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Fruits and Roots: A Celebration and Forward Look

Beakbane and Thompson (1939, East Malling) Had It Right: Scion Vigour is Physiologically Linked to the Xylem Anatomy of the Rootstock

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Summary

In 1939 A.B. Beakbane and E.C. Thompson published research that showed a correlation between the xylem anatomy of apple rootstocks and the vigour that those rootstocks imparted to scion cultivars grafted on them. However, Beakbane and his colleagues never made a clear functional link between rootstock xylem anatomical characteristics and the vigour that rootstocks impart to scions. Subsequently numerous researchers have reported relationships between rootstock xylem anatomy and scion vigour in several fruit tree species. Researchers have also reported that the leaf or stem water potential of trees growing on size-controlling rootstocks is often somewhat more negative than trees growing on vigorous rootstocks in the same environment. Recent research with dwarfing peach rootstocks has documented clear linkages between rootstock xylem anatomy, theoretical and measured rootstock axial hydraulic conductance, scion stem water potentials and scion shoot growth rates in composite peach trees. This paper will review the core evidence that links rootstock xylem anatomy to scion vigour and demonstrate that linkage using L-PEACH, a dynamic functional-structural tree model of tree physiology, architecture and growth.

Key words: Fruit trees, dwarfing rootstocks, leaf and stem water potential, shoot extension growth, hydraulic conductance, xylem vessel diameter, L-PEACH

Introduction

Composite trees, formed by a scion grafted onto a rootstock, are commonly used in commercial fruit orchards. The use of composite trees allows for efficient clonal propagation of scion cultivars and selection of rootstock genotypes with important rootstock traits. One of those traits is the control that rootstocks can exert on scion vigour (Webster, 2002). The most famous vigour controlling rootstocks (the Malling series of apple rootstocks) were initially selected at the East Malling Research Station (Ferree & Carlson, 1987; Fallahi *et al*., 2002). The adoption of the Malling series of rootstocks has had a tremendous impact of apple production world-wide and has revolutionized orchard system concepts for many other fruit crops. A series of new peach rootstocks that provides a wide range of vigour controlling capacity has recently been developed at the University of California, Davis, (DeJong *et al*., 2004; Tombesi *et al*., 2011) and there is hope that production efficiency gains based on incorporating dwarfing rootstocks into apple and cherry systems (Webster, 1993) can be achieved with peach (Reighard & Loreti, 2008).

The development of virtually all dwarfing rootstocks has occurred based on empirical evaluations of rootstock performance with scion cultivars grafted onto them and an understanding of the physiological mechanism involved in causing dwarfing is still under debate (Rogers & Beakbane, 1957; Webster, 2004). In 1939 A.B. Beakbane and E.C. Thompson published research that showed a correlation between the xylem anatomy of apple rootstocks and the vigour that those rootstocks imparted to scion cultivars grafted on them. Specifically, dwarfing apple rootstocks had roots with fewer and smaller xylem vessels than invigorating rootstocks (Beakbane & Thompson, 1939). However in a review of proposed mechanisms involved in rootstock control of scion vigour Rogers & Beakbane (1957) dismissed the idea that xylem anatomical differences could be involved because the prevailing view at the time was that xylem vessels were in substantial excess compared to what was necessary to efficiently move water through a tree. One of the first functional experimental confirmations that water relations could be involved occurred when Giulivo & Bergamini (1982) reported that midday leaf water potentials of 'Golden Delicious' apple trees grafted on dwarfing 'M.9' and 'M.26' rootstocks were significantly lower than trees on vigorous 'M.11' and seedling rootstocks, whereas trees with intermediate-high vigour (grafted on 'M.111', 'MM.104', 'MM.106', and 'M.7') had intermediate values. Later, Olien & Lakso (1984, 1986) provided convincing evidence that midday stem water potential measured on apple trees grafted on dwarfing 'M.9' and 'M.26' dwarfing rootstocks was significantly lower than that of trees grafted on more vigorous rootstocks ('MM.104', 'M.7' and 'MM.106'). Similar results have been reported not only for apple (Cohen & Naor 2002), but also for peach (Basile *et al*., 2003*a*; Motisi *et al*., 2004; Solari *et al*., 2006*a*) and sweet cherry (Gonçalves *et al*., 2006; Hajagos & Vegvari, 2013).

The remainder of this paper will review research related to the physiological mechanism involved in causing vigour reduction that has been conducted on a series of size-controlling peach rootstocks developed at the University of California, Davis, in cooperation with USDA-ARS researchers in Parlier, CA (DeJong *et al*., 2004; Tombesi *et al*., 2011).

Linkage between Shoot Growth Characteristics and Xylem Water Potential

Dwarfing peach rootstocks reduce both shoot length as well as the number of shoots per tree while the number of internodes per shoot is not generally affected by rootstock vigour (Weibel *et al*., 2003). Stem water potentials tended to be more negative in trees on dwarfing rootstocks compared to control trees when measured in June, however subsequent measurements in August did not show significant differences (unpublished data). Basile *et al*. (2003*a*) reported that differences in daily shoot growth rates of trees on dwarfing and invigorating rootstocks were correlated with differences in daily patterns of stem water potential, particularly during the spring vegetative growth period. Subsequently, by doing manipulative studies in the field to modify canopy transpiration rates Solari *et al*. (2006*a*) confirmed that young trees on dwarfing rootstocks had lower midday stem water potential values than trees on vigorous rootstocks and that there was a direct linkage between daily patterns of shoot extension growth and daily patterns of stem water potential in trees on both vigorous and dwarfing rootstocks..

Linkage between Xylem Stem Water Potential and Hydraulic Conductance

It is well known that there is a connection between patterns of stem water potential and hydraulic conductance (Tyree & Sperry, 1988) and this was confirmed to be the case for peach trees on rootstocks that imparted various degrees of vigour. Basile *et al*. (2003*b*) reported that a size controlling peach rootstock clearly had decreased measured xylem hydraulic conductance compared to the vigorous 'Nemaguard' rootstock and that the differences in conductance were primarily found in the rootstock itself and not in the rootstock/scion graft union or the scion growing on the dwarfing rootstock. Differences in rootstock hydraulic conductance also corresponded with differences in diurnal shoot growth and water potential patterns measured on the same trees (Solari *et al*., 2006*b*). Subsequently Solari & DeJong (2006) documented that shoot growth could be manipulated by pressurizing the root system and thus overcoming hydraulic conductance differences between dwarfing and invigorating rootstocks, resulting in similar shoot extension growth rates irrespective of rootstock. These experiments confirmed direct links between stem water potential, stem hydraulic conductance and shoot growth rates.

Linkage between Rootstock Hydraulic Conductance and Xylem Anatomy

Axial hydraulic conductance in plants is a function of the anatomical characteristics of xylem (Tyree & Zimmermann, 2002). Xylem vessel diameters are especially important because of the Hagen-Poisseuille law which states that the hydraulic conductance of a tube is a function of the diameter of the tube raised to the fourth power (Tyree & Ewers, 1991). Measurements of xylem vessel anatomy clearly showed that differences in rootstock-induced tree vigour were associated with differences in mean xylem vessel diameters and theoretically calculated xylem vessel conductance of a range of rootstock genotypes (Tombesi *et al*., 2010*a*). Further research documented that dwarfing peach rootstocks have very limited influence on the xylem vessel characteristics of the scion and differences in xylem anatomy also explain the partial vigour reductions obtained when a dwarfing rootstock genotype is used as an inter-stem (Tombesi *et al*., 2010*b*).

How can Xylem Vessels be Limiting? Or, where did Rogers and Beakbane go wrong?

It is now known that the majority of water conduction in species with ring porous wood anatomy occurs in the large vessels of the latest formed ring of xylem and that the large vessels from earlier years of cambial growth are often essentially non-functional (Elmore & Ewers, 1985). This appears to be especially the case in peach (Ameglio *et al*., 2002). Thus the bulk of water flow up the tree during a given growing season occurs in the xylem vessels formed during that same season. This means that the efficiency of xylem flow early in the season is largely dependent on newly formed xylem in the spring and is probably highly dependent on the characteristics of that xylem and the rate at which it is being formed. Thus hydraulic conductance during the spring period is likely limited by the rate of xylem development as well as the xylem vessel characteristics. If this is true, then the strongest differences in stem water potential between trees on rootstocks with small *vs* large vessel diameters would occur during the grand period of growth that occurs during the spring because the potential rate of xylem vessel formation may lag behind the potential rate of canopy growth. When canopy growth in mature trees slows in early summer due to phenological control mechanisms (DeJong *et al*., 1987), the development of new xylem may regain balance with the canopy size and then tree hydraulic capacity would match transpiration demands of the canopy and differences in measured water potentials between trees on dwarfing and invigorating rootstocks would be minimal.

Support for this hypothesis has recently been provided by a girdling experiment in peach. Mature peach trees that had the base of their scaffolds girdled (a 6 mm wide strip of bark and cambium removed) early in the spring vegetative growth period (approximately 3 weeks after bloom) had decreased midday stem water potentials for more than 8 weeks after girdling with correspondingly decreased shoot growth rates and fewer vigorous shoots compared to non-girdled control trees (Tombesi *et al.*, 2014). Trees that were girdled 2 weeks later subsequently had midday stem water potentials that were intermediate between the early girdled and non-girdled trees indicating that hydraulic conductance was apparently not as limiting in the later girdled trees.

Additional corroboration for a hydraulic conductance mediated rootstock size-controlling mechanism in peach trees has been provided by testing this mechanism in the L-PEACH functional-structural virtual tree simulation model (Da Silva *et al*., 2011). The L-PEACH model (Allen *et al*., 2005, Lopez *et al*., 2008, Da Silva *et al*., 2011) simulates the development and growth of a peach tree's architecture, tracks all functional elements during growth, exchanges carbon and water between the plant's elements while individual components are sensitive to local availability of carbon and water as well as environmental factors. This model has no set carbohydrate allocation patterns; instead carbohydrate distribution is governed by relative carbon demands of each carbohydrate sink, the proximity of the sinks to carbohydrate sources and resistances along the transport pathways. The model runs using hourly environmental parameters recorded at a field weather station, calculates leaf/canopy photosynthesis and transpiration as well as water flow through the soil-plant-atmosphere continuum, and estimates stem water potential throughout the simulated canopy. Shoot growth in the model is sensitive to stem water potential both through direct effects on shoot growth and indirect effects on photosynthesis and thus carbon supply. The hydraulic conductance mediated rootstock size-controlling mechanism was tested running two simulations with the L-PEACH model. One simulation used values for hydraulic conductance that corresponded with values for vigorously growing peach trees and in the other simulation the hydraulic conductance of the segment of the hydraulic pathway in the rootstock portion of the tree was simply reduced by 50%. The screen captures after each year of the two four-year simulations (Fig. 1) show the cumulative effect of the reduced rootstock hydraulic conductance over time. The simulations also clearly demonstrate an often under-appreciated aspect of scion growth on dwarfing rootstocks; that the apparent effects of dwarfing rootstocks on tree size increase over time because tree vigour at the beginning of the season is a function of the pruning severity during the dormant season and the amount of storage carbohydrates available to initially support growth the following spring (Mika, 1986). Thus the vigour of trees on dwarfing rootstocks tends to decrease each year relative to trees on vigorous rootstocks also because they are usually pruned less and the mass of the wood available for storing carbohydrates is also less per tree (Pernice *et al*., 2006).

Conclusions

Anatomical analysis of size-controlling rootstocks in comparison with their vigorous counterparts indicates a clear mechanism that can account for the size-controlling behavior of a series of peach rootstocks that is consistent with a large body of accumulated research on the same, or similar, peach rootstocks. This research indicates that normally vigorous scion cultivars growing on dwarfing rootstocks have reduced shoot growth and numbers of vigorous shoots than the same scion cultivars growing on vigour inducing rootstocks. Reductions in shoot growth are related to decreased mid-day stem water potentials. Decreased mid-day stem water potentials are related to decreased measured root hydraulic conductance. Decreased measured root hydraulic conductance is related to xylem vessel characteristics and decreased theoretical xylem hydraulic conductance of the outer ring of xylem. There is mounting evidence that water conductance and consequently, spring vegetative growth in peach are dependent on newly formed spring xylem vessels and thus the xylem characteristics of newly formed xylem in a rootstock are a probable cause for differences in scion vigour related to dwarfing rootstocks.

While the size-controlling behavior of apple rootstocks were initially associated with xylem vessel characteristics by Beakbane & Thompson (1939), and more recently in other species (Goncalves *et al*., 2007; Olmstead *et al*., 2006*a,b*); there is also evidence that hydraulic conductance is reduced

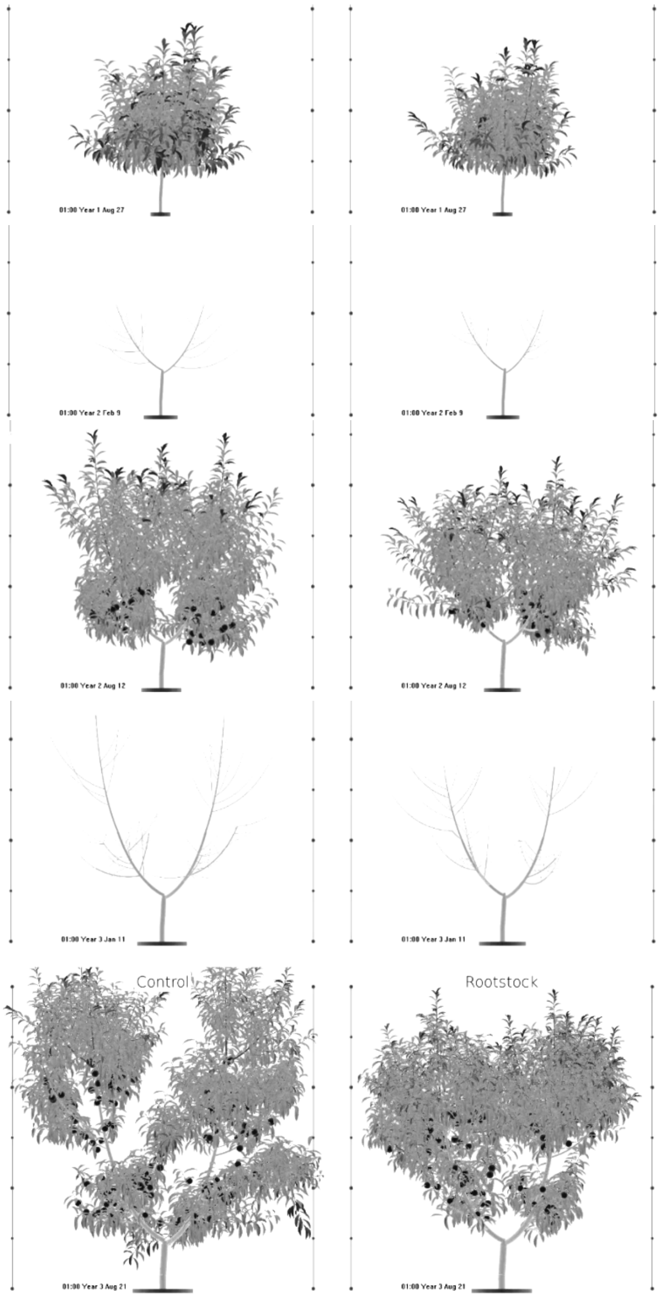

Fig. 1. Pictures of virtual trees generated from simulation runs of the L-PEACH model over a series of 4 years. The trees on the left are from simulations using normal values for stem and rootstock hydraulic conductance. The trees on the right are results from running the model with exactly the same parameters as for trees on the left except that xylem hydraulic conductance of the rootstock section of the tree was reduced by 50%. The trees at the top show the size of the trees at the end of the summer during the 2nd year of growth. The second row of trees shows the trees after they have been pruned in the following dormant season. The 3rd and 4th row shows corresponding sizes of trees during and after the 3rd year of growth. The bottom row shows the difference in size of the trees toward the end of the 4th year of growth. The trees were selectively pruned at the end of each growing season and fruit were thinned to crop loads corresponding to the amount of fruiting shoot length on each tree.

in dwarfing compared with vigorous apple rootstocks (Atkinson *et al*., 2003). Furthermore there is now evidence of co-localization of genes in apple controlling traits linked to tree growth and fruit bearing with traits linked to xylem development (Lauri *et al*., 2011). However more research is necessary to document clear mechanistic linkages between xylem anatomy and rootstock vigour as has been done with peach. It is likely that these linkages can be established, at least for trees within the family Rosaceae. Thus, Beakbane & Thompson (1939) were on the right track after all.

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