

Modeling Seasonal Patterns of Carbohydrate Storage and Mobilization in Peach Trees

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Highlights: Storage of carbohydrate is essential for perennial plants survival, but its modeling is often unsatisfactory. We studied the dynamics of reserve storage and mobilization in Peach trees and introduced a modeling approach that consider storage as an active sink rather than a passive buffer as frequently done in carbon-based models of tree growth.

Keywords: carbon budgets, carbon reserves, stored carbohydrates, perennial plants, tree carbon budget modeling, xylem storage

INTRODUCTION

Carbohydrate reserves, defined as carbohydrate resources accumulated in plant tissues that can mobilized at a later date, are recognized to play an essential role in the survival and productivity of temperate deciduous fruit trees. They provide a source of carbohydrate for growth and metabolism during periods when current photosynthetic supply of carbohydrates is not adequate to meet demands required to sustain normal organ growth and functioning. Carbohydrate reserves have been studied in many types of forest and fruit trees (Priestley 1970, Oliviera and Priestley 1988, Kozlowski 1992). There is not a clear understanding 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 and deplete reserves when the potential rate of carbohydrate utilization exceeds the rate of current photosynthate production (Oliviera and Priestley 1988, Kozlowski *et al.* 1991, Millard and Grelet 2010). In 1994, Cannell and Dewar challenged this concept and argued that because storage reserves are so important for the survival of perennial plants at times when current photosynthates are inadequate to meet growth demands, it may not be correct to treat storage sinks as passive reservoirs.

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), and was often ignored (Génard *et al.* 2008). Viewing reserve storage as a passive buffer means that carbohydrate partitioning into storage is modeled passively when all other sinks are satisfied. However, seasonal patterns of reserve storage and mobilization indicates that some storage often occurs when there are many other active carbohydrate sinks. Thus the concept of active carbohydrate reserve sinks and sources proposed by Cannell and Dewar (1994) seems more appropriate.

The first objective of this research was to experimentally determine the concentration of non-structural carbohydrates present in the bark and wood of mature peach trees under conditions when it was likely that those concentrations would represent the maximum and minimum concentrations during a growing season. The second objective was to use the data from the field experiment to fully implement the long term carbohydrate storage sub-model in the functional-structural L-PEACH model.

MATERIALS AND METHODS

To achieve the first objective and insure that the results of the field study would reflect the “capacity” of peach trees to mobilize and replenish carbohydrate reserves in their trunks we used an experimental treatment that was designed to “maximize” utilization of reserves. On March 1, prior to bud-break, 24 16-year-old peach trees (‘O’Henry’ scion grafted on ‘Lovell’ rootstock) growing in a semi-commercial orchard at the University of California Wolfskill Experimental Orchard, were selected for uniformity. At that time six trees were cut down and the stumps and major roots were removed from the soil. Two radial slices (~1cm thick) of the trunk (~20 cm above the graft union) and root crown (~10 cm below the graft union) were sampled for carbohydrate analyses. The top of the two main scaffolds of 18 remaining trees were removed to a height of about 1 m above the ground. This treatment was designed to eliminate reproductive sinks and stimulate strong vegetative regrowth in the form of epicormic shoots (Pernice *et al.* 2006) and therefore, mobilize all available carbohydrate reserves. On June 6, August 5 and November 5, six additional trees were cut down, removed

from the soil and sample slices of the trunk and root crown were obtained as described above for the initial six trees. The tissue samples were subsequently dried to a constant mass at 60 °C, weighed, ground to pass a 40-mesh (0.60 mm) screen, and analyzed for starch and soluble nonstructural carbohydrates by standard methods (Smith 1968). Starch was hydrolyzed with amyloglucosidase, and glucose, sucrose, fructose and sorbitol were analyzed by HPLC (Johansen *et al.* 1996) with a fast carbohydrate column. Concentrations of total glucose after starch hydrolysis, sucrose, fructose and sorbitol were summed to give an estimate of total nonstructural carbohydrates (TNC).

MODELING

The L-PEACH functional-structural plant model (Allen *et al.*, 2005, Lopez *et al.* 2008) simulates the development and growth of a plant’s architecture based on carbon and water exchanges (Da Silva *et al.* 2011). This model has no set carbohydrate allocation patterns; instead carbohydrate distribution is driven by competition among individual plant organs acting as semi-autonomous components sensitive to local availability of carbon and water as well as environmental factors. In this model the underlying mechanism for carbon transport treats the plant as a network of components and uses an analogy with an electrical circuit to compute the flow of carbohydrate between every component. The stored carbohydrate that can be mobilized was modeled as a capacitor within the electrical sub-circuit representing the organ storage. This capacitor discharged when carbohydrate storage was mobilized, thus acting as an active source, and charged when storage was a sink. However, the switch between source and sink, i.e. the remobilization period, was user-defined. Moreover, the carbohydrate demand of the storage sink and the maximum carbohydrate available for mobilization needed to be defined and quantified. Since storage in woody tissue represents the majority of carbohydrates stored in perennial tissues of deciduous trees, the concentration of stored carbohydrates in the active sapwood of a tree under conditions in which the storage sinks would be expected to be saturated, was used as the potential sink storage. By the same reasoning the maximum carbohydrates available for mobilization was assumed to be represented by the difference between the maximum concentration of carbohydrates in the sapwood and the minimum concentration under conditions when it would be expected that all available reserves have been mobilized, the severe pruning treatment in our study. The corresponding experimental values that were used for parametrization are shown in Table 1.

Table 1: Mean (\pm SE) non-structural carbohydrate concentrations (% dry wt.) for root crown and trunk tissues of peach trees at their potential, (March) and at the sampling date when the minimum was measured (June), and the percent decline in the concentration between the two sampling dates.

	Potential	Min	% Decline
Root	12.89 \pm 0.48	7.08 \pm 0.16	45.05 \pm 3.91
Trunk	8.48 \pm 0.34	4.86 \pm 0.35	42.71 \pm 5.55

In the electrical analogy, sources and sinks are defined by their electromotive force (ef) that can be viewed as their “strength”. The electromotive forces of the whole system are subsequently used to determine the voltage (or carbohydrate concentration) at each attachment point of sources and sinks. Simply put, for a pure sink $ef = 0$ while for a pure source $ef = 1$. In the case of a process that can act as both, source and sink, a shift between these values is necessary to simulate the passage from sink to source and vice-versa. However, such a drastic change is unlikely to be a natural process and moreover, it requires additional information about when and why this switch occurs. To tackle this, we defined the storage ef as a function of the capacitor charge, it is 0 as long as the TNC is below the minimum value (Table 1. Min) and increases along a simple logistic curve to reach the value of 1 when TNC reaches its potential value (Table 1. Potential). In that way, source or sink activity depends on the local conditions of carbohydrate allocation and, as the pattern of TNC along the season, is an emergent property of the model.

RESULTS AND DISCUSSION

The simulated results were obtained on the 6th year run of a tree that was severely pruned to reproduce the field experiment. During the first 5 years, the tree was grown and pruned to simulate the commercial practices of the orchard. As shown in Fig.1, the TNCs at the beginning of the season were the potential ones as defined in Table 1. The TNCs then decrease, as storage mobilization takes place, and reach a minimum value slightly

above the one indicated in Table 1. The mobilization period is followed by a period when carbohydrates are accumulated again toward their initial ratio. The overall behavior of mobilization and refill of storage carbohydrate matches the experimental pattern (whisker dots in Fig1). However its slight offset suggests that mobilization occurs sooner than only as a function of demand. It is likely that spring carbohydrate mobilization starts as a signal activated process with stored starch being hydrolyzed and sugars being unloaded into xylem vessels (Sauter *et al.* 1973). Additionally, replenishing storage sinks appears to be a slower process than mobilization and what occurred in the simulations. The slower rate of storage refill might be due to the differences between the biochemical processes necessary to transform starch into sugar and those to hydrolyze starch in the spring. Further research is needed before this can be explicitly modeled within the framework of L-PEACH since, at present, all carbohydrate allocation in the model is sink driven.

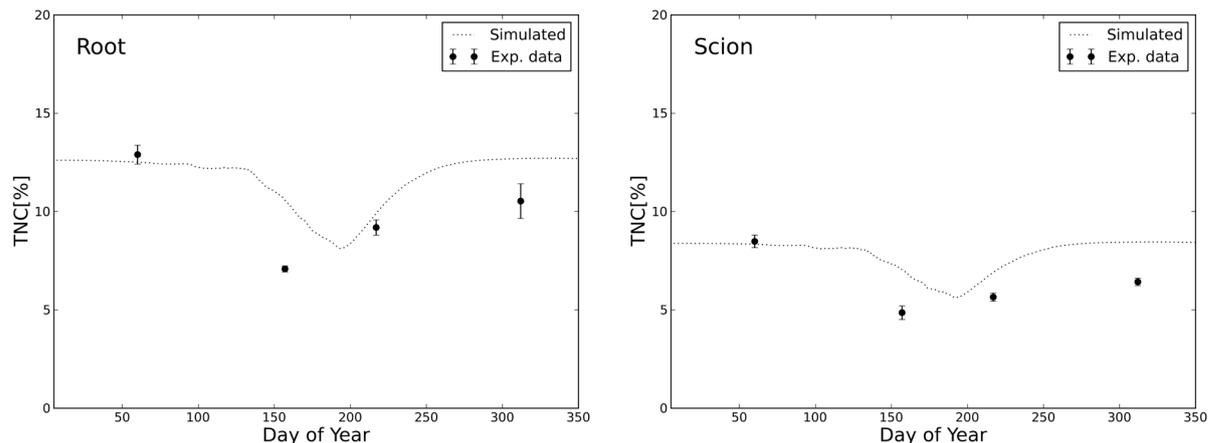


Figure 1: Seasonal patterns of TNC for root (left) and scion (right). Experimental data are displayed as points representing the mean (\pm SE) TNC measured at the different sampling dates. The dashed lines are the simulated patterns.

These improvements allowed the model to reproduce the general pattern of TNC using a simple approach and without a user-defined period of mobilization. However, the discrepancies in behavior suggest that additional mechanisms are involved and detailed modeling of these processes may require specific parameterization for a given species. Indeed, the more detail we incorporate into modeling specific processes, the closer we get to a connection with genetic specificity. Being able to determine what parameters/processes are genetically altered among genotypes and incorporating them into functional-structural models is a major challenge for the future.

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