Dormant Carbohydrate Reserves of Two Peach Cultivars Grafted on Different Vigor Rootstocks

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Keywords: *Prunus persica*, vegetative growth, dwarfing

Abstract

In temperate fruit trees, early spring shoot growth depends on carbohydrate reserves accumulated in the previous season. Vigorous rootstocks can accumulate more reserves, which contribute to a higher initial flush of shoot growth. Total dormant, non-structural carbohydrates (TNC) in above and below ground tissues were studied in mature 4-year-old 'Redhaven' and 5-year-old 'Redtop' peach trees at three different locations (California, Georgia and South Carolina), and in 1-year-old 'Redhaven' trees grown near Clemson, South Carolina. The rootstocks included Lovell (*Prunus persica*), Pumiselect® (*P. pumila*), Krymsk® 1 (P. tomentosa × P. cerasifera), Cadaman®-Avimag *(P. persica × P. davidiana)*, Controller® 5 (*P. salicina × P. persica*) and Cornerstone (*P. persica × P. dulcis*). Shoot and root samples were taken for tissue analysis from the mature trees concurrently when the 1-year-old peach trees were removed from the ground. Carbohydrates were also quantified in bark and wood tissues in the mature 'Redtop' trees. Greater concentrations of TNC were found in roots of 'Redhaven' and 'Redtop' trees in California compared to the other two sites; however, shoot TNC did not differ significantly among sites. Concentration of TNC in roots was at least two-fold more than in shoots. Lovell roots had the greatest accumulation of reserves and Krymsk® 1 the lowest. Rootstock bark accumulated the largest amount of TNC, followed by scion bark, and Lovell had the greatest TNC content. One-year-old 'Redhaven' trees had the highest TNC accumulation in Lovell roots. About 70% of TNC were accumulated in root tissues, and smaller roots accounted for most of the carbohydrates (>80%). The more vigorous rootstocks, in this case Lovell, not only had the greatest accumulation of dormant carbohydrates, but also had the greatest root and shoot dry weights per tree, suggesting that the initial differences in spring shoot growth could be attributed to both.

INTRODUCTION

There are different theories about rootstock dwarfing mechanisms but none have yet been proved experimentally. One potential mechanism that could influence scion vigor when budded to different rootstocks is the capacity of the rootstock to store carbohydrates. Roots contain the highest concentration of nonstructural carbohydrates (TNC) and other reserves at the end of the growing season, and these reserves are mobilized during the winter and finally depleted as new leaf and shoot growth starts in the spring (Loescher et al., 1990). Carbon reserves are poorly incorporated, if not neglected, in most carbon-based tree growth models, and the major reason why carbon reserves are often neglected is because the lack of knowledge about dynamics of carbon reserves (Le Roux et al., 2001). Storage carbohydrates are very important for temperate perennial trees because new spring growth depends on the previous season's reserves. The carbohydrate storage pool is used during periods of low photosynthesis to fuel maintenance respiration, to cope with water stress and to build new leaves in spring (Kozlowski, 1992). All perennial parts show alternate depletion and replenishment, but this behavior is most pronounced in roots. Roots contain the highest concentration of nonstructural carbohydrates (TNC) and other reserves at the end of the growing season. Once sufficient leaf area is gained in spring, new photosynthates are synthesized again to support the rest of the season's growth (Marchi and Sebastiani, 2005). Total non-structural carbohydrate accumulation, especially starch, peaks in the fall, and this is followed by a drastic reduction in concentration at the end of the winter in order to support new growth in spring.

Preliminary results from experiments investigating the physiological mechanisms involved in size-controlling rootstocks for peach trees indicated that there is a relationship between dormant season root carbohydrate storage and tree growth characteristics associated with different rootstocks. In this study, the differences in root starch concentrations between the most vigorous and least vigorous rootstocks combined with the clear differences in early spring shoot growth behavior of trees on the different rootstocks (Weibel et al., 2003) and the knowledge that spring growth is largely dependent on overwintering stored starch (Koslowski, 1992), suggests some relationship between rootstocks and initial spring growth. The objective of this study was to determine if there is a specific relationship between rootstock TNC and vigor of scion growth on a range of size-controlling peach rootstocks that were previously reported to induce different scion vigor when grown under orchard field conditions.

MATERIALS AND METHODS

Four-year-old 'Redhaven' peach trees and five-year-old 'Redtop' peach trees grafted on different rootstocks were grown at three different locations: Kearney Agricultural Center, Parlier, CA; USDA Southern Fruit & Nut Tree Laboratory, Byron, GA and Musser Fruit Research Center, Seneca, SC. Trees were part of two NC-140 rootstock trials (www.nc140.org), and they were planted at 5×6 m. Lovell, Pumiselect®, Krymsk® 1, Cadaman®, Controller® 5 and Cornerstone were used as rootstocks. Cadaman® and Cornerstone were vigorous rootstocks, Lovell had standard vigor, Pumiselect® had intermediate vigor, Controller® 5 also had intermediate vigor but less than Pumiselect®, while Krymsk® 1 was the most size-controlling rootstock. Trees were planted in a completely randomized block design with 4-8 replications for the adult bearing trees and 6 replications for the young non-bearing trees.

Stem and root samples were taken in January 2006 from trees at the three research sites. Each sample was a composite of 3 shoots and 3 roots per tree. Depending on the site and combinations, 4 to 8 trees were used at each site as replicates. On 'Redtop' trees at Kearney Agricultural Center, Parlier, CA, a small cylinder of woody tissue (1-cm-diameter) was taken from the rootstock and scion at 7-10 cm below and above the graft union.

In another experiment, one-year-old 'Redhaven' peach trees, grafted on Lovell, Pumiselect®, Krymsk® 1 and Cadaman® were planted in double rows at 1.5 m × 1.5 m in the row and 6 m between rows. Three shoots and three roots were used to study the concentration of TNC on different dates during Winter 2006-07.

In a third experiment, whole trees planted at the same time and distance as previously described were removed from the ground in January 2007. The above and below ground material was separated in different shoot and root sizes. This plant material was dried at 60°C for at least 2 weeks before grinding for tissue analysis. For carbohydrate analyses, all samples were frozen in liquid nitrogen, stored at -70°C and subsequently freeze-dried. Dried samples were ground through a 40-mesh screen. Ground plant tissues were stored in a desiccator. TNC were determined as described by Somogyi (1945). Data were analyzed by SAS (9.1 version) using the GLM procedure.

RESULTS

Shoot TNC concentration of bearing 'Redhaven' and 'Redtop' trees did show an interaction between rootstocks and the three locations. Greater concentrations of TNC were found in 'Redhaven' (Table 1) and 'Redtop' (data not shown) roots from California compared to the other two sites; however, shoot TNC did not differ significantly among sites (data no shown). In these trees, concentrations of TNC in roots were at least two-fold greater than in shoots. Lovell roots had the greatest accumulation of reserves and Krymsk® 1 the lowest (Table 1).

When the concentrations of TNC were studied from bark and wood tissues of five-year-old 'Redtop' trees grafted on Lovell, Pumiselect®, Controller® 5 and Krymsk® 1 rootstocks at Kearney Agricultural Center, CA, differences were observed at the scion and rootstock tissue levels (Table 2). When similar tissues were compared among the different rootstocks, Lovell generally had higher concentrations of total dormant nonstructural carbohydrates (Table 2). Scion bark tissues from 'Redtop' trees grafted on Lovell rootstock had the highest concentration of TNC, while scions on Controller® 5 had the lowest. Scion wood tissue from trees grafted on Lovell and Pumiselect® rootstocks had significantly higher concentrations than Controller® 5. In the roots, bark TNC values were highest in Lovell, while Krymsk® 1 and Controller® 5 had the lowest concentrations. TNC concentration in woody root tissue was greater in Lovell and Pumiselect® than in Krymsk® 1 and Controller® 5.

During Winter 2006-2007, one-year-old peach trees had differences in TNC concentration. Roots at all sample dates had significantly higher concentrations of TNC in Lovell compared to the rest of the rootstocks on the first three dates (Fig. 1), while Krymsk® 1 had the lowest TNC concentration. Root TNC concentrations increased until 20 January 2006, and after that they declined (Fig. 1). The TNC concentration in shoots tended to decrease after January in trees on all rootstocks, and the differences between trees on the various rootstocks were less than for the roots.

In the second part of the young non-bearing 'Redhaven' tree experiment, the TNC of all tissues were analyzed, and trees grafted on Lovell rootstocks had the highest TNC values (Fig. 2), trees on Pumiselect® intermediate values, and Krymsk® 1 the lowest ones. Trees grown on Pumiselect® and Krymsk® 1 rootstocks did not differ in the percentage of TNC distribution related to those grown on Lovell (data not shown). Roots contained about 70% of the TNC, so almost 3/4ths of the TNC were accumulated below ground.

DISCUSSION

The importance of TNC as reserves for woody tree species, and in particular for fruit trees, is to support initial growth in the spring. Considering that about one-half to two-thirds of the carbohydrate reserves in fruit trees can be used for flowering, early fruit growth and early shoot growth (Kozlowski, 1992), it is important to understand the relationship between scion growth vigor associated with different rootstocks and the total nonstructural carbohydrates present as reserves during the winter.

The concentration of TNC found in shoots and roots were similar to those reported in peach by others for peach trees (Dichio et al., 2007). In general, the concentration of TNC in 'Redhaven' and 'Redtop' shoots from mature bearing trees at the three sites (CA, GA and SC) were not significantly different in January 2006. For the roots, the higher TNC concentrations of the more vigorous rootstocks (Lovell, Cadaman® and Cornerstone) suggest that the vigorous rootstocks have a higher capacity to store carbohydrates per unit of root tissue or a greater availability of carbohydrates for storage at the whole tree level (Table 1).

The results from bark and wood tissues followed a similar pattern for both shoots and roots. Generally, TNC concentrations reported in the literature are higher in bark than wood; such as was found in peach (Dowler and King, 1966). The higher content of TNC in bark compared to wood is reported to be a consequence of its proximity to sieve tubes (Jordan and Habib, 1996), but the high TNC accumulation in root bark compared to scion bark suggests that a higher specialization of root tissue acts as a reserve or sink organ

(Kozlowski, 1992). All trees had the same general pattern of TNC distribution with a higher concentration in bark tissues. At the same time, root bark TNC content was higher than the shoot bark.

In young non-bearing trees, shoot TNC concentrations among trees on the different rootstocks decreased by the end of winter (Fig. 1). At the end of dormancy, scion TNC concentrations were less in the shoots of trees on Lovell rootstock compared to the more size-controlling rootstock, Krymsk® 1, suggesting an earlier mobilization of TNC in this vigorous rootstock.

Lovell roots always had higher TNC concentrations than the rest of the rootstocks. After reaching maximum values in January, root TNC concentrations began decreasing in all rootstocks, presumably due to remobilization of carbohydrates to support spring growth (Fig. 1). The change in the pattern of TNC concentration through the winter was consistent with other studies in peach (Dowler and King, 1966; Ellis, 1993), where the concentration declined toward the end of winter due to remobilization of carbohydrates from the roots to the growing points.

When whole one-year-old ‘Redhaven’ trees were removed from the soil, the TNC concentration of above-ground tissues (shoots, branches and trunk) followed a similar pattern as bearing trees (Fig. 1 and Table 1). The differences in TNC content of the whole tree (but mainly in the roots) might account for some quantitative differences in the spring flush of growth. Differences in TNC concentration were correlated with the vigor of the rootstocks, where the more vigorous ones had higher TNC concentrations; however, larger differences were found for total TNC per tree (Fig. 2). The high TNC content in the vigorous rootstock was a consequence of the large dry weight per tree (data not shown). It appeared that the differences observed in growth, especially the initial growth in spring, might be due to a larger amount of TNC in the trees grafted on the more vigorous rootstocks rather than the concentration of TNC by itself.

These differences between concentration and total TNC per tree indicate that the vigorous rootstocks have higher initial growth potential due to larger total reserves, especially in their root tissues. The size of the root system, and to a lesser extent the concentration of TNC, could be the reason for the observed differences in the early flush of growth. However, how much of this reserve-dependent initial growth may be responsible for the season’s growth differences observed between dwarfing and vigorous rootstocks is still unclear.

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Tables

Table 1. Dormant total nonstructural carbohydrates (mg g^{-1} DW) in 5-mm-diameter roots of bearing Redhaven trees grafted on different rootstocks at Kearney, California (CA); Byron, Georgia (GA) and Musser Fruit Research Center, South Carolina (SC), in January 2006.

	Root TNC concentration (µg g^{-1} DW)[z]
Location	
CA	265 a
GA	237 b
SC	233 b
Rootstocks	
Lovell	321 a
Cadaman	279 a
Pumiselect	207 c
Krymsk 1	232 b
Analysis of variance	Probability
Places	0.0037
Rootstocks	0.00001
Places × rootstocks	0.0206

[z]Different letters within a column indicate significant differences at P <0.05.

Table 2. Concentration of dormant total nonstructural carbohydrates in bark and wood tissues (µg g^{-1} DW) from sampled patches located at 7 to 10 cm above and below the graft union of five-year-old Redtop trees grafted on four different rootstocks.

Rootstock	Total nonstructural carbohydrates concentration (µg g^{-1} DW)			
	Scion		Root	
	Bark[z]	Wood	Bark	Wood
Lovell	296 a	173 a	413 a	214 a
Pumiselect	238 b	154 a	357 b	220 a
Krymsk 1	234 b	171 ab	256 c	139 b
Controller 5	236 b	141 b	262 c	166 b

[z]Different letters within a column indicate significant differences at P<0.05 (Duncan's multiple range test).

Figures

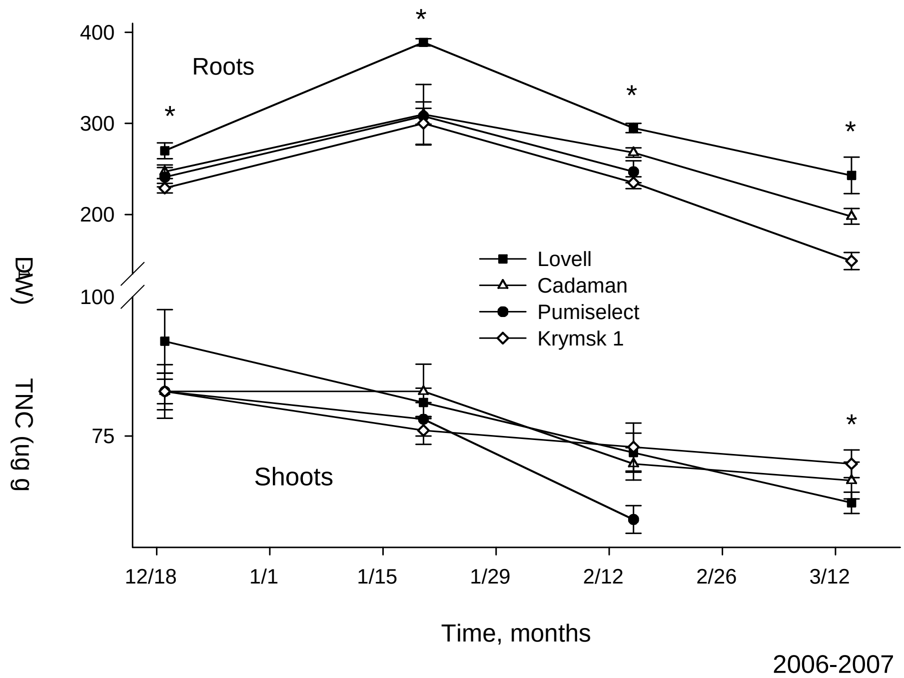

Fig. 1. Concentration of nonstructural carbohydrates in root and shoot tissues of one-year-old Redhaven trees grafted on different rootstocks in Winter 2006-2007. Standard errors are given for each point. Asterisks represent significant rootstock treatment differences at each point at P<0.05 (Duncan's multiple range test).

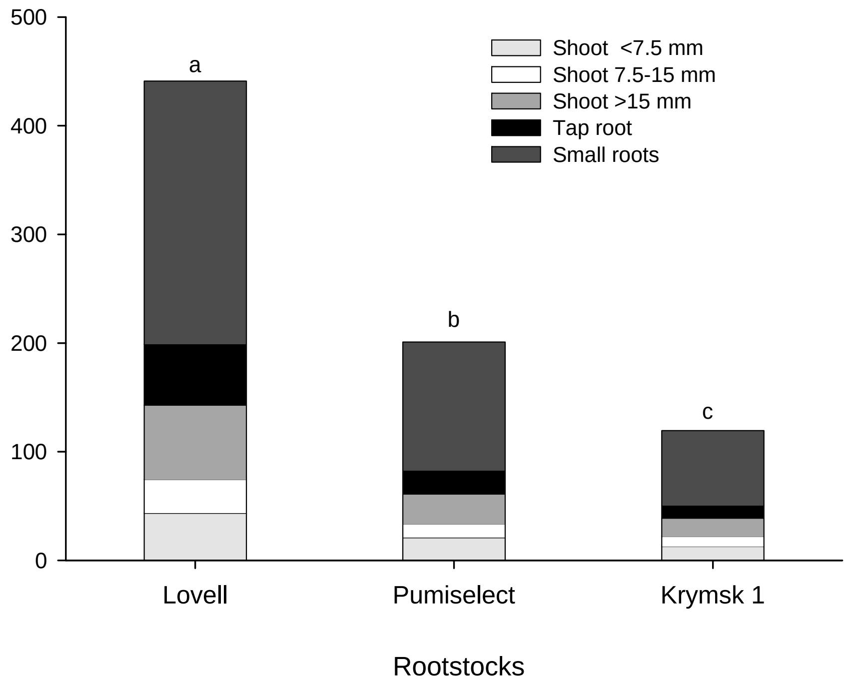

Fig. 2. Total amount of dormant nonstructural carbohydrates in different organs of one-year-old 'Redhaven' peach trees grafted on three different rootstocks in January 2006. Different letters indicate significant differences for TNC dry weight per tree at P<0.05 (Duncan's multiple range test).