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# DWARFING MECHANISMS OF PRUNUS SPECIES AS INTERSTEMS AND ROOTSTOCKS ON PEACH [PRUNUS PERSICA (L.) BATSCH] TREE VEGETATIVE GROWTH AND PHYSIOLOGY

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DWARFING MECHANISMS OF PRUNUS SPECIES AS INTERSTEMS AND  
ROOTSTOCKS ON PEACH [PRUNUS PERSICA (L.) BATSCH] TREE  
VEGETATIVE GROWTH AND PHYSIOLOGY

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A Dissertation  
Presented to  
the Graduate School of  
Clemson University

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In Partial Fulfillment  
of the Requirements for the Degree  
Doctor of Philosophy  
Plant and Environmental Sciences

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by  
Antonio Marcelo Weibel  
December 2008

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## ABSTRACT

The use of small trees in orchard systems reduces manual labor (pruning, thinning and harvesting), and induces precocity, thus making high-density plantations economically advantageous, which has elicited an interest in size-controlling rootstocks. However, the mechanisms involved in the reduction of scion growth by the rootstock are not well understood. The main objective of this study was to gain a better understanding of the dwarfing mechanism induced by size-controlling peach rootstocks. The relationship among different rootstocks (dwarfing to invigorating range) as to stored carbohydrates, tree water status, and interstem and grafting height was evaluated on young and mature ‘Redhaven’ and ‘Redtop’ peach trees in California, Georgia and South Carolina. The main rootstocks involved in the study were Cadaman® (vigorous), Lovell (control), Pumiselect® (semivigorous), Controller® 5 (semivigorous), and Krymsk® 1 (more size-controlling).

Greater concentrations of TNC were found in ‘Redhaven’ and ‘Redtop’ roots in California compared to the other two sites; however, shoot TNC did not differ significantly among sites. Concentration of TNC in roots were at least two fold compared to shoot TNC concentration. About 70% of total non-structural carbohydrates were accumulated in root tissues, where smaller roots accounted for most of the carbohydrates (>80%). The more vigorous rootstocks not only had the higher accumulation of dormant carbohydrates but also the highest root and shoot dry weight per tree, suggesting that the initial difference in new spring growth could be the result of these growth components.

Rootstock genotypes used as interstems and not the grafting height affected the size of 'Redhaven' trees in the studied combinations. Krymsk® 1 and Pumiselect® interstem trees were 81% and 88%, respectively, the size of Lovell trees at the end of the first year, while Krymsk® 1 interstem trees were almost 50% of the control at the end of second year. Budding height did not affected significantly scion growth, however a tendency was observed when trees on Krymsk® 1 had reduced growth when grafted at higher height. These data suggest the dwarfing mechanism in some *Prunus* rootstocks involves other plant tissues rather than roots.

There was a positive correlation between scion vegetative growth as affected by rootstock and tree water status. In addition, the results suggested that the seasonal changes in dry matter production and partitioning found in two peach cultivars may be influenced, at least in part, by seasonal variations in stem water potential, stomatal conductance and transpiration rates. Xylem vessel diameters of Lovell rootstocks were two fold greater than those of Krymsk® 1 rootstocks. The results also suggested that in peach rootstocks the main hydraulic resistance might be located at the root such as the case of Krymsk® 1 or graft union interface as in Pumiselect®; so, depending on genotype combinations.

## DEDICATION

I wish to dedicate this thesis to my mother and the memory of my loving father, who gave me the example of life. To my wife, Diana, I give my undying gratitude and love for the support, concern, patience and sacrifice she always gave and to my children, María Luz, Joaquín and Nicolás, who are inexhaustible sources of happiness and help me forget any frustration.

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## CHAPTER I

### INTRODUCTION

The use of rootstocks for fruit trees has become widely expanded in the last several hundred years. The characteristics needed in rootstocks have become more sophisticated over the years, where disease and pest resistance and adaptation to poorly drained or wet soils are very important factors in choosing rootstocks. However, limiting tree vigor, enhancing crop efficiency and increasing fruiting precocity are primary objectives in newly established fruit orchards.

More than two millenia have passed since the practice of growing trees in pots or cutting the roots were used to control tree size. In the past half-century, selective breeding programs have produced many dwarfing rootstocks especially for apples and more recently for cherries. However, the use of dwarfing rootstocks has been extended to other tree fruit crops because of the economic advantages, which include reducing hand labor (pruning, thinning, harvest), pesticides, fertilizer, and enhancement of cropping efficiency and precocity.

Despite efforts to understand the mechanisms involved in the reduction of the scion size due to rootstock, these mechanisms still remain unclear. Different theories exist that try to explain this reduction in scion growth. Plant hormones by direct or indirect effects are suggested to influence scion growth either via their synthesis, metabolism or transport from roots to shoots and from shoots to roots. Measurement of

hormone concentration in sap flow of active transpiring trees is difficult because of the constant changes in the sap flow rate throughout the day. In general, roots are the focus of most studies that try to understand how dwarfing rootstocks influence scion growth. Root anatomy and physical size might limit water, nutrient and hormone transport to the shoot. On the other hand, graft unions might present a physiological and physical barrier for compounds (minerals, hormones, etc) and water, respectively.

Less attention has been directed to the effect of interstems and budding heights on scion growth, except in apples, where interstem studies have shown that interstocks reduce scion growth as much as a dwarfing rootstock. This research would indicate that other factors besides a root effect is involved in the dwarfing mechanism of rootstocks. Higher accumulation of non-structural carbohydrates that are stored for winter and broken down in spring might induce more shoot growth in trees grafted on vigorous rootstocks. However, the theory that supports the relevance of tree water status to tree dwarfing has attracted the attention of many researchers in the past decade. This theory suggests that dwarfing rootstocks generate a water deficit in the scion, which reduces shoot and overall tree growth. Dwarfing rootstocks have been reported to induce a higher resistance to water movement in roots (peaches) and the graft union (apples and cherries); however, graft unions of dwarfing rootstocks in apple and cherries often seem to have incompatibility issues.

Our hypothesis supports the theory that water status of the scion is affected by the rootstock where dwarfing rootstocks reduce the water available to the scion. Roots and graft union could play an important role in the reduction of water transport to the scion.

In addition, we think that winter non-structural carbohydrate content of the tree would affect initial spring growth. If interstems and budding heights affect the vegetative growth of peach scions, then roots are not the only explanation for the dwarfing mechanism of peach rootstocks. It is likely that the dwarfing mechanism can not be readily explained by individual tissues and organs, and possibly the scion growth could be regulated by more complex pathways.

In order to better understand the dwarfing effect of rootstocks, our objectives were i- to determine the concentration of non-structural carbohydrates in different rootstocks, which could be tied to the new spring vegetative growth; ii- study the effect of the interstem and budding height on scion vegetative growth and water status; and iii- to establish relationships among tree water status, some physiological parameters (i.e., transpiration rate and stomata resistance), vegetative growth, root anatomy and rootstocks.



## CHAPTER II

### LITERATURE REVIEW

#### **Overview**

Rootstocks are used in fruit orchards to tolerate different soil conditions such as dry, saline, heavy, wet soils, presence of disease organisms and soil-borne insects. But one of the most important uses of rootstocks is their capacity to reduce the size of the scion, and increase precocity and efficiency at the same time. Even though this rootstock effect was suspected 2000 years ago, the mechanisms involved are hardly known (Crasweller and Schupp, 2006).

Hand labor involves more than half of the annual cost of growing peaches in the United States due to the pruning, thinning and harvesting that is done, often with ladders because of the large size of trees (DeJong et al., 1999). For that reason production costs could be substantially reduced and orchard operations made safer if the size of the trees could be reduced enough to eliminate the need for ladders (Hayden and Emerson, 1976; Green, 1991; Reed, 1975). The benefit of dwarf and size-controlling rootstocks has been clearly demonstrated in apples and revolutionized the apple industries in Europe and the U.S. (Rom and Carlson, 1987). In the past few decades, apple researchers and farmers introduced spur varieties and dwarfing rootstocks to control tree size, reducing the hand labor costs and increasing tree precocity. The tendency toward high-density apple

plantations has become more widespread in Europe, U.S. and other countries. The increasing density of orchard plantings to obtain high yields and the accompanying high cost of hand-assisted operations emphasized the necessity of developing size-controlling rootstocks. Unlike in apples, there are no widely acceptable size-controlling rootstocks for peaches and nectarines. New rootstocks have become available mostly from Europe, but their use is still very limited mainly because of the restricted range of compatibility among cultivars (Felipe, 1989; Loreti, 1994; Atkinson and Else, 2001; Atkinson et al., 2003 and Zarrouk et al., 2006).

In spite of the potential importance of size-controlling rootstocks to production of peaches and nectarines as well as other tree crop species, the development of size-controlling rootstocks in these crops has been very slow. Most of the development research is strictly empirical since there is no specific analyzable genetic trait that has been identified with the size-controlling mechanism. The production research involving these rootstocks also tends to be strictly empirical since the actual physiology involved in the size-controlling behavior is poorly understood (Rom and Carlson, 1987; Webster and Wertheim, 2003; Costes and García-Villanueva, 2007).

In grafted fruit trees, the scion and the rootstock develop in different environments, the air and the soil, respectively. Interaction between the two genotypes is very complex because the scion uses water, hormones and nutrients while the rootstock depends on carbohydrates, hormones and other compounds from the scion. The transported nutrients and other compounds crossing the bud union influence the scion and rootstock and produce changes that affect tree size, fertility, longevity, pathogen

resistance, fruit quality, yield, etc. In some cases, these influences are stronger than the effects produced by soil or climatic conditions (Rom and Carlson, 1987; Webster and Wertheim, 2003).

It is known the effect that rootstocks have on the structure and physiology of fruit trees. Rootstocks can affect Trunk Cross Sectional Area (TCSA) (Westwood and Roberts, 1970; Ferree, 1988; Loreti et al., 1993, Weibel et al., 2003; Santos et al., 2004; Reighard et al., 2006), tree height, shoot length, leaf size and weight (Ferree and Barden, 1971; Westwood 1978; Weibel, 2003; Costes and García-Villanueva, 2007; Tworkoski and Miller, 2007), canopy diameter (Tubbs, 1980; Crabbé, 1984; Ferree, 1988; Loreti et al., 1993, Giorgi et al., 2005; Tworkoski and Miller, 2007), fruit yield (Bernhard 1985; Bussi et al., 1995; Carusso et al., 1996, 1997; Weibel, 1999 and Reddy et al., 2003), fruit quality (Reddy et al., 2003, Gil-Izquierdo et al., 2004; Giorgi et al., 2005; Drogoudi and Tsipouridis, 2007), fruit soluble solids (Murase et al. 1990, Camara et al., 2003ab, 2004; Whiting and Lang, 2004), bloom date (Durner and Goffreda, 1992; Young and Houser, 1980), tree nutrition (Brown and Cummins, 1989, Giorgi et al., 2005), foliar nutrient content (Knowles et al., 1984, Camara et al., 2004), leaf net photosynthesis (Ferree and Barden, 1971; Lichev and Berova, 2004; Koshita et al., 2006), branch crotch angle (Crabbé, 1984; Warner, 1991) and bark thickness (Yadava and Doud, 1978). However, the mechanisms that induce these effects are unknown. The complexity is clearly seen when reciprocal grafts are made between two varieties, showing a different behavior of the genotypes when they work as scion or as root (Swarbrick et al., 1946, Tubbs, 1977). There are several theories about the effects and the mechanisms involved in dwarfing

(Lockard and Schneider, 1981; Crabbé, 1984; Rom and Carlson, 1987; Atkinson et al., 2001; Atkinson and Else, 2001; Webster and Wertheim, 2003; Costes and García-Villanueva et al., 2007), but none of these theories has been definitively proved.

### **Dwarf theories**

Different theories have been proposed to explain the mechanisms involved in the reduction of scion growth by the rootstocks. The theories are related to the effects of hormones and other compounds, stored carbohydrates, hydraulic conductivity of roots, and the graft union. These theories are explained below.

#### **Hormone, bark tissue and other compounds**

Theories on the dwarfing effect come from different research approaches but hormones appear to be related to the dwarfing mechanism in some way. One theory hypothesizes that the roots or graft union or both could alter hormone concentration or the ratio among hormones, where auxins, gibberellins, cytokinins and abscisic acid are involved (Webster and Wertheim, 2003). One of the main hormones involved in this mechanism might be indole acetic acid (IAA). IAA may act on roots, increasing the growth of the root system in the vigorous rootstocks. More recently, Chong and Andrew (2006) found in cherry that the more vigorous ‘Mazzard’ rootstock had a lower activity of the IAA oxidase than the more dwarfing rootstocks, ‘Gi 148/1’ and ‘Gi 148/8’. Kamboj et al. (1997) reported greater auxin movement to roots in the apple cultivar ‘Fiesta’ when it was grafted on the invigorating M.114 and M.111 rootstocks compared to the dwarfing

M.9 and M.27 rootstocks, suggesting that auxin increases root size. In the same work, it was found that the ratio of abscisic acid (ABA) to IAA present in the rootstock bark was inversely related to rootstock vigor. In addition, Kamboj et al. (1997) found that cytokinin concentration in shoot sap of 'Fiesta' apple was found higher on the invigorating rootstocks than on the dwarf rootstocks. It has also been suggested that endogenous gibberellins (GAs), may be associated with the dwarfing mechanism (Webster and Wertheim 2003). Richards et al. (1986) studied the gibberellin effect on apple tree cultivar 'Northern Spy'. These last authors found a small amount of radioactive [<sup>3</sup>H]GA<sub>4</sub> was found in shoot and leaf tissues when M.9 (dwarfing) was used as an interstock; whereas, trees grafted on the invigorating MM.115 rootstock had high radioactive GA in their leaves. This reduced uptake of [<sup>3</sup>H]GA<sub>4</sub>, which was applied to the rootstock xylem, appears to be related to reduced transport from root to scion. In another study, Soumelidou et al. (1994) assessed that the rate of polar auxin transport in shoot segments of apple rootstocks was reduced in the dwarfing rootstocks compared with the invigorating ones. Noda et al. (2000) also found a positive correlation between the shoot tip IAA content and the shoot growth of lemon scions grafted on rootstocks characterized by different invigorating properties. In a more recent study, Sorce et al. (2002), working on grafted and ungrafted *Prunus* rootstocks, found a correlation between the level of auxins and cytokinins and invigorating peach rootstocks, where high levels of IAA were found in exudates from roots of ungrafted vigorous rootstocks. However, the results showed some contradictions, probably due to the fact the 2-year-old trees were confined to small 1.7 liter containers. The latter authors hypothesized about the existence

of a feedback loop between IAA and cytokinins. In this feedback loop, a decrease in the basipetal flow of IAA would stimulate the synthesis and the export (via xylem sap) of cytokinins from the roots. This rise of cytokinin concentration in the xylem sap would increase the synthesis and translocation of IAA out of the shoot apex, which would in turn reduce cytokinin levels in the xylem sap (Bangerth, 1994).

The action of hormones could also be involved in changes in the tree frame by affecting branch crotch angles. The apple rootstock M.9 induced dwarfing in an M.2 scion. Although the elongation of the leader shoot was not affected by the dwarf rootstock, the crotch angle of the lateral shoots dominated by the apex was wider (Crabbé 1984). These wide angles may be a consequence of hormonal effects. Wider angles reduce apical dominance and consequently control of shoot size, especially in the upper part of the tree.

Bark tissue has been used to explain the dwarfing mechanism in apples. When Lockard and Schneider (1981) grafted a single piece of bark tissue of M.26 onto 'Gravenstein/MM.111' trees, the resulting trees were dwarfed. Growth regulators (IAA) and phenol compounds in the bark tissue could interact, thus reducing the size of the scion. The presence of thick bark in apples has been associated with the dwarfing response. The reduction in growth has been related to an increased proportion of bark tissue in roots, smaller vessel size, and enlarged wood-ray tissue (McKenzie, 1961). The growth inhibiting properties of the bark tissue may be caused by phenols (Lockard and Schneider, 1981).

Simons and Chu (1984) analyzed calcium concentrations in conductive and non-conductive phloem of bark tissues in dwarf and vigorous apple rootstocks. They found a higher accumulation of calcium in dwarf rootstocks. The presence of calcium was associated with necrotic tissue. Dwarfing rootstocks also had more non-conducting phloem tissue compared to vigorous rootstocks.

Graft unions alone may affect the scion by other mechanisms such as those suggested by xylem exudate studies in apples and cherries (Jones 1984). Xylem exudates from apple trees on dwarfing rootstocks had lower nutrient and hormone concentrations in the scion sap compared to the invigorating rootstocks. This indicated that the graft union, especially the region near to the scion, could reduce the amounts of growth regulators and nutrients to the scion, and may cause a reduction in size or vigor. In the same study, the dwarfing mechanism in cherry appeared to be associated with growth regulators produced in the scion that affects the rootstocks. The dwarfing mechanism appeared to differ between the two species.

Atkinson and Else (2001) support the hormone theory, but they were concerned about the appropriate methodology necessary to measure the amount of a hormone in the sap flow. It is known that changes in transpiration rate lead to a variation of the xylem solutes (Atkinson and Else, 2001). By increasing the transpiration rate the solute concentration is reduced but this change is not proportional, so in order to measure the hormone concentration in vigorous and dwarf rootstocks, it would be important to measure those trees under the same transpiration rate. On the other hand, measuring the hormone concentration in a tissue from excised braches or roots will not give a realistic

result compared to a transpiring tree. It is evident that the dwarfing effect is not a simple signaling hormone mechanism, so it likely is intertwined with a complex system of signaling pathways acting in tandem rather than in isolation.

### **Stored carbohydrates**

In many higher plants the primary photosynthetic products are sugars and starch. These compounds may be stored in the leaf blade and other organs during photosynthesis. Excess carbohydrates are accumulated in shoot, branches and specially roots by the end of the summer. Starch is the main storagerage carbohydrate at the end of the growing season in perennial trees and is subsequently transformed to sugar during the winter, where the increase in soluble ‘free’ sugar accounts essentially for the decrease in starch (Winkler and Williams, 1945).

Carbohydrate reserves in deciduous trees are very important for reproductive and vegetative development in the initial growth stages (Quinlan, 1969; Loescher et al., 1990; Gaudillère et al., 1992; Teng et al. 1999). Furthermore, not only carbohydrate content but also the total amount of carbohydrates in each part is important for maintaining tree vigor (Yano et al., 2002). The contribution of reserves to the annual tree carbon balance is one of the keys to understanding tree vegetative and reproductive growth. The storage pool is used during periods of low photosynthesis to fuel maintenance of respiration (Ögren, 2000), to cope with water stress, and to build leaves in spring (especially broad-leaved species) (Barbaroux and Dufrêne, 2003).

Carbon allocation within a plant is very complex because of complex linking between carbon source organs (mainly leaves) and carbon sink organs (mainly sapwood



of stems, branches and roots, and fruits). The complexity comes essentially from regulations due to feedback mechanisms, interactions between different functions, and the special distribution of the different plant compartments (Génard et al., 2008). 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).

Roots are the main organ of carbohydrate storage. Allocation of reserves to roots can be influenced by several factors: carbohydrate biochemistry, respiration, hormones, phloem loading and unloading, and genetic control (Friend et al., 1994). Water availability, light, nutrition and temperature exert an influence over the allocation of carbohydrates and can modify the shoot/root ratio in woody species (Tromp, 1983; Keller and Loescher, 1989; Friend et al., 1994; Jordan and Habib, 1996; Tagliavini et al., 1999; Esparza et al., 2001; Allen et al. 2005, Cheng and Fuchigami, 2002; Eschenbach, 2005; Dichio et al., 2007 and Génard et al., 2008). In addition, it is well known that cultural practices, such as fertilization, girdling, pruning and fruit thinning can modify the allocation of reserves (Priestly, 1976; Worley, 1979; Schnelle and Klett, 1992; Tagliavini et al., 1999). Root reserves are mobilized during the winter and finally depleted as soon as new leaf and shoot growth start in the spring (Loescher et al., 1990). 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). Numerous studies have covered the effect of carbohydrate accumulation in forest trees (Hansen et al., 1996; Kainulainen et al., 1998; Kosola et al. 2001, Piispanen and Saranpaa, 2001; Jaggi et al., 2002; Li et al.,

2002; Newell et al. 2002). It was mentioned that early spring growth is highly dependent on remobilization of stored carbohydrate reserves (Kozlowski 1992) in woody species, and the rate and amount of accumulation depend on species. Barbaroux et al. (2003) found significant differences in the amount of reserves used by oaks and beeches. Oaks doubled the reserves used from October to June, probably due to differential needs for spring growth and winter maintenance between these two genera.

Fewer studies have been carried out in fruit trees as compared to forest trees. One of the big differences in these two kinds of trees is the influence exerted by fruits, the most powerful sink of carbohydrates. The importance of TNC as reserves for woody species, and in particular for fruit trees, for initial growth in the spring has been reported by Crane and Al-Shalan, 1977; Gaudillière et al., 1992; Nzima et al., 1997 and Allen et al., 2005. 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 of scion growth vigor associated with different rootstocks and the total non-structural carbohydrates present as reserves during the winter.

Non-structural carbohydrates of heavy cropping ("on") trees compared to light cropping ("off") pistachio trees showed large differences in starch and soluble sugar degradation (Nzima et al., 1997). Soluble sugars and starch in "on" trees declined in all organs (leaves, inflorescence buds, rachises, nuts, current 1-year-old wood, and primary and tertiary branches and roots) as nut growth occurred. In contrast, all organs of "off"

trees accumulated greater concentrations of soluble sugars and starch indicating a strong effect of fruit in the allocation of reserves.

Three-year-old walnut trees were lifted from the field, and starch and soluble sugars from different organs were analyzed (Lacointe et al., 1993). The authors found that 90% of the reserves were located in roots, mainly in the taproots, in autumn. In addition, they found a significant hydrolysis of starch to soluble sugars in winter. They also reported that autumn reserves were mobilized massively in spring; whereas, those accumulated in the summer were mobilized only slightly, suggesting that autumn starch is more readily available than summer starch.

The effect of fruits has been studied on fruit trees and related to the partitioning of carbohydrates. It is known that dry matter production above ground is directly related to the radiation intercepted by the crop (Hsiao, 1993). However, fruit yield per ground unit area may increase not only with increases in canopy photosynthesis caused by increments in the light intercepted, but also because of changes in the dry matter partitioning. This change in the distribution of dry mass in fruit trees may be attributed to rootstocks, which can send either more or less carbohydrates to fruits, shoots, branches, trunk or roots (Forshey and Elfving, 1989). Fruits act as strong sinks for carbohydrates and the availability of carbohydrates for an individual fruit depends on the supply from source organs and the demand of the sink organs (Grossman and DeJong, 1995abc). In terms of assimilate partitioning; fruits are considered irreversible storage sinks that import carbohydrates without exporting assimilates (Ho, 1992).

It was found that allocation of assimilates to fruits in 'Loring' peach trees on 'Halford' rootstock was lower in the fruit stages I and II than in stage III. Less shoot and root growing points were active in stage III, leaving more available carbohydrates for fruits (Miller and Walsh, 1988).

Above ground mass partitioning is affected by crop load, and although fewer works have involved root growth, it has been reported that carbohydrates partitioned to roots are strongly reduced with heavy crop loads (Maggs, 1963; Avery, 1969; Richard and Rowe, 1977; Forshey, 1982). The number of new white roots is reduced when fruited peach trees are compared to non-fruited trees. This effect was especially observed during the final stage of fruit growth and the last part of the vegetative season, implying that fruits are stronger sinks than roots (Williamson and Coston, 1986).

Palmer (1992) found that increases in crop load of 'Crispin' apple on M.27 rootstock slightly reduced leaf dry matter production but produced a large decrease of shoot and root dry weight. In addition, he found that growth of roots appeared to be more reduced than shoots, and this effect was more marked in the dwarf rootstocks compared to the invigorating rootstocks.

Rogers and Booth (1964), working with 'Lane's Prince Albert' apple on five different rootstocks, showed that after a heavy crop load the vegetative growth of the following season was reduced by 53% when the more dwarfing M.IX rootstock was used compared to 9% when the trees were on the more vigorous M.VI rootstocks. In peach, dwarf rootstocks had a higher accumulation of dry matter in fruits compared to more vigorous rootstocks (Weibel, 1999)

One of the proposed mechanisms that would cause the reduction of scion size is the capacity for storage carbohydrates. Rootstocks influence carbohydrates and biomass partitioning, and some studies document this specific behavior. The differences in root starch concentrations between the most vigorous and least vigorous rootstocks were uncovered in a preliminary study (DeJong 2006, personal communication). The differences observed in early spring shoot growth of trees on different rootstocks (Basile et al., 2003, Weibel et al., 2003; Balkhoven-Baart and Maas, 2004; Massai and Loretto, 2004) and the knowledge that this spring growth is largely dependent on overwintering stored starch (Koslowski, 1992; Nzima et al., 1997) suggest that differences in scion growth could be attributed to the rootstock effect.

### **Hydraulic conductivity**

The mechanism of dwarfing due to rootstocks in fruit trees seems to be related to the hydraulic status of the whole tree, where water uptake and transport play a central function. Different studies have attempted to explain the dwarfing mechanisms using the water status theory as far back as 30 to 40 years ago (Avery 1969, 1970).

Water relations were studied in apple rootstocks by Olien and Lakso (1984). They suggested that differences in mean midday stem water potential could be attributed to reduction of water flow due to graft union or root resistance. In another study, apple canopy conductance was lower in apple trees grafted on M.9, a more dwarfing rootstock, compared to trees grafted on the more vigorous MM.106 and Hashabi rootstocks. (Cohen and Naor, 2002)

In peaches and pears, Chalmers et al. (1984) found that when water stress was applied, shoot growth was markedly reduced but the number of fruits and fruit growth was not reduced as much as shoot growth. Similar results were found by Avery (1969, 1970) where number and size of fruits were not affected as much as vegetative growth when apple trees grew on dwarfing rootstocks. These two papers in peach, pear and apple, suggested that dwarfing rootstocks may reduce the scion water potential in the same way the tree reduces shoot growth when it is affected by water stress conditions.

The primary effect of water deficits is the reduction of expansive growth (Hsiao, 1973, Hsiao and Xu, 2000). Tissue growth involves some biochemical processes such as solute transport and wall loosening and formation, in addition to physical parameters (turgor pressure and water transport) (Hsiao and Jing, 1987, Hsiao and Xu, 2000).

Seasonal growth is assumed to be the integrated result of diurnal growth over many days (Berman and DeJong, 1997b). Temperature, solar radiation and water status of the plant affect the diurnal growth (Hsiao and Bradford, 1983; Hsiao, 1993; Hsiao and Xu, 2000; McDonald et al., 1991; Tsuda and Tyree, 2000). Diurnal changes in plant water status have been described for many species including perennial plants (Panterne et al., 1998) and peach trees (Chalmers and Wilson, 1977; Larson et al., 1988; Berman and DeJong, 1996, 1997ab; Basile et al., 2003; Weibel et al., 2003). Simmoneau et al. (1993ab) found that the diurnal variations in peach tree stem diameter were correlated with water potential changes in the same tree and a lag of ten minutes was observed between changes in the plant water potential and in the stem diameter. In another study, vegetative growth was clearly reduced when water stress was applied to peach trees

(Chalmers et al, 1984; Berman and DeJong, 1997a). Berman and DeJong (1997b) modeled peach stem growth rate using temperature and stem water potential as the main variables to predict the daily stem growth. These results showed that under constant stem water potential, temperature affected the growth rate, but changes in the stem water potential markedly influenced the extension growth of stems. In the same work, it was demonstrated that the pattern of peach diurnal growth rate was similar for plum, apricot, almond, prune and cherry. Water relations studies of 'Empire' apple on five different rootstocks (Olien and Lakso 1984) indicated that stem water potential of the most dwarfing rootstocks were lower than the more vigorous rootstocks, especially at midday and the first hours of the afternoon; however, no differences in stem water potential were recorded among rootstocks in the early morning and in the evening.

It has been shown that under conditions of high air humidity and soil field capacity the water potential of peach trees growing under different rootstocks (dwarf to invigorating ones) tends to equilibrate (Basile et al., 2003a; Weibel et al., 2003). Under conditions of high air humidity, low temperatures ( $< 30^{\circ}\text{C}$ ), and soil field capacity the water potential of peach trees growing under different rootstocks (dwarfing to vigorous) tends to equilibrate (Basile et al., 2003; Weibel et al.; 2003). Under this low transpiration condition, where the water status of the tree would be maximum, there would be a small effect of the hydraulic resistance in all the trees, so the vegetative growth would not be affected. However, when the air humidity is reduced and temperature increased, the transpiration increases and concurrently the gradient of water potential between soil and leaves also increases (Tyrré and Ewers, 1991). Under this last condition, the hydraulic

resistance should be over expressed in the more size-controlling rootstocks causing a reduction of scion growth. In many cases, the reduction in hydraulic conductivity will reduce the carbon uptake and growth potential (Clearwater et al., 2004; Hubbard et al., 2001; Sperry 2000), suggesting this could be another effect produced by dwarfing rootstocks.

The differences in water potential at midday, which were mentioned earlier, could be produced by high hydraulic resistances at the graft union or root level, and may partially explain the mechanism for the reduction in the diurnal extension shoot growth rate. In general, most studies on the hydraulic architecture of trees have not taken into account the presence of two genetically different tissues. Most studies assume continuous vascular systems, where the estimation of conductance and resistance appear to follow some continuity (except at node levels) (Tyree and Ewers 1991). However, the graft union has a high degree of discontinuity, which could have strong effects on water flow, particularly when dwarfing rootstocks are involved. Olien and Lakso (1984) suggested that differences in mean midday stem water potential were a result of reduced water flow due to the graft union or root hydraulic resistance. Atkinson et al. (2003) found that root system and graft union were responsible for most of the resistance when a dwarf rootstock was used in apples. In cherries, graft union conductivity was reduced in the graft union when the combinations involved dwarfing rootstocks (Olmstead et al., 2004, 2006). When vines of kiwifruit were grafted on four different rootstocks, they showed a positive correlation between growth and hydraulic conductivity (Clearwater et al., 2004). The graft union in this study did not represent a high resistance to water, indicating that



such a reduction in the water pathway could originate at the roots. However, peaches seem to have a different behavior, showing high resistance in the root system and low resistance in the graft union (Basile et al., 2003b, 2007; Solari et al., 2006ab). Glenn and Scorza (1992) compared the root water resistance of reciprocal combinations of dwarf and vigorous peach cultivars and found that largest phenotypes presented the lowest root water resistance. Basile et al. (2003b) showed that the reduced midday water potential of size-controlling rootstocks was most likely from reduced hydraulic conductance at the root level.

#### **Graft union anatomic structure**

The main tree structures involved in water transport from the rootstock to the scion are the roots and the graft union. Vessels are the most important elements involved in the transport of water in vascular plants (Comstock and Sperry, 2000). By increasing the number and size of the vessels, the hydraulic conductivity is higher. A similar result occurs if the conducting elements have a clear continuity along the different tissues (roots, graft union, trunk). Zimmermann (1983) supported the theory that vessel size (cross-sectional area), vessel number and total vessel surface might well affect the efficiency of water conductance by roots, indicating that a larger total cross-sectional area of vessels should facilitate transport of greater volumes of water per unit time to the scion.

Studies with apples and cherries suggest that dwarfing interstocks and rootstocks are associated with a marked depletion of the constituents of xylem sap compared to vigorous rootstocks, and the graft union with the scion appears to contribute to this effect

(Olmstead et al., 2004, 2006ab). In cherries, rootstock vigor decreased as vessel surface decreased (Olmstead et al., 2004, 2006ab). Childers (1983) found less cross-sectional area of the xylem root tissue and smaller and fewer xylem vessels in dwarfing rootstocks compared to the more vigorous ones. Also in apple, graft union resistance was related to high hydraulic resistance and reduced active xylem when trees were grafted on dwarfing rootstocks (Atkinson et al. 2003). In this work, the total area of stained stem xylem, calculated as a percentage, was significantly greater for the semi-vigorous rootstock (MM.106, 47%) compared to the dwarfing one (M.27, 24%). The measured reduction in stained area of the scion stems grafted onto dwarfing rootstocks (M.27) relative to those on semi-vigorous rootstocks indicated a reduction in the functional area of xylem above the graft union.

Tissues showing abnormal growth might indicate the effect of dwarf rootstocks on apple cultivar (Simons, 1986). Simons (1986) working in one-year-old apple trees found that the outer bark of the graft union of dwarf rootstocks was thicker than the semi-dwarf ones, and their phloem was hardly functional compare to the invigorating rootstocks. In the same research it was found that the vascular tissues showed a swirling pattern and some senescent tissues became important at this level. Differences in vessel frequency and lumen area in graft union tissues were smaller in ‘Rainer’/’Gi 5’ (dwarfing combination) cherry than in ‘Rainier’ grafted on the non-dwarfing rootstock, ‘Colt’ (Olmstead et al., 2006a). Also, when ‘Lapins’ cultivar grew on ‘Gi 5’ rootstock (dwarfing) the vascular elements tended to grow obliquely to the longitudinal axis of the tree, and the xylem vessel elements had smaller diameters than those trees on ‘Colt’

rootstock (vigorous). These abnormal structures in the vascular system have been suggested to be involved in some kind of incompatibility present at the beginning of the formation of the graft union or during the subsequent growth as consequence of biochemical or physiological interaction between the two tissues (Simons and Chu, 1984).

A common feature of dwarfed apple trees is the swollen, distorted tissues composed mainly of xylem elements that are produced in the region of the graft interface between rootstock and scion (Jones 1986). Soumelidout et al. (1994) studied the early development of graft unions in the apple cultivars 'Gala' and 'Bramley'. These cultivars exhibited pronounced differences in the pattern of xylem production during subsequent growth when they were grafted on different rootstocks. In the case of M.9 (dwarf rootstock), the xylem linking the bud to the rootstock contained fewer vessels than in the semi-dwarfing MM.106. In other work, where the apple cv 'Golden Delicious' was grafted on apple seedling, MM.106, M.26, M.7 and M.9 rootstocks, the more vigorous rootstocks had longitudinal orientation of vascular tissues with normal cambial development occurring between the stock and the scion while the more dwarfing rootstocks exhibited swirling phloem, abnormal orientation of the xylem rays and different degrees of necrosis within the graft union (Ussahatanonta and Simons, 1988). Beakbane and Thompson (1939) reported that xylem vessel size and number in the scion was not significantly different among rootstocks, but they showed a tendency of the biggest xylem elements to belong to the more vigorous apple rootstocks. A later work of these authors probed the living tissue in the wood and bark of roots, which was found to

be related to the vigor and fruitfulness of the scion variety (Beakebane and Thompson, 1947).

In peaches, some works showed that most of the hydraulic resistance is found in the roots instead of the graft union. Roots represented the major resistance to water flow when different peach rootstocks were compared by Basile et al. (2003). In addition, the dwarf rootstock recorded a higher water resistance when it was compared with the vigorous one, but no anatomical studies were done. Rieger and Litvin (1999) comparing plants from different genus found a negative correlation between root hydraulic conductance and root diameter. More recently, Basile et al. (2007) and Solari et al. (2006ab) confirmed earlier studies on peaches where the highest hydraulic resistance was found in the root system.

However, dwarfing mechanisms supporting the theory that roots are involved in reducing the size of the scion have been controversial when interstems are used. Different reports, in apple (Czynczyk, 1980; Seleznyova et al., 2003) and citrus (Camara et al., 2003ab) showed an effect of interstems. Thus, the effect of interstems should be considered in future studies that investigate dwarfing theories.

### **Radial and axial transport**

In most cases when considering a whole plant, the highest resistance to water transport occurs in the root system (Liu et al., 1978; Pasioura, 1988). There are two main components in the movement of water: the axial and radial conductance. The first component represents the movement of water through the vessel elements up to the stem

and the second one belongs to the conductance of water from the root surface to the xylem vessels.

In general, the axial conductance in fruit trees is assumed to be large enough to not limit the water pathway due to secondary radial growth, which increases the number of xylem vessels (Vercambre et al. 2002). These authors, working with a peach cultivar grafted onto 'Damas GF 1869' plum rootstock, found that the woody roots had higher conductance than the fine roots. They concluded that fine roots had the highest resistance to the axial water movement. However, they agreed that axial resistance does not limit the transport of water unless some limitations were present such as very deep soil (Jackson et al. 2000) or some kind of restriction of the root system that might reduce the water flow (Yamauchi et al., 1995). In the same work, the authors found a positive correlation between root diameter and conductance; however, the slope was lower for the fine roots. Fine roots had larger variability in conductance due mainly to the difference in the number of vessels as compared to woody roots.

Green and Clothier (1999) developed an experiment where they examined the spatial and temporal pattern of water uptake in a mature apple orchard. They found that when the soil was uniformly wet, 70% of the water uptake belonged to the roots localized in the first 0.40 m as well as 70% of the fine roots were also in this first soil layer. They measured the water flow of roots and found significant variability among roots. Additionally, when they dried half of the soil (one side row of the tree) the uptake of the roots in the wet part increased almost two-fold. In the same study when water was applied again, the roots that were inactive in the drier soil recovered to the original uptake

within hours. This suggested there was a complex mechanism involving water uptake and conductivity in the root system.

Frensch and Hsiao (1993) found that the highest resistance to water movement was in the radial flow unless the tracheid elements are cavitated during water stress or the roots were very long. The water from the soil to the lumen of xylem vessels needs to travel through complex pathways that involve both apoplastic and symplastic mechanisms (Taiz and Zeiger, 2006). Water flow variation should depend on the apoplastic or cell-to-cell pathways and this variation needs to be related to the different species (Barrowclough et al., 2000; Steudle and Peterson, 1998). One likely candidate to modify the cell-to-cell path is the water channel, which modifies the membranes conductance. These water channels are represented mainly by transmembrane proteins, which allow passive movement of single water molecules through plasmalemma and tonoplast membranes that are generally called aquaporins (Clarkson et al., 2000; Tyerman et al., 1999; Vandeuleur et al., 2005; Taiz and Zeiger, 2006; Kaldenhoff et al., 2008).

Aquaporins are proteins that belong to the major intrinsic proteins (MIP) family. In this family, two different protein groups have been identified in the plasma membrane and in the tonoplast: the plasma membrane intrinsic protein (PIPs) and the tonoplast intrinsic protein (TIPs), respectively. Aquaporins form a large family with 35 members in higher plants. In Arabidopsis, 35 aquaporin genes have been identified; while in maize 36 genes have been reported (Chaumont et al., 2005). It is estimated that over 50% of the plant water needs travel through aquaporins in root membranes and in membranes

associated with sugar and water storage (Vandeleur et al., 2005). Aquaporins have been shown to control the transport of water from roots to leaves, and also regulate other processes such as transport of assimilates into the sieve elements. In addition, they are involved in the regulation of permeability to CO<sub>2</sub> and hydrogen peroxide, boric acid uptake, transport of small alcohols, closure or aperture of stomata, movement of the leaves and control of cytoplasmic homeostasis (Tyerman et al., 2002).

These water channels also have been shown to be interconnected with ABA signal transduction (Kaldenhoff et al., 2008). HgCl<sub>2</sub> was found to block most aquaporins by binding to the sulfhydryl group (SH) of Cys residues located in the proximity of the aquaporin pore. Several experiments showed a decrease of 20 to 90% in the movement of water (Javot and Maurel, 2002). In corn, it was found that oxidation by hydrogen peroxide (H<sub>2</sub>O<sub>2</sub>) reduced dramatically the water flow in roots and cortical cells (Henzler et al., 2006). Eight cDNA encoding putative aquaporins were studied in the stress tolerant *Vitis* hybrid rootstock 'Richter-110' by Baiges et al. (2001). The authors found that most of the aquaporins had higher expression in roots rather than in stems and leaves. Aquaporins were associated with water transport between xylem parenchyma cells and embolized vessels in walnut (Sakr et al., 2003). In addition, aquaporins seem to be related to differences in growth associated with dwarfing rootstocks in olives (Lovisololo et al., 2007). These authors found a clear correlation between the dwarfing rootstock and low aquaporin expression; whereas, the expression of aquaporins was high when the vigorous rootstock was considered. Importance of aquaporins is still probably underestimated due their relativity recent discovery.

### **Interstems and budding height**

The effects produced by dwarf rootstocks on apples, pears, cherries, plums and peaches have been well documented; however, fewer studies have taken in account the effect of interstems (interstocks) since most of the focus has been on the roots and graft union. In general, interstems have been used to overcome incompatibility between rootstocks and scions, such as for pear cultivars ('Williams' or 'Bartlett') on quince rootstocks. In this case, when an interstem is used ('Old Home' or 'Beurre Bosc') the three-graft combination is completely compatible and tree growth is normal (Hartman et al., 1998).

Clonal dwarfing rootstocks for pear and apple reduce scion growth when used as interstock (Olmstead et al., 2004, 2006ab) (or interstems) and the longer the interstock length, the greater is the effect (Webster, 1995). Some studies have demonstrated that the length of the dwarfing interstem controlled the tree size (Parry and Rogers, 1972; Carlson and Oh, 1975). Most interstem research has been done in apples (Czynczyk, 1980; Seleznyova et al., 2003, 2008; Tojnko et al., 2004) showing that interstems affect tree growth and fruit quality. More recently, other fruit species have been tested by using interstems such as in cherries (Rozpara and Grzyb, 2004) and citrus (Cámara et al., 2003ab, 2004; Gil-Izquierdo et al., 2004) and several in peaches (Yano et al., 2002; Rufato et al., 2006). Interstems not only affect tree growth and fruit quality, they increase tolerance to salt in citrus (Cámara et al., 2003a, 2004) and cold resistance in apples (Webster and Wertheim, 2003). In two sweet cherry cultivars, 'Van' and 'Buttner's Red', which were grafted on several interstems and two common rootstocks,



*Prunus avium* and *P. mahaleb*, leaf mineral content except for phosphorous was found to be different because of the interstem (Rozpara et al., 1990). It is apparent that interstocks could produce similar results as rootstocks (Czynczyk, 1980), indicating that there is a common effect, which might not be related only to roots as most of the works suggest.

A similar increase in scion dwarfing, at least with apple and pear, is associated with stem characteristics of the rootstock and is not entirely attributable to its root characteristics (Webster, 1995). Recent studies have reported the effect of the increase of budding height on the shank or stem of a dwarfing rootstock (Mielke and Smith, 2002; Hrotko and Maguar, 2004; Kviklys and Lanauskas, 2007; Kviklys et al., 2007). Hrotko and Magyar (2004) suggested that the budding height effect might be the result of the longer rootstock portion (shank) exposed to the sun. These authors planted at different depths 'Idared' apples trees grafted at 30 cm from the root system. The authors suggested auxin transport loss and decomposition in the rootstock bark was believed to be higher due to sun exposure. In another study, buried apple interstocks gave a reduction of 15% in tree growth compared to the exposed ones (Domoto, 2001). Overall, the majority of grafting height studies have been done in apple trees where there is a reduction in growth as the budding height is increased (Parry, 1986; Kumar and Ananda, 2004; Sosna, 2004; Kviklys et al., 2007). Budding height did not affect scion growth in the first growing season when Kviklys et al. (2007) studied young 'Auksis' apple trees grafted at 0, 10, 20 and 30 cm from the ground. However, in the same study budding height reduced scion growth in the second and third season. In another study, budding height did not follow a clear pattern when Grzyb et al. (2002) budded two plum cultivars

at 10, 20 and 30 cm from the ground. This work showed that 'Bluefre' plum trees grew the least when they were budded at 30 cm; whereas, 'Ammers' plum trees had the most vegetative growth when they were budded at 10 cm. Besides other factors, budding height had significant effects on the growth and yield characteristics observed primarily in apple trees; however, peaches were not included in any of those studies.

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## CHAPTER III

### DORMANT CARBOHYDRATE RESERVES OF TWO PEACH CULTIVARS GRAFTED ON DIFFERENT ROOTSTOCKS

#### **Introduction**

The increasing density of the orchard plantings to obtain high yields and accompanying high cost of the manual operations emphasized the necessity of size-controlling rootstocks. In past decades, apple researchers and farmers introduced spur cultivars and dwarfing rootstocks to control tree size. Small plants made high-density apple plantations widespread in Europe and America. The use of small trees reduces cost of hand labor for pruning, thinning and harvest, while inducing precocity, making high-density plantations economically advantageous (Reed, 1975; Hayden and Emerson, 1976; Green, 1991; and DeJong et al., 1999). Unlike apples, there are no widely acceptable size-controlling rootstocks for peaches. New peach rootstocks have become available from Europe since two decades but their use is still very limited because of the restricted range of compatibility among cultivars (Felipe, 1989; Loreti, 1994).

There are different theories on rootstock dwarfing mechanisms (Lockard and Schneider, 1982; Crabbé, 1984; Rom and Carlson, 1987; Atkinson and Else, 2001; Atkinson et al., 2003; Webster and Wertheim, 2003). One potential mechanism that could influence scion vigor when budded to different rootstocks is the capacity of the

rootstock to store carbohydrates. 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 (DeJong, 2006, personal communication). The differences observed in early spring shoot growth of trees on different peach rootstocks (Weibel et al., 2003; Balkhoven-Baart and Maas, 2004; Massai and Loretto, 2004; Reighard et al. 2006) and the knowledge that this spring growth is largely dependent on overwintering stored starch indicate a rootstock TNC and scion vigor interaction.

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). Carbohydrate reserves 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, 1996). 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. These reserves are mobilized during the winter and finally depleted as new leaf and shoot growth starts in the spring (Loescher et al., 1990). 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).

Allocation of reserves to roots can be influenced by several factors: carbohydrate biochemistry, respiration, hormones, phloem loading and unloading, and genetic control (Friend et al., 1994). Water availability, light, nutrition and temperature exert an influence over the allocation of carbohydrates and can modify the shoot/root ratio in woody species (Tromp, 1983 ; Keller and Loescher, 1989; Friend et al., 1994; Jordan and Habib, 1996; Tagliavini et al., 1999; Esparza et al., 2001; Allen et al. 2005, Cheng and Fuchigami, 2002; Eschenbach, 2005; Dichio et al., 2007 and Génard et al., 2007). In addition, it is well known that cultural practices, such as fertilization, girdling, pruning and fruit thinning can modify the allocation of reserves (Priestly, 1976; Worley, 1979; Schnelle and Klett, 1992 and Tagliavini et al., 1999).

Numerous studies have described carbohydrate accumulation in forest trees (Hansen et al., 1996; Kainulainen et al., 1998; Kosola et al., 2001; Piispanem and Saranpää, 2001; Li et al., 2002; Jäggi et al., 2002 and Newell et al., 2002) and showed that early spring growth is highly dependent on remobilization of stored carbohydrate reserves in woody species. Barbaroux et al. (2003) found significant differences in the amount of reserves used by oaks and beeches. Oaks used double the amount of reserves from October to June, probably due to differential needs for spring growth and winter maintenance between these two genera. However, fewer studies related to nonstructural carbohydrates have been done on fruit trees where fruits can exert a fundamental effect because they are the most powerful sink for carbohydrates. Lacoïnte et al., (1993)

studied three-year-old potted walnut trees and analyzed starch and soluble sugars from different organs. In autumn, 90% of the reserves were located in roots, primarily in the taproots. Significant hydrolysis of starch to soluble sugars occurred in winter, mainly at the end of the dormancy period to help support the new growth.

Large differences in starch and soluble sugar degradation has been reported between pistachio trees with heavy crops ('on') and light crop loads ('off') (Nzima et al., 1997). Soluble sugars and starch in "on" trees declined in all organs (leaves, inflorescence buds, rachises, 1-year old wood, and primary and tertiary branches and roots) as nut growth occurred. In contrast, all organs in "off" trees accumulated greater concentrations of soluble sugars and starch indicating a strong effect of the fruit on the allocation of reserves.

Conditioning of the previous season's growth altered the availability of carbohydrates for initial spur foliage development in spring of 'Golden Delicious' trees (Tustin et al., 1992). When natural or artificial shade was applied around fruiting spurs, both in the previous season and in the current year, the foliar number of leaves produced on the spurs was reduced. This reduction in number of leaves was attributed to an early termination of bourse shoot growth of the previous-season shaded spurs.

Changes in the distribution of dry mass in fruit trees may be attributed to rootstocks, which can alter the relative proportion of carbohydrates allocated to fruits, shoots, branches, trunk or roots (Forshey and Elfving, 1989). Palmer (1992) found that increases in crop load of "Crispin" apple on M.27 rootstock slightly reduced leaf dry matter production and had a large reduction in shoot and root dry weight. In addition, he



found that root growth appeared to be reduced more than shoots, and this effect was more pronounced in the dwarfing rootstocks compared to vigorous rootstocks. On the other hand, Barden and Ferree (1979) did not find differences in photosynthesis, dark respiration and transpiration of apple trees grafted onto several rootstocks, but they worked with trees confined to small containers, which might have altered the normal development of those trees, thereby reducing the chance to express normal tree growth.

In peach trees, heavy crop loads increased the proportion of dry mass in fruits relative to shoots and roots more in size-controlling rootstocks compared to vigorous ones (Inglese et al., 2002 and Weibel, 1999). In winter, root starch concentration of 'Redhaven' peach trees was significantly different among three different vigorous rootstocks (Ellis, 1993). Total nonstructural carbohydrate concentration in roots did not show a relationship to rootstocks. The observed changes in TNC depended on the sample date (Ellis, 1993). In the same study, the concentration of starch and total nonstructural carbohydrates were higher in roots than shoots.

Preliminary studies on size-controlling rootstocks of peach showed a high correlation between dormant season root carbohydrate storage and characteristics of tree growth associated with several rootstocks (DeJong, 2006, personal communication). Peach trees grafted on *Prunus tomentosa* (dwarfing rootstock) had lower root TNC compared to trees grafted on *Prunus persica* (vigorous rootstock) (Yano et al., 2002). They also found that roots smaller than 2-mm-diameter had high TNC concentration. However, Gaudillère et al. (1992), working on a range of size-controlling rootstocks for

prune trees, could not demonstrate any correlation between the rootstock vigor and level of carbohydrate reserves in the perennial parts before spring bud burst.

Seasonal patterns of carbohydrate concentrations in perennial tissues have been reported to be quite similar for several fruit tree species such as pistachio (Nzima et al., 1997), cherry (Roper et al., 1988 and Keller and Loescher, 1989), apple (Tromp, 1983 and McQuen et al., 2004), pecan (Worley, 1979), walnut (Lacointe et al., 1993) and peach (Layne and Ward, 1978; Ellis, 1993; Jordan and Habib, 1996; Marquat et al., 1999 and Yano et al., 2002). 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.

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. It is hypothesized that dormant season rootstock total non-structural carbohydrates storage capacity is functionally associated with scion vigor characteristics of a range of size controlling rootstocks, where dwarfing or size-controlling rootstocks could store less carbohydrates than the more invigorating rootstocks. It is expected that more carbohydrates are stored in roots compared to the above ground tissue mass.

## Materials and methods

### Experiment one: Shoot and root TNC of adult bearing peach trees

Four-year-old peach trees [*Prunus persica* (L.) Batsch cv. Redhaven] and five-year-old peach trees [*Prunus persica* (L.) Batsch cv. Redtop] 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, and they were planted at 5 m x 6 m. Lovell (*Prunus persica*), Pumiselect® (*P. pumila*), Krymsk® 1 (formerly called VVA-1) (*P. tomentosa* x *P. cerasifera*), Cadaman®-Avimag (*P. persica* x *P. davidiana*), Controller® 5 (formerly called K-146-43) (*P. salicina* x *P. persica*) and Cornerstone (formally called SLAP) (*P. persica* x *P. dulcis*) were used as rootstocks. Cadaman® and Cornerstone were vigorous rootstocks, Lovell had standard vigor, Pumiselect® and Controller® 5 had intermediate vigor, while Krymsk® 1 was the most size-controlling rootstock (least vigor).

Stem and root samples were taken in January 2006 from trees at the three research sites (January 12, 20 and 24 for California, South Carolina and Georgia respectively). Each sample was a composite of 3 shoots or 3 roots per tree. Depending on the site and combinations, 4 to 8 trees were used at each site as replicates. Stem samples were taken from sun-exposed “hangers” (i.e. shoots) located at about 1.5 m from the ground. Four- to 6-mm-diameter shoot sections of about 15 cm in length were taken from the middle part of one-year-old shoots. Four- to 6-mm-diameter roots were collected at 40 to 60 cm

from the trunk and at a depth of 5 to 15 cm. In addition, samples from 'Redhaven' trees at the Musser Fruit Research Center were collected for TNC analyses on 15 December 2006 and 20 January 2007 to compare with those taken the prior winter.

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. Trunk bark was sampled by removing the bark patch from the cylinder. Trunk wood was sampled by removing a core of 10 mm depth. Samples were taken from trees grafted on Lovell, Pumiselect®, Controller® 5 and Krymsk® 1 rootstocks.

#### **Experiment two: Shoot and root TNC of young non-bearing trees' shoot and root sampling**

One-year-old 'Redhaven' peach trees grafted on Lovell, Pumiselect®, Krymsk® 1 and Cadaman® were planted in January 2006 and used for nonstructural carbohydrate studies in January 2007. Trees were planted in double rows at 1.5 m x 1.5 m in the row and 6 m between rows. Three shoots and three roots similar to adult trees were used to study the concentration of total nonstructural carbohydrates from the one-year-old trees on different dates (19 December, 2006, 20 January, 2 February and 14 March 2007) during the Winter of 2006-07.

#### **Experiment three: Young non-bearing trees' analysis of total TNC**

In a third experiment, whole trees planted at the same time and distance as previously described were removed from the ground in January 2007 after a season of growth. The above ground material was separated into three different groups: 1) shoots

with diameter less than 7.5 mm; 2) shoots with diameter between 7.5 and 15 mm; and 3) shoots with diameter greater than 15 mm. Roots were divided into two groups: - Primary, which included the main root system originating from the graft union (including the rootstock trunk), and secondary roots, which represented all the roots coming from the main system. Fresh weight of all groups of material were determined and then the material was dried at 60°C for at least 2 weeks before grinding as previously described. Carbohydrate analyses were also done as described previously for adult trees. Six trees per treatment were analyzed.

#### **Experiment design and data analysis**

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. Data were analyzed by SAS (9.1 version) using the GLM procedure.

All samples were frozen in liquid nitrogen, stored at -70°C and subsequently freeze-dried. Dried samples were ground with a Wiley Mill (Thomas® Wiley® Mini-Mill) through a 40-mesh screen. Ground plant tissues were stored in a desiccator.

Nonstructural carbohydrates were determined as described by Somogyi (1926, 1936 and 1945) and Nelson (1944). Two to three sub-samples of 50 mg each were used from each treatment for TNC analysis. For each sample 5 ml ethanol 80% and 10 ml Na-acetate buffer (pH 4.5) were added and boiled for 2 hours in a water bath. After cooling, 1 ml each of invertase (5 units ml<sup>-1</sup>) and amyloglucosidase (50 units ml<sup>-1</sup>) were added. The samples were incubated for 3 days at 45°C with periodic stirring to break down starch and complex sugars to glucose. After a 3-day incubation period, 25 µl of

supernatant were placed into a test tube and 1 ml of Copper Reagent added and boiled for 2 hours in order to reduce the copper by glucose. After boiling, 1 ml of AMSO reagent was added to react with the reduced copper. The solution was cooled and the absorbance was measured at 520 nm. Glucose in samples was quantified against glucose standards of 0, 50, 100, 250, 500, 1000 and 2000 ppm.

## Results

### Shoot and root TNC of adult bearing peach trees

Shoot total nonstructural carbohydrates (STNC) concentration of 'Redhaven' and 'Redtop' trees did show interaction between rootstocks and the three places (CA, GA and SC). At Byron, GA, shoot TNC concentrations varied from 94 to 124 mg g<sup>-1</sup> dry weight (DW) and was not different among rootstocks. In California, 'Redhaven' trees grafted on Pumiselect® and Krymsk® 1 rootstocks had the highest significant accumulation of shoot TNC (134 and 135 mg g<sup>-1</sup> DW respectively) while Cadaman® and Lovell had the lowest (114 and 116 mg g<sup>-1</sup> DW respectively). Shoots from 'Redtop' trees were not significantly different with regard to the accumulation of carbohydrates, and shoot TNC values ranged from 84 to 110 mg g<sup>-1</sup> DW. Shoot TNC of 'Redhaven' or 'Redtop' were not significantly different in trees grown at the Musser Fruit Research Center in South Carolina (data not shown). Shoot TNC values ranged from 76 to 129 mg g<sup>-1</sup> DW.

Root TNC of 'Redhaven' trees had a significant interaction between locations and rootstocks (Table 3.1). Higher root TNC concentration was found in trees grown at

California compared to those grown at GA or SC. Root TNC concentrations were the highest in Lovell and Cadaman®, while Pumiselect® had the lowest TNC concentration and Krymsk® 1 intermediate TNC concentration (Table 3.1).

Roots from 'Redtop' trees grafted on Cornerstone (SLAP) rootstock had the highest TNC concentration in GA and SC, while the lowest concentrations were found in Pumiselect® and Krymsk® 1 roots. Lovell roots had intermediate concentrations at Georgia and SC (Table 3.2). In California, 'Redtop' trees on Lovell rootstock had the highest concentrations of root TNC; while Pumiselect® roots had the lowest concentration. In Redtop trees growing in South Carolina, significant differences were found in the different root genotypes (Table 3.2), with the more vigorous rootstocks having more TNC than less vigorous ones.

Samples collected from 'Redhaven' trees at Musser Fruit Research Center on two different dates (15 December 2006 and 20 January 2007) indicated that shoot TNC was significantly greater in those grafted on Cadaman® than trees on Controller® 5 and Pumiselect® (Table 3.3). On the same dates, Lovell roots had the highest concentration of total dormant nonstructural carbohydrates and Krymsk® 1 roots the lowest.

When the concentrations of TNC were studied on 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 3.4). When similar tissue was compared among the different rootstocks, Lovell generally had higher concentrations of total dormant nonstructural carbohydrates (Table 3.4). Scion bark tissues from 'Redtop' trees grafted

on Lovell rootstock had the greater concentration of TNC, while than on Controller® 5, Pumiselect® or Krymsk® 1. 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.

The concentration differences of TNC in similar tissues above and below the graft union was analyzed in order to determine if there was an effect of the graft union on the accumulation of TNC above and below the graft union in the 'Redtop' trees grafted on four rootstocks (Table 3.4). Bark tissues of Lovell and Pumiselect® had significantly larger differences between the TNC accumulated above and below the graft union compared to Krymsk® 1 and Controller® 5. In general, bark tissues had larger differences in TNC concentrations compared to the wood (Table 3.4). Woody tissues from trees grafted on Pumiselect® and Lovell rootstocks had significantly larger differences in TNC than Krymsk® 1. Moreover, Krymsk® 1 was the only rootstock which had an inverse concentration of TNC; that is, it was higher in the scion than the root (Table 3.4).

#### **Experiment two: Young non-bearing trees' shoot and root sampling**

During Winter 2006-2007, one-year-old peach trees grafted on different rootstocks were analyzed for the content of TNC in different tissues. Five-mm-diameter roots at all sample dates had significantly higher concentrations of TNC in Lovell roots compared to the rest of the rootstocks (Fig. 3.1). Lovell roots had the highest



concentrations while Krymsk® 1 the lowest. Root TNC concentrations increased until 20 January 2006, and after that they declined (Fig. 3.1). 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.

### **Experiment three: Young non-bearing trees' analysis of total TNC**

Concentrations of TNC in dormant shoots with <7.5-mm-diameter and those with >15-mm-diameter were not significantly different among the three studied rootstocks. Only shoots between 7.5- and 15-mm-diameter on Krymsk® 1 had significantly lower TNC concentrations than Lovell and Pumiselect® (Table 3.5). The main root system (tap root) and the rest of the roots (smaller roots) on Krymsk® 1 had significantly lower TNC concentrations than the other two rootstocks (Table 3.5).

'Redhaven' trees grafted on Lovell had the greatest total dry weights (Table 3. 6), while those on Krymsk® 1 and Pumiselect® had the least. However, trees on Krymsk® 1 tended to produce the smallest dry weights. When the TNC of all tissues were analyzed, trees grafted on Lovell rootstocks had the highest TNC values (Table 3.7). Trees on Pumiselect® tended to have higher amounts of TNC in all tissues than Krymsk® 1, although the differences in the first year in the field for these trees were not statistically significant.

Figure 3.2 shows the distribution by percentage of TNC in the different dormant tissues of one-year-old 'Redhaven' trees on Lovell rootstock. 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. The distribution of TNC in the trees was similar when the shoot/root TNC ratio was analyzed. Shoot: root ratios were 0.47, 0.48 and 0.49 for trees on Lovell, Pumiselect® and Krymsk® 1 respectively. The main root had about 20% of the dormant TNC of the root system, while near 80% of the root TNC was concentrated in roots that originated from the main axis (Fig. 3.2).

## **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 (Crane and Al-Shalan, 1977; Gaudillière et al., 1992; Nzima et al., 1997 and Allen et al., 2005). 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 (Kozłowski, 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. Presence of large amount of TNC in trees grown on vigorous rootstocks could support the theory where these rootstocks generate a larger vegetative growth early in the spring, leading to larger trees at the end of the season.

### **Bearing peach trees**

The concentration of TNC found in shoots and roots were similar to those reported in peach by Dichio et al. (2007), Dowler and King (1966), Ellis (1993) and Stassen et al. (1981a,b), in almond by Esparza et al. (2001), in cherry by Keller and

Loescher (1989) and in pecan by Worley (1979). In general, the concentration of TNC in the 5-mm-diameter '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 (Tables 3.1-3.3). The greater partitioning of carbohydrates to fruits reported for the more size-controlling rootstocks (Caruso et al., 1995, 1997; Weibel, 1999) suggests less availability of carbohydrates for root storage in these trees due to the strong sink strength of the fruits.

Even though the tissue samples from mature bearing trees represented a very small fraction of the total mass volume (5-mm-diameter shoots and roots), 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 and pistachio wood (Dowler and King, 1966; Crane et al., 1976, 1977). 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 a higher specialization of root tissue to act as a reserve or sink organ (Tromp, 1983; Loescher et al., 1990; Kozlowski, 1992, 1996). 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.

The pattern of TNC concentrations found in our study in the bark and wood tissues of the scion trunk was similar to those reported for peach by Dowler and King (1966) and Jordan and Habib (1996). Similar patterns also were observed by Keller and Loescher (1989) in cherry trees although the values of TNC were lower than the results obtained in peaches. The more vigorous rootstocks exhibited a clear tendency to have higher concentrations of TNC in bark and wood tissues (Table 3.4). Tabuenca (1973) found that the accumulation of TNC were higher in the scion than in the roots in the cases of graft incompatibility between peach and plums. In our study, the higher concentration of TNC in the root bark and wood tissues compared to those in the scion, suggested that the present combinations were compatible, and the differences in growth were caused by other factors. The larger differences between scion (lower) and rootstock (higher) observed in the bark TNC concentrations for the more vigorous rootstocks indicate either more selective pathways of TNC transport or a higher capacity for carbohydrate storage of root tissues in the vigorous rootstocks due to differences in anatomy.

#### **Young non-bearing trees**

In young non-bearing trees, shoot TNC concentrations among trees on the different rootstocks decreased during the winter (Fig. 3.1). 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, which could allow it to grow earlier in the spring.

Lovell roots always had higher TNC concentrations than the rest of the rootstocks, consistent with the observed values in the 5-mm roots of mature trees. 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. 3.1). The change in the pattern of TNC concentration through the winter was consistent with other studies in peach (Dowler and King, 1966; Stassen et al., 1981ab; Ellis, 1993; Jordan and Habib, 1996; Singh and Kanwar, 2004), where the concentration declined toward the end of winter due to remobilization of carbohydrates from the roots to the growing points (Génard et al. 2007). Root TNC was higher in the young non-bearing trees than bearing trees, possibly due to a greater availability of TNC in non-bearing trees. Moreover, it has been demonstrated that fruiting in general decreases carbohydrate reserves, although there is little evidence of the reduction of carbohydrates in the roots (Goldschmidt and Golomb, 1982; Loescher et al., 1990; Nzima, 1997).

When whole one-year-old 'Redhaven' trees were removed from the soil, the TNC concentration of above-ground tissues (shoots, branches and trunk) did not differ very much; however, the more size-controlling rootstocks tended to have lower values (Table 3.5). In the roots the differences were more marked. The main root and the rest of the roots in the more size-controlling rootstocks had lower concentrations of carbohydrates. 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. TNC concentrations of smaller roots were considerably higher than the main roots on a dry weight basis. In *Quercus*, the carbohydrate reserves varied considerably with the root size, while the starch content of oak roots was inversely related to root diameter (Wargo 1976). Wargo found that as root diameter decreased, the rays were closer together and the proportion of

ray tissue (high starch storage capacity) to woody tissues (low starch storage capacity) was higher. Our data confirmed that shank or main roots had lower concentrations of TNC than the smaller diameter roots. Yano et al. (2002) reported rootstock trunks had lower TNC concentrations than roots that were smaller than 10-mm-diameter. This was the apparent reason for the relatively high amount of carbohydrates found in young trees on Pumiselect® (Table 3.5), which had (at this age) most of its root system dominated by small roots (data not shown), compared to Lovell roots, which were larger in diameter. The distribution of TNC between the root and shoot and the shoot/root TNC ratio in trees grafted on the three different rootstocks was similar (Fig. 3.2) indicating that differences in growth were not due to TNC distribution in the trees.

As mentioned previously, 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 (Table 3.7). The high TNC content in the vigorous rootstock was a consequence of the large dry weight per tree. 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. A comparison of Krymsk® 1 and Lovell data exemplify this concept. Krymsk® 1 had an average root TNC concentration that was 20 % (tap root) to 30% (small roots) less than Lovell, but at the same time, Krymsk® 1 had 70% (main root) and 74% (small roots) less total TNC (g DW tree<sup>-1</sup>) than Lovell. A similar picture develops from an analysis of concentration of carbohydrates and the total TNC per tree in the above ground parts. Krymsk® 1 had 23%

less TNC concentration than Lovell in above ground tissues, but when the analysis considered the total TNC in the above-ground bio mass, Krymsk® 1 had 73% less total TNC than Lovell in those tissues.

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.

Table 3.1. Dormant total nonstructural carbohydrates ( $\text{mg g}^{-1}$  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.

<b>Root TNC concentration (<math>\text{mg g}^{-1}</math> DW)<sup>z</sup></b>	
<b>Location</b>	<b>Means</b>
CA	265 a
GA	237 b
SC	233 b
<b>Rootstocks</b>	
Lovell	321 a
Cadaman	279 a
Pumiselect	207 c
Krymsk 1	232 b
<b>Analysis of variance</b>	<b>Probability</b>
Places	0.0037
Rootstocks	0.00001
Places x rootstocks	0.0206

<sup>z</sup>Different letters within a column indicate significant differences at  $P < 0.05$ .



Table 3.2. Dormant total nonstructural carbohydrate (TNC) concentration ( $\text{mg g}^{-1}$  DW) in 5-mm-diameter roots of adult bearing Redtop trees grafted on different rootstocks at Kearney, California (CA); Byron, Georgia (GA) and Musser Fruit Research Center, South Carolina (SC), in January 2006.

<b>Root TNC concentration (<math>\text{mg g}^{-1}</math> DW)</b>			
<b>Redtop</b>			
<b>Rootstocks</b>	<b>CA</b>	<b>GA</b>	<b>SC</b>
<b>Lovell</b>	313 a	209 b	226 b
<b>Pumiselect</b>	164 d	175 c	-
<b>Krymsk 1</b>	271 b	146 c	188 c
<b>Cadaman</b>	-	-	-
<b>Controller 5</b>	197 cd	-	201 bc
<b>Cornerstone</b>	230 c	249 a	306 a

<sup>2</sup>Different letters within a column indicate significant differences at  $P < 0.05$  (Duncan's multiple range test).

Table 3.3. Total dormant nonstructural carbohydrate (TNC) concentration ( $\text{mg g}^{-1}$  DW) in one-year-old shoots and roots of Redhaven peach trees grafted on different rootstocks at the Musser Fruit Research Center, South Carolina on two different dates (December 15, 2006 and January 20, 2007).

<b>TNC concentration (<math>\text{mg g}^{-1}</math> DW)</b>		
<b>Rootstocks</b>	<b>Roots<sup>z</sup></b>	<b>Shoots</b>
<b>Lovell</b>	246 a	118 ab
<b>Pumiselect</b>	191 b	104 b
<b>Krymsk 1</b>	142 c	114 ab
<b>Cadaman</b>	201 b	121 a
<b>Controller 5</b>	184 b	106 b

<sup>z</sup>Different letters within a column indicate significant differences at  $P < 0.05$  (Duncan's multiple range test).

Table 3.4. Concentration of dormant total nonstructural carbohydrates (TNC) in bark and wood tissues ( $\text{mg g}^{-1}$  DW) and differences in bark and wood TNC concentration between scion and rootstock tissues 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. The same tissues were compared among the different rootstocks.

<b>TNC concentration (<math>\text{mg g}^{-1}</math> DW) in bark and wood tissues among different rootstocks.</b>						
	<b>Scion</b>		<b>Root</b>		<b>Differences between rootstock and scion</b>	
	<b>Bark<sup>z</sup></b>	<b>Wood</b>	<b>Bark</b>	<b>Wood</b>	<b>Bark</b>	<b>Wood</b>
<b>Lovell</b>	296 a	173 a	413 a	214 a	117 a	41 ab
<b>Pumiselect</b>	238 b	154 a	357 b	220 a	119 a	65 a
<b>Krymsk 1</b>	234 b	171 ab	256 c	139 b	22 b	-32 c
<b>Controller 5</b>	236 b	141 b	262 c	166 b	26 b	25 b

<sup>z</sup>Different letters within a column indicate significant differences at  $P < 0.05$  (Duncan's multiple range test).

Table 3.5. Concentration of total dormant nonstructural carbohydrates (TNC) ( $\text{mg g}^{-1}$  DW) in different tissues of one-year-old Redhaven peach trees grafted on three different rootstocks.

TNC concentration ( $\text{mg g}^{-1}$ DW)					
Rootstocks	Shoots <sup>z</sup>			Roots	
	<7.5 mm	7.5-15.0 mm	>15.0 mm	Tap	Small
<b>Lovell</b>	73 a	68 a	72 a	83 a	219 a
<b>Pumiselect</b>	73 a	66 a	66 a	88 a	251 a
<b>Krymsk 1</b>	60 a	51 b	57 a	59 b	176 b

<sup>z</sup>Different letters within a column indicate significant differences at  $P < 0.05$  (Duncan's multiple range test).

Table 3.6. Dry weight (g DW) from different tissues of one-year-old Redhaven peach trees grafted on different rootstocks.

Dry weight in tissues of one-year-old Redhaven trees					
Rootstocks	Shoots <sup>z</sup>			Roots	
	<7.5 mm	7.5-15.0 mm	>15.0 mm	Large	Small
<b>Lovell</b>	604.4 a	458.8 a	1020.6 a	680.4 a	1122.0 a
<b>Pumiselect</b>	352.8 b	263.2 b	488.3 b	249.2 b	457.5 b
<b>Krymsk 1</b>	185.8 b	141.2 c	243.3 b	201.8 b	402.8 b

<sup>z</sup>Different letters within a column indicate significant differences at  $P < 0.05$  (Duncan's multiple range test).

Table 3.7. Weight (g DW/tree) of dormant total nonstructural carbohydrates per tree in different tissues of one-year-old Redhaven peach trees grafted on three different rootstocks.

<b>TNC dry weight (g DW/tree) in tissues of one-year-old Redhaven trees</b>					
<b>Rootstocks</b>	<b>Shoots<sup>z</sup></b>			<b>Roots</b>	
	<b>&lt;7.5 mm</b>	<b>7.5-15.0 mm</b>	<b>&gt;15.0 mm</b>	<b>Tap</b>	<b>Small</b>
<b>Lovell</b>	43.4 a	31.1 a	68.3 a	56.2 a	242.0 a
<b>Pumiselect</b>	20.9 b	12.7 b	27.5 b	21.6 b	118.2 b
<b>Krymsk 1</b>	12.9 b	9.4 b	16.5 b	11.4 b	69.1 b

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

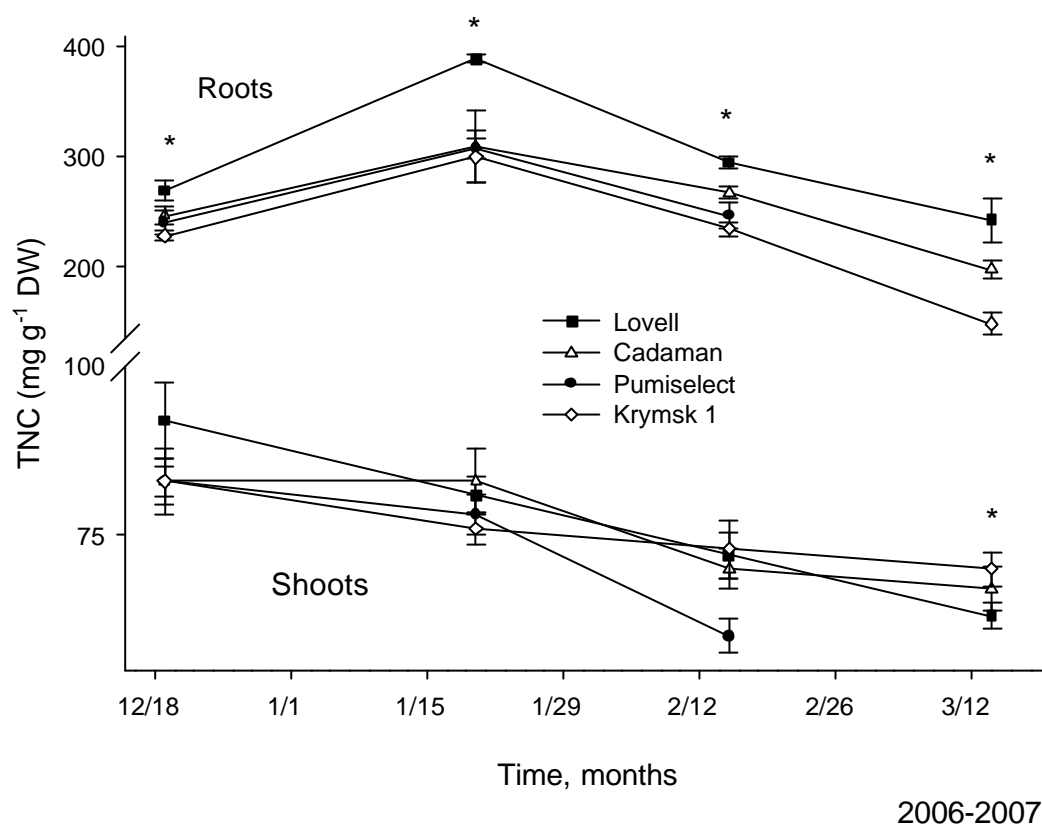


Fig. 3.1. Concentration of nonstructural carbohydrates (TNC) in root and shoot tissues of one-year-old Redhaven trees grafted on different rootstocks in Winter 2006-2007. Standard errors are given for each point. Asterisks represent significant rootstock treatment differences at each point at  $P < 0.05$  (Duncan's multiple range test).

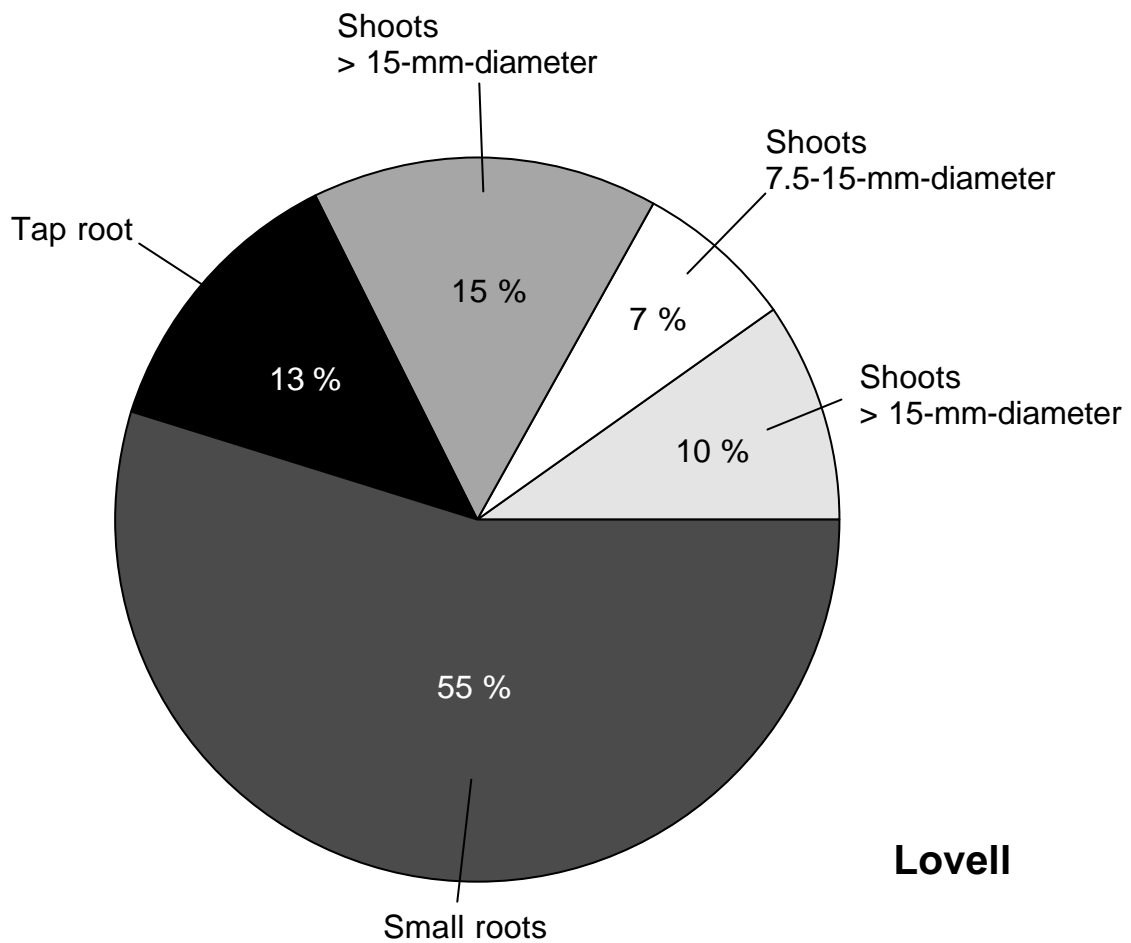


Fig. 3.2. Percentage distribution of total dormant nonstructural carbohydrates in different tissues of one-year-old Redhaven peach trees grafted on Lovell rootstock. Above ground mass: shoots less than 7.5-mm-diameter, shoots between 7.5 and 15-mm-diameter and shoots bigger than 15-mm-diameter. Below ground mass: tap root represents the main root (shank) and small roots were the rest of the roots coming from the main one. One hundred represents total weight of nonstructural carbohydrates per tree.

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## CHAPTER IV

### EFFECT OF INTERSTEM AND GRAFTING HEIGHT ON VEGETATIVE GROWTH OF YOUNG PEACH TREES

#### **Introduction**

Dwarfing mechanism studies have focused mainly on the root and graft unions where hormones, nutrients and water status are correlated with the functionality of these tissues (Soumelidou et al., 1994; Hartmann, 1998; Atkinson and Else, 2001, 2003; Basile et al., 2003; Olmstead et al., 2006ab; Solari et al., 2006ab). The effects of dwarfing or semi-dwarfing rootstocks on apple, pear, cherry, plum and peach scion growth has been fairly well studied but little research has done the effects of interstems (interstocks) and grafting height is not well understood. In addition, most of this type of work has been done on apples, but the literature is sparse on interstem or grafting height effects on peach trees.

In general, interstems have been used to circumvent incompatibility between rootstocks and scions. An example is found in pear trees where some cultivars are not compatible with quince (rootstock), such as the case of ‘Bartlett’ (‘Williams’) when it is grafted on quince for dwarfing induction. In this case, when an interstem is used (e.g., ‘Old Home’ or ‘Beurre Bosc’) the twice-grafted combination is completely compatible, and trees are healthy (Hartman et al., 1998; Wertheim and Vercaemmen, 2000).



In the 1980s in Washington state, several 'Granny Smith' and 'Delicious' apple orchards were top-worked with new and more commercially valuable apple cultivars. Therefore, 'Granny Smith' and 'Delicious' became interstocks in these orchards. Drake et al., (1997), demonstrated that 'Fuji' fruits growing on Granny Smith interstock had higher soluble solids concentration, more red skin color and calcium, and less scald, bitter pit and internal breakdown than fruits grown on 'Delicious' interstems. Taylor (2001) working on several apple interstem and rootstock combinations showed how the interstock affected tree size as much as when the same genotype was used as a rootstock. At the same time, vigorous rootstocks did not vary the scion size when they were used as an interstock, indicating a similarity between the rootstock and interstem effect.

In two sweet cherry cultivars, 'Van' and 'Buttner's Red', which were grafted on several interstems and two common rootstocks, *Prunus avium* and *P. mahaleb*, leaf mineral content was analyzed (Rozpara et al., 1990). Rozpara et al. (1990) found that interstems affected the concentration of all the nutrients in leaves except for phosphorous. Ebel et al. (2000) found apple foliar nutrient differences on trees grafted on different interstocks and rootstocks but only when the nutritional levels were close to toxicity or deficiency. In comparison, 'Verna' lemon trees grafted on seven interstocks experienced only small changes in flavonoid content of lemon juice among the interstem treatments (Gil-Izquierdo et al., 2004).

Interstems reduced final size of 'Valencia Late' orange trees when the cultivar grew on the interstock 'Salustiano' orange (Camara et al., 2003). Also in citrus, other work has showed that the length of the dwarfing interstem controlled tree size (Parry and

Rogers 1972). Most interstem studies have been done in apples (Carlson and Oh, 1975; Czynczyk, 1980; Samad et al., 1999; De Rossi et al. 2003; Seleznyova et al., 2003; Tojnko et al. 2004) and the effects of the interstem were on tree growth and fruit quality. More recently, other fruit species have been tested with interstems including cherries (Rozpara and Grzyb, 2004), persimmon (Koshiva et al. 2006), citrus (Cámara et al. 2003ab, 2004; Gil-Izquierdo et al., 2004), and peaches (Yano et al. 2002, Rufato et al., 2006). Interstems not only affect tree growth and fruit quality; they also increase salt tolerance in citrus due to chloride exclusion (Cámara et al. 2003b, 2004) and improved cold resistance in apples (Webster and Wertheim 2003).

In mango, no differences in growth were observed with interstems (Perez et al., 1988; Sampaio and Simao, 1996; Veloso et al., 2004). Jones and Quinlan (1981), working on cherries, did not find differences in scion growth when trees were grafted with the interstock 'Clone 15'. In the same work, the authors found a 20-30% reduction in scion growth when the interstock was allowed to develop some small lateral shoots. The authors suggested the possible production of some scion growth inhibitors in interstem leaves.

Scion growth reduction were found when height of budding on the shank or stem of a dwarfing rootstock was increased (Mielke and Smith, 2002; Hrotko and Maguar, 2004; Kviklys and Lanauskas, 2007; Kviklys et al., 2007). However, budding height is rarely considered in most fruit studies. Although, a few studies refer to the use of differences in graft height as a methodology to reduce scion size (Kumar and Ananda, 2004). Santos et al. (2004) working on sweet cherry trees grafted on different rootstocks

and at different graft heights, found an inverse correlation between budding height and trunk cross-sectional area both in the nursery and in the orchard. However, they also found that sweet cherry was more affected by interstock than by the budding height. In another work, 'Beurré D'Anjou' pear trees budded on 'Old Home' at different heights had a growth reduction of 60% when the scion bud was located at 38 cm above ground compared to the control at 7 cm (Mielke and Smith 2002). Similar results were reported with 'Amers' and 'Bluefre' plum trees grown on 'Wangenheim' prune seedlings when those trees were budded at different heights (Grzyb et al. 2002). Although some reports showed a reduction in scion size with each increment of budding height, others did not or on the contrary, they suggested an inverse relationship between vigor and budding height, such as the report on 'Auksis' apple trees on different rootstocks and budding heights by Kviklys and Lanauskas (2007). In their research, trees budded at 30 cm were taller than those budded at 10 or 20 cm from the ground.

Budding height effect might be the result of the longer rootstock portion (shank) exposed to the sun (Hrotko and Magyar, 2004). They suggested that auxins might be involved in the scion growth reduction as the budding height increases. They suggested that auxin transport may be reduced and decomposition is greater in the rootstock bark that was exposed to sun. Tree dwarfing effects were correlated with planting depth, the deeper the planting the higher the dwarfing effect. In the same study, apples trees grafted on an interstem showed similar results as planting depth when the interstems were planted below ground. In another study, buried apple interstocks gave a reduction of 15% in tree growth compared to the exposed ones (Domoto, 2001).

Interstocks and grafting height may produce similar results as rootstocks, indicating that there is a common effect, which might not be related only to roots as most of the previous work attempted to demonstrate. Reduction in growth may involve changes in xylem or phloem anatomy. Moreover, these tissues may inhibit or reduce the action of some growth promoters in the scion.

The objective of this experiment was to determine the dwarfing effect of interstem budding height on peach scion growth.

## **Materials and methods**

### **Interstems**

In June 2005, Lovell [*Prunus persica* (L.) Batsch], Pumiselect® (*P. pumila*) and Krymsk® 1 (formerly called VVA-1) (*P. tomentosa* x *P. cerasifera*) rootstocks grown in the nursery at the Musser Fruit Research Center, near Clemson, South Carolina, were budded with 'Redhaven' [*Prunus persica* (L.) Batsch], Pumiselect® (*P. pumila*) and Krymsk® 1 (formerly called VVA-1) (*P. tomentosa* x *P. cerasifera*). At the end of the growing season in October 2005, all trees were chip budded with 'Redhaven' at 10 cm above the initial graft union. This 10 cm portion of 'Redhaven', Pumiselect® and Krymsk® 1 trees represented the interstem portion. In winter, all interstem trees were cut back just above the Redhaven buds (i.e., chip buds). Also in winter, trees were transplanted to the field in double rows at 1.5 m x 1.5 m, 1.5 m x 2.5 m and 1.5 m x 3.0 m spacing within the row and 6 m between rows. Trees were planted in a completely

randomized block design with nine replications per combination. In the following spring (March 2006), only one bud was allowed to grow from each tree. During the 2006 growing season all trees developed a main shoot, which was allowed to grow without interference. At the end of the season, all trees had one main shoot, which had come from the initial bud. Trees were not pruned during the studied period to avoid interaction between tree growth and reactions to pruning, but all fruits were taken off 3 weeks after blooming in Spring 2007 to direct all carbohydrates to the vegetative growth. The plots were managed according to standard commercial practices with an herbicide strip in the row and a mowed grass strip between rows. Trees were micro-sprinkler irrigated to replace 100% estimated evapotranspiration.

Vegetative growth was recorded by measuring trunk cross-sectional area (TCSA), tree height (main terminal) and number of growing shoot apices. TCSA was calculated from diameter measurements. Trunk diameter was measured 1) at 5 cm above the 'Redhaven' bud union for the scion TCSA; 2) in the middle of the interstem portion; and 3) at 5 cm below the rootstock-interstem graft union on the rootstock (shank) portion. Number of growing shoot apices were represented by all apices that were growing at the time of the measurements, including apices coming from main, secondary, tertiary and sylleptic shoots.

Midday stem water potential was measured on mature leaves, close to the main shoot at about 1.5 m from the ground. Leaves were covered with aluminum bags at least one hour before measurements (McCutchan and Shackel, 1992). After this period, it was assumed the leaf water potential was equilibrated with that of the xylem sap to which the

leaf was attached. Then, leaves were cut at the petiole base and put in the pressure chamber. Two leaves per tree were used to measure stem water potential.

At the end of the first growing season, the whole tree was removed from the ground and then fresh and dry weighed. The above ground material was separated in three different groups: shoots with diameters less than 7.5 mm; shoots and branches with diameters between 7.5 and 15 mm; and branches with diameters larger than 15 mm. Roots were divided in two groups: primary or shank roots, which included the primary root and including the rootstock trunk, and secondary roots (secondary, tertiary and smaller roots). Whole trees, previously divided in the above mentioned groups, were dried at 60°C for at least 2 weeks before taking dry weights.

### **Grafting heights**

In order to determine the effect of height of grafting on the vegetative growth of ‘Redhaven’ peach trees, Lovell, Pumiselect® and Krymsk® 1 rootstocks were grafted at different heights above the ground. In October 2005, rootstocks were propagated by semi-hardwood cuttings in greenhouses and then transplanted to the field in April 2006. Trees were planted in a single, double row at 0.75 m x 1.5 m, in a 3 x 3 completely randomized factorial design.

In June 2006 all trees were chip budded with ‘Redhaven’ at 3 different heights above the ground: 5, 25 and 45 cm, respectively. Trees were cut back above the ‘Redhaven’ buds three weeks later. Only one bud from the scion (‘Redhaven’) was allowed to grow above the interstem union.

Vegetative growth, as measured in TCSA, was recorded in 2006 and 2007. At the end of the second year of growth during Winter 2007, trees on Lovell and Krymsk® 1 were cut just above (1 cm) the graft union, and then fresh and dry weighed following the same procedure described for interstem trees. At three different dates, midday stem water potential was measured to establish any relationship between plant water status and vegetative growth on June 20, July 17 and August 14, 2007. Data were analyzed by SAS (9.1 version) using the GLM procedure.

## **Results**

### **Interstems**

Interstems and rootstocks significantly affected TCSA of 'Redhaven' peach trees in both the first and second years of growth (Table 4.1; Fig. 4.1). Krymsk® 1 rootstock produced the smallest trees; whereas trees on Lovell rootstock were the largest at the end of both periods. Krymsk® 1 rootstock and Pumiselect® rootstock and interstem produced TCSA values intermediate of those of the Lovell and Krymsk® 1 rootstocks at the end of the first year of growth. Unfortunately, there was no chance to compare trees on Pumiselect® in the second year since those trees had to be removed. 'Redhaven' TCSA on Krymsk® 1 interstem was significantly different from Lovell and Krymsk® 1 rootstocks in the second year, where Lovell rootstocks produced the largest trees and Krymsk® 1 the smallest ones.

At the same time, the annual increment of scion TCSA in the first and second year of growth followed the same pattern; where Lovell was the more vigorous and Krymsk® 1 rootstock the smallest. Differences in TCSA growth were observed in the first month after bud break (Fig. 4.1) and differences increased with time. At the end of the second year of growth, trees on Lovell rootstock had almost double the TCSA as on the Krymsk® 1 interstem and more than three times the TCSA of trees on Krymsk® 1 rootstock. This is in comparison to the first year, when TCSA of trees on Lovell were only 20% and 100% larger than Krymsk® 1 interstem and Krymsk® 1 rootstocks, respectively (Fig. 4.2). These differences are shown in Fig. 3.2, where Lovell rootstock is the reference treatment (100%). Here, scion TCSA of 'Redhaven' trees grafted on Krymsk® 1 rootstock were 46 % and 30 % on November 2006 and 2007, respectively. In the case of Krymsk® 1 interstem, scion TCSA was 78 % and 56 % of Lovell in the first and second year, respectively. Pumiselect® interstem TCSA had mean values between Lovell and Pumiselect® rootstocks for the first year of growth. In general, differences in trunk growth enlargement at the rootstock and scion level were not very visible in the field. Small TCSA differences were found suggesting no incompatibility symptoms in the studied combinations (Table 4.1).

The seasonal height growth pattern of the main shoot was similar to the TCSA growth during the first year (Fig. 4.3). Since the beginning (first month), trees budded on Lovell rootstocks were bigger than trees on Krymsk® 1 rootstocks, and these differences were larger at the end of the first year, while both interstems, Krymsk® 1 and Pumiselect®, had intermediate values (Table 4.1).



Generally, during the season, the total number of active growing apices for each 'Redhaven' tree grafted on Lovell rootstock was the greatest, while Krymsk® 1 had the least number (Fig. 4.4). Shoots of 'Redhaven' on Lovell rootstock grew longer into the season, while shoots from 'Redhaven' on Krymsk® 1 rootstock ceased growing earlier. Shoots from 'Redhaven' trees on Pumiselect® rootstocks and the two interstems, Krymsk® 1 and Pumiselect®, stopped growing later than for Krymsk® 1 rootstock but ceased earlier than on Lovell rootstock (data not shown). At the end of the first year of growth, two groups were significantly different: the Lovell rootstock group, which included the two interstems and the second group with Pumiselect® and Krymsk® 1 rootstocks, which had the fewest number of grown apices per tree (Table 4.1). At the end of the season, 'Redhaven' trees grafted on Lovell rootstock and Krymsk® 1 and Pumiselect® interstems had the highest number of shoots or growing points. There was a high correlation ( $r^2 = 0.908$ ) between trunk cross-sectional area and the number of growing points (terminal buds) at the end of the first season (Fig. 4.5).

At the end of the first season, trees on Lovell rootstock had the greater total shoot length; while those on Pumiselect® and Krymsk® 1 rootstocks the least total shoot length (Table 4.2). Trees with Krymsk® 1 and Pumiselect® interstems had total shoot lengths significantly larger than trees on Krymsk® 1 rootstocks. Trees on Lovell had the greatest length of shoots less than 7.5-mm-diameter. Shoots between 7.5 and 15.0-mm-diameter were also affected by rootstock and interstem. Trees on Lovell and both interstems had the largest total length of these intermediate shoot diameters. The largest branches and trunks (greater than 15.0-mm-diameter) also had significant differences

where trees on Lovell rootstocks had larger length than on Pumiselect® and Krymsk® 1 rootstocks. Total length of the largest branches of trees grafted on Pumiselect® and Krymsk® 1 interstems were significantly larger than those trees on Krymsk® 1 rootstock.

Rootstock and interstem genotypes significantly affected the fresh (data not shown) and dry weights of the different types of shoots (Table 4.3). The results followed a similar pattern for shoot length. Trees on Lovell roots, including those with Pumiselect® and Krymsk® 1 interstems, had larger total shoot fresh and dry weights than trees on Pumiselect® and Krymsk® 1 rootstocks. The lowest mean values for shoots smaller than 7.5-mm-diameter were found in trees on Krymsk® 1 rootstocks. These thin shoots had the highest mean dry weights on ‘Redhaven’ trees on Lovell rootstock, which was significantly higher than trees on Pumiselect® and Krymsk® 1 rootstocks. A similar trend was observed in shoots and branches between 7.5 and 15.0-mm-diameter. Trees on Lovell roots had the largest dry weights for those shoots larger than 15-mm-diameter.

Rootstocks and interstems affected fresh (data not shown) and dry weight of roots (Table 4.4). Total root dry weight was highest in Lovell rootstocks; whereas Pumiselect® and Krymsk® 1 rootstocks had the lowest weights. Total root dry weight means from ‘Redhaven’ trees grafted on the two interstems had intermediate values. Both interstems and rootstocks significantly influenced the shoot and root dry weight ratio. Krymsk® 1 and Lovell rootstock had a shoot:root ratio close to one (0.92 and 1.13, respectively); whereas Pumiselect® and both interstems had a significantly higher

accumulation of dry weight in the above ground tissues compared to the whole root system, with a shoot:root ratio between 1.4 and 1.6. At the end of the first season of growth, total tree dry weight was significantly higher when trees were grafted on Lovell rootstocks compared to Pumiselect® and Krymsk® 1 rootstocks (Fig. 4.6). Trees with Pumiselect® and Krymsk® 1 interstems had significantly more dry weight than on Krymsk® 1 rootstock. 'Redhaven' on Krymsk® 1 and Pumiselect® rootstocks had the smaller percentage of total dry weight when Lovell rootstock was considered as the control (100%) (Fig. 4.6). Percentage of total dry weight per tree relative to Lovell was intermediate for 'Redhaven' with Pumiselect® and Krymsk® 1 interstems.

In order to correlate the differences in vegetative growth observed in the first year and the water status of the plant, on three different dates, stem water potential was taken in all the combinations (Table 4.5). For these three measurements, trees with Krymsk® 1 and Pumiselect® interstems were not different from trees grafted on Lovell rootstocks, but they had a significantly higher stem water potential compared to trees on Krymsk® 1 and Pumiselect® rootstocks, especially when the data were pooled.

### **Grafting heights**

First- and second-year growth of 'Redhaven' in trunk cross sectional area (TCSA) did not show a significant interaction (data not shown) between rootstocks and grafting height. Trees had a short period of growth from July to November 2006, because they were budded in June 2006. Budding height had no effect on scion diameter (Table 4.6). Trees on Krymsk® 1 rootstock were significantly smaller than those trees on Pumiselect® and Lovell rootstocks at the end of the first year of growth (Table 4.6). In

the second year of growth, 'Redhaven' trees grafted on Krymsk® 1 rootstock were smaller than those trees grafted on Lovell rootstock, independent of the grafting height (Fig. 4.6). Grafting height did not affect above ground dry weight, but differences occurred among rootstocks, where scions on Lovell rootstock had significantly larger dry weights than those on Krymsk® 1 (Table 4.7).

In Summer 2007, which was the second year of growth, midday stem water potential averaged over three different measurement dates (June 20, July 17 and August 14) were significantly different among rootstocks. Trees grafted on Krymsk® 1 had lower stem water potential than trees on Lovell rootstocks (Table 4.7). On the other hand, grafting height did not significantly affect midday day stem water potential.

## **Discussion**

The objective of the study was to determine the effect of interstocks and budding height on scion vegetative growth in order to understand the dwarfing mechanism in peach rootstocks. In the interstem study, TCSA results agreed with two earlier peach experiments (Hossain et al. 2005; Rufato et al. 2006). In our study, interstems significantly affected the size of the trees (Tables 4.1-4.3; Figs. 4.1-4.3). Krymsk® 1, the more dwarfing rootstock, reduced the size of the tree at the end of the first year to almost 50% of the control (Lovell), but by the end of the second year, Krymsk® 1 controlled the vigor to 35% of Lovell. Trees with a Krymsk® 1 interstem reduced TCSA up to 19% compared to trees on Lovell rootstocks in the first season, while the reduction was close

to 50% at the end of the second season. Moreover, annual TCSA increments for trees on Krymsk® 1 rootstocks compared to trees on Lovell were 47.9 % for the first season and 26.8 % for the second year (Table 4.1). In the case of trees with a Krymsk® 1 interstem, trees were 80.9% of the control TCSA for the first season, and the percentage was reduced to 43.3% after the second growing season. ‘Redhaven’ trees grafted on Krymsk® 1 rootstock and interstem had a two-fold reduction in the annual TCSA increment in the second year compared to the first season and to Lovell (control). These results confirmed what was reported by Samad et al. (1999), who when working on apple interstems found the greatest effect of scion control was in the second season. According to Costes and García-Villanueva (2007) and Seleznyova et al. (2003, 2008) dwarfing effects are cumulative and superimposed year-to-year. Moreover, differences in TCSA growth were observed very early from the first month after initial bud break (Fig. 4.1), so the cumulative effect started to show very early due to a reduction of leaf area (data not shown) and stem growth.

During the first season, the number of active growing apices of ‘Redhaven’ trees grown on Krymsk® 1 and Pumiselect® rootstocks was significantly lower than that on Lovell rootstock (Fig. 4.4 and Table 4.1). Differences in number of active growing points between trees on Lovell rootstock and trees on Krymsk® 1 and Pumiselect® interstems were significantly lower only at the latter part of the season, indicating an earlier set of the terminal bud in trees on Krymsk® 1 and Pumiselect® interstems. This effect was even more noticeable in those trees grown on Krymsk® 1 rootstock. In their study of branch pattern of ‘Royal Gala’ apple trees, where MM.106 and MM.9 were used

as both rootstock and interstems, Seleznyova et al. (2003) found that dwarfing rootstocks produced shorter shoots, which had fewer internodes. This reduction in the number of internodes generated fewer buds in the following year, which reduced whole tree growth. With this mechanism repeated every year, annual growth of trees on a dwarfing rootstock would be exponentially smaller every year, giving a higher reduction in growth as the plant ages. Costes and García-Villanueva (2007) and Seleznyova et al. (2008) agreed that dwarfing rootstocks and interstems tend to produce more flower buds than invigorating rootstocks. These authors reported that there was a reduction in the proportion of vegetative buds related to flower buds which lead to less growth in the trees grafted on dwarfing rootstocks and interstocks.

Although at the end of the first season there were no significant differences in total above ground dry weight among trees on Lovell rootstock and those on both interstems, significant differences were found in root dry weight. ‘Redhaven’ with Krymsk® 1 interstems had lower root dry weights. Similarly, trees grown on Pumiselect® interstems, although not significantly different, tended to have lower root dry weight than trees on Lovell.

In summary, ‘Redhaven’ trees with Pumiselect® and Krymsk® 1 interstems had 76% and 66 % dry weight of above ground biomass, respectively relative to trees on Lovell rootstocks, but this percentage changed when the root dry weight was included. Trees grafted with Pumiselect® and Krymsk® 1 interstems had 89% and 78% dry weight of roots, respectively of that of Lovell roots. This would suggest that trees grown on both interstems, although having the same root genotype (Lovell), need a proportionally larger

root system to get similar above ground growth as suggested by the differences in the shoot:root ratio.

Trunk cross-sectional area of the interstem trunk portion was smaller than TCSA on both the rootstock and scion. This reduction of interstem trunk diameter might suggest a reduction in xylem and phloem pathways (Webster, 1995).

No differences were observed when midday stem water potential was measured on Lovell and both interstems (Table 4.5). Trees on Krymsk® 1 and Pumiselect® rootstocks had the lowest midday stem water potential, which correlated with a higher reduction in their vegetative growth. Our results did not agree with Camara et al. (2003) who worked on orange interstocks where they found a significant reduction in leaf water potential due to interstock.

Rufato et al. (2006) found a negative linear correlation between interstock length and scion vegetative growth when 'Jubileu' peach was intergrafted with 5, 10, 15 and 20 cm of the peach cultivar 'Granada'. De Rossi et al. (2003) found a similar effect of interstem length on 'Imperial Gala' apple trees when these trees were grafted with EM.9 interstems of different lengths. Therefore, it might be possible to make a parallel between the effect of interstock length and budding height relative to the effect of controlling scion growth.

In our budding height experiment, no differences were found in TCSA due to grafting height. Only a tendency toward a decrease in TCSA when the budding height was increased, which was observed in the second year of growth in trees budded on Krymsk® 1 rootstocks (Fig. 4.7). Midday stem water potential was consistent with

TCSA growth because differences were found only among rootstocks and no grafting height effect was observed.

Our results of budding height effect on scion growth agreed with other researchers who did not find differences in sweet cherry (Sadowski et al., 1996, Webster, 1998). Rozpara and Zygmunt (2006) compared the growth, yield, and fruit quality of five sweet cherry cultivars with 'Northstar' interstem grafts of two different lengths (50 and 70 cm) and with trees of the same cultivars grafted on Mazzard seedlings and the 'P-HL A' rootstocks. Only one of the five cultivars had significant differences in growth due to interstem length after 8 years of growth.

Some contradictory reports related to the effect of budding height were found in the literature. For example, when a local peach rootstock was grafted at four different heights (10, 15, 20 and 25 cm) with 'Fazali Manani' plum cultivar, scion size was affected by grafting height and the 25 cm height produced the largest trees (Ullah et al. 1997). However, the peach rootstock did not control scion growth. Similar results were found by Kviklys and Lanauskas (2007) in apples, where trees grafted at 30 cm were taller and larger than those grafted at 10 cm.

A significant but opposite effect of budding height was found in pear by Mielke and Smith (2002) where the highest budding height resulted in the smallest trees. Moreover, results presented by Grzyb et al. (2002), where two plum cultivars were budded at 10, 20 and 30 cm showed that 'Bluefre' plum trees grew the least when they were budded at 30 cm; whereas 'Ammers' plum trees had the highest vegetative growth when they were budded at 10 cm.



Overall, the majority of grafting height studies have been done in apple trees where there was a reduction in growth as the budding height was increased (Parry, 1986; Kumar and Ananda, 2004; Sosna, 2004; Kviklys et al., 2007). Budding height did not affect scion growth in the first growing season when Kviklys et al. (2007) studied young ‘Auksis’ apple trees grafted at 0, 10, 20 and 30 cm from the ground. However, in the same study budding height reduced scion growth in the second and third season.

In our study, the trends in the reduction of scion growth due to budding height observed on trees budded on Krymsk® 1 at the end of the second year suggested that budding height could affect tree growth in future years due to annual reductions in TCSA from the dwarfing effect (Seleznyova et al. 2003, 2004, 2008).

The results from our work indicated that interstems, and probably budding height, affected peach scion growth. So, different processes, other than root and graft union effects, are involved in dwarfing peach rootstocks, making the understanding of these mechanisms more complex.

Table 4.1. Tree height, number of growing apices (NPG) per tree, scion, interstem and rootstock TCSA (2006), and scion annual TCSA increment (2006-2007) of non-bearing Redhaven trees growing on different rootstocks and interstems.

Rootstocks	Height (cm)	NGP	Trunk Cross-Sectional Area (cm <sup>2</sup> )			
	Tree height <sup>z</sup> (2006)	NGP/tree (2006)	Scion (2006)	Interstem (2006)	Rootstock (2006)	Annual indec. (2006-07)
<b>Lovell</b>	245.2 a	233.7 a	20.5 a	-	20.5 a	35.1 a
<b>Lovell/ Krymsk 1</b>	221.2 ab	182.0 a	16.0 b	12.5 a	16.7 b	15.3 b
<b>Lovell/ Pumiselect<sup>y</sup></b>	200.0 bc	202.0 a	17.8 b	13.1 a	17.1 b	-
<b>Pumiselect<sup>y</sup></b>	207.3 b	114.2 b	15.6 b	-	17.4 b	-
<b>Krymsk 1</b>	176.5 c	63.8 b	9.5 c	-	10.5 c	9.4 c

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

<sup>y</sup>Trees on Pumiselect were removed prior to the second year.

Table 4.2. Influence of rootstock and interstem on the above ground tissue length (shoots, branches and trunk) of one-year-old Redhaven trees.

<b>Redhaven shoot length (cm) <sup>z</sup></b>				
<b>Shoot diameter<sup>y</sup></b>				
<b>Rootstocks</b>	<b>&lt; 7.5 mm</b>	<b>7.5-15.0 mm</b>	<b>&gt; 15.0 mm</b>	<b>Total</b>
<b>Lovell</b>	<b>7493.0 a</b>	<b>921.2 a</b>	<b>364.5 a</b>	<b>8778.7 a</b>
<b>Lovell/Krymsk 1</b>	<b>6076.0 ab</b>	<b>785.7 a</b>	<b>312.2 ab</b>	<b>7174.0 ab</b>
<b>Lovell/Pumiselect</b>	<b>6745.0 ab</b>	<b>761.8 a</b>	<b>351.5 a</b>	<b>7858.3 ab</b>
<b>Pumiselect</b>	<b>4487.0 bc</b>	<b>496.0 b</b>	<b>184.0 ab</b>	<b>5167.0 bc</b>
<b>Krymsk 1</b>	<b>2047.0 c</b>	<b>284.3 b</b>	<b>90.0 c</b>	<b>2421.3 c</b>

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

<sup>y</sup> Material was classified as three different kinds of shoots and trunks: shoots smaller than 7.5-mm-diameter, shoots and branches between 7.5 and 15.0-mm-diameter, and branches and trunks larger than 15.0-mm-diameter.

Table 4.3. Influence of rootstock and interstem on the above ground tissue dry weight (shoots, branches and trunk) of one-year-old Redhaven trees.

<b>Redhaven shoot dry weight (g)</b>				
	<b>Shoot diameter <sup>z,y</sup></b>			
<b>Rootstocks</b>	<b>&lt; 7.5 mm</b>	<b>7.5-15.0 mm</b>	<b>&gt; 15.0 mm</b>	<b>Total</b>
<b>Lovell</b>	<b>598.8 a</b>	<b>449.3 a</b>	<b>1014.5 a</b>	<b>2062.7 a</b>
<b>Lovell/Krymsk 1</b>	<b>492.2 ab</b>	<b>395.3 a</b>	<b>922.0 a</b>	<b>1809.5 a</b>
<b>Lovell/Pumiselect</b>	<b>510.0 ab</b>	<b>371.0 ab</b>	<b>956.0 a</b>	<b>1837.0 a</b>
<b>Pumiselect</b>	<b>352.8 bc</b>	<b>263.2 b</b>	<b>488.3 b</b>	<b>1104.3 b</b>
<b>Krymsk 1</b>	<b>185.8 c</b>	<b>141.2 c</b>	<b>234.2 b</b>	<b>561.2 b</b>

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

<sup>y</sup>Material was classified on three different kinds of shoots and trunks: shoots smaller than 7.5-mm-diameter, shoots and branches between 7.5 and 15.0-mm-diameter, and branches and trunks larger than 15.0-mm-diameter.

Table 4.4. Influence of rootstock and interstems on the root dry weight of one-year-old Redhaven trees.

<b>Redhaven root dry weight (g) <sup>z</sup></b>			
<b>Rootstocks</b>	<b>Tap root</b>	<b>Small roots</b>	<b>Total</b>
<b>Lovell</b>	<b>679.0 a</b>	<b>1116.8 a</b>	<b>1795.8 a</b>
<b>Lovell/Krymsk 1</b>	<b>472.3 a</b>	<b>719.0 bc</b>	<b>1191.3 b</b>
<b>Lovell/Pumiselect</b>	<b>509.5 a</b>	<b>862.2 ab</b>	<b>1371.7 ab</b>
<b>Pumiselect</b>	<b>249.2 b</b>	<b>457.5 c</b>	<b>706.7 c</b>
<b>Krymsk 1</b>	<b>224.0 b</b>	<b>443.3 c</b>	<b>667.3 c</b>

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

<sup>y</sup>Material was classified on two different kinds of roots: rootstock portion below the graft union plus tap root (tap root), and the remainder of the root system (small roots).

Table 4.5. Effect of rootstocks and interstem on midday stem water potential (Mpa) of Redhaven trees at different dates during the first year of growth.

<b>Stem water potential (Mpa) <sup>z</sup></b>				
<b>Rootstocks</b>	<b>05/12</b>	<b>07/07</b>	<b>09/06</b>	<b>Season average</b>
<b>Lovell</b>	<b>-0.51 ab</b>	<b>-0.83 ab</b>	<b>-0.74 a</b>	<b>-0.69 a</b>
<b>Lovell/Krymsk 1</b>	<b>-0.44 a</b>	<b>-0.76 a</b>	<b>-0.72 a</b>	<b>-0.63 a</b>
<b>Lovell/Pumiselect</b>	<b>-0.48 ab</b>	<b>-0.81 ab</b>	<b>-0.67 a</b>	<b>-0.62 a</b>
<b>Pumiselect</b>	<b>-0.59 b</b>	<b>-0.95 bc</b>	<b>-0.91 b</b>	<b>-0.79 b</b>
<b>Krymsk 1</b>	<b>-0.58 b</b>	<b>-1.02 c</b>	<b>-0.94 b</b>	<b>-0.85 b</b>

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

Table 4.6. Effect of grafting height and rootstock on trunk cross-sectional area of one- and two-year-old Redhaven trees grafted on Lovell, Pumiselect® and Krymsk® 1 rootstocks at the Musser Fruit Research Center in December 2006 and 2007.

<b>Redhaven trunk cross-sectional area (cm<sup>2</sup>)<sup>z</sup></b>						
	<b>Budding heights</b>			<b>Rootstocks<sup>y</sup></b>		
<b>Season</b>	<b>5 cm</b>	<b>25 cm</b>	<b>45 cm</b>	<b>Lovell</b>	<b>Pumiselect</b>	<b>Krymsk 1</b>
<b>First year</b>	2.8 a	2.5 a	2.5 a	3.2 a	3.1 a	1.5 b
<b>Second year<sup>z</sup></b>	13.7 a	15.0 a	12.7 a	21.9 a	-	5.6 b

<sup>z</sup>Different letters within a row for budding heights and rootstocks indicate significant differences at P < 0.05 (Duncan's multiple range test).

<sup>y</sup>Trees on Pumiselect were removed prior to the second year.

Table 4.7. Effect of grafting height on above ground biomass and midday stem water potential of Redhaven trees grafted to two rootstocks.

<b>Grafting height</b>	<b>Dry weight per plant (kg)<sup>zy</sup></b>		<b>Stem water potential (Mpa)<sup>x</sup></b>	
	<b>Lovell</b>	<b>Krymsk 1</b>	<b>Lovell</b>	<b>Krymsk 1</b>
<b>5 cm</b>	<b>1.54 a</b>	<b>0.41 b</b>	<b>-0.87 a</b>	<b>-1.04 b</b>
<b>25 cm</b>	<b>1.81 a</b>	<b>0.43 b</b>	<b>-0.85 a</b>	<b>-1.01 b</b>
<b>45 cm</b>	<b>1.56 a</b>	<b>0.24 b</b>	<b>-0.85 a</b>	<b>-1.00 b</b>

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

<sup>y</sup>Dry weight at the end of the second year (November 2007).

<sup>x</sup>Midday stem water potential was represented by the average of three measurements in Summer 2007 (June 20, July 17 and August 14, 2007).

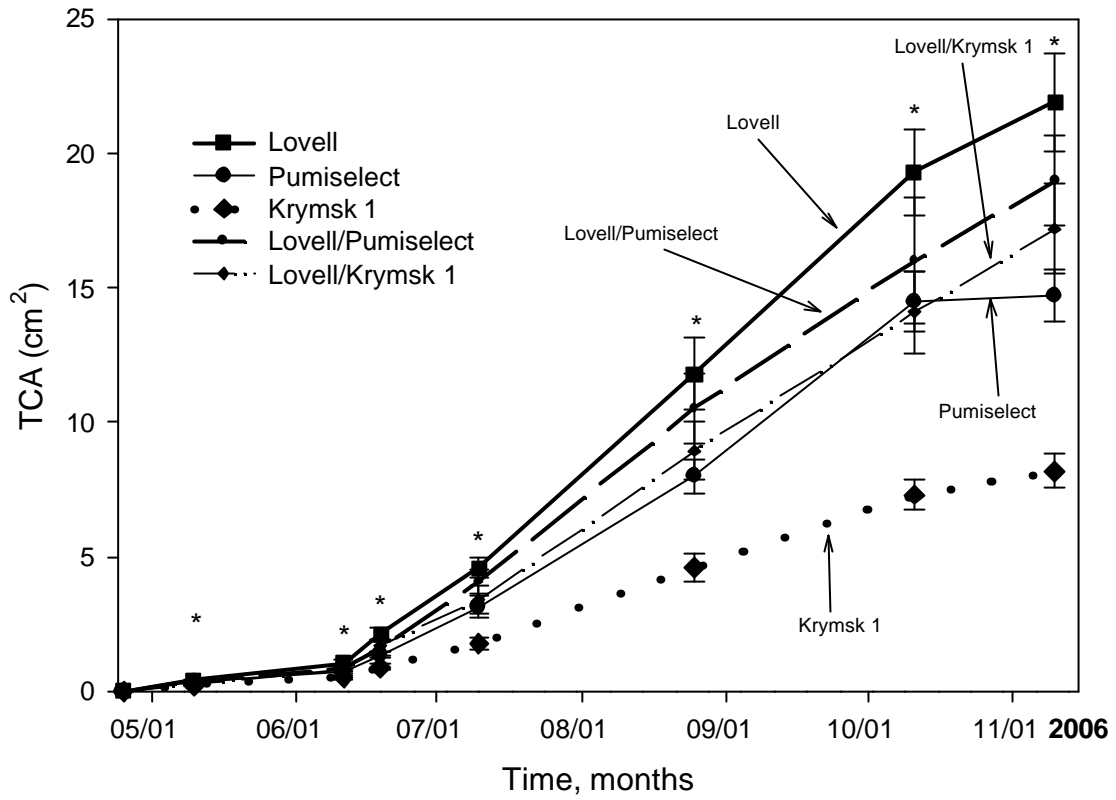


Fig. 4.1. The seasonal pattern of trunk cross-sectional area (TCSA) growth of Redhaven trees growing on different rootstocks and interstems in 2006. Standard errors are given for each point. Asterisks represent significant rootstock treatment differences at each point at  $P < 0.05$  (Duncan's multiple range test).

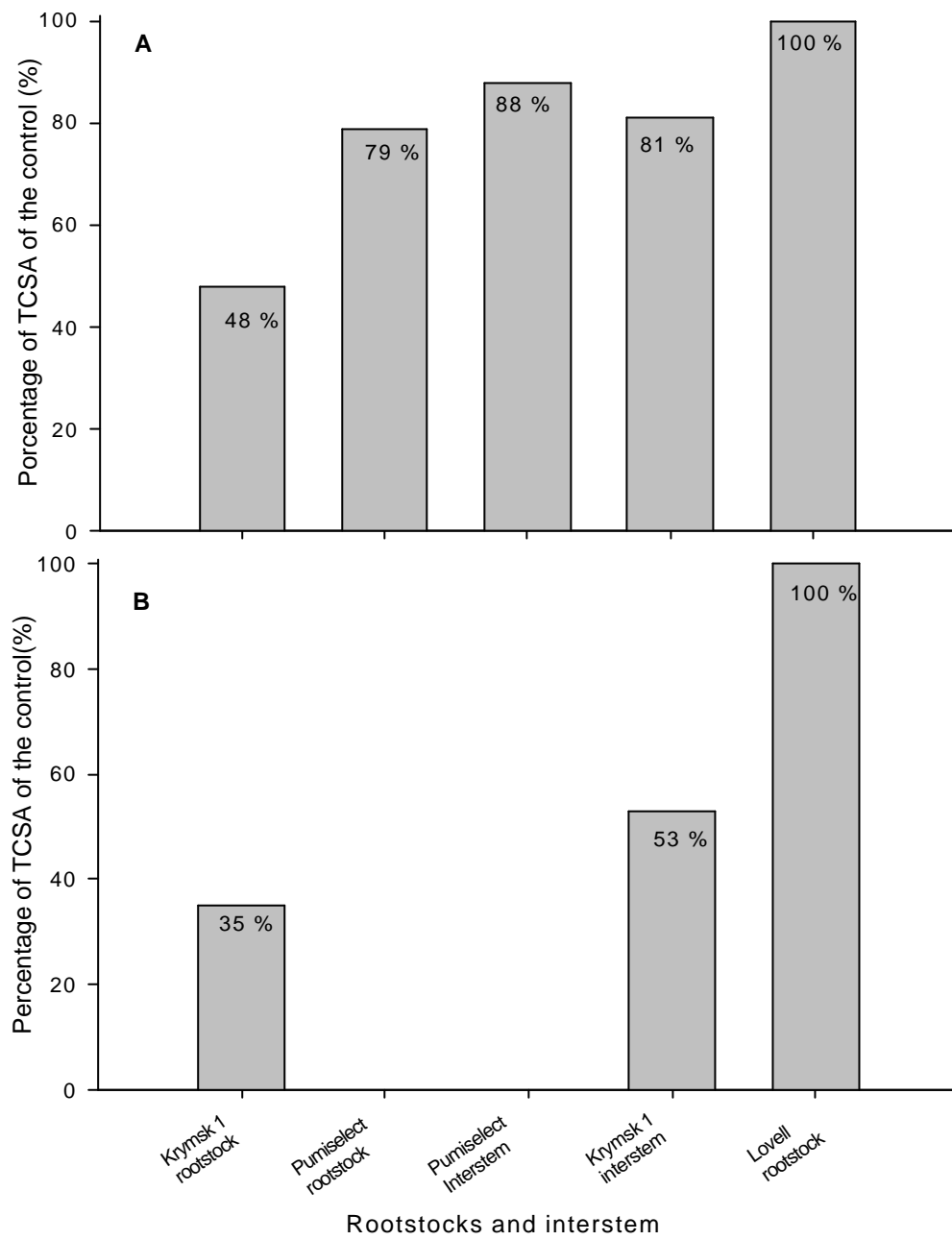


Fig. 4.2. The size (TCSA) of Redhaven trees grown on different rootstocks and interstems relative to trees on Lovell (e.g., 100). First year growth (A) and second year growth(B).



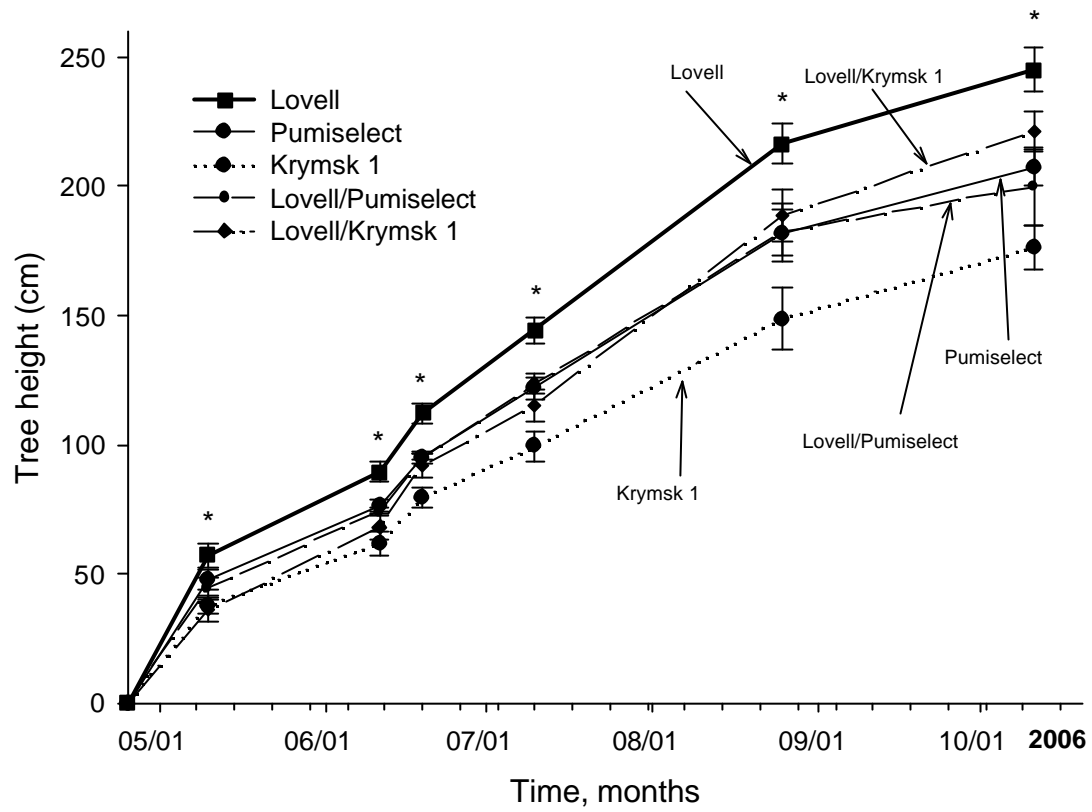


Fig. 4.3. Seasonal pattern of height growth of Redhaven trees grown on different rootstocks and interstems in 2006, representing the first year of growth. Standard errors are given for each point.

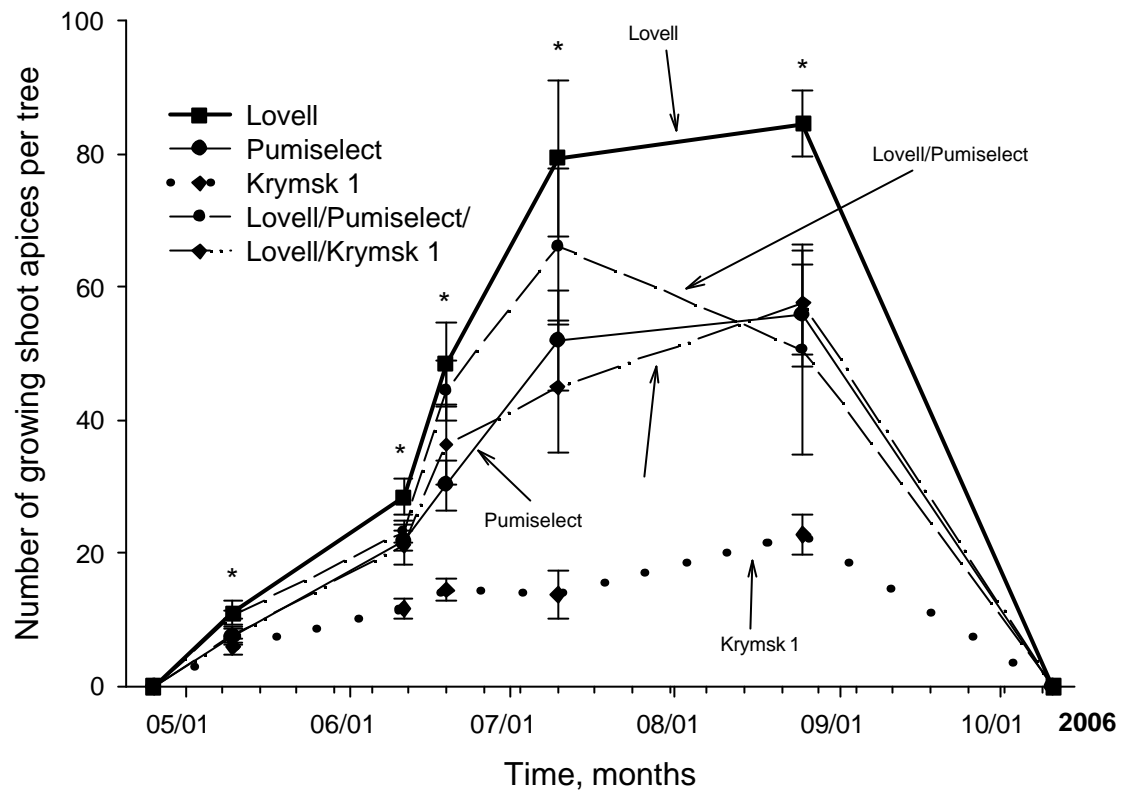


Fig. 4.4. Seasonal pattern of number of growing points for Redhaven trees grown on different rootstocks and interstems in 2006, representing the first year of growth. Standard errors are given for each point.

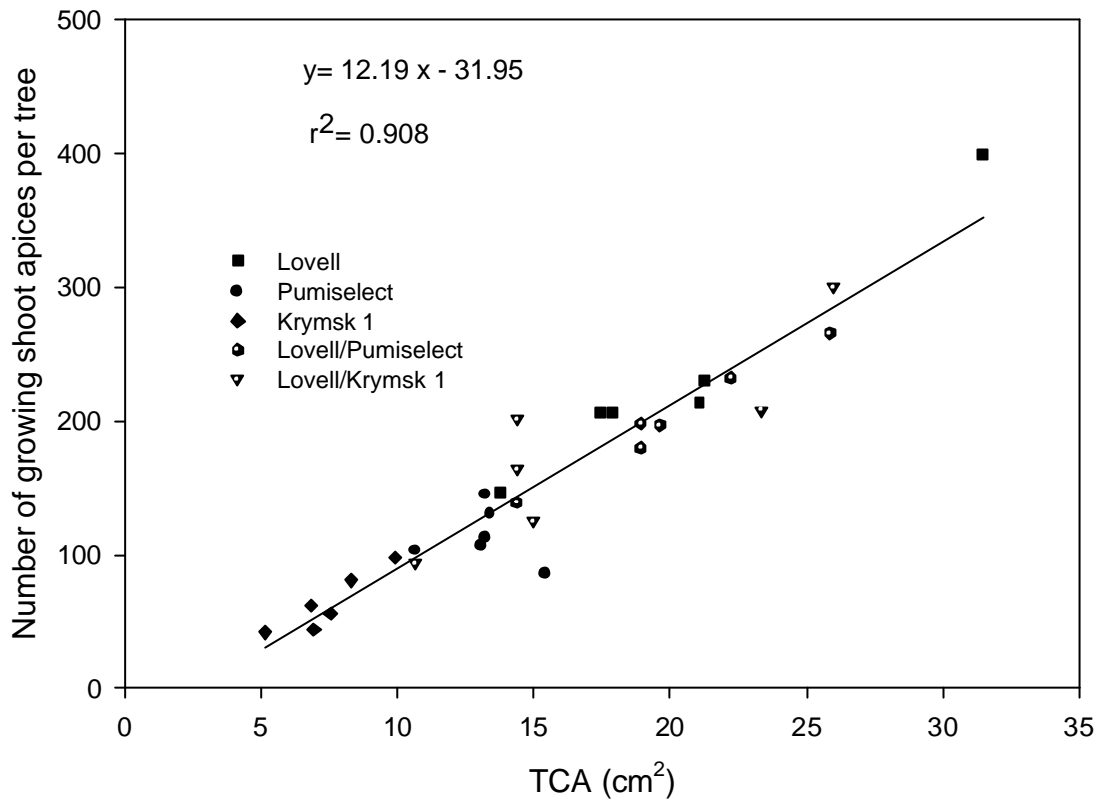


Fig. 4.5. Relationship between total number of growing points during the season and trunk cross-sectional area of one-year-old Redhaven trees grafted on different rootstocks and interstems.

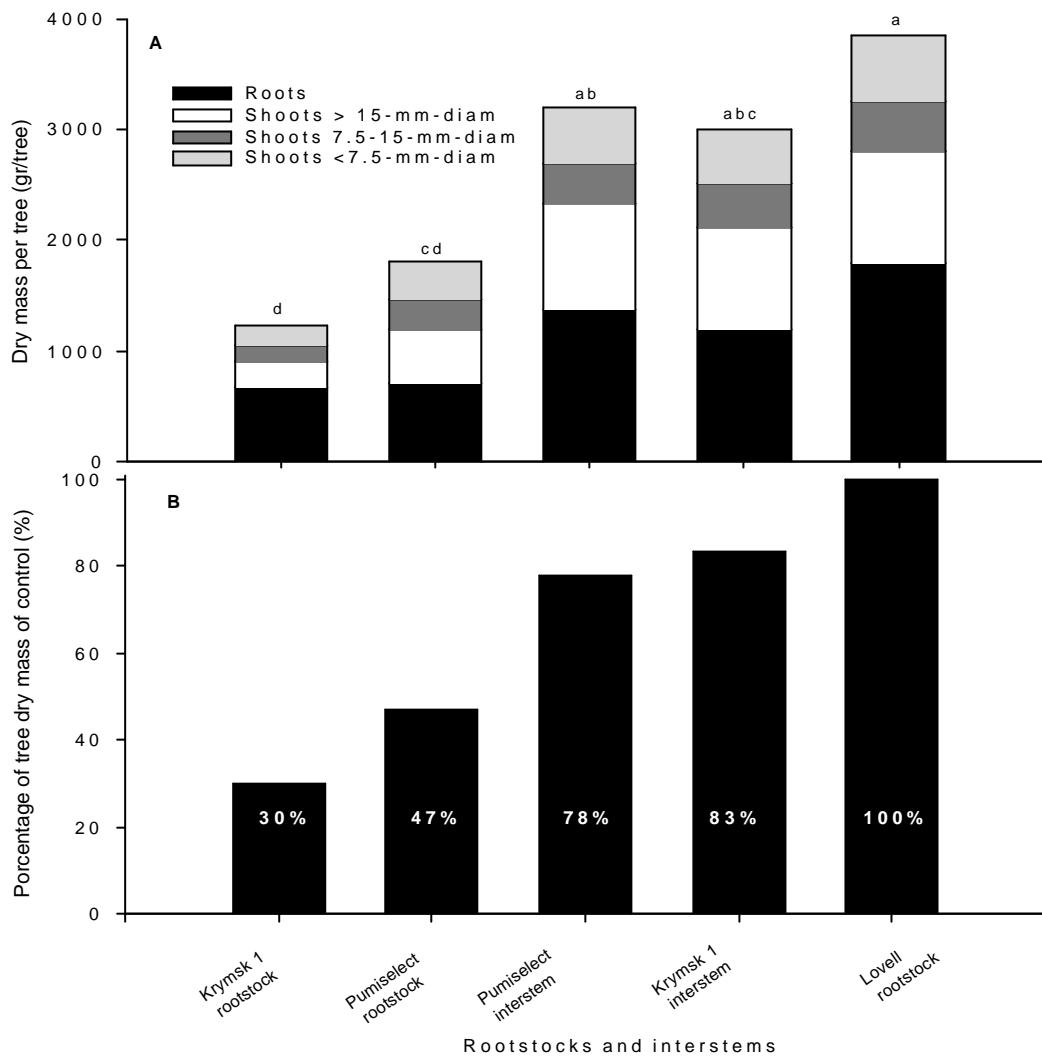


Fig. 4.6. Distribution of total dry mass from roots (tap root and small roots) and shoots (shoots < 7.5-mm-diameter, shoots and branches between 7.5 and 15-mm-diameter, and branches and trunk > 15-mm-diameter) of one-year-old Redhaven trees grafted on different rootstocks and interstems. Dry matter harvested per tree (A) and total dry mass (roots and shoots) relative to trees on Lovell rootstock (control) (B). Different letters indicate significant differences for total dry weight from whole trees (shoots + roots) at  $P < 0.05$  (Duncan's multiple range test).

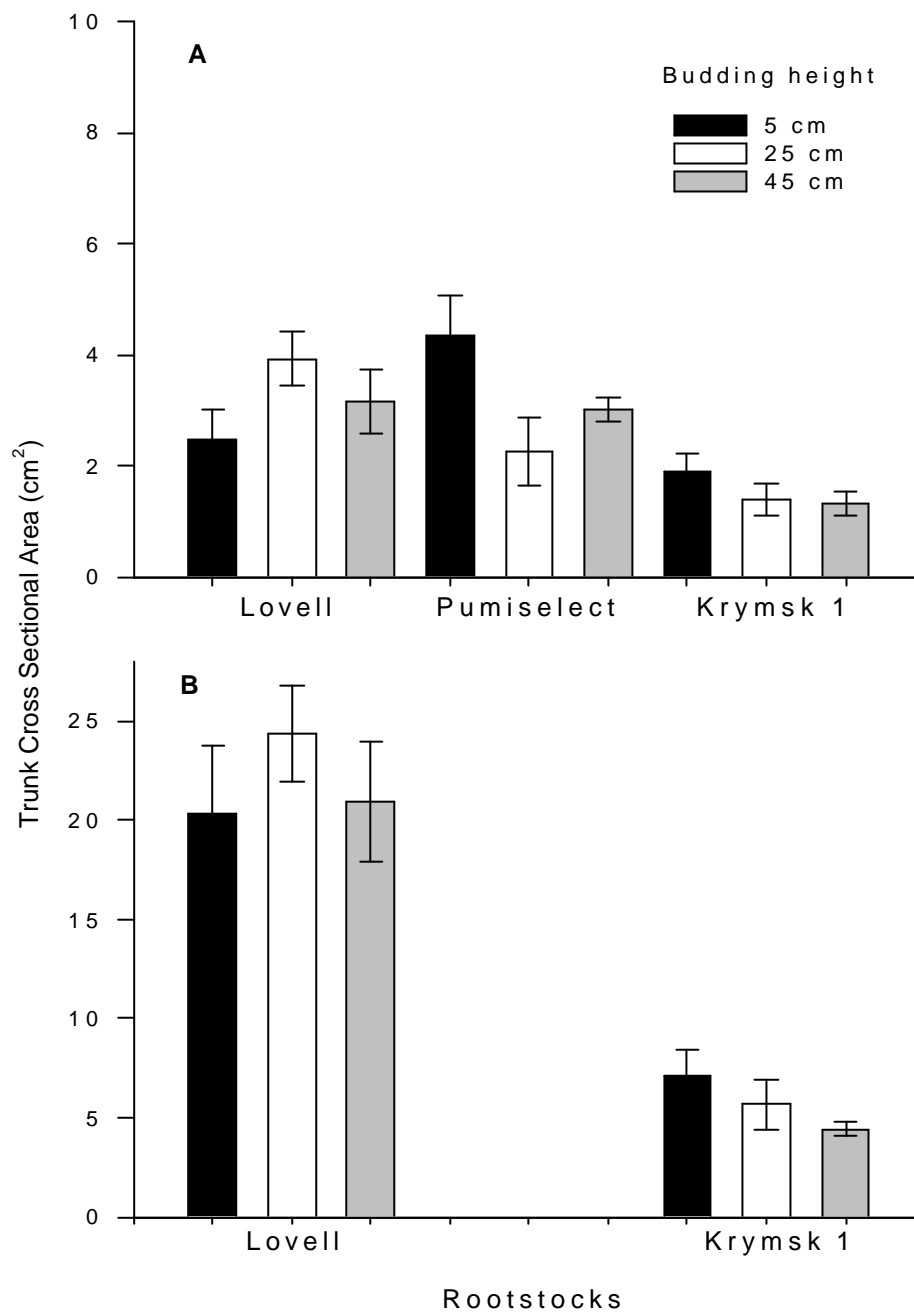


Fig. 4.7. Effect of rootstock and budding height on TCSA after the first (A) and second (B) year of growth of Redhaven trees at the Musser Fruit Research Center, Seneca, South Carolina. Error bars represent  $\pm 1$  standard error of the mean.

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## CHAPTER V

### WATER STATUS AND THE DWARFING MECHANISM OF PEACH ROOTSTOCKS

#### **Introduction**

Rootstocks have a profound influence on the reproductive and vegetative growth of a tree scion (Averi, 1970; Czynczyk, 1980; Bussi et al., 1995; Carusso et al., 1997; Reighard et al., 2006). Unique rootstocks allow trees to tolerate different edaphic conditions, such as dry, saline, heavy or wet soils, and the presence of disease organisms and soil-borne insects. Perhaps the most important use of a specialized rootstock is to reduce the size of the scion while at the same time, increase its efficiency of fruit production (Mika et al., 1980). Even though the dwarfing effect of the rootstock was suspected over 2000 years ago, the mechanisms involved are not well understood. Several theories about the effects and the mechanisms involved in dwarfing have been published (Lockard and Schneider, 1981; Crabbé, 1984; Rom and Carlson, 1987; Atkinson and Else, 2001; Atkinson et al., 2003; Webster and Wertheim 2003). Recent studies link the hydraulic status of the whole tree with the dwarfing capacity of a particular rootstock; therefore, water uptake and transport may play a central function in the dwarfing of trees.

Olien and Lakso (1984) studied water relations of 'Empire' apple on five rootstocks and suggested that differences in the mean midday stem water potential could

have been associated with either resistance to flow at the graft union or to root hydraulic resistance. Cohen and Naor (2002) found a lower conductance in the canopy of apple trees when grown on the dwarfing rootstock M.9 as compared to the conductance recorded when trees were grown on the more vigorous MM.106 and 'Hashabi' rootstocks. Li et al. (2002) also reported a reduction in the canopy conductance when apple trees were grafted on M.9 rootstocks. Chalmers et al. (1984) found that when water stress was applied to peach and pear trees, shoot growth was markedly reduced but the reduction in number of fruits produced and fruit growth was not as great as the reduction in shoot growth. Costes and Garcia-Vilanueva (2007) and Seleznyova et al. (2008) both reported that dwarfing rootstocks reduced the number of shoots as a consequence of the early transition to flowering induced by the rootstocks. In trees grafted on dwarfing rootstocks, the proportion of reproductive buds was greater than the number of vegetative buds.

Seasonal vegetative growth is the integrated result of diurnal growth over many days (Berman and DeJong, 1997b.). Diurnal growth is affected by temperature, solar radiation, and the water status of the plant (Hsiao and Bradford, 1983; McDonald et al., 1992; Hsiao, 1993; Hsiao and Xu, 2000; Tsuda and Tyree, 2000). Any tissue growth involves some biochemical processes such as loosening and formation of cell walls and solute transport in addition to the effects of physical parameters: turgor pressure and water transport (Hsiao and Jing, 1987). Thus, the primary effect of water deficit is the reduction of expansive growth (Hsiao, 1973; Hsiao and Xu, 2000). Diurnal changes in plant water status have been described for many perennial species including peach trees

(Chalmers and Wilson, 1978; Larson et al., 1988; Berman and DeJong, 1996, 1997ab; Basile et al., 2003, Weibel et al., 2003). Putting these concepts together, it is possible to infer that dwarfing rootstocks may reduce the scion water potential and the scion would then respond as if under conditions of water stress.

When vapor pressure deficit is increased (high temperature and low relative humidity), transpiration increases as does the gradient of water potential between soil and leaves (Tyree and Ewers, 1991). In dwarfing rootstocks that mimic this condition, hydraulic resistance would be over expressed causing the observed reduction of scion growth. Reduction in hydraulic conductivity will reduce the carbon uptake and growth potential (Sperry, 2000; Hubbard et al. 2001; Clearwater et al., 2004); thus producing a secondary effect of a reduction in the rate of photosynthesis.

It is clear there is a correlation among vegetative growth, water status and rootstocks, but the question remains as to which tissue is mainly responsible for the reduction in the water pathway? The graft union has a high degree of discontinuity, which could have strong effects on water flow, particularly when dwarfing rootstocks are involved. Olien and Lakso (1984) related their findings about the growth of 'Empire' apple on five rootstocks to either high resistance to flow at the graft union or to high root hydraulic resistance.

Atkinson et al. (2003) found that the root system and graft union were responsible for most of the resistance when a dwarf rootstock was used in apples. In cherries, graft union conductivity seems to reduce water transport in dwarfing rootstocks (Olmstead et al., 2004, 2006ab). However, peaches seem to behave differently and show higher

resistance to water movement in the roots and lower resistance to water movement at the graft union (Basile et al. 2003b, 2007; Solari and DeJong, 2006; Solari et al., 2006ab). Glenn and Scorza (1992) compared root water resistance of reciprocal combinations of dwarf and standard cultivars of peaches and found that the tallest phenotypes had the lowest root water resistance. When vines of kiwifruit were grafted on four different rootstocks, there was a positive correlation between growth and hydraulic conductivity (Clearwater et al. 2004). The graft union in this study did not show a high resistance to water movement, indicating that roots could be the origin of the observed reduction in water movement.

Mechanisms by which a fruit rootstock affects the scion could be explained by changes in the anatomical structure of cells and tissues (Olmstead, 2006ab). Water transport could explain the behavior of dwarfing rootstocks in those cases where graft union and roots would be the main structures involved in these mechanisms. Studies with cherries also would support this theory (Olmstead et al., 2004, 2006ab). In apples, Simons (1986), working in one-year-old trees, found that the vascular tissues showed a swirling pattern and some senescent tissues became important at this level. These abnormal structures in the vascular system have been suggested to be involved either in some kind of incompatibility present at the beginning of the formation of the graft union or during the subsequent growth as a consequence of biochemical or physiological interaction between the two tissues (Simons and Chu, 1984). A common feature of dwarfed apple trees is the swollen, distorted tissues composed mainly of xylem elements that are produced in the region of the graft interface between rootstock and scion (Jones

1986). Soumelidou et al. (1994) studied the early development of graft unions in the apple cultivars 'Gala' and 'Bramley'. This study showed that in the case of M.9 (a dwarf rootstock) the xylem linking the bud to the rootstock contained fewer vessels than in the semi-dwarfing MM.106.

In peaches, past works showed that most of the hydraulic resistance was found in the roots instead of the graft union. Roots were the major resistance to water flow when different peach rootstocks were compared by Basile et al. (2003b) and rootstocks that gave the greatest size control had the highest water resistance.

In most cases that examine a whole plant, the highest resistance to water transport occurs in the root system (Liu et al., 1978; Molz, 1981; Pasioura, 1988; Tyree, 2003). Rieger and Litvin (1999) comparing different species found a negative correlation between root hydraulic conductance and root diameter. There are two main components involved in the movement of water: the axial and radial conductance. The first component represents the movement of water through the vessel elements up to the stem, and the second term describes the conductance of water from the root surface to the xylem vessels. In general, the axial conductance in fruit trees is assumed to be sufficient to allow normal growth and not to limit the water pathway due to a secondary growth that increases the number of xylem vessels (Vercambre et al. 2002). In the same study, Vercambre et al. (2002), working on a peach variety grafted on to 'Damas GF 1869' plum rootstock, found that woody roots had a higher conductance than the fine roots. However, they agreed that axial resistance did not reduce water transport unless some limitations were present such as very deep soil (Jackson et al., 2000) or some kind of



restriction of the root system that might reduce the water flow (Yamauchi et al., 1995). Fine roots exhibited larger variation in the conductance due mainly to the difference in the number of vessels compared to woody roots.

We hypothesized that dwarfing mechanisms of peach rootstocks are linked to the water status of the tree and the differences in scion growth are a consequence of water stress caused by the more-size controlling rootstocks. Our study attempted to establish a relationship between the impaired growth of peach scions caused by rootstocks and the physiological responses of the scion, so as to understand the dwarfing mechanism in peach trees.

## **Materials and methods**

### **Experimental sites and plant materials**

#### **Bearing trees at Georgia and South Carolina**

Data were collected in 2005 and 2006 on trees of two peach [*Prunus persica* (L.) Batsch] cultivars, 'Redhaven' and 'Redtop', grafted on different rootstocks: Lovell (*Prunus persica*), Pumiselect® (*P. pumila*), Krymsk® 1 (formerly called VVA-1) (*P. tomentosa* x *P. cerasifera*), Cadaman®-Avimag (*P. persica* x *P. davidiana*) and Controller® 5 (formerly called K-146-43) (*P. salicina* x *P. persica*). Cadaman® is a vigorous rootstock. Lovell is of standard vigor, while Pumiselect® and Controller® 5 are of semi-dwarf vigor. The Krymsk® 1 rootstock produces the greatest control in size. Bearing trees were grown at two different locations: USDA Southeastern Fruit & Nut

Tree Laboratory, Byron, GA and Musser Fruit Research Center, Seneca, SC. Trees were part of two NC-140 rootstock trials, and were planted at 5 m along the row and 6 m between rows. The NC-140 'Redhaven' peach tree trial was planted in 2002 while the NC-140 'Redtop' peach plot was planted in 2001. Depending on the site and combinations, 4 to 6 repetitions were used per treatment.

### **Young trees at South Carolina**

Young non-bearing 'Redhaven' and 'Redtop' peach trees were grown at the Musser Fruit Research Center. On June 2005, Lovell, Pumiselect®, Krymsk® 1 and Cadaman® rootstock trees, grown at the nursery, were budded with 'Redhaven', 'Redtop' and self-grafted. The dormant trees were cut back to 10 cm above the graft union and then transplanted into a field site in January 2006. These trees were planted in double rows at 1.5 m x 1.5 m, 1.5 x 2.5 m and 1.5 x 3.0 m in the row and 6 m between rows. In the spring (March 2006), only a single shoot was allowed to grow. This shoot was the single main trunk of the tree. Trees were not pruned during the experimental period, but all fruits were removed in Spring 2007. Trees were irrigated as needed using micro-sprinklers to replace 100% estimated evapotranspiration.

### **Nursery trees at South Carolina**

Lovell, Pumiselect® and Krymsk® 1 rootstocks were planted at the Musser Fruit Research Center nursery, Seneca, SC, at 0.5 m between plants and 1.5 m between rows in April 2006, then either budded with 'Redhaven' or self-grafted on June 2006, and then used for water potential and root studies in the following season (2007). All trees were cut back in January 2007 as described above.

All plots were managed according to standard commercial practices. Rows of trees received herbicide treatments, but a mowed grass strip was maintained between the rows, except in the nursery, where all areas between the rows were also treated with herbicide. Mature and young non-bearing trees on the field were irrigated with micro-sprinklers to replace 100% estimated evaporation. Trees at the nursery were drip irrigated.

### **Data collection**

#### **Rootstock effect on the scion**

Vegetative growth was monitored by measuring trunk cross-sectional area (TCSA), tree height (main shoot) and number of active growing points. For young non-bearing trees TCSA was calculated based on the diameter of the tree 5 cm above the graft union. For bearing trees, TCSA was calculated using the diameter 20 cm above the ground. Trees were planted in a Complete Randomized Block Design (CRBD).

#### **Graft union effect on scion growth and scion effect on rootstock growth**

Vegetative growth measurements similar to those described above were recorded on one-year-old self-grafted trees to determine the effect of the graft union on vegetative growth and on midday stem water potential when the same genotype was used as scion and rootstock in an individual tree. In addition, to determine differences in dry matter partitioning, whole trees planted in the field at 1.5 m x 1.5 m in January 2006, were removed from the ground at the end of the first year of growth, weighed, dried and then weighed again to obtain fresh and dry weights. Total shoot length and dry weight were

also measured. To correlate tree growth with tree water status, midday stem water potential was measured on mature fully expanded leaves, close to the main shoot on May 31, June 1 and August 3, 2006. Two leaves per tree were used for measurement of stem water potential. Leaves were covered with aluminum bags (McCutchan and Shackel, 1992) at least one hour before measurements. After this period, it was assumed that leaf water potential was equilibrated with that of the xylem sap of the stem to which the leaf was attached. Then, leaves were cut and put in a pressure chamber. The excised leaves were pressurized with a 3005-model pressure chamber (Soil Moisture Equipment, Santa Barbara, CA). Trees in these experiments were planted in a CRBD.

In another experiment to determine the effect of the scion ('Redhaven') on the rootstock, one-year-old 'Redhaven' trees were compared to self-grafted rootstocks. Measurements and design were as described for the graft union study.

#### **Diurnal shoot growth and stem water potential**

Diurnal stem extension rate (SER) was measured on six well exposed shoots of three-year-old 'Redhaven' peach trees at the Musser Fruit Research Center on July 27-28, 2005. SER was measured by making fine ink marks with permanent marker on the stem. Only actively growing stems were chosen, while those showing reduction of growth, non-growth or excessive growth (watersprouts) were discarded. Distance between marks was measured with a digital caliper. SER was determined by dividing the length increment (amount of change in distance between marks) by the amount of time between measurements (Berman and DeJong, 1997). Measurements were made at approximately 4-hour intervals during the day and 6-hour intervals during the night. Stem water

potential was measured on the same trees to correlate shoot growth and tree water status. Stem water potential was measured on mature leaves, close to the main shoot at about 1.5 m from the ground. Water potential was recorded at the time of shoot growth measurements, following the same methodology as described above. Each treatment was replicated 5 times in a Complete Randomized Design (CRD). Treatments were: Lovell, Cadaman®, Controller® 5, Pumiselect® and Krymsk® 1. Diurnal stem extension rate and total number of actively growing shoot apices were measured to estimate the diurnal total growth per tree. In addition, diurnal shoot growth and number of growing points were also measured on 3-year-old 'Redhaven' peach trees grafted on Lovell, Cadaman®, Controller® 5, Pumiselect® and Krymsk® 1 rootstock at the USDA Southeastern Fruit & Nut Tree Laboratory, on July 20-21, 2005. Trees were irrigated the previous day until soil field capacity was reached to ensure water was not a limiting factor.

In another experiment, SER, number of shoot growing apices, and water potential studies were done on one-year-old 'Redhaven' peaches trees grafted on Lovell, Cadaman®, Pumiselect® and Krymsk® 1 rootstocks at the Musser Fruit Research Center on June 22-23, 2006. The experiment was set up as described above for the 3-year-old trees.

### **Midday stem water potential**

Different experiments on bearing and non-bearing trees were done to determine the effect of rootstock on tree water status in Spring and Summer of 2005, 2006 and 2007. Measurements of stem water potential at midday were made on 'Redhaven' and 'Redtop' bearing trees at the USDA Southeastern Fruit & Nut Tree Laboratory and the

Musser Fruit Research Center in 2005 and 2006. In these studies treatments included: Lovell, Cadaman®, Controller® 5, Pumiselect® and Krymsk® 1 rootstocks. In addition, similar studies were done on one-year-old ‘Redhaven’ and ‘Redtop’ trees grafted on Lovell, Cadaman®, Pumiselect® and Krymsk® 1 rootstocks at the Musser Fruit Research Center in 2006.

Water potential at Midday was also measured on young ‘Redhaven’ peach trees (less than one-year-old) on Lovell, Pumiselect® and Krymsk® 1 rootstocks at the Musser Fruit Research Center. In addition, the water potential of these ‘Redhaven’ peach trees was compared with the water potential of those of rootstock trees, which had not been budded with a scion (own rooted).

In another study, Lovell, Pumiselect®, Cadaman® and Krymsk® 1 rootstock trees were budded with ‘Redhaven’ peach cultivar at 20 cm from the ground. Leaves situated on the rootstock portion of the tree were retained in order to measure water potential in the rootstock and scion stem at the same time and on the same tree. Differences in scion and rootstock stem water potential would be attributed to the graft union hydraulic resistance. As a control, some rootstock trees were self-grafted. Trees were planted in January 2006, budded in July 2006 and water potential measurements were done in Summer 2007. In addition, the work was repeated on younger ‘Redhaven’ trees at the nursery of the Musser Fruit Research Center in Summer 2007 with Lovell, Pumiselect® and Krymsk® 1 rootstocks as treatments.

### **Transpiration rate and stomata resistance measurements**

Resistance offered by stomata was measured using a steady-state porometer (Li 1600, LICOR, Inc., Nebraska, USA) and expressed in  $s\ cm^{-1}$ . Transpiration was also assessed using the steady state porometer readings and expressed in  $\mu g\ H_2O\ cm^{-2}\ s^{-1}$ . One sun-exposed and fully expanded leaf per tree and 6 trees per treatment (replications) were selected for measurement. In order to reach the steady state conditions, it was necessary to hold the leaves attached to the instrument for at least 1.5 minutes before measuring stomatal resistance and transpiration rate.

On one-year-old 'Redhaven' peach trees grafted on Lovell, Cadaman®, Pumiselect® and Krymsk® 1 rootstocks, diurnal measurements of transpiration rate as well as stomatal conductance were conducted on September 29 and October 6, 2006. The measurements were made six to seven times at about 2-hour intervals from 9 am to 7 pm.

At midday on different dates, stem water potential, transpiration rate and stomatal resistance were simultaneously measured to estimate correlations between tree water status and physiological responses of the stomata under these conditions. Leaves from one- and four-year-old 'Redhaven', and one-year-old 'Redtop' peach trees grown at the Musser Fruit Research Center were used for the study in addition to rootstock trees that had not been budded.

### **Evaporative method: tree hydraulic resistance**

One-year-old peach trees grown in greenhouses at Clemson University, SC, were used to measure tree hydraulic resistance. The experiment included 4 treatments: 'Redhaven' peach cultivar budded on Lovell and Krymsk® 1 rootstocks and trees of both

rootstocks which had not been budded. In the field after growing one year, trees that had not been budded were cut at 20 cm from the ground, while those grafted with the scion were cut back at 10 cm above the graft union. Then all trees were transplanted to pots and moved to the greenhouses. For 3.5 months trees were grown under 16 photoperiod and 26°C air temperature during the day and 20°C at night. Light was provided at  $\sim 700 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$  photosynthetic photon flux density. Trees grew in 57-l plastic containers filled with a mixture of 45% peat moss, 15% perlite, 15% vermiculite and 25% bark (3B-Mix, C. Fafard, Inc., Agawan, MA) and amended with 0.4 kg per pot of 18-6-12 Multicote fertilizer (N-P-K, Schultz Co., Bridgeton, MO). Trees were planted at the end of February 2006 and the experiment was continued until June 21, 2006. Trees were irrigated daily to maintain the soil media at near maximum water holding capacity. The experiment was a Completely Randomized Design with 5 replications (trees).

The evaporative flow method involved the measurement of tree transpiration rates and water potential gradients. The plastic containers in which the trees were growing were enclosed in plastic bags that were sealed around the base of the trunk to avoid evaporation from the soil medium during the experiment.

All calculations were completed assuming that water relations had reached a steady state. It was assumed that all water loss came from the shoots and especially the leaves, and no losses were due to evaporation from the soil. Hydraulic resistance ( $R$ ) and leaf-area-specific resistances ( $R_l$ ) were calculated. Hydraulic resistance was calculated for the whole tree ( $R_{tree}$ ) and also partitioned between the stem and roots ( $R_{stem} + R_{root}$ ).



$$R_{tree} = - \frac{\Psi_{leaf} - \Psi_{soil}}{E}$$

where  $\Psi_{leaf}$  represents leaf water potential,  $\Psi_{soil}$  the soil water potential and  $E$  the evaporative flux density, which was calculated gravimetrically.  $\Psi_{soil}$  was measured in covered leaves at night, assuming an equilibrium between soil and stem water potential under low transpiration conditions.  $E$  was calculated through the following equation:

$$E = \frac{\Delta W}{\Delta t}$$

Where  $\Delta W$  is the weight change (kg) and  $\Delta t$  is the time change (s).

At steady state, stem + root hydraulic resistance ( $R_{stem} + R_{root}$ ) was calculated as:

$$R_{stem} + R_{root} = - \frac{\Psi_{stem} - \Psi_{soil}}{E}$$

Where  $\Psi_{stem}$  is the stem water potential measured on bagged non-transpiring leaves and  $\Psi_{soil}$  is the stem water potential measured at night.

$R_l$  was calculated as follows:

$$E_l = \frac{\Delta W}{A \Delta t}$$

Where  $A$  is leaf area ( $m^2$ ) and  $E_l$  is the evaporative flux density related to leaf area.

Transpiration rate was gravimetrically measured with an ES100L digital scale (Ohaus Corp., Pine Brook, NJ) every 2.5 hours, four times during the light period. Trees were irrigated after weighing to replace transpired water and maintain the soil media at maximum water holding capacity. Conductivity (K) and leaf-area specific conductivity (K<sub>l</sub>) were calculated as 1/R and 1/R<sub>l</sub>, respectively.

### **Fine root length and density**

Fine root development from 2-year-old 'Redhaven' peach trees grafted on Lovell, Cadaman®, Pumiselect® and Krymsk® 1 rootstocks was measured using root density cores. Four 20 cm deep and 5.3 cm diameter cores were taken at 40 cm from the base of each tree trunk in April 2006. These cores were taken in opposite directions from the trunk. Total of six trees (repetitions) were used for the experiment. Cores were stored at 4°C until processing. Soil was washed from the rootstock roots by hand. Length of fine roots (less than 3-mm-diameter) per sample was measured and converted with a WinRhizo system (Regent Instruments, Montreal, Quebec, Canada) and used to calculate the root length density (cm root cm<sup>-3</sup> soil) of the soil surrounding the tree trunks.

An additional experiment involved roots of young 'Redhaven' peach trees grafted on Lovell, Pumiselect® and Krymsk® 1 rootstocks grown at the Musser Fruit Research Center nursery, Seneca, SC, in September 2007. Whole trees were removed from the ground, while trying to keep the root system intact. Each tree root system was washed by hand and roots with diameter smaller than 3 mm were separated. Three intact fine root branches (< 3-mm-diameter) per tree were scanned for length with WinRhizo software. After scanning, the three fine root branches were dried. Also, the remaining

fine roots (< 3-mm-diameter) from each tree were dried and weighed to calculate total root length of fine roots. The rest of the material was separated in rootstock shank or tap root (included the trunk portion below the graft union), and roots > 3-mm-diameter (coarse roots). All these tissues were dried for two weeks at 60°C and weighed thereafter. The ratio dry weight: root length from the 3 fine roots was used to calculate the total length of roots smaller than 3-mm-diameter.

Leaf area and fresh and dry weights from above ground tissues (shoot, branches and trunk) was also measured. The experiment included 5 trees per rootstock as replications. All data were analyzed by SAS (9.1 version) using the GLM procedure.

## **Results**

### **Rootstock vegetative growth comparison**

Differences in tree vegetative growth were observed in three- to five-year-old ‘Redhaven’ peach trees at the Musser Fruit Research Center. TCSA of trees grafted on Lovell and Cadaman® rootstocks were the greatest (Fig. 5.1). Controller® 5 and Pumiselect® had intermediate values for TCSA, while Krymsk® 1 had the smallest trunk growth.

When one-year-old trees were compared, ‘Redhaven’ and ‘Redtop’ trees budded on Lovell had the greatest TCSA (Fig. 5.2). Growth reduction was observed in trees on Cadaman® rootstock relative to those trees grafted on Lovell, probably due to the fact

that those trees on Cadaman® were planted later than the rest of the rootstocks, which reduced their initial and probably final size.

Trunk cross-sectional area did not differ significantly when one-year-old 'Redhaven' and 'Redtop' trees were compared on the same rootstock, with the exception of trees on Lovell rootstock. In addition, trees on Lovell had larger TCSA after the second year of growth, while trees on Krymsk® 1 were the smallest (Fig. 5.2; Table 5.1). Similar results were found in the number of one-year-old shoots and tree height in the first season. Generally, the 'Redhaven' cultivar grew more than 'Redtop', except when trees were grown on Krymsk® 1 rootstock (Fig. 5.2; Table 5.1).

#### **Graft union effect.**

The effect of the graft union on tree growth and water status was studied on self-grafted and non-grafted rootstock trees. No differences were recorded when budded and non-budded trees on the same rootstock were compared. Figure 5.3 and Table 5.2 show differences in vegetative growth patterns due to rootstock genotypes independently of the graft unions. Graft union, in these compatible combinations (self-grafted), did not affect the number of grown shoots per tree, tree height and TCSA at the end of the first season when the same root genotype was considered. Differences were attributed only to root genotypes (Table 5.2).

The effects of the graft union on the midday stem water potential followed the same pattern as vegetative growth. No significant differences were found for most of the combinations when the same genotype was studied. Only self-grafted Krymsk® 1 trees had significantly higher values (less negative) of water potential than those non-grafted

(Table 5.2). Significant differences were found among genotypes, where Pumiselect® trees had the highest (less negative) midday stem water potential, whereas Krymsk® 1 rootstock, in concurrence with the lowest vegetative growth, had the lowest (more negative) water potential at midday (Table 5.2).

### **Scion effect on rootstock**

Generally, self-grafted Lovell trees had the largest trunks (Table 5.3), while Krymsk® 1 trees had the smallest trunks at the end of the first season. The most vigorous rootstock, Lovell (self-grafted), had a reduction in TCSA when the material was grafted with ‘Redhaven’ scions; whereas, Pumiselect® and Krymsk® 1 trees increased their trunk diameter when grafted with ‘Redhaven’. Similar results were found when the number of grown shoot apices and total shoot length per tree were considered. However, in the case of trees grown on Lovell rootstocks, there were no differences in both number of growing points and total shoot length (Table 5.3).

Shoot, root, total tree dry weight, and shoot: root ratios were significantly affected by the scion (‘Redhaven’) when the same root genotype was compared. Generally, the scion reduced the vegetative tree growth of Lovell rootstocks. Even though no significant differences in total tree dry weight were found on Pumiselect® and Krymsk® 1 rootstocks due to scion effect, these rootstocks showed an increase tendency when trees were budded with the scion (Table 5.3). TCSA was significantly greater when Pumiselect® and Krymsk® 1 rootstocks were grafted with ‘Redhaven’. Clear significant differences were found when root genotypes were compared. Krymsk® 1 had the lowest shoot, root and total tree dry weights while Lovell the highest. Shoot: root ratio values

depended on the rootstock and were not affected by the scion. Krymsk® 1 had the lowest ratios, while Pumiselect® had the highest ones (Table 5.3).

### **Diurnal shoot growth**

Diurnal shoot extension growth rate of 3-year-old 'Redhaven' peach trees was higher on trees grafted on Lovell and Cadaman® rootstocks as compared with the rest of the combinations (Fig. 5.4). Krymsk® 1, especially at midday, had the lowest shoot extension growth rate on the tagged shoots on July 27-28, 2005. Table 5.4 shows the effect of rootstocks on the total number of active growing shoot apices per tree on July 27-28, 2005. 'Redhaven' trees grafted on Lovell and Cadaman® rootstocks had a significantly greater number of growing shoots per tree. Controller® 5 had intermediate number of shoots per tree, while Pumiselect® and Krymsk® 1 had the least. Average diurnal growth of the selected shoots on Krymsk® 1 rootstock was significantly lower than shoots on Cadaman® and Lovell rootstocks. The estimated total diurnal shoot growth per tree was calculated by multiplying the number of growing shoots per tree by the mean daily shoot growth. Differences were directly correlated with the number of growing shoots per tree: Trees on Lovell and Cadaman® rootstocks grew approximately 2 m per day. Trees on Controller® 5 approximately 1 m per day and trees on Pumiselect® and Krymsk® 1 grew less than 0.4 m per day. Trees grown in Georgia had similar results to those grown in South Carolina (Table 5.4). Three-year-old 'Redhaven' trees on Lovell and Cadaman® rootstocks had significantly greater total estimated diurnal shoot growth (length) per tree than Pumiselect® and Krymsk® 1 rootstocks, and these differences were mainly due to the number of active growing shoots per tree (Table 5.4).

Controller® 5 had intermediate mean values and only differed significantly from Krymsk® 1 in the number of growing shoots per tree.

One-year-old 'Redhaven' trees on Pumiselect® and Krymsk® 1 rootstocks had low stem water potentials, especially at midday and during the early hours of the afternoon (Fig. 5.5). At the same time, trees on Cadaman® and Lovell rootstocks had high growth on the tagged shoots. Water potential was related to the temperature, since high temperatures corresponded with low stem water potentials. Trees grafted on Lovell rootstocks had the highest number of growing shoots, and daily and total shoot growth per tree (Table 5.5). Cadaman® trees had the highest diurnal growth of the tagged shoots; however, total estimated shoot growth was lower than Lovell because of the reduced size of the plants due to the fact that Cadaman® trees were planted later. Both Pumiselect® and Krymsk® 1 had the smallest amount of growth.

### **Midday stem water potential measurements**

#### **Bearing trees**

In order to relate scion vegetative growth, tree water status, and rootstocks, different studies were done in bearing and young non-bearing peach trees based on the stem water potential at midday. Midday stem water potential of mature bearing 'Redhaven' and 'Redtop' peach trees at the Musser Fruit Research Center and the USDA Southeastern Fruit & Nut tree Laboratory were measured on different dates. Similar trends were observed at both sites (Table 5.6). Trees on Cadaman® and Lovell rootstocks had greater stem water potential (less negative) than on Pumiselect and Krymsk® 1 the lowest (more negative).

### **Young non-bearing trees**

During the season, one-year-old 'Redhaven' trees on the more vigorous rootstocks, Lovell and Cadaman®, had higher mean stem water potential at midday than the less vigorous rootstocks, Pumiselect® and Krymsk® 1. In general, trees on Krymsk® 1 rootstock had the lowest stem water potentials (Fig. 5.6). When all dates were averaged, 'Redhaven' trees on Cadaman® and Lovell had the highest stem water potential at midday (-0.75 and -0.85 Mpa, respectively), while Pumiselect® had intermediate stem water potential values (-1.04 Mpa) and Krymsk® 1 the lowest values (-1.14 Mpa). Young 'Redtop' trees on Cadaman® and Lovell rootstocks had significantly higher mean stem water potential (-0.90 and -0.92 Mpa, respectively) during the season than those trees on Pumiselect® and Krymsk® 1 rootstocks (-1.02 and -1.06 Mpa, respectively). 'Redhaven' and 'Redtop' cultivars did not affect the stem water potential of those trees grafted on different rootstocks over two different dates (data not shown).

In another experiment, self-rooted 'Redhaven' trees were compared with 'Redhaven' on different rootstocks. No significant differences were observed between self-rooted 'Redhaven' trees and the rest of the combinations except with Krymsk® 1. Midday stem water potential for trees grafted on Krymsk® 1 had -1.10 Mpa, while the rest of the combinations ranged between -0.82 and -0.94 Mpa.



### **Stem water potential comparison between rootstock and scion in different and same trees**

Midday stem water potential was measured on one-year-old ‘Redhaven’ peach trees grafted on four different rootstocks and in self-grafted rootstock trees on 3 different days (May 31, June 1 and July 11, 2006). The most noticeable result was found in the combinations ‘Redhaven’ on Pumiselect® and self-grafted Pumiselect® trees. In these cases, ‘Redhaven’ trees on Pumiselect® had the lowest mean midday water potential (-1.41 Mpa), while self-grafted Pumiselect® trees had the highest midday water potential (-0.71 Mpa). ‘Redhaven’ trees on Lovell rootstock (-0.96 Mpa) did not differ from self-grafted Lovell trees (-0.99 Mpa). Differences between ‘Redhaven’ and self-grafted trees were the greatest when ‘Redhaven’ on Pumiselect® were compared to self-grafted Pumiselect® trees (Table 5.7).

Measurements of midday stem water potential were made below and above the graft union on the same tree. Because leaves were left on the rootstock, as well as on the cultivar, it was possible to measure the rootstock and scion (‘Redhaven’) stem water potential at the same time and on the same tree. Differences between stem water potential above and below the graft union could be attributed to the graft union hydraulic resistance.

Midday stem water potential differences between rootstock and scion were also measured on young ‘Redhaven’ trees at the nursery of the Musser Fruit Research Center (Table 5.7). Similar to one-year-old trees, the RH/Pumiselect® combination had the largest difference between rootstock and scion stem water potential at midday. Krymsk®

1 rootstock trees had the lowest rootstock water potential. Mean scion midday stem water potential was lowest on trees grafted on Krymsk® 1 and Pumiselect® rootstocks.

In another study, self-rooted rootstock trees were studied on two different days in June (June 10, 16, 2007). In agreement with previous results, self-grafted Pumiselect® trees had the highest average midday stem water potential (-0.49Mpa), whereas Krymsk® 1 trees had the lowest (-0.91Mpa). Lovell trees had intermediate stem water potential values (-0.70 Mpa).

### **Transpiration rate and stomatal resistance**

The rootstock had a significant effect on the stomatal resistance of 'Redhaven' leaves on September 29, 2006 (Fig. 5.7). Leaves from trees on Pumiselect® rootstock had significantly greater stomatal resistance, especially at midday, as compared to leaves of trees grafted on Cadaman® rootstock. Leaf stomatal resistance at midday remained at  $\sim 1.5 \text{ s cm}^{-1}$  in Pumiselect® trees and  $\sim 1 \text{ s cm}^{-1}$  in Cadaman® trees. Thus, the Pumiselect® genotype caused an increase (i.e.,  $\sim 50\%$  higher) in stomatal resistance compared to Cadaman® (Fig. 5.7). During the day, trees on Pumiselect® had the greatest average stomatal resistance ( $1.92 \text{ s cm}^{-1}$ ), while trees on Cadaman® had the lowest ( $1.30 \text{ s cm}^{-1}$ ). Stomatal resistance for those trees on Krymsk® 1 ( $1.72 \text{ s cm}^{-1}$ ) did not differ from Lovell ( $1.60 \text{ s cm}^{-1}$ ); however, the stomatal resistance observed in Lovell was greater than that observed in Pumiselect®. During the same period transpiration rate followed an inverse relationship to that of stomatal resistance (Fig. 5.7). Leaves on trees grafted on Cadaman® rootstocks increased the transpiration rate at midday to  $\sim 13 \mu\text{g m}^{-2} \text{ s}^{-1}$ , while leaves on Pumiselect® increased to  $\sim 10 \mu\text{g cm}^{-2} \text{ s}^{-1}$ . Although the differences

in transpiration rate between Pumiselect® and Cadaman® were significant at midday, trees on Cadaman® tended to show a 30 to 40% greater transpiration rate during the sunlit hours when compared to that of Pumiselect®.

Stomatal resistance and transpiration rate of different rootstock genotypes in one-year-old 'Redhaven' trees were also studied on October 6, 2006 (Fig. 5.8). Results were similar to those recorded on September 29, 2006. Leaf stomatal resistance of trees grown on Pumiselect® rootstock was close to  $1.5 \text{ s cm}^{-1}$ , while those on Cadaman® and Lovell rootstocks were approximately  $1.0 \text{ s cm}^{-1}$ . Stomatal resistance increased remarkably at the end of the afternoon due to sunlight reduction. The mean tendency showed that there was approximately a 50% increase in stomatal resistance for the Pumiselect® genotype as compared to trees on Cadaman® rootstock. During sunlit hours, mean stomatal resistance was  $2.06$  and  $2.03 \text{ } \mu\text{g cm}^{-2} \text{ s}^{-1}$  for Krymsk® 1 and Pumiselect®, respectively and was significantly greater than the stomatal resistance observed for Cadaman® and Lovell ( $1.52$  and  $1.40 \text{ } \mu\text{g cm}^{-2} \text{ s}^{-1}$ , respectively). Transpiration rate during the day averaged  $8.50 \text{ } \mu\text{g cm}^{-2} \text{ s}^{-1}$  for Pumiselect® rootstock,  $9.43 \text{ } \mu\text{g cm}^{-2} \text{ s}^{-1}$  on Krymsk 1,  $11.02 \text{ } \mu\text{g cm}^{-2} \text{ s}^{-1}$  for Lovell and  $11.06 \text{ } \mu\text{g cm}^{-2} \text{ s}^{-1}$  for Cadaman®. Leaf transpiration on Cadaman® and Lovell was significantly greater than on Pumiselect® and Krymsk® 1.

In another experiment, root genotypes, stomatal resistance, leaf transpiration rate and midday stem water potential at midday were studied on one-year-old 'Redhaven'. Water vapor pressure deficit was expected to be highest at midday, where it might lead to increased stomatal resistance due to closing of stomata. Results (Table 5.8) showed that trees on Lovell and Cadaman® rootstocks had significantly higher midday stem water

potentials, than trees on Krymsk® 1 rootstocks. Trees on Pumiselect® had intermediate stem water potential. Under these conditions, leaves on Cadaman® had the greatest transpiration rate. Transpiration rate for leaves on Cadaman® rootstock was 35 and 50% greater than those leaves on Pumiselect® and Krymsk® 1 rootstocks, respectively. In contrast, stomatal resistance was the highest in leaves on Krymsk® 1 rootstock and the lowest in leaves on Cadaman® rootstock.

#### **The evaporative method: tree hydraulic resistance**

Tree growth was significantly affected by the treatments (Table 5.9). Above ground tree dry mass was higher in 'Redhaven' (RH) trees on Lovell (L) rootstock and in self-grafted Lovell trees when compared to self-rooted Krymsk® 1 rootstock trees. Root dry weight was lower in self-grafted Krymsk® 1 trees than in RH/L and Lovell. Total tree dry weight was also affected by treatments; where RH/L tree dry weight was greater than trees on Krymsk® 1 roots. In addition, shoot: root ratio was higher in the own-rooted Krymsk® 1 trees compared to the other combinations. Leaf area was significantly greater in RH/L and Lovell trees (4.36 and 4.91 m<sup>2</sup>, respectively). Krymsk® 1 trees had significantly smaller leaf area (2.19 m<sup>2</sup>), while intermediate results were found in RH/K trees (3.03 m<sup>2</sup>). Results from this study suggested that potted trees could suffer root growth limitations, which might prevent and modify tree vegetative growth potential.

Significant differences were found in specific-leaf-area conductance (*K<sub>l</sub>*) where self-grafted Krymsk® 1 trees had the least *K<sub>l</sub>* when the whole tree and stem + root were considered (Table 5.10). Although no differences were shown among the rest of the combinations, trees on Lovell roots tended to have a higher *K<sub>l</sub>* than those on Krymsk® 1

roots. Hydraulic conductance (K) did not differ among treatments; however, trees grafted on Lovell rootstock had a higher K value than those grafted on Krymsk® 1 rootstocks (Table 5.10).

### **Root system: root length and density**

Vegetative growth of young ‘Redhaven’ trees grown in the nursery was significantly affected by root genotype. Lovell roots induced a high vigor as compared to the ‘Redhaven’ cultivar; whereas Krymsk® 1 roots significantly reduced tree size (Table 5.11). In addition, the relationship between shoot and root dry weight was affected by the different rootstocks. Trees on Krymsk® 1 had the lowest shoot: root ratio compared to the other two rootstocks.

Lovell had significantly higher shank and total root dry weight (Table 5.12). However, fine root (<3-mm-diameter) dry weight was significantly higher in Pumiselect® than in Lovell, while Krymsk® 1 fine (small) root dry weight was intermediate between Pumiselect® and Lovell. Dry coarse roots weighted more in Lovell than in Krymsk® 1. No significant differences were found in total fine root length; however, the root system of Pumiselect® tended to have a greater total length of fine roots. This was readily observed when whole trees were pulled from the ground. Pumiselect® had long fine roots and most of them were located near the surface. Lovell roots had 90% of the total root dry weight as shank and coarse roots (>3-mm-diameter) although these two tissues represented less than 60% of total root dry weight in the case of the Pumiselect® root system. When soil samples were taken near one-year-old

'Redhaven' trunks, no major differences were found either in root length or in root dry weight per soil volume among the treatments (Table 5.12).

### **Discussion**

In our study, rootstocks significantly affected scion growth. These results were comparable to those reported by Reighard et al. (2006) and DeJong et al. (2005). Using 'Redhaven' on Lovell as the control, TCSA of bearing 4-year-old 'Redhaven' trees grafted on Krymsk® 1 rootstock were only 30% of those control plants. TCSAs of trees on Pumiselect® rootstock were only 60% of the control trees. Trees on Cadaman® had similar growth to those on Lovell.

In young trees, differences among rootstocks were smaller when recorded for the first year than for the second season. 'Redhaven' on Krymsk® 1 rootstock was about 50% of the size of those trees on Lovell after the first year of growth and 35% at the end of the second season. Seleznyova et al. (2004) suggested that dwarfing effects are cumulative and superimposed year-to-year. This would be explained by the reduction in the number of internodes and buds at the end of every season, with the consequent reduction in the number of shoots coming in the following spring. This annual behavior found in dwarfed trees year after year would end in smaller trees at the end of each year compared to trees grown on vigorous rootstocks. In our study, differences in the number of current year shoots between trees on dwarfing and vigorous rootstocks at the end of the first year supported this supposition.

The effect of rootstock on the scion has been widely studied; however, less attention has been devoted to the scion effect on the rootstock. The most vigorous rootstock, Lovell, had a reduction in total tree dry weight up to 20% when it was grafted with 'Redhaven'. However, Krymsk® 1 trees increased 2.6 fold in dry weight when they were grafted with 'Redhaven'. Pumiselect® had an increment of 30% in dry weight after having been budded with 'Redhaven'. When total dry weight of self-grafted Lovell trees was considered as 100%, self-grafted Pumiselect® trees grew only about 25% of Lovell, while Krymsk® 1 grew only about 9% (Tables 5.2 and 5.3). Thus, when tables 5.1-5.3 were considered, the dwarfing effects of rootstocks were remarkably dependent on rootstock genotype; the smaller the rootstock the greater the dwarfing effect.

The reason why trees on dwarfing rootstocks are smaller should be directly connected to the mechanism that induces the reduction of the scion vegetative growth. Therefore, we focused this research on hydraulic conductance as the major cause of growth reduction, which has been suggested as a possible dwarfing mechanism by previous works (Atkinson and Else, 2001; Atkinson, 2003; Basile et al., 2003b; Webster and Wertheim, 2003; Weibel et al., 2003; Nakano et al., 2004; Solari and DeJong, 2006).

The effect of the graft union on the resistance to water flow has been studied in apples (Beakbane and Thompson, 1939; Simons and Chu, 1980,1984; Soumelidou et al., 2004; Atkinson et a., 2003), peaches (Basile et al., 2003b), and cherries (Olmstead et al., 2004, 2006ab). In this study, when rootstock trees were self-grafted, no effect was observed in either vegetative growth or in stem water potential. Similarly, when good compatibility between rootstock and scion tissues is present, the newly formed

conducting elements (xylem and phloem) do not reduce the water pathways (Gascó et al., 2007). On the contrary, when species or cultivars are partially compatible or incompatible, discontinuities or distortion of the xylem or phloem are present (Moing and Carde, 1988; Olmstead et al., 2006; Zarrouk, 2006).

Berman and DeJong (1997b), Basile et al. (2003a) and Weibel et al. (2003) showed that seasonal vegetative growth depends on the diurnal stem extension growth, which is directly related to the water status of the plant. In our work, diurnal shoot growth rates were comparable to those found by these authors in peach trees. However, in order to quantify the effect of rootstocks it was necessary to consider the total number of shoots that were growing at the same time. On a daily basis, shoots from 4-year-old ‘Redhaven’ trees grew 0.18 m on Krymsk® 1, 2.17 m on Cadaman® and 1.88 m on Lovell.

It is known that apple dwarfing rootstocks exhibit increased water flow resistance at the graft union (Atkinson et al., 2003) similar to cherries (Olmstead et al., 2004). However, studies done in peaches showed that the major resistance to water transport was found in the roots (Basile et al., 2003b; Solari et al., 2003ab). The results in peach were similar to those found in most plants where the major hydraulic resistance was accounted for by the root system (Passioura, 1988; Barrowclough et al., 2000; Tyree, 2003). We found that at midday self-grafted Pumiselect® trees had higher stem water potentials than Krymsk® 1, suggesting a lower tree hydraulic resistance, compared to other self-grafted rootstocks. When Krymsk® 1 rootstock was grafted with ‘Redhaven’, the scion water potential dropped less than 10%; however, when Pumiselect® was budded with ‘Redhaven’, scion water potential dropped about 42% relative to the self-grafted



rootstock trees. No change was observed in stem water potential at midday between self-grafted Lovell trees and those grafted with 'Redhaven'. In addition, when leaves were left on the rootstock portion, the stem water potential from rootstock to scion dropped 9% and 34% for Krymsk® 1 and Pumiselect® trees, respectively. Although no quantification of hydraulic resistance was made, the results suggested that in the case of Pumiselect®, the graft union might considerably increase the tree hydraulic resistance. Furthermore, it appeared that the major source of hydraulic resistance in Krymsk® 1 was the root system as was reported by Basile et al. (2003b) and Solari et al. (2006ab).

Decrease in scion growth by dwarfing rootstocks is thought to be due mainly to the reduction in shoot and leaf growth because of low water potential. Low water potential of stressed trees grafted on dwarfing rootstock directly affect biochemical processes such as solute transport and cell wall loosening and formation. In addition, physical parameters are affected such as turgor pressure and water transport (Hsiao and Jing, 1987; Hsiao and Xu, 2000). Moreover, limitations on photosynthesis might affect growth in the long term by reducing carbohydrate availability for biochemical processes and reserves (Loreto and Chartzoulakis, 2003; Taiz and Zeiger, 2006). In our study, leaf temperature, measured with the porometer, did not differ among rootstocks at any time. Even though photosynthesis was not measured in our work, transpiration rate and stomatal resistance were significantly different among rootstocks. These differences were found particularly at midday and in the early afternoon hours; however, trends in transpiration and stomatal resistance tendencies during the high light intensity hours showed that the more dwarfing rootstocks, Krymsk® 1 and Pumiselect®, had the lowest

transpiration rate and the highest stomatal resistance. Solari and DeJong (2006) working on both a semi-dwarfing (Controller® 5) and a vigorous rootstock (Nemaguard) found through root pressurization that higher increments in leaf water potential, transpiration rate and leaf conductance were expressed in the invigorating rootstock. Similar results were found in apple rootstocks by Li et al. (2002) who concluded that differences in the lower canopy conductance in M.9 dwarfing rootstocks were caused by resistance in the water transport in the roots or graft union. In contrast, Wilkins et al. (2002) did not find differences in leaf conductance, internal CO<sub>2</sub>, and leaf transpiration among several peach rootstock selections, although they worked with non-dwarfing rootstocks. Our results showed increments in stomatal conductance and transpiration rate at higher stem water potentials, which were associated with the more vigorous rootstocks.

The evaporative method, as studied in potted trees, measured tree hydraulic conductance. In this study, significant differences were found among treatments in dry weight and leaf area; however, these differences were much smaller in magnitude than those observed in the same combinations growing in the field. Effects of root confinement on vegetative growth, such as in containers, have been widely reported (Williamson and Coston, 1990; Rieger and Marra, 1994; Webster et al, 2000), to cause severe reduction in shoot and root growth. Webster et al. (2000) demonstrated that there were no differences in tree dry weight when different apple rootstocks were grown in containers, even though the large differences in rootstock vegetative growth potential had been observed previously in the field under normal growth conditions. In our experiment, tree hydraulic resistance values were similar to those found by Solari et al.

(2006a); however, we did not find differences among treatments as Solari et al. (2006a) did. Constriction effects could have been more magnified in our trees because they grew in pots in the greenhouse where root growth conditions were more limiting; whereas trees observed by Solari et al. were growing in pots located outside (in the field).

Trunk cross-sectional area, shoot: root ratio, leaf area, and shoot, root, leaf and total tree dry weight were all affected by treatments when young trees were grown in the nursery. Significant differences were observed between Lovell, Pumiselect® and Krymsk® 1 rootstocks, and these differences were associated with the vegetative growth potential linked to each rootstock. Total fine root length (<3-mm-diameter) did not differ statistically; however, the trends in total fine root length indicated that Pumiselect® roots had more fine roots than the other rootstocks, whereas Lovell roots had the smallest total length of fine roots. Pumiselect® had the highest midday stem water potential, thus the greater amount of fine roots, which are responsible for most of the water uptake (Barrowclough et al. 2000; Tyree, 2003) would support an explanation for the high hydraulic conductivity noted in Pumiselect®. High root conductivity in Lovell could be explained as a consequence of high radial conductivity in the fine roots. Basile et al. (2007), working on 5 different peach rootstocks, found differences in fine root length only in K-119-50 (*Prunus salicinia* x *P. dulcis*), which produced the greatest amount of fine roots, whereas there were no differences among the other 4 rootstocks. In our work, trends observed in Pumiselect® fine roots agreed with our previous studies when one-year-old 'Redhaven' peach trees were removed from the ground, and where Pumiselect® accounted for the largest amount of small roots (< 5-mm-diameter). Vercambre et al.

(2002) reported that main roots in *Prunus* L. did not appear to limit axial water transport, so limitation in water uptake and transport should be limited to the fine roots. In our experiment, Krymsk® 1 root system had similar total fine root length and dry weight to Lovell; however, larger roots (>3-mm-diameter) were found in Lovell. Assuming that Krymsk® 1 had a larger root hydraulic resistance than Lovell roots; a larger radial hydraulic conductance is to be expected in the more vigorous rootstock (Lovell). When the roots are very long or the water conducting elements are largely cavitared, the greatest resistance to the water flow in plants is located at the radial level (Frensch and Hsiao, 1993; Steudle and Peterson, 1998; Vercambre et al., 2002; Tyree, 2003).

Although measurements of hydraulic conductance of roots were not assessed by the present study, the results suggested that in peach rootstocks the main hydraulic resistance might be located at the root or graft union interface, depending on genotype combinations. Differences observed between apple and peach hydraulic resistance might not be generally applicable for the species but probably is limited to specific combinations. In addition, root system architecture which was not evaluated in our study might play an important role in hydraulic conductance (Huang and Eissenstat, 2000).

After studying different cultivars, locations, tree ages, and rootstocks, the present work showed a relationship between scion vegetative growth and how it is affected by rootstock and tree water status. In addition, the results of our study suggest that the seasonal changes in dry matter production and partitioning found in two peach cultivars may be influenced, at least in part, by seasonal variations in stem water potential, stomatal conductance and transpiration rates.

Table 5.1. Trunk cross-sectional area (TCSA) (2006-2007), number of growing points per tree (NGP) (2006) and tree height (2006) of ‘Redhaven’ (RH) and ‘Redtop’ (RT) peach trees grafted on different rootstocks. Trees were planted in January 2006.

<b>Redhaven (RH) and Redtop (RT) vegetative growth<sup>y</sup></b>				
<b>Combinations</b>	<b>TCSA one - year-old trees (cm<sup>2</sup>)</b>	<b>TCSA two - year-old trees (cm<sup>2</sup>)</b>	<b>NGP one - year-old trees</b>	<b>Height one - year-old trees (cm)</b>
<b>RH/ Cadaman<sup>z</sup></b>	16.01 bc	43.12 b	145.9 b	209.5 ab
<b>RT/ Cadaman<sup>z</sup></b>	13.18 c	38.14 b	83.63 cd	177.2 cde
<b>RH/ Lovell</b>	19.78 a	55.92 a	202.7 a	224.5 a
<b>RT/ Lovell</b>	16.65 b	51.76 a	145.1 b	208.7 ab
<b>RH/ Pumiselect</b>	16.03 bc	-	139.6 b	192.0 bc
<b>RT/ Pumiselect</b>	14.92 bc	-	107.9 c	189.8 bcd
<b>RH/ Krymsk 1</b>	9.47 d	18.89 c	68.6 de	171.9 de
<b>RT/ Krymsk 1</b>	7.82 d	11.47 c	42.4 e	160.2 e

<sup>y</sup>Different letters within columns indicate significant differences at P <0.05 (Duncan’s multiple range test).

<sup>z</sup>Trees were planted in April 2006.

Table 5.2. The TCSA, annual TCSA increment, number of grow points per tree (NGP), tree height and midday stem water potential (MSW) of rootstock trees self-grafted and non-grafted. Trees were planted at the Musser Fruit Research Center, South Carolina, in January 2006. Midday stem water potential was measured on May 31, June 1 and August 3, 2006.

<b>Graft union effect <sup>y</sup></b>						
<b>Rootstocks</b>	<b>TCSA 2006 (cm<sup>2</sup>)</b>	<b>TCSA 2007 (cm<sup>2</sup>)</b>	<b>TCSA incred. (cm<sup>2</sup>)</b>	<b>NGP</b>	<b>Tree height (cm)</b>	<b>MSW (Mpa)</b>
<b>Cadaman/ Cadaman</b>	29.3 a	-	-	179.3 b	294.4 a	-1.17 bc
<b>Cadaman</b>	25.0 ab	65.4 a	41.4 a	152.0 b	282.3 ab	-1.25 c
<b>Lovell/ Lovell</b>	26.8 ab	-	-	225.7 a	232.7 d	-1.06 ab
<b>Lovell</b>	23.9 b	57.2 b	33.7 b	218.3 a	228.8 d	-1.08 ab
<b>Pumiselect/ Pumiselect<sup>z</sup></b>	9.5 c	-	-	28.8 c	233.1 d	-0.98 a
<b>Pumiselect<sup>z</sup></b>	9.9 c	-	-	29.8 c	227.3 d	-0.97 a
<b>Krymsk 1/ Krymsk 1</b>	3.2 d	8.4 c	5.3 c	8.1 c	264.8 bc	-1.29 c
<b>Krymsk 1</b>	3.3 d	9.6 c	6.3 c	9.8 c	242.8 dc	-1.44 d

<sup>y</sup>Different letters within a column indicate significant differences at P <0.05 (Duncan's multiple range test).

<sup>z</sup> Combinations were removed for dry weight studies in January 2007.

Table 5.3. Effect of the scion (Redhaven) on trunk cross-sectional area (TCSA), number of growing points (NGP), total shoot length, shoot, root and total tree dry weight of one-year-old rootstock trees in Winter 2006-07. Trees were planted at the Musser Fruit Research Center, South Carolina in January 2006.

<b>Scion effects on the rootstocks<sup>z</sup></b>							
<b>Combinations</b>	<b>TCSA (cm<sup>2</sup>)</b>	<b>NGP /tree</b>	<b>Shoot length (cm)</b>	<b>Shoot dry weight (g)</b>	<b>Root dry weight (g)</b>	<b>Total tree weight (g)</b>	<b>Shoot: root ratio</b>
<b>Redhaven/ Lovell</b>	20.5 b	233.7 a	8787 a	2063 b	1796 b	3859 b	1.13 dc
<b>Lovell</b>	27.7 a	229.7 a	10512 a	2796 a	2121 a	4917 a	1.31 bc
<b>Redhaven/ Pumiselect</b>	13.1 c	114.2 b	5167 b	1104 c	707 c	1811 c	1.60 a
<b>Pumiselect</b>	8.4 d	31.2 dc	2719 c	768 dc	494 c	1261 c	1.53 ab
<b>Redhaven/ Krymsk 1</b>	7.44 d	63.8 c	2408 c	561 dc	600 c	1161 dc	0.93 d
<b>Krymsk 1</b>	3.04 e	8.0 d	756.5 d	236 d	211 d	447 d	1.12 dc

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

Table 5.4. Effect of rootstocks on the number of active growing points (NGP), average diurnal shoot growth (ADSG) and estimated total diurnal shoot growth (EDSG) per tree of 3-year-old Redhaven peach trees grown at the USDA Southeastern Fruit & Nut Tree Laboratory, Byron, Georgia and the Musser Fruit Research Center, South Carolina, July 20-21 and 27-28, 2005, respectively.

<b>Diurnal shoot growth and NGP per tree<sup>z</sup></b>						
<b>Rootstocks</b>	<b>Georgia</b>			<b>South Carolina</b>		
	<b>NGP</b>	<b>ADSG (mm/d)</b>	<b>EDSG (cm)</b>	<b>NGP</b>	<b>ADSG (mm/d)</b>	<b>EDSG (cm)</b>
<b>Lovell</b>	221.8 a	8.0 a	175.8 a	252.2 a	7.3 ab	187.6 a
<b>Cadaman</b>	194.0 a	7.5 a	147.1 a	248.6 a	8.8 a	217.2 a
<b>Controller 5</b>	151.0 ab	6.5 ab	104.8 ab	128.6 b	8.9 a	112.8 b
<b>Pumiselect</b>	55.7 bc	3.9 b	36.4 b	53.0 c	6.5 ab	37.6 c
<b>Krymsk 1</b>	23.4 c	7.8 a	20.5 b	28.2 c	5.2 b	18.3 c

<sup>z</sup>Different letters within a column indicate significant differences at P <0.05 (Duncan's multiple range test)



Table 5.5. Effect of rootstocks on the number of growing points (shoots) and estimated total diurnal shoot growth of one-year-old Redhaven peach trees grown at the Musser Fruit Research Center, June 22-23, 2006. Trees were planted in January 2006.

Rootstocks	Diurnal shoot growth <sup>z</sup>		
	Number of growing points per tree	Average diurnal shoot growth (mm/d)	Total diurnal shoot growth per tree (cm)
<b>Lovell</b>	44.2 a	11.0 a	475.5 a
<b>Cadaman<sup>y</sup></b>	19.8 b	13.4 a	259.9 b
<b>Pumiselect</b>	27.2 b	7.7 b	215.8 b
<b>Krymsk 1</b>	14.2 b	6.4 b	91.5 b

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

<sup>y</sup>Trees on Cadaman were planted in April 2006.

Table 5.6. Midday stem water potential of bearing Redhaven and Redtop peach trees grafted on different rootstocks at the Musser Fruit Research Center, Seneca, South Carolina and USDA Southeastern Fruit & Nut Tree Laboratory, Byron, Georgia, 2005-2006. Redtop trees were planted in 2001 and Redhaven trees in 2002.

<b>Midday water potential (Mpa)<sup>z</sup></b>				
	<b>Georgia</b>		<b>South Carolina</b>	
<b>Rootstocks</b>	<b>Redhaven<sup>y</sup></b>	<b>Redtop<sup>w</sup></b>	<b>Redhaven<sup>v</sup></b>	<b>Redtop<sup>u</sup></b>
<b>Lovell</b>	-0.55 a	-0.46 a	-0.78 a	-0.42 a
<b>Cadaman</b>	-0.58 a	-	-0.78 a	-0.48 b
<b>Controller 5</b>	-0.63 a	-0.68 b	-0.93 b	-0.54 c
<b>Pumiselect</b>	-1.04 c	-0.85 c	-1.17 c	-
<b>Krymsk 1</b>	-0.80 b	-0.85 c	-0.98 b	-0.54 c

<sup>z</sup>LSmeans within a column with different letters are significantly different (P <0.05).

<sup>y</sup>Measured on 5/12 and 7/19/2005.

<sup>w</sup>Measured on 5/12/2005.

<sup>v</sup>Measured on 5/18, and 7/27/2005, and 7/12 and 7/28/2006.

<sup>u</sup>Measured on 5/18/2005.

Table 5.7. Mean midday stem water potential comparison between one-year-old Redhaven (RH) peach trees (scion) grafted on different rootstocks and self-grafted rootstock trees (root) in 2006, and rootstock (root) and scion midday stem water potential of young Redhaven peach trees measured on the same tree in 2007 at the Musser Fruit Research Center, Seneca, South Carolina.

<b>Midday stem water potential of (Mpa)<sup>z</sup></b>						
<b>Different tree (2006)<sup>y</sup></b>				<b>Same tree (2007)<sup>w</sup></b>		
<b>Combinations</b>	<b>Scion</b>	<b>Root</b>	<b>Differ.</b>	<b>Scion</b>	<b>Root</b>	<b>Differ.</b>
<b>RH/Lovell</b>	-0.96 a	-0.99 b	-0.03 b	-0.77 a	-0.65 a	0.11 b
<b>RH/Pumiselect</b>	-1.21 b	-0.71 a	0.50 a	-1.00 b	-0.66 a	0.34 a
<b>RH/Krymsk 1</b>	-1.17 b	-1.07 b	0.10 b	-0.98 b	-0.81 b	0.16 b

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

<sup>y</sup>Measured on May 31, June 1 and July 11, 2006.

<sup>w</sup>Measured on July 20, August 17 and September 4, 2007.

Table 5.8. Average midday stem water potential, leaf transpiration rate and stomata resistance of one-year-old Redhaven peach trees grafted on 4 different rootstocks at the Musser Fruit Research Center, Seneca, South Carolina on June 29 and July 12, 2006.

<b>Redhaven<sup>z</sup></b>			
<b>Rootstock</b>	<b>Water potential (Mpa)</b>	<b>Stomatal resistance (s cm<sup>-1</sup>)</b>	<b>Transpiration (µg cm<sup>-2</sup> s<sup>-1</sup>)</b>
	<b>1-year-old</b>	<b>1-year-old</b>	<b>1-year-old</b>
<b>Lovell</b>	-0.96 a	0.47 bc	37.4 b
<b>Cadaman</b>	-0.92 a	0.36 c	44.8 a
<b>Pumiselect</b>	-1.18 b	0.59 ab	33.6 bc
<b>Krymsk 1</b>	-1.31 c	0.69 a	29.6 c

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

Table 5.9. Tree dry weight (DW), leaf area (m<sup>2</sup>), and shoot: root ratio (S:R) of 15-gal potted Redhaven trees grafted on Lovell and Krymsk 1 rootstocks and own-rooted Lovell and Krymsk® 1 trees after 3.5 months of growth in a greenhouse at Clemson, SC harvested June 21, 2007.

<b>Dry weights<sup>z</sup> (DW) (g)</b>						
<b>Combinations</b>	<b>Shoots</b>	<b>Leaves</b>	<b>Shoots + leaves</b>	<b>Root</b>	<b>Total DW (g)</b>	<b>S:R ratio</b>
<b>Redhaven/Lovell</b>	448 a	227.4 a	675 a	258 a	934 a	2.75 b
<b>Lovell</b>	397 ab	236.7 a	634 a	227 a	861 ab	2.93 b
<b>Redhaven/Krymsk 1</b>	305 b	164.0 b	469 b	206 ab	675 b	2.36 b
<b>Krymsk 1</b>	472 a	99.8 c	572 ab	135 b	706 b	4.23 a

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

Table 5.10. Hydraulic conductance (K in  $\text{kg Mpa}^{-1} \text{ s}^{-1} \times 10^{-5}$ ) and leaf-area-specific conductance (Kl in  $\text{kg Mpa}^{-1} \text{ m}^{-2} \text{ s}^{-1} \times 10^{-5}$ ) of young Redhaven trees grafted on Lovell and Krymsk 1 rootstocks, and self-grafted Lovell and Krymsk 1 rootstock trees after 3.5 months of growth in the greenhouse, harvested on June 21, 2007.

<b>Hydraulic conductance</b>				
<b>Combination</b>	<b>K (tree)</b> ( $\text{kg Mpa}^{-1} \text{ s}^{-1} 10^{-5}$ )	<b>K (Stem + root)</b> ( $\text{kg Mpa}^{-1} \text{ s}^{-1} 10^{-5}$ )	<b>Kl (tree)</b> ( $\text{kg Mpa}^{-1} \text{ m}^{-2} \text{ s}^{-1} 10^{-5}$ )	<b>Kl (stem + root)</b> ( $\text{kg Mpa}^{-1} \text{ m}^{-2} \text{ s}^{-1} 10^{-5}$ )
<b>Redhaven/ Lovell</b>	6.87 a	9.96 a	19.25 b	3,789 b
<b>Lovell</b>	6.92 a	9.17 a	19.13 b	3,530 b
<b>Redhaven/ Krymsk 1</b>	5.25 a	8.10 a	14.43 b	4,392 b
<b>Krymsk 1</b>	3.49 a	7.72 a	7.34 a	6,327 a

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

Table 5.11. Effect of rootstocks on scion trunk cross-sectional area ( $\text{cm}^2$ ), leaf area ( $\text{cm}^2$ ), leaf, root, shoot and total tree dry weight (g), and shoot: root ratio dry weight (S:R) of young Redhaven peach trees grown in nursery at the Musser Fruit Research Center, Seneca, South Carolina.

<b>Redhaven<sup>z</sup></b>							
<b>Rootstocks</b>	<b>TCSA</b> ( $\text{cm}^2$ )	<b>Leaf area</b> ( $\text{cm}^2$ )	<b>Leaves</b> (g)	<b>Stems</b> (g)	<b>Roots</b> (g)	<b>Tree</b> (g)	<b>S:R</b>
<b>Lovell</b>	6.9 a	32,586 a	202.6 a	352.7 a	208.4 a	763.7 a	2.7 a
<b>Pumiselect</b>	4.4 b	19,822 b	120.0 b	190.1 b	118.8 b	428.8 b	2.65 a
<b>Krymsk 1</b>	2.0 c	6,759 c	47.9 c	56.5 c	71.8 c	176.2 c	1.44 b

<sup>z</sup>Different letters within a column indicate significant differences at  $P < 0.05$  (Duncan's multiple range test).

Table 5.12. Effect of rootstocks on root dry weight (DW) (g) and total fine root length (cm) of young Redhaven peach trees grown at a nursery, and root length (cm) and dry weight (mg) per unit of soil volume (cm<sup>3</sup>) of one-year-old Redhaven trees grown in the field at the Musser Fruit Research Center, Seneca, South Carolina, 2007.

<b>Redhaven</b>								
<b>Rootstocks</b>	<b>Less than one-year-old (nursery trees)</b>					<b>One-year-old trees (field trees)</b>		
	<b>Shank DW (g)</b>	<b>Coarse roots DW (g)</b>	<b>Small roots DW (g)</b>	<b>Total DW (g)</b>	<b>Fine root length (cm)</b>	<b>Fine root length/ soil vol.</b>	<b>Fine root DW/soil vol.</b>	
<b>Lovell</b>	112.2 a	59.0 a	19.0 b	190.2 a	17,221 a	3.32 a	0.894 a	
<b>Pumiselect</b>	27.2 b	39.6 ab	40.5 a	107.3 b	32,705 a	3.51 a	0.868 a	
<b>Krymsk 1</b>	22.7 b	22.7 b	22.4 ab	66.4 c	21,846 a	2.86 a	0.819 a	

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

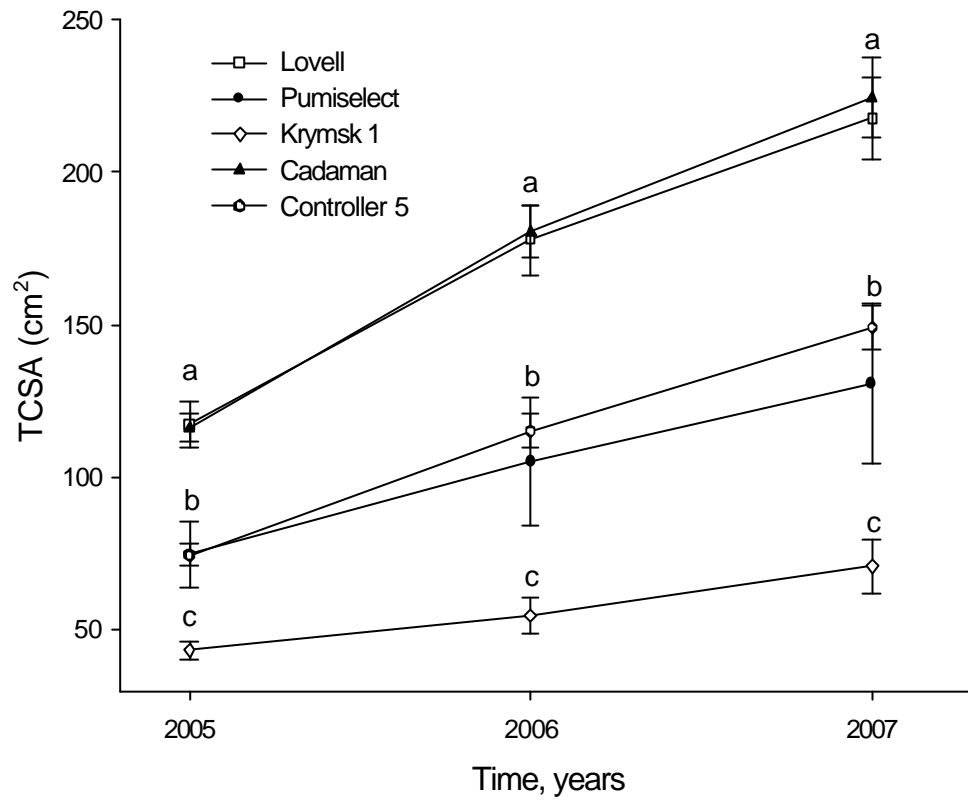


Fig. 5.1. Winter trunk cross-sectional area (TCSA) of Redhaven open vase trees grafted on different rootstocks, Musser Fruit Research Center, Seneca, SC, 2005-2007. Standard errors are given for each point. Different letters indicate differences at  $P < 0.05$  (Duncan's multiple range test).

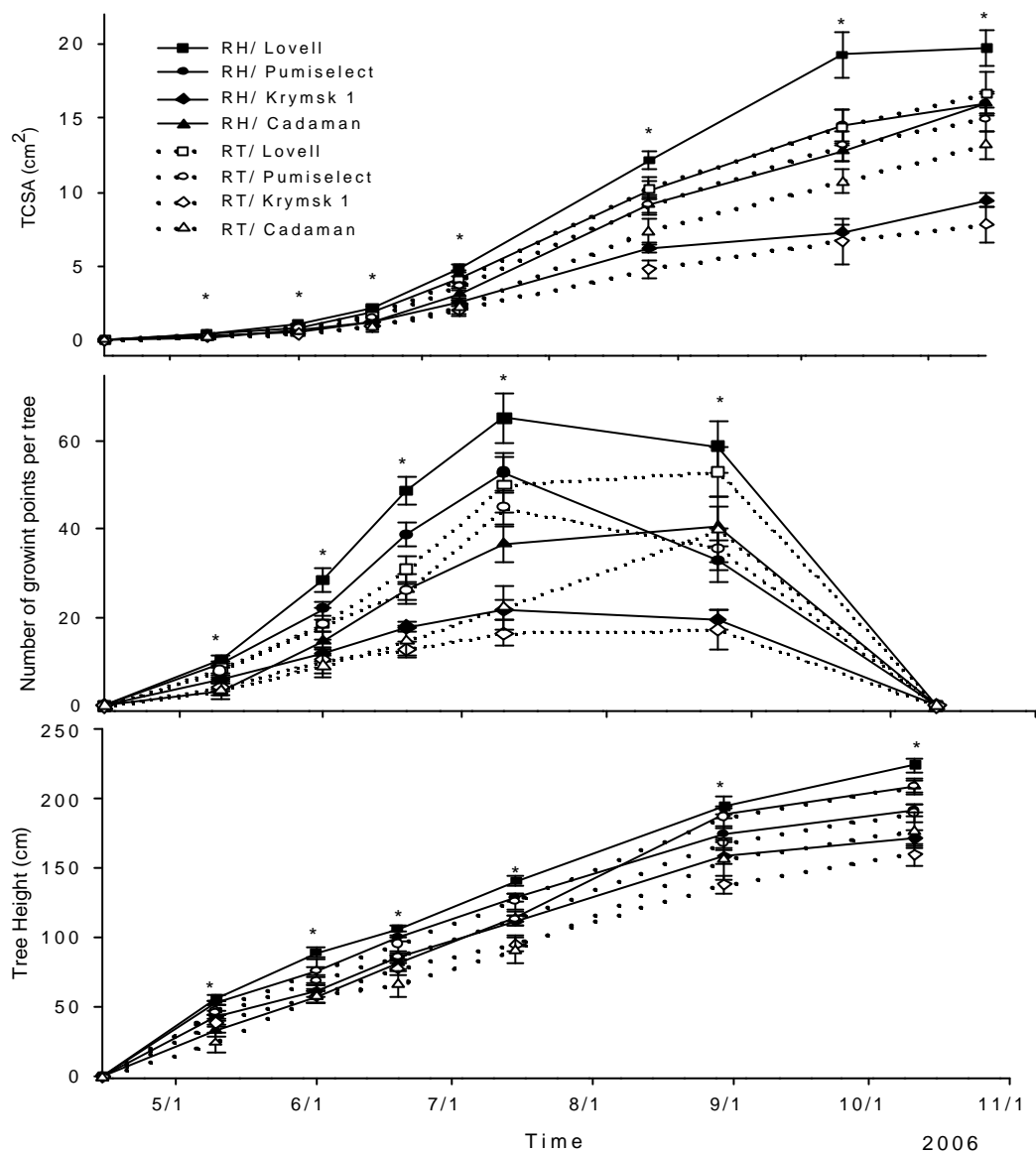


Fig. 5.2. The seasonal pattern of trunk cross-sectional area (TCSA) growth (A), number of growing shoot apices per tree (B), and tree height (C) of one-year-old 'Redhaven' trees growing on different rootstocks in 2006. Standard errors are given for each point. Asterisks indicate significant differences at  $P < 0.05$  (Duncan's multiple range test).



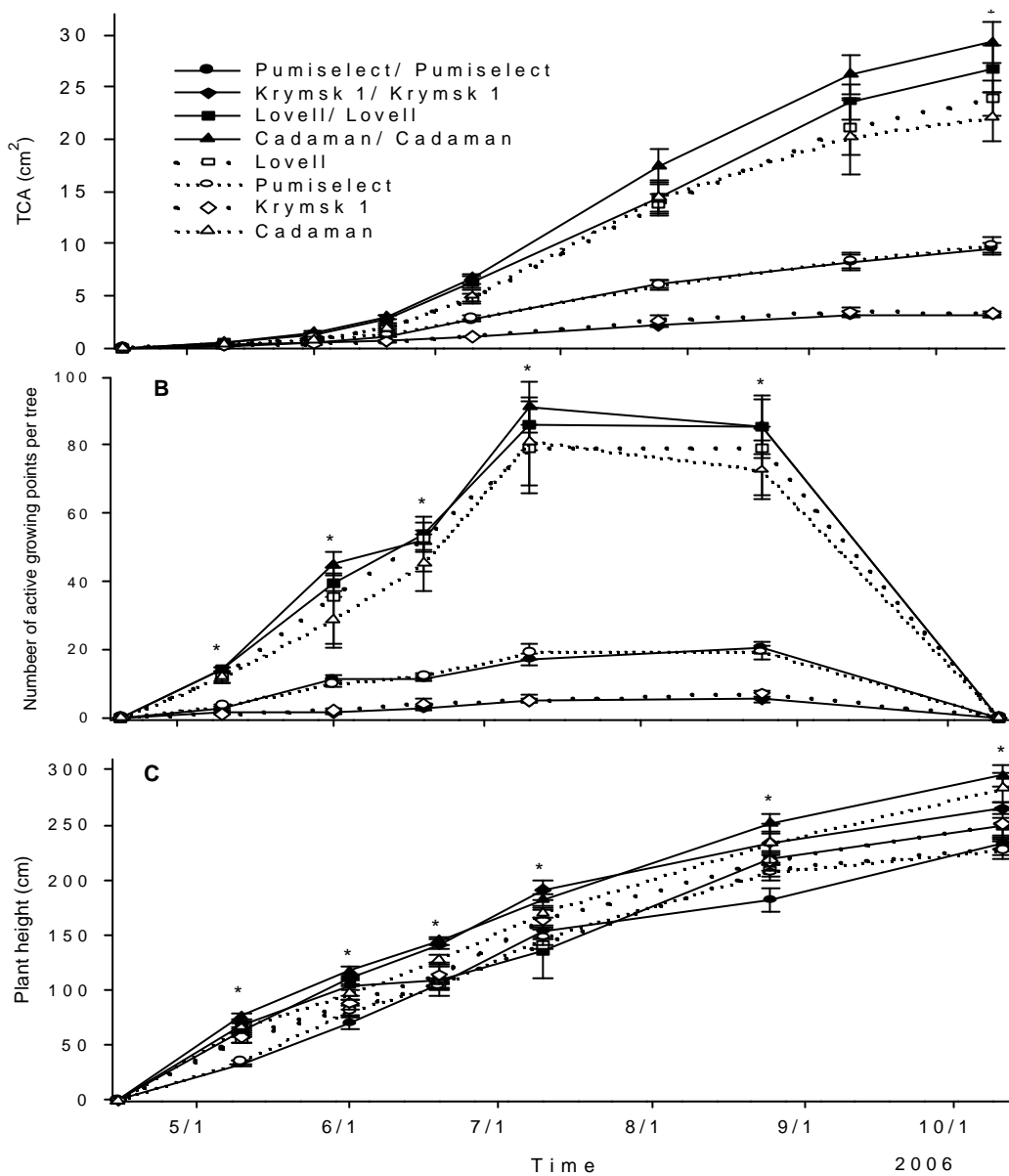


Fig. 5.3. The seasonal pattern of trunk cross-sectional area (TCSA) (A), number of active growing shoot apices per tree (B), and tree height (C) of one-year-old rootstock trees growing in 2006. Rootstock trees were self-grafted while others were not grafted. Standard errors are given for each point. Asterisks indicate significant differences at  $P < 0.05$  (Duncan's multiple range test).

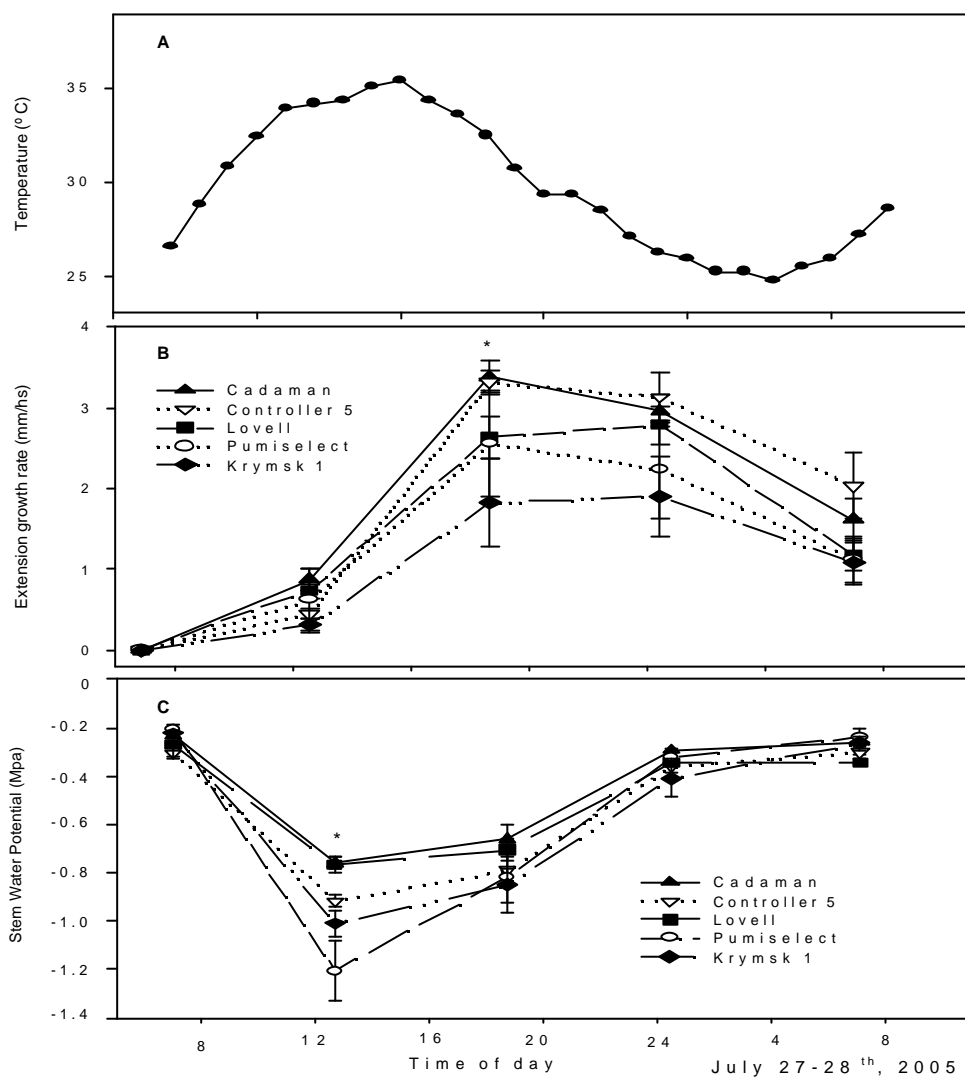


Fig. 5.4. The diurnal extension growth rate of shoots of 3-year-old Redhaven, open vase trees growing on five different rootstocks at the Musser Fruit Research Center, Seneca, SC, for July 27-28, 2005. (A) Average air temperature; (B) hourly shoot extension rate ; (C) stem water potential. Error bars represent  $\pm 1$  standard error of the mean. Asterisks indicate significant differences at  $P < 0.05$  (Duncan's multiple range test)

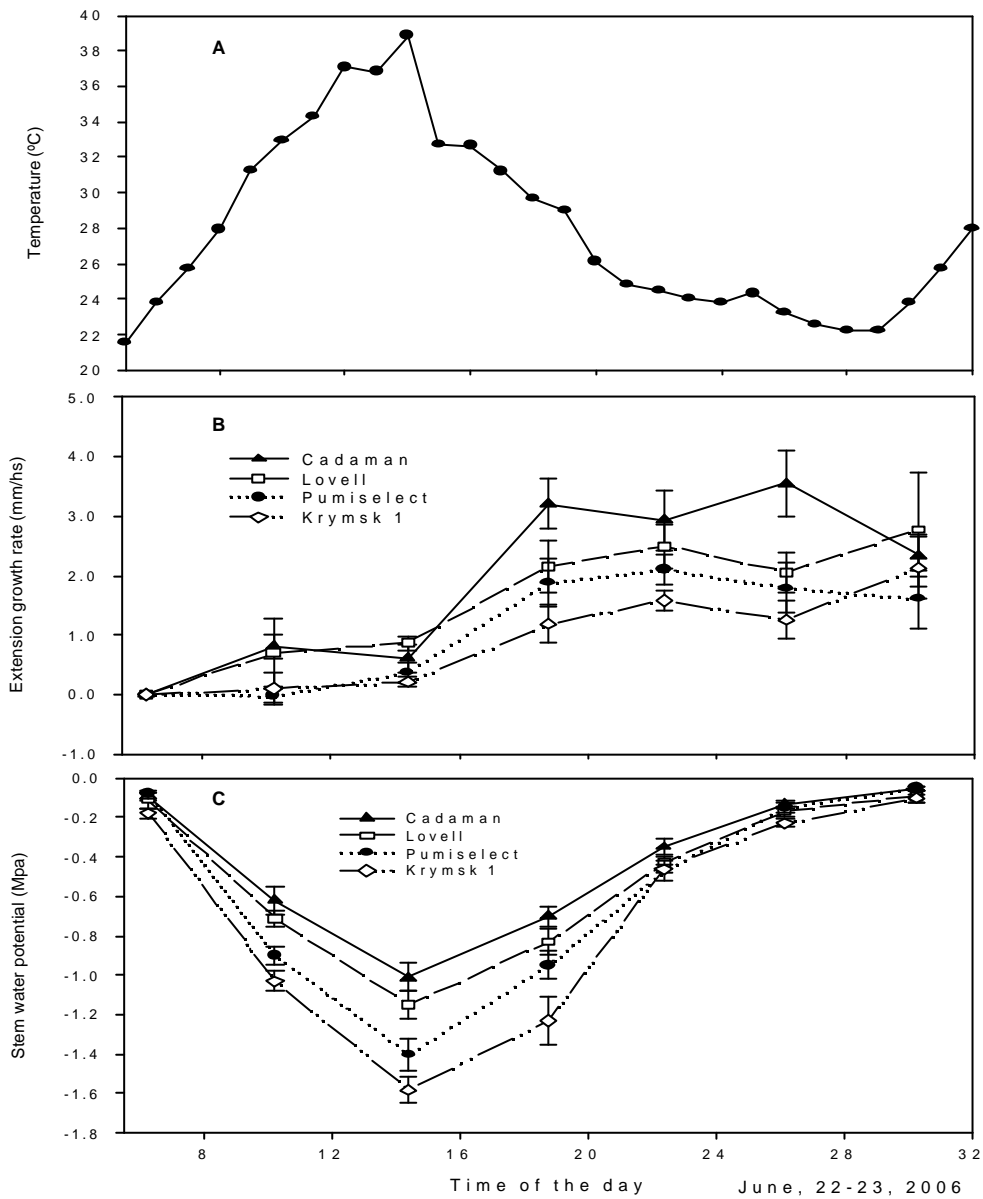


Fig. 5.5. The diurnal extension growth rate of shoots of one-year-old Redhaven peach trees growing on four different rootstocks, at the Musser Fruit Research Center, Seneca, SC for June 22-23, 2005. (A) Average air temperature; (B) hourly shoot extension rate; (C) stem water potential. Error bars represent  $\pm 1$  standard error of the mean.

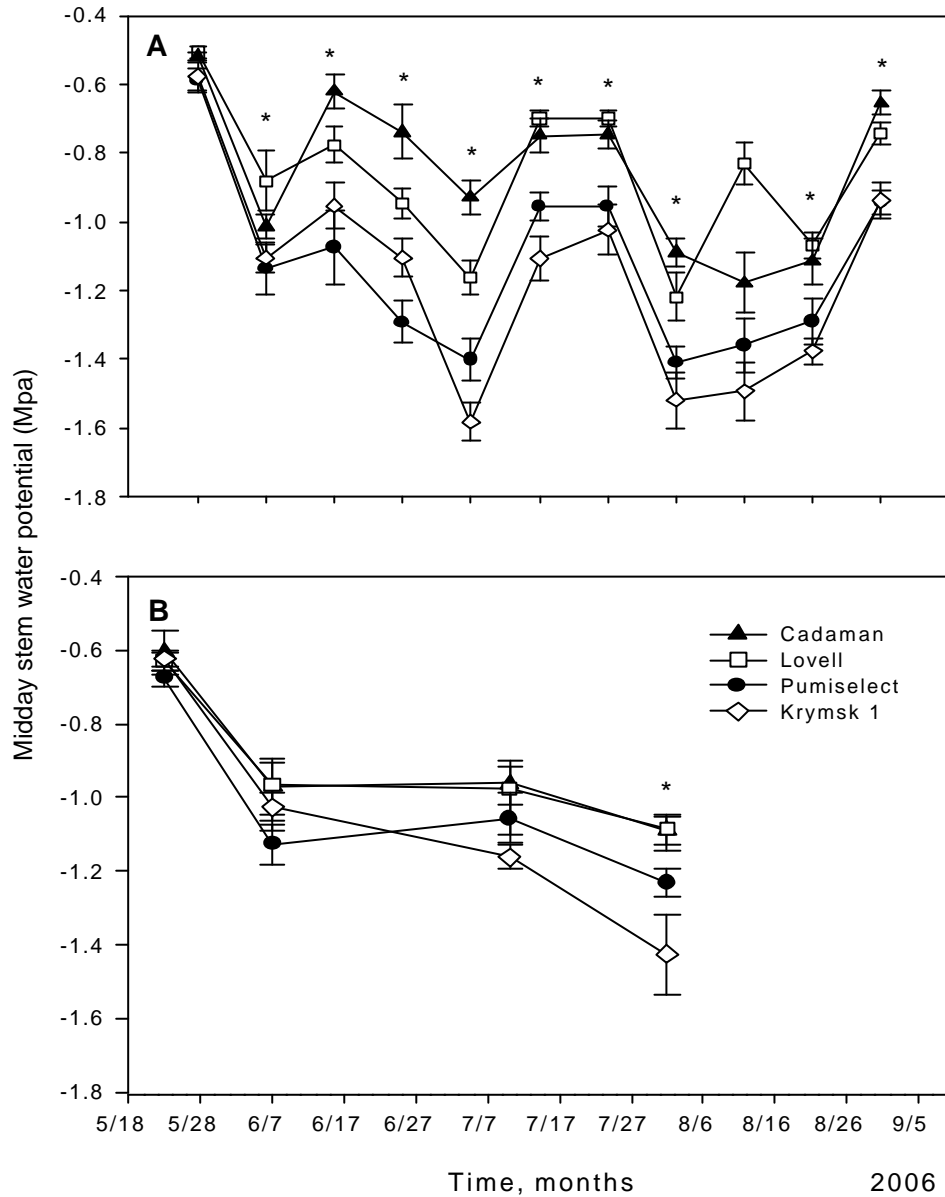


Fig. 5.6. Seasonal pattern of midday stem water potential of one-year-old Redhaven (A) and Redtop (B) peach trees grafted on four different rootstocks at the Musser Fruit Research Center. Standard errors are given for each point. Asterisks indicate significant differences at  $P < 0.05$  (Duncan's multiple range test).

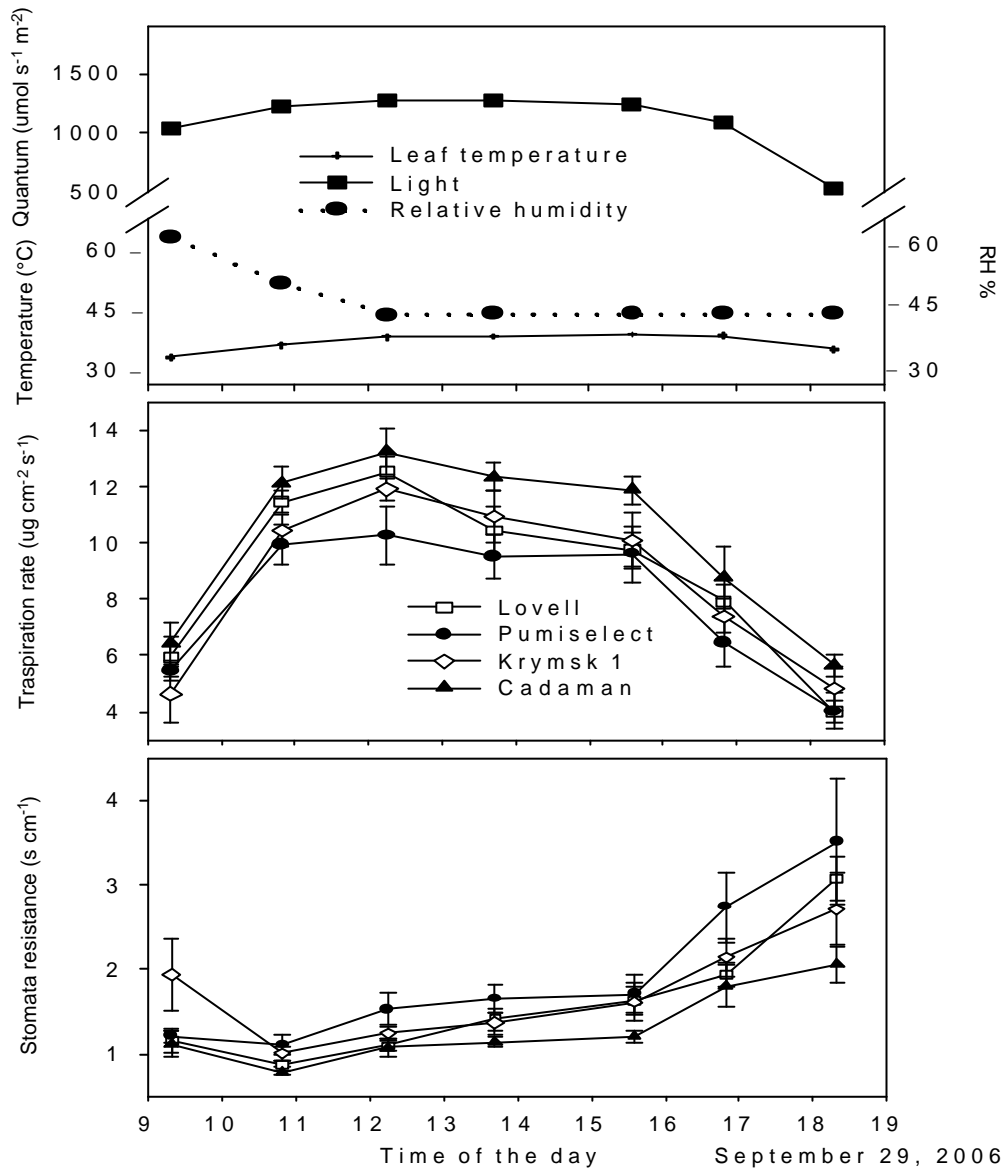


Fig. 5.7. Changes in stomatal resistance and transpiration rate of one-year-old Redhaven peach trees growing on four different rootstocks at the Musser Farm Research Center on September 29, 2006. (A) Leaf temperature, relative humidity and light; (B) Transpiration rate; and (C) Stomatal resistance. Each point represents the mean  $\pm$  the standard error.

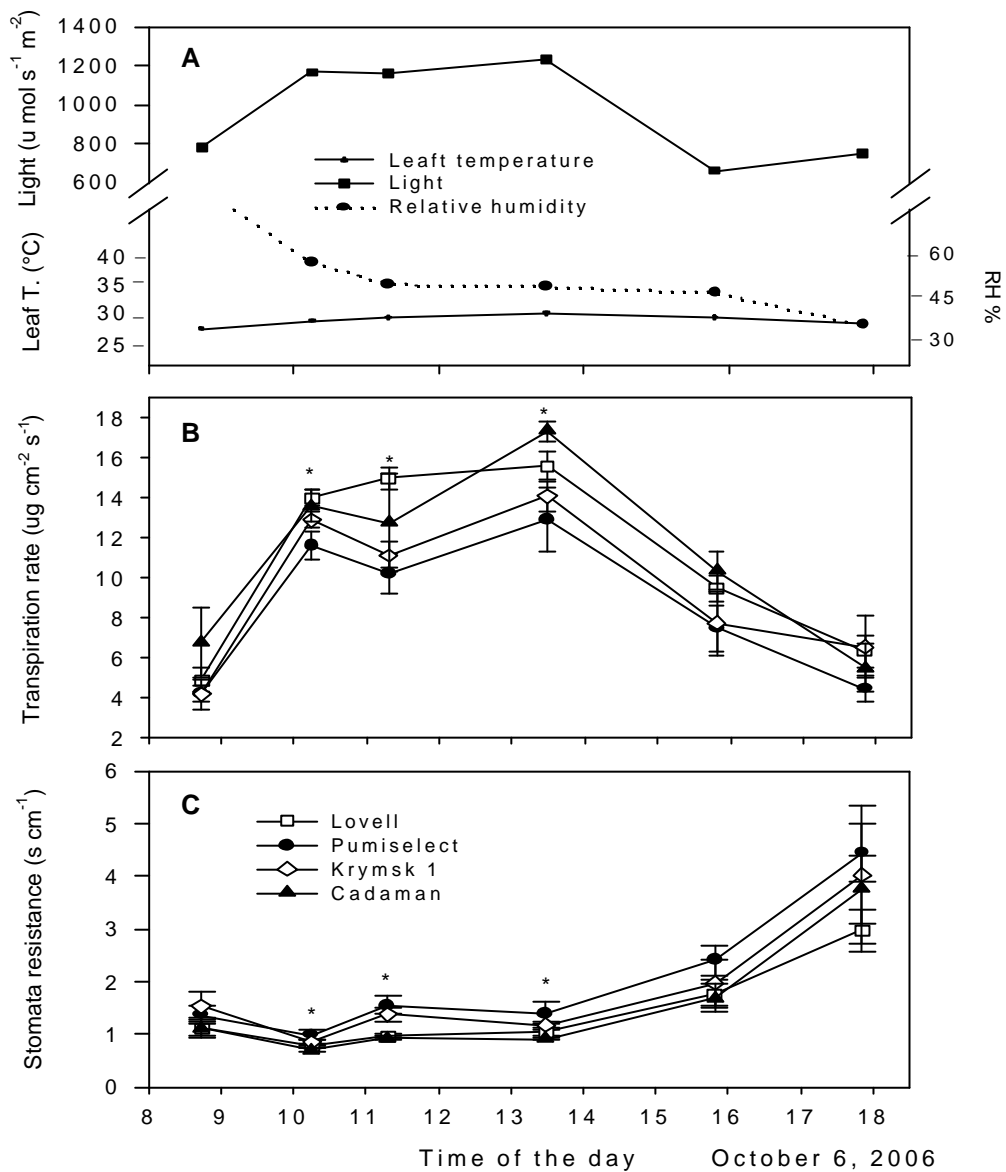


Fig. 5.8. Changes in stomatal resistance and transpiration rate of one-year-old Redhaven peach trees growing on four different rootstocks at the Musser Farm Research Center on October 6, 2006. (A) Leaf temperature, relative humidity and light; (B) Transpiration rate; and (C) Stomatal resistance. Each point represents the mean  $\pm$  the standard error. Asterisks indicate significant differences ( $P < 0.05$ ).

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## CHAPTER VI

### SCION AND ROOTSTOCK XYLEM VESSEL SURFACE

#### **Introduction**

Mechanisms by which fruit rootstock affects the scion still remain unclear despite extensive investigation. Water relations might explain the behavior of dwarfing rootstocks where graft union and root system would be the main structures involved in these mechanisms. Zimmermann (1983) supported the theory that vessel size (cross-sectional area), vessel number and total vessel area might affect the efficiency of water conductance by roots, indicating that a larger total cross-sectional area of vessels should facilitate transport of greater volumes of water per unit time to the scion. Also, the graft union is considered to be important in apples and it is related to the hydraulic conductivity (Atkinson et al., 2003). Tissues showing abnormal growth might indicate the effect of dwarfing rootstocks on apple cultivars by reducing the water and nutrient transport from the rootstock to the scion. Simons (1986) working in one-year-old apple trees found that the vascular tissues showed a swirling pattern and some senescent tissues became important at this level.

However, roots represented the major resistance to water flow when different peach rootstocks were compared by Basile et al. (2007) and Solari et al. (2006ab). In these works, a dwarfing rootstock had higher root water resistance when it was compared

with the more vigorous ones. Rieger and Litvin (1999) compared different species and found a negative correlation between root hydraulic conductance and root diameter. When Atkinson et al. (2003) compared the root hydraulic conductivity of excised roots, the dwarfing rootstocks showed about 50% lower conductivity than trees onto semi-dwarf rootstocks. In the same work, when two ungrafted apple rootstocks, M.27 (dwarfing) and M.M.106 (semi-vigorous) were studied, the authors found that root hydraulic conductivity (ratio between water flow and driving force) was highest in the semi-dwarf rootstock tree. These researchers found a lower leaf and stem section conductivity in the dwarfing trees, suggesting that the dwarfing effect might be a consequence of the reduction in the number and/or size of the vessels.

Vessels conduct large amounts of water in spring (Zimmermann, 1983). Once the water deficit starts developing (low soil water availability, high vapor pressure deficit), the sizes of the newly formed vessels are reduced. Most of the vessels originated in the previous season are able to conduct water very early in the spring, before new xylem is generated by the cambium; however, these old vessels start to plug with tyloses or air (embolism) (Zimmermann, 1983)

Based on the Hagen-Poiseuille equation, the flow rate ( $dV/dt$ ) in a capillary is proportional to the hydraulic conductivity ( $L_p$ ) and to the pressure driving force or pressure gradient between two points at a determined distance ( $dP/dl$ ). Where  $dV$  is the velocity and  $dt$  is time. Considering that  $L_p = \frac{r^4}{8\eta}$ , where  $r$  = radius of the capillary, and  $\eta$  is the viscosity of the liquid. Conducting vessels are quite different from perfect tubes because they are not infinite, have pits, pit diameter is variable, vessel surface is not



smooth (especially for the pits) and conductivity of pit membranes are quite variable too. For that reason the predicted and real measurement of hydraulic conductivity could have a difference in 26 to 67%. However, to obtain an approximation the Hagen-Poiseuille is useful for this proposal. By this equation, the flow rate is increased by the fourth power of the radius. So, for vessels with large diameters, the conductivity of the xylem is increased in an exponential way; however, tree vessels are not pipes (Lewis, 1998, 1992).

In ring porous trees, most of the old conducting xylem becomes non-functional with the age (Zimmermann, 1983; Tyree, 2003). However, the levels of conductance are surprisingly higher for these trees, when they are compared to small diameter vessels of diffuse porous trees. By doubling the size of a capillary (vessel), the flow rate is increased sixteen times.

The objective of this study was to compare the average vessel diameter and area developed in spring at above (scion) and below (rootstock) the graft union, to determine the relationship between low water status observed in dwarfing or semi-dwarfing rootstocks and lumen area of xylem vessels.

### **Materials and methods**

Rootstock cultivars were planted in the nursery at the Musser Fruit Research Center, Seneca, South Carolina, in April 2006. Three rootstocks were used and classified by their dwarfing effect: Lovell (standard, non-dwarfing), Pumiselect® (semi-dwarfing) and Krymsk® 1 (dwarfing) rootstocks. Trees were planted at 0.5 m between plants and

1.5 m between rows, and then budded with 'Redhaven' in June 2006. The dormant trees were cut back to 10 cm above the graft union in January 2007. These trees were used for vessel studies in Summer 2007. The nursery was managed according to standard commercial practices. Rows of trees and areas between the rows received herbicide treatments. Trees were drip irrigated. Vegetative growth measurements were described previously in Chapter IV in the section of fine root length and density of trees grown in the nursery.

Transverse sections from above (scion) and below (rootstock) the graft unions were harvested in September 2007. Samples were divided into the physical location: scion and rootstock for the three combinations and collected to 5 cm below and above the graft union. After harvesting, the samples were sectioned into transverse sections (25  $\mu\text{m}$ ) with a sliding microtome, and placed in Petri dish in a 1:1 alcohol-water solution until analyzing the images under the microscope.

Images were captured with a microscope and vessel area was measured within the current year's growth. Vessel measurements were restricted to similar cell lineage, considering the last growth ring and the first lines of vessels, which represented the first growth in Spring 2007. In order to estimate the highest hydraulic conductivity, only the first 10 largest vessels were considered from the new growth in each sample. These vessels were expected to have the highest hydraulic conductance. Vessel area was determined through the vessel diameter, which was calculated from the mean of two measurements perpendicular to each other across the widest part of the lumen for each

vessel. Diameter measurements were done by hand, from the images taken with the microscope

## Results

Radius and surface of xylem vessels were affected significantly by rootstocks in the scion ('Redhaven') and rootstock portions of the trees. Trees grafted on Lovell rootstocks had greater xylem vessel radius than Pumiselect® and Krymsk® 1 in the scion portion of the trunk, and these differences in xylem lumen radii were greater in the rootstock portions (Fig. 6.1, Table 6.1). In the rootstock section, Lovell rootstocks had the greatest radii, while Krymsk® 1 rootstock the smallest. In this last trunk section, Pumiselect® had intermediate xylem lumen radii (Table 6.1). The fourth exponent of the radius ( $\text{radius}^4$ ), which is related to the hydraulic conductivity, followed the same pattern as the radius. For the rootstock section of the tree, the mean  $\text{radius}^4$  of those trees grafted on Lovell were  $1,128,375 \mu\text{m}^4$ ,  $479,930 \mu\text{m}^4$  for Pumiselect® and  $145,173 \mu\text{m}^4$  for Krymsk® 1. At the scion portion no significant differences were observed (data not shown).

Differences in vessel surfaces between those found at the scion and rootstock portion of the trunk were not significantly different in 'Redhaven' trees grafted on the three different rootstocks. However, a trend was observed where Pumiselect® ( $1,660 \mu\text{m}^2$ ) and Krymsk® 1 ( $1,617 \mu\text{m}^2$ ) had higher differences than trees on Lovell ( $796 \mu\text{m}^2$ ). In addition, graft union tissues from all the combinations showed normal development

(data not shown) and no abnormal tissue was visually observed. Vegetative growth patterns of trees are shown in Tables 5.11 and 5.12 in Chapter V.

## Discussion

Average lumen areas of the largest vessels were greater than those found in 3-year-old *Populus sieboldii* by Sano et al. (2005) and less than one-year-old cherry rootstock trees reported by Olmstead et al. (2006ab); however these authors based their works on average xylem vessels instead of the largest ones, which were used in our research. Gonçalves et al. (2007), who worked with mature cherry trees grafted to five different rootstocks, found a higher vessel frequency (number of vessels per mm<sup>2</sup>) in roots of dwarfing rootstocks compared to those roots from trees grafted on vigorous rootstocks. However, in the same research vessel diameter was significantly larger in roots from vigorous rootstocks than from dwarfing rootstocks. Our study showed that the more vigorous rootstock, Lovell, had a vessel radius about 20% larger than Pumiselect® and almost 40% larger than Krymsk® 1. When the vessel surface is considered, differences among rootstocks become larger, where vessel surface of Lovell was 3-fold of those vessel of Krymsk® 1. Differences in vessel diameter were correlated with the vigor imparted by cherry rootstocks (Gonçalves et al. (2007), and these differences were also correlated with the hydraulic conductivity.

In addition, our work found significant differences between the largest vessel diameters in the scion portion of trees when 'Redhaven' was grafted onto Lovell

rootstocks. These results agree with those reported in apple (Beakbane and Thompson, 1939; Soumelidou et al., 1994) and cherry (Olmstead et al. 2007ab).

In conclusion, the vessel diameter differences observed in the scion and rootstock portion of the peach trees from the new spring growth used in our experiment would indicate that differences in growth imparted by the rootstocks were associated with the hydraulic conductivity. The smaller hydraulic conductivity of more size-controlling rootstocks would be primarily affected by smaller vessel diameter in the rootstock portion and secondary by the smaller vessel area in the scion portion of those trees. Because only the largest vessels were used in the present work, further study involving all of the vessels would be needed to confirm the results observed in our work.

Table 6.1. Radius, radius<sup>4</sup> and surface ( $\mu\text{m}^2$ ) of the ten largest xylem vessels from the initial spring growth of ‘Redhaven’ trees grafted on three different rootstocks.

Average vessel surface				
Scion portion <sup>z</sup>			Rootstock portion	
Rootstock	Radius ( $\mu\text{m}$ )	Surface ( $\mu\text{m}^2$ )	Radius ( $\mu\text{m}$ )	Surface ( $\mu\text{m}^2$ )
<b>Lovell</b>	36.5 a	4,224 a	31.8 a	3,226 a
<b>Pumiselect</b>	30.7 b	3,041 b	25.7 b	2,106 b
<b>Krymsk 1</b>	29.7 b	2,798 b	19.3 c	1,180 c

<sup>z</sup>Different letters within a column indicate significant differences at  $P < 0.05$  (Duncan’s multiple range test).

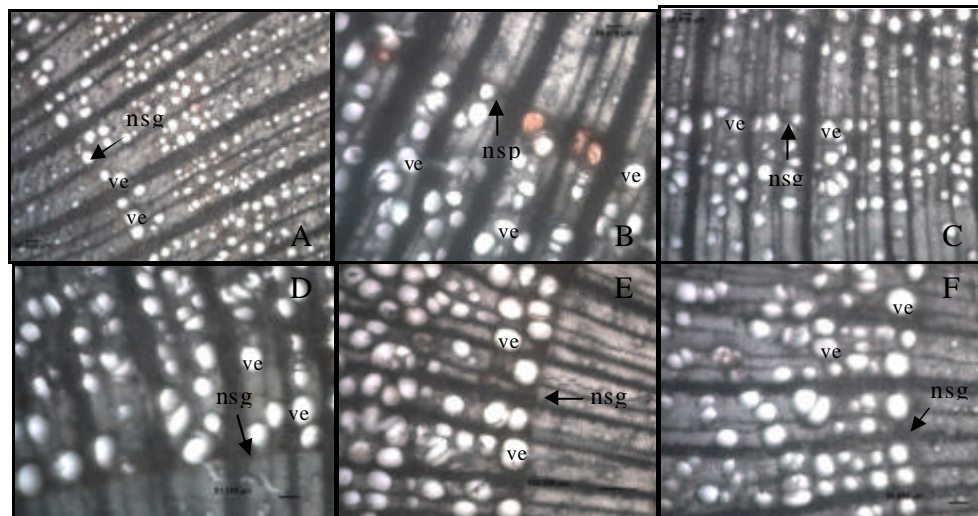


Fig. 6.1. Image captured using a microscope of the vessels in the rootstock section of Redhaven peach trees grafted on Krymsk® 1 (A), Lovell (B) and Pumiselect (C) rootstocks; and those vessels in the scion portion (Redhaven) of trees grafted on Krymsk® 1 (D), Lovell (E) and Pumiselect (F) rootstocks. Sections were taken at the same height and zoom, nsg = new spring growth, ve = vessel elements.

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## CHAPTER VII

### CONCLUSIONS

Unique rootstocks allow trees to tolerate different edaphic conditions such as dry, saline, heavy or wet soils, and the presence of disease organisms and soil-borne insects. Probably, the most important use of a specialized rootstock is to reduce the size of the scion while at the same time increases its precocity and efficiency of fruit production. Even though the dwarfing effect of the rootstock was suspected over 2000 years ago, the mechanisms involved are not well understood.

Differences in TCSA growth were observed very early from the first month after initial bud break, thus the cumulative effect started to show very early mainly due to a reduction in leaf area and stem growth. The experiments demonstrated a significant effect of rootstocks on vegetative growth. Krymsk® 1, the most dwarfing rootstock, reduced the size of the tree at the end of the first year to almost 50% of the control (Lovell), and by the end of the second year, Krymsk® 1 controlled the vigor to just 35% of Lovell. Our results showed that dwarfing effects are cumulative and superimposed year-to-year. In addition, when self-grafted rootstock trees were studied, dwarfing effects of rootstocks were remarkably dependent on rootstock genotype; the smaller the tree rootstock cultivar, the greater the dwarfing potential effect.

Root TNC concentration was at least twice the shoot TNC concentration, where Lovell roots had the highest accumulation of reserves and Krymsk® 1 the lowest.

Rootstock bark accumulated the largest amount of TNC, followed by scion bark; where Lovell had the highest TNC content. Accumulation of TNC in bark tissues indicated an important location of storage in fruit trees. 'Redhaven' trees had the highest accumulation of TNC in roots of the more vigorous rootstock (Lovell). About 70% of TNC were accumulated in root tissues, where smaller roots accounted for most of the carbohydrates (>80%). The more vigorous rootstocks, not only had the higher accumulation of dormant carbohydrates but also the highest root and shoot dry weight per tree, suggesting that the initial difference in new spring growth could be the result of both effects. 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 amount of early flush of growth. However, how much of this reserve-dependent initial growth may be responsible for the season's growth differences that were observed between dwarfing and vigorous rootstocks is still unclear.

Trees with a Krymsk® 1 interstem reduced TCSA up to 19% compared to trees on Lovell rootstocks in the first season, while the reduction was close to 50% at the end of the second season. Our results indicated that interstems, and probably budding height, affected peach scion growth. In addition, the interstock effect was related to the tree water status. Thus, different processes other than root and graft union effects were involved in scion dwarfing by peach rootstocks, thereby indicating a more complex mechanism exists for dwarfing in peach.

When high compatibility between rootstock and scion tissues was present, the newly formed conducting elements (xylem and phloem) did not reduce the water

pathway. Although hydraulic resistance was not quantified, stem water potential measurements taken below and above the graft union suggested that in the case of Pumiselect®, the graft union might considerably increase the tree hydraulic resistance. However, it would be possible that the major source of hydraulic resistance in Krymsk® 1 would be the root system. In addition, rootstock xylem diameter appears to be related to the hydraulic conductance where the more vigorous rootstocks had larger xylem diameter than the more size-controlling rootstocks.

There were significant differences in leaf transpiration rate and stomatal resistance among rootstocks. These differences were found particularly at midday and in the early afternoon hours, where trees grafted on Krymsk® 1 and Pumiselect® had the lowest transpiration rate and the highest stomatal resistance. Moreover, our results showed greater shoot growth, stomatal conductance and transpiration rate at higher stem water potentials, which were associated with the more vigorous rootstocks.

After studying different cultivars, locations, tree ages, and rootstocks, the present work found a relationship among scion vegetative growth as affected by rootstock, winter carbohydrate content, tree water status and rootstocks. Greater accumulations of carbohydrates in invigorating rootstocks ensured a greater initial vegetative growth in spring which was a characteristic of trees on vigorous rootstocks.