

Demystifying carbohydrate allocation to storage in fruit trees

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Abstract

In spite of the essential nature of long-term carbohydrate reserves for tree survival and productivity there has been confusion about how allocation of carbohydrates to storage reserves occurs in trees. 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. However this concept has been challenged because storage reserves are so important for the survival of perennial plants and thus it is probably not correct to treat storage sinks as passive reservoirs. The lack of understanding or clear concepts regarding the dynamics of reserve storage and mobilization in perennial plants has been a major limitation in carbon budget models of tree growth and is a substantial unresolved issue facing pomologists, tree physiologists and ecologists. This paper reviews a logical basis for considering carbohydrate storage as an active sink and provides a method for quantifying and simulating annual carbohydrate storage and mobilization potential in temperate deciduous fruit trees. This view of carbohydrate storage leads to the hypothesis that the capacity for carbohydrate storage is largely a function of xylem and phloem anatomy and is created as trees grow. The amount of carbohydrate that is actually stored is a function of that capacity and the ability of storage sinks to actively compete for carbohydrates during and shortly after the growing season.

Keywords: CHO reserves, carbon partitioning, starch storage, starch mobilization, xylem parenchyma

INTRODUCTION

Carbohydrate reserves, defined as carbohydrate resources accumulated in mobilizable form, are recognized to play an essential role in the survival and productivity of temperate deciduous fruit trees, providing sources of carbohydrate for growth and metabolism during periods when current photosynthates are not adequate to meet demands required to sustain normal organ growth and functioning. This latter condition is particularly prevalent during early spring growth, after winter dormancy, when many parts of the plant increase metabolism and begin active growth but there are no leaves on the tree (Oliveira and Priestley, 1988). Carbohydrate reserves have been studied in trees for more than a century (Hartig, 1858) and their nature, location and seasonal behavior have been documented in many types of forest and fruit trees (Priestley, 1970; Oliveira and Priestley, 1988; Dickson 1991, Kozlowski, 1992).

Starch is usually the most prevalent form of long term storage reserves in many temperate deciduous trees during the growing season up until autumn but during the transition from autumn to winter many species convert starch into soluble carbohydrates (Zimmermann, 1971). While carbohydrate concentrations can be very high in bark tissues of some tree species, reserves stored in the woody parenchyma tissues of the root, trunk and stems are quantitatively most important (Kozlowski and Keller, 1966).

The seasonal dynamics of carbohydrates reserves have been studied in numerous tree species and almost all temperate deciduous tree species are characterized by having high concentrations of reserves in late autumn and winter followed by depletion during the grand



period of growth in spring and a gradual build-up of reserves during the summer and early autumn (Kozłowski et al., 1991). In deciduous fruit trees several studies have reported low rates of reserve accumulation during summer or early autumn periods that correspond to peak times of fruit growth (Ryugo and Davis, 1959; Priestley, 1970).

In spite of the essential nature of carbohydrate reserves for tree survival and productivity there is not a clear understanding about how allocation of carbohydrates to storage reserves occurs in trees (Epron et al., 2012). Sala et al. (2012) stressed the need for clearer understanding of factors that control allocation of carbohydrates to storage reserves in trees. 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 occurs when photosynthates are in excess.

In 1994, Cannell and Dewar challenged the passive concept of CHO storage and argued that storage reserves are too important to treat storage sinks as passive reservoirs. They argued that reserves are not an “optional extra” and cited examples of when there appear to be control mechanisms for the use of carbohydrate reserves and that storage sinks are refilled at the same time as the growth of other sinks for carbohydrates (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 probably not saturated (Ryugo and Davis, 1959; Priestley, 1970). Similarly, although autumn appears to be the main period for accumulation of carbohydrate reserves in temperate deciduous trees there are significant amounts of reserves that are accumulated while growth is still occurring in the summer period (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 reserve storage of that species may have priority for transported carbohydrates over growth.

The lack of understanding and clear concepts regarding the dynamics of reserve storage and mobilization in perennial plants has been a major limitation in carbon-based models of tree growth (Lacointe, 2000; Le Roux et al., 2001; Epron et al., 2012). Our work with the functional-structural L-Peach model has provided a novel approach to understanding and addressing this problem. The L-Peach model simulates the structural growth and physiology of virtual peach trees over multiple years. As a virtual L-Peach tree grows, canopy photosynthesis is calculated and photosynthate is distributed as a function of the calculated sink demands of specific organs (Allen et al., 2005). Thus photosynthate distribution in the tree is primarily a function of the respiration and growth potential of all of the individual organs that make up the tree (DeJong, 1999). Using this concept of photosynthate distribution, all that was needed to simulate carbohydrate allocation to storage was to quantify the storage sink(s) of a tree. Since it is widely recognized that the reserves stored in the woody parenchyma tissues of the root, trunk and stems of trees are quantitatively most important (Kozłowski and Keller, 1966), 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: 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 aging. In 2005 we conducted a field experiment to quantify these parameters and subsequently used these data to develop a sub-model within the L-Peach model to simulate carbohydrate storage and mobilisation in a virtual L-Peach tree. Details of the field experiment, data developed and the modelling can be found in Da Silva et al. (2014).

DISCUSSION

The important point of this research is that the collective carbohydrate storage organ of a fruit tree can be conceptualized as the sum of the xylem and phloem parenchyma of that tree. Thus the capacity of this collective organ to store carbohydrates is finite and can be estimated from the overall volume of xylem and phloem parenchyma cells and the storage capacity of those cells. Since, on a volume basis, the active xylem parenchyma (located in the sapwood) is much more prevalent than active phloem parenchyma (in the latest layer of phloem) and the xylem parenchyma is imbedded in woody tissue, most of a tree's incremental increases in storage capacity are determined as each annual ring of xylem develops. Therefore tree carbohydrate storage capacity is mainly a function of the anatomical development of wood and the size and ratio of parenchyma cells compared to the other cells in that wood.

There has been much speculation about "strategies" of carbohydrate storage in trees in response to environmental events (Franklin et al., 2012). But if carbohydrate storage capacity of trees is primarily determined as wood is formed and only current-year sapwood 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 avenues for future research into the effects of growing conditions on development of carbohydrate storage capacity in trees. It is known that stressful conditions such as a water stress (Larson et al., 1988) or over cropping (Grossman and DeJong, 1995b) lead to decreases in incremental diameter growth of wood. Thus stress could result in less incremental xylem parenchyma cell volume and potentially have long-term effects on carbohydrate storage and subsequent tree vigour.

In addition to factors affecting overall carbohydrate storage capacity there are also numerous researchable questions about how much of the carbohydrate stored in parenchyma cells is available for mobilization and transport out of the cells in spring. Our experiments indicated that approximately 45% of stored carbohydrates in peach tree xylem were mobilized and this decreased slightly as the xylem aged (Da Silva et al., 2014). Others have reported similar or greater changes in carbohydrate storage and mobilization capacity with tree age in other species (Barbaroux and Bréda, 2002; Keller and Loescher, 1989; Lacoïnte et al., 1993). Much more research needs to be done to differentiate the genetic and environmental factors that govern these processes.

There are also numerous questions regarding the dynamics of carbohydrate storage and mobilization over time. It is generally thought that carbohydrates stored in woody tissues of fruit trees are primarily mobilized in spring during the grand period of growth. Subsequently storage occurs during the growing season and/or primarily during the fall when leaves are actively photosynthesizing but most other growing sinks are minimally active. This connotes that carbohydrates mainly come out of storage tissues during winter and spring and go into tissues during summer and fall. However, research by Nzima et al. (1997) and Spann et al. (2008) documented that carbohydrates that went into pistachio shoots during early summer were mobilized during the primary period of kernel fill in late summer and then storage was replenished by leaf fall the same year. Furthermore, Zwieniecki et al. (pers. commun.) have recently provided evidence of daily movement of carbohydrates out and in to xylem parenchyma cells in pistachio trees. Clearly much more research is needed in this area.

Associated with spring mobilization from xylem parenchyma is the question of how these carbohydrates are transported to the growing tips of the tree when the phloem is largely non-functional during this period (Evert, 1963). It is clear that most of the carbohydrate movement up a tree or vine in winter or early spring is in the xylem vessels. Cells adjacent of xylem vessels have the capacity to exude sugars into the vessels and this can help to create a positive hydraulic pressure in the xylem (Zwieniecki and Holbrook, 2009; Wegner, 2014). The result of this xylem pressure is often observed as exudation when species with large xylem vessels (walnut, grape and kiwifruit) are pruned in late winter (Ryugo, 1988). The signals involved in timing this process are unknown and interesting because the roots are not thought to experience true dormancy (Kramer and Kozlowski,

1979). There is also no efficient mechanism to transfer hormones from the top of the tree to the roots prior to bud-break because the phloem is non-functional during the winter in temperate deciduous trees (Evert, 1963).

Another very interesting aspect of carbohydrate storage in woody tissues is that typically carbohydrate concentrations in woody tissues are higher in roots than in the above-ground parts of the tree (Basile, Day and DeJong, unpublished data; Da Silva et al., 2014; Esparza et al., 2001; Keller and Loescher, 1989). Given that carbohydrate storage in wood is dependent on the proportion of xylem parenchyma in the wood, it may be that carbohydrate storage capacity is limited by the need for the wood to serve other major functions such as structural support and xylem transport. Roots are known to have higher proportions of parenchyma cells than do stems (Esau, 1953). This may be because roots require less structural support than the top of the tree. It would be interesting to experimentally determine whether there is a trade-off between stems providing structural support and carbohydrate storage capacity.

DeJong (2014) has argued that a potential avenue of research for increasing yields of early maturing peach yield 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 (1995a) 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 during the previous growing season. If early maturing cultivars could be bred to store an amount of carbohydrate equivalent to the amount that the later maturing cultivars put into fruit growth by maturing fruit later in the season, then the yields of early maturing cultivars could be substantially increased. It may be possible to select for greater winter carbohydrate storage capacity by selecting for higher proportions of parenchyma cells in the xylem if doing so does not compromise tree structure.

CONCLUSIONS

The concept of active carbohydrate allocation to storage in fruit trees that is primarily governed by the relative proportion of parenchyma cells in xylem sapwood and current year phloem is easy to understand and provides clarity to what has been a mystery for horticulturists. Within this conceptual framework quantification of the long-term storage capacity of trees is dependent on several factors (total amount of active sapwood, maximum and minimum carbohydrate concentrations in the sapwood, change in these concentrations with sapwood age, etc.) but all of these factors are experimentally quantifiable. In addition this concept opens up several new paths for future research and potentially even provides traits to select for if a tree breeder is interested in increasing overwintering carbohydrate storage capacity to increase initial fruit set and crop loads, especially in early maturing cultivars.

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