Modeling Size-Controlling Rootstock Effects on Peach Tree Growth and Development Using L-PEACH-h

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Abstract

Vigorous peach scion cultivars, growing on graft-compatible rootstocks, exhibit differing amounts of vegetative growth, depending on the rootstock used. Recent research on the physiology of peach size-controlling rootstocks has indicated that the primary factor, that limits the vegetative growth, appears to be the hydraulic conductance characteristics of the rootstocks. There is good evidence that the size-controlling rootstocks have smaller mean xylem vessel diameters that lead to decreased axial hydraulic conductance, and therefore, to slightly decreased water potentials in the scion stems. Previous research has also documented direct (relative stem extension growth rates) and indirect (decreased leaf photosynthesis rates) linkages between stem water potentials and shoot growth rates. In the past year, a functional-structural plant model, for simulating peach tree growth and physiology, L-PEACH, was modified to simulate, on an hourly basis, the uptake, transport and transpiration of water, simultaneously with the carbohydrate assimilation and distribution. Thus, the new model, L-PEACH-h, can estimate stem water potentials for each hour and for each node in the tree, and use these water potential values to modify simulated shoot growth and physiological functioning of the leaves. In this presentation, we demonstrate how these new developments allow simulation of cumulative effects of size-controlling rootstocks on peach tree growth.

INTRODUCTION

A series of new peach rootstocks, that provide a wide range of size-controlling capacity, have recently been developed at the University of California, Davis (Tombesi et al., 2011). The development of these rootstocks led to studies of the physiological mechanism involved in controlling scion vigour in graft-compatible peach rootstocks. Weibel et al. (2003) reported that dwarfing rootstocks reduced both shoot length, as well as the number of shoots per tree, while the number of internodes per shoot was not generally affected by rootstock vigour. Basile et al. (2003) reported that shoot growth of trees, on dwarfing rootstocks, was correlated with differences in seasonal patterns of stem water potential. Subsequently, Solari et al. (2006a) confirmed that trees on dwarfing rootstocks had lower midday stem water potential values than trees on vigorous rootstocks. Stem water potential is closely related to hydraulic conductance (Tyree and Sperry, 1988), and Solari et al. (2006b) reported that dwarfing rootstocks had lower leaf-specific hydraulic conductance than a vigorous rootstock. In a subsequent study, Solari et al. (2006c) documented that shoot growth was affected by manipulating stem water potential in trees with dwarfing and vigorous rootstocks, thus confirming the links between stem water potential, stem hydraulic conductance and shoot growth rates.

This series of work led to an investigation of the physiological basis for the reductions of hydraulic conductance, in dwarfing rootstocks. Axial hydraulic conductance, in plants, is a function of the anatomical characteristics of xylem. Xylem vessel diameters are especially important because, as the Hagen-Poisseuille law states, the hydraulic conductance of a tube is a function of the radius of the tube raised to the fourth power (Vercambre et al., 2002). Subsequent research documented that differences in rootstock-induced tree vigour, of a range of peach rootstock genotypes, were correlated with differences in mean xylem vessel diameters and their densities in xylem tissue

(Tombesi et al., 2010a,b, 2011).

In a parallel project, our lab has been involved in developing the L-PEACH functional-structural model of tree growth. This model is based on the concept that carbon partitioning is driven by competition among individual plant organs, acting as semi-autonomous components interacting with each other and the environment (Allen et al., 2005; Lopez et al., 2008). In this model, the underlying mechanism for carbon transport treats the plant as a network of components and uses an analogy with an electrical circuit to compute the flow of carbohydrate throughout the plant (Prusinkiewicz et al., 2007). Recently, this model was substantially improved by revising the model to operate on an hourly time-step, instead of a daily time-step (Da Silva et al., 2011). This latest version of the model is named L-PEACH-h.

L-PEACH-h can simulate hourly development and growth of each individual organ and whole tree, in response to environment and management practices over multiple years. The revision of the model, to hourly time-steps, made it feasible to simulate diurnal responses to factors, such as light and temperature that vary widely during a typical day. The hourly time-step also made it possible to contemplate simulating diurnal patterns of plant water potential, and diurnal responses to water availability.

Water availability is a key factor governing tree development that affects growth, directly and indirectly, through reduced organ growth, and decreases production and transport of carbohydrates. Plant responses to water availability are complex, and dramatically change over short periods of time. Plant or organ water potential is the most often measured variable used to evaluate plant water status. Additionally, the physiological status of plants and the principles of the movement of water, from the soil through the plant to the atmosphere, are described on the basis of water potential concepts (Nobel, 1999). Thus, a xylem circuit was built into the L-PEACH-h model, so that the diurnal water potential of each organ could be simulated along with their physiological functioning and growth (Da Silva et al., 2011). In plants, water moves from soil through roots, up through the xylem of the stems and eventually evaporates from the leaves. Therefore, in addition to the xylem circuit, modeling water transport in a tree required simulating both water uptake from the soil and leaf transpiration; i.e., modeling soil water availability and the soil-plant-atmosphere interactions (Slatyer, 1967; Thornley and Johnson, 1990). The current version of the L-PEACH-h model has sub-models for simulating decreases in soil water availability at the soil-root interface, water uptake by the root, water transport within the plant, and leaf transpiration behavior in addition to all the previously described sub-models for organ growth and carbon assimilation, distribution and utilization (Da Silva et al., 2011).

Previous research documented that the size-controlling behavior of a new series of peach rootstocks was based on alterations of stem water potential, caused by differences in the xylem conductance behavior of the rootstock genotypes and we recently included a water circuit in the L-PEACH-h functional-structural plant model, that made it possible to calculate stem water potential, at each node of a virtual plant, and simulate water stress effects on tree growth and physiology. Therefore, the next logical step was to test if the growth and physiological behavior of different peach rootstocks could be simulated by varying the conductance characteristics of the rootstocks used in simulations.

METHODS

The approach used for testing the hypothesis that the behavior of trees growing on dwarfing rootstocks, in comparison to standard rootstocks, could be simulated by adjusting rootstock hydraulic conductance was very straightforward. The L-PEACH-h simulation model simulates tree growth starting with a single metamer containing a leaf primordia, an internode segment with an apical meristem and a rudimentary root. When the model is run, growth of the tree begins and, after developing several nodes, budding is simulated by cutting the shoot, back to the initial couple of nodes, stimulating a lateral bud to function as a new apical meristem and resuming tree growth. This creates a clear separation between the shoot that grows above that cut (the “scion”), and the base of the tree that grows from the original metamer (the "rootstock"). In a normal simulated tree, the hydraulic conductance values, assigned to both the "scion" and the "rootstock", are the same. In order to simulate the size controlling effect of a dwarfing rootstock, on tree growth and water relations, the hydraulic conductance of the 'rootstock" piece, at the base of the trunk, was reduced by modifying the vessel diameters and their density, according to the data collected by Tombesi et al. (2011), in a significantly size-controlling rootstock. The resulting reduction, in hydraulic conductance, was approximately 50%. Comparative simulations of tree growth and physiology were then run for four simulated years, using the same initial starting parameters and weather data input files, except for varying the hydraulic conductance of the "rootstock". The trees were "pruned" manually, in silico, after each of the years of simulated growth, and fruit were thinned (in the last two simulated years), using the automatic thinning feature of the L-PEACH-h model, that allows the user to specify the date of thinning (set to day of year 130) and the minimum number of nodes allowable between each fruit after thinning (set to 4).

RESULTS AND DISCUSSION

Decreasing the hydraulic conductance of the "rootstock" in the simulated tree, on the size-controlling rootstock, had a substantial effect on the simulated diurnal pattern of stem water potential of trees on the dwarfing rootstock, compared to the simulated trees on the standard rootstock (Fig. 1). These simulated diurnal patterns of stem water potential were similar to the differences in patterns of stem water potential among rootstocks, previously measured, in spring conditions, in the field (Basile et al., 2003).

The differences in the simulated growth of the trees, on control and dwarfing rootstocks, became clear during the first simulated year of growth in the orchard (second year of simulated growth), as differences, in canopy size, became accentuated and simulated canopy transpiration placed, increasing demands on the hydraulic conductance of the rootstocks (Fig. 2). After four years of simulated growth, the virtual tree on the dwarfing rootstock was substantially smaller than the virtual tree on the control rootstock (Fig. 3). Although the model still requires more refinement, in terms of calibration, interactions between trunk growth, xylem vessel development and growth and hydraulic conductance, as well as the interactions between simulated xylem water potential, organ growth and leaf physiology, the results of these simulations clearly document how reductions, in axial hydraulic conductivity of a rootstock, can lead to substantial reductions in scion growth. The ability of the L-PEACH-h model, to simulate such behavior, is due to the fact that it is a dynamic system and dynamic structure model, that simulates tree development and growth based on the notion that trees are composed of a collection of semi-autonomous organs, that are dependent on other organs to supply carbohydrates, nutrients and/or water (Allen et al., 2005). This allows changes in only one parameter, rootstock hydraulic conductance, to influence the development and growth of the whole tree. The fact that L-PEACH-h can simulate growth, over multiple years, also allows a clear understanding of how rootstock dwarfing effects are cumulative, over the lifetime of a tree, a fact that is often difficult to fully appreciate when doing experimental research with these trees.

Recent research indicates that the size-controlling behavior, of selected cherry rootstocks, may be also associated with differences in xylem anatomy and hydraulic conductance of the rootstocks (Gonçalves et al., 2007; Olmstead et al., 2006), so the implications of this modeling experiment may pertain to other species besides peach. However, there may be many other situations in which rootstock size-controlling effects may be due to other factors, such as partial graft incompatibility between the scion and the rootstock (Webster, 1995), and modeling this would require an entirely different approach.

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Figures

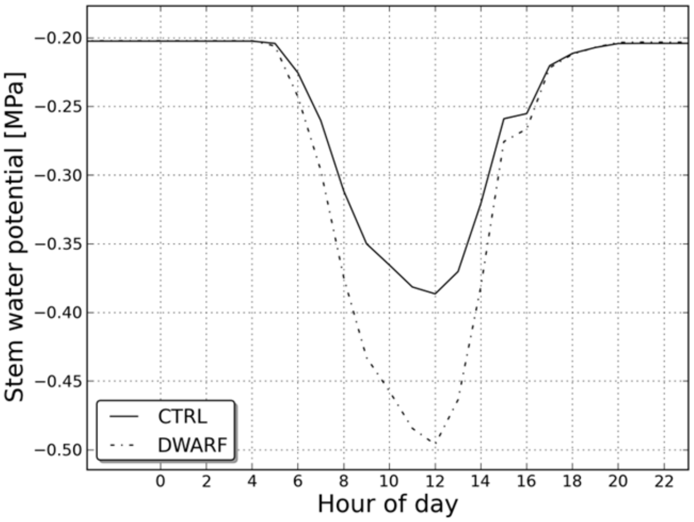

Fig. 1. Simulated diurnal patterns of stem water potential of trees on control and dwarfing (hydraulic conductance reduced by 50%) rootstocks during a typical spring day under California weather conditions.

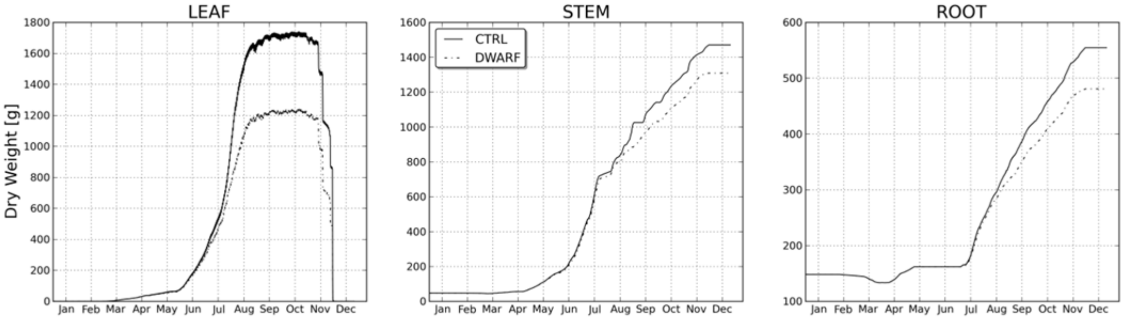

Fig. 2. Comparison of simulated leaf, stem and root dry weight accumulation of trees grown on control and dwarfing rootstocks during the first year of growth in an orchard (second year of simulated growth).

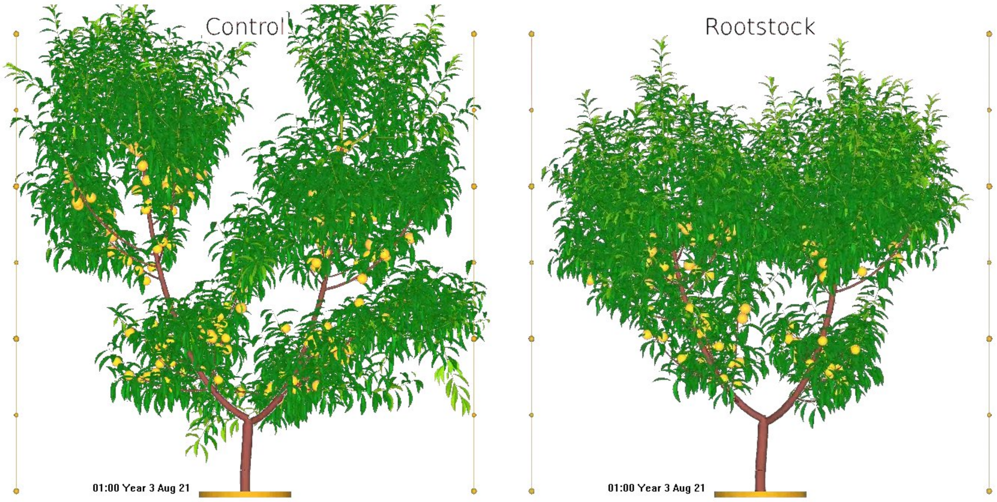

Fig. 3. Comparison of simulated peach trees growing on a control and dwarfing rootstock in August of the fourth year of growth (third year in the orchard). Trees were pruned and trained in silico to a perpendicular 'V' shape (DeJong et al., 1995) with two scaffolds.