983). *Arboriculture*. Prentice-Hall. Englewood Cliffs, NJ.
- Heerema, R. J., Weinbaum, S. A., Pernice, F. and DeJong, T. M. (2008). Spur survival and return bloom in almond [*Prunus dulcis* (Mill.). D.A. Webb] varied with spur fruit load, specific leaf weight, and leaf area. *Journal of Horticultural Science and Biotechnology* 83:274-81.
- Ho, L. C. (1988). Metabolism and compartmentation of imported sugars in sink organs in relation to sink strength. *Annual Review of Plant Physiology* 39:355-78.
- Horton, P. (2000). Prospects for crop improvement through the genetic manipulation of photosynthesis: Morphological and biochemical aspects of light capture. *Journal of Experimental Botany* 51:475-85.
- Johnson, R. S. and Lakso, A. N. (1986). Carbon model of a growing apple shoot: 1. Development of the model. *Journal of the American Society for Horticultural Science* 111:160-4.
- Kozlowski, T. T., Kramer P. J. and Pallardy, S. G. 1991. *The Physiological Ecology of Woody Plants*. Academic Press, San Diego, CA, 657p.
- Lacointe, A. (2000). Carbon allocation among tree organs: A review of basic processes and representation in functional-structural models. *Annual Forestry of Science* 57:521-34.
- Lakso, A. N., Corelli-Grappadelli, L. and Goffinet, M. C. (1995). An exponential model of the growth pattern of the apple fruit. *Journal of Horticultural Science* 70:389-94.
- Lakso, A. N., Wünsche, J. N. and Palmer, J. W. (1999). Measurement and modeling of carbon balance of the apple tree. *HortScience* 34:1040-7.
- Lampinen, B. D., Tombesi, S., Metcalf, S. G. and DeJong, T. M. (2011). Spur behaviour in almond trees: Relationships between previous year leaf area, fruit bearing and mortality. *Tree Physiology* 31:700-6.
- 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. *HortTechnology* 22:237-44.
- Lampinen, B. D., Edstrom, J. P., Metcalf, S. G., Stewart, W. L., Negron, C. M. and Contador, M. L. (2015). How walnut trees can be brought into bearing without annual pruning. *California Agriculture* 69:123-8.
- Landhäuser, S. M. and Lieffers, V. J. 2003. Seasonal changes in carbohydrate reserves in mature northern *Populus tremuloides* clones. *Trees* 17:471-6.
- Lang, G. A. (2001). Critical concepts for sweet cherry training systems. *The Compact Fruit Tree* 34:70-3.
- Lang, G. A., Olmstead, J. W. and Whiting, M. D. (2004). Sweet cherry fruit distribution and leaf populations: Modeling canopy dynamics and management strategies. *Acta Horticulturae* 636:591-9.
- Lauri, P.-É. (2002). From tree architecture to tree training – An overview of recent concepts developed in apple in France. *Journal of the Korean Society for Horticultural Science* 43:782-8.
- Lauri P.-É., Willaume, M., Larrive, G. and Lespinasse, J.-M. (2004). The concept of centrifugal training in apple aimed at optimizing the relationship between growth and fruiting. *Acta Horticulturae* 636:35-42.
- 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* 9:173-88.

- Lescourret, F., Moitrier, N., Valsesia, P. and Génard, M. (2011). QualiTree, a virtual fruit tree to study the management of fruit quality. I. Model development. *Trees* 25:519-30.
- Li, K.-T. and Lakso, A. N. (2004). Photosynthetic characteristics of apple spur leaves after summer pruning to improve exposure to light. *HortScience* 39:969-72.
- Lopez, G., Favreau, R. R., Smith, C., Costes, E., Prusinkiewicz, P. and DeJong, T. M. (2008). Integrating simulation of architectural development and source-sink behavior of peach trees by incorporating Markov models and physiological organ function sub-models into L-Peach. *Functional Plant Biology* 35:761-71.
- Lopez, G., Echeverria, G., Bellvert, J., Mata, M., Behboudian, M. H., Girona, J. and Marsal, J. (2016). Water stress for a short period before harvest in nectarine: Yield, fruit composition, sensory quality, and consumer acceptance of fruit. *Scientia Horticulturae* 211:1-7.
- Maggs, D. H. (1963). The reduction in growth of apple trees brought about by fruiting. *Journal of Horticultural Science* 38:119-28.
- Marcelis, L. F. M. (1994). A simulation model for dry matter partitioning in cucumber. *Annals of Botany* 74:43-52.
- 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* 119:180-4.
- 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* 23:313-23.
- Marsal, J., Casadesus, J., Lopez, G., Mata, M., Bellvert, J. and Girona, J. (2016). Sustainability of regulated deficit irrigation in a mid-maturing peach cultivar. *Irrigation Science* 34:201-8.
- 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* 113:309-14.
- Neales, T. F. and Incoll, L. D. (1968). The control of leaf photosynthesis rate by the level of assimilate concentration in the leaf: A review of the hypothesis. *Botanical Review* 34:107-25.
- Negron, C., L. Contador, B. D. Lampinen, S. G. Metcalf, Y. Guedon, E. Costes and DeJong, T. M. (2013). Systematic analysis of branching patterns of three almond cultivars with different tree architectures. *Journal of the American Society for Horticultural Science* 138:407-15.
- Niinemets, Ü. (1995). Distribution of foliar carbon and nitrogen across the canopy of *Fagus sylvatica*: Adaptation to a vertical light gradient. *Acta Oecologia* 16:525-41.
- Oliveira, C. M. and Priestley, C. A. 1988. Carbohydrate reserves in deciduous fruit trees. *Horticultural Reviews* 10:403-30.
- Palmer, J. W., Wünsche, J. N., Meland, M. and Hann, A. (2002). Annual dry-matter production by three apple cultivars at four within-row spacings in New Zealand. *Journal of Horticultural Science and Biotechnology* 77:712-17.
- Palmer, J. W., Wünsche, J. N., Greer, D. H., Laings, W. A. and Palmer, J. W. (2005). Physiological and biochemical leaf and tree responses to crop load in apple. *Tree Physiology* 25:1253-63.
- Pavel, E. W. and DeJong, T. M. (1993a). Relative growth rate and its relationship to compositional changes of nonstructural carbohydrates in the mesocarp of developing peach fruits. *Journal of American Society for Horticultural Science* 118:503-8.

- Pavel, E. W. and DeJong, T. M. (1993b). Seasonal CO₂ exchange patterns of developing peach (*Prunus persica*) fruits in response to temperature, light and CO₂ concentration. *Physiologia Plantarum* 88:322-30.
- Pearcy, R. W. and Ehleringer, J. (1984). Comparative ecophysiology of C3 and C4 plants. *Plant, Cell and Environment* 7:1-13.
- Priestley, C. A. (1970). Carbohydrate storage and utilization. In: *Physiology of Tree Crops*. L. C. Luckwill and C. V. Cutting, eds. Academic Press, London, pp. 113-27.
- 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* 71:103-9.
- Renton, M., Guédon, Y., Godin, C. and Costes, E. (2006). Integrating Markov chain models and L-systems to simulate the architectural development of apple trees. *Acta Horticulturae* 707:63-70.
- Reyes, F. DeJong, T. Franceschi, P. Tagliavini M. and Gianelle D. (2016). Maximum growth potential and periods of resource limitation in apple trees. *Frontiers of Plant Science* 7:233.
- Robinson, T. L., Lakso, A. N. and Ren Z. (1991). Modifying apple tree canopies for improved production efficiency. *HortScience* 26:1005-12.
- Ro, H.-M., Kim, P.-G., Lee, I.-B., Yiem, M.-S. and Woo, S.-Y. (2001). Photosynthetic characteristics and growth responses of dwarf apple (*Malus domestica* Borkh. cv. Fuji) saplings after 3 years of exposure to elevated atmospheric carbon dioxide concentration and temperature. *Trees* 15:195-203.
- 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* 19:173-80.
- 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* 20:271-6.
- Rosati, A., DeJong, T. M. and Esparza, G. (2002). Physiological basis for light use efficiency models. *Acta Horticulturae* 584:89-94.
- Rufat, J. and DeJong, T. M. (2001). Estimating seasonal nitrogen dynamics in peach trees in response to nitrogen availability. *Tree Physiology* 21:1133-40.
- Ryugo, K. and Davis, L. D. 1959. The effect of the time of ripening on the starch content of bearing peach branches. *Proceedings of the American Society for Horticultural Science* 74:130-3.
- 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* 122:772-7.
- Seleznyova, A., Thorp, G., White, M., Tustin, S. and Costes E. (2003). Structural development of branches of 'Royal Gala' apple grafted on different rootstock/interstock combinations. *Annals of Botany* 91:1-8.
- Sorce, C., Massai, R., Picciarelli, P. and Lorenzi, R. (2002). Hormonal relationships in xylem sap of grafted and ungrafted *Prunus* rootstocks. *Scientia Horticulturae* 93:333-42.
- 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* 100:242-4.

- Sperling, O., Silva, L. C. R., Tixier, A., Th eroux-Rancourt, G. and Zwieniecki, M. A. (2017). Temperature gradients assist carbohydrate allocation within trees. *Science Reports* 7:3265.
- Sprugel, D. G., Hinkley, T. M. and Schaap, W. (1991). The theory and practice of branch autonomy. *Annual Review of the Ecology System* 22:309-34.
- Stephenson, A. G. (1981). Flower and fruit abortion: Proximate causes and ultimate functions. *Annual Review of Ecology and Systematics* 12:253-79.
- Taiz, L., Zaiger, E., Moller I. M. and Murphy, A. (2015). *Plant Physiology and Development*. Sinauer Associates Inc., Sunderland, MA, 761pp.
- Tixier, A., Sperling, O., Orozco, J., Lampinen, B., Roxas, A. A., Saa, S., Earles, J. M. and Zwieniecki, M. A. (2017). Spring bud growth depends on sugar delivery by xylem and water recirculation by phloem M unch flow in *Juglans regia*. *Planta* 246:495-508.
- Tombesi, S., Lampinen, B. D., Metcalf, S. and DeJong, T. M. (2011). Relationships between spur- and orchard-level fruit bearing in almond (*Prunus dulcis*). *Tree Physiology* 31:1413-21.
- Tustin, D. S., Dayatilake, G. A., Henriod, R. E., Breen, K. C. and Oliver, M. (2011). Changes in fruiting behaviour and vegetative development of 'Scifresh' apple in response to artificial spur extinction using centrifugal training. *Acta Horticulturae* 903:603-10.
- Wargo, P. M. 1979. Starch storage and radial growth in woody roots of sugar maple. *Canadian Journal of Forest Research* 9:49-56.
- Watson, M. A. and Casper, B. B. (1984). Morphogenetic constraints on patterns of carbon distribution in plants. *Annual Review of Ecology and Systematics* 15:233-50.
- 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* 23:418-28.
- Weinstein, D. A., Beloin, R. M. and Yanai, R. D. (1991). Modelling changes in red spruce carbon balance and allocation in response to interacting ozone and nutrient stresses. *Tree Physiology* 9:127-46.
- White, J. (1979). The plant as a metapopulation. *Annual Review of Ecology and Systematics* 10:109-45.
- Wilson, B. F. (1970). *The Growing Tree*. University of Massachusetts Press, Amherst, MA, 152pp.
- Wong, B. L., Baggett, K. L. and Rye, A. H. 2003. Seasonal patterns of reserve and soluble carbohydrates in mature sugar maple (*Acer saccharum*). *Canadian Journal of Botany* 81:780-8.
- W unsche, J. N. and Lakso A. N. (2000). The relationship between leaf area and light interception by spur and extension shoot leaves and apple orchard productivity. *HortScience* 35:1202-6.
- W unsche, J. N., Palmer, J. W. and Greer, D. H. (2000). Effects of crop load on fruiting and gas-exchange characteristics of 'Braeburn'/M.26 apple trees at full canopy. *Journal of the American Society for Horticultural Science* 125:93-9.
- Zwieniecki, M. A., Tixier, A. and Sperling, O. (2015). Temperature-assisted redistribution of carbohydrates in trees. *American Journal of Botany* 102:1216-18.