Growth patterns and morphology of fine roots of size-controlling and invigorating peach rootstocks

BORIS BASILE,[1] DAVID R. BRYLA,[2] MICHELLE L. SALSMAN,[3] JORDI MARSAL,[4] CHIARA CIRILLO,[1] R. SCOTT JOHNSON[5] and THEODORE M. DEJONG[5,6]

[1] *Dipartimento di Arboricoltura, Botanica e Patologia Vegetale, Università degli Studi di Napoli Federico II, Via Università 100, 80055 Portici, Napoli, Italy*

[2] *USDA ARS, Horticultural Crop Research Laboratory, 3420 NW Orchard Avenue, Corvallis, OR 97330, USA*

[3] *USDA ARS Water Management Laboratory, 9611 S. Riverbend Avenue, Parlier, CA 93648, USA*

[4] *Institut de Recerca i Tecnologia Agroalimentàries (IRTA), Area de Tecnologia Frutícola, Centre UdL-IRTA, Avda Rovira Roure 177, E-25198 Lleida, Spain*

[5] *Department of Plant Sciences, University of California, 1035 Wickson Hall, One Shields Avenue, Davis, CA 95616, USA*

[6] *Corresponding author (tmdejong@ucdavis.edu)*

Summary We compared growth patterns and morphology of fine roots of size-controlling and invigorating peach (*Prunus persica* (L.) Batsch) rootstocks. Peach trees were grafted on five rootstocks: a vigorous control (Nemaguard), three intermediate vigor rootstocks (K119-50, P30-135 and Hiawatha), and a semi-dwarfing rootstock (K146-43). Minirhizotron tubes were installed at the base of trees on each rootstock and root images captured with a minirhizotron digital camera system. Number, visible length, and diameter of new roots were recorded at fixed soil depths from April 19, 2000 to December 19, 2001. Root diameter, specific root length, root tissue density and root length density were also measured periodically for each rootstock on roots collected from in-growth cores. Rootstocks had similar seasonal patterns of new root production. Fine root production was lowest in winter and appeared to decline during the final stages of fruit growth. A rootstock with almond in its genetic background (K119-50) produced the greatest quantity of fine roots and had the greatest number of new roots below 69 cm, whereas there were no differences among the other four rootstocks in the total number of roots produced. Rootstock K146-43 had thicker fine roots than the other rootstocks. Independent of rootstock, fine roots produced during spring had greater specific root length than those produced later in the season. The seasonal pattern of fine root production did not appear to be associated with the previously reported effects of these dwarfing rootstocks on shoot growth and stem water potential early in the growing season.

Keywords: dwarfing rootstocks, in-growth core, minirhizotron, root diameter.

Introduction

Roots provide the aboveground part of the tree with water and nutrients, and the root system is dependent on the aboveground tree organs for carbohydrates and other organic compounds (Rom and Carlson 1987). Production and transport of growth regulators from roots to shoots (abscisic acid, cytokinins, and gibberellins) and from shoots to roots (auxin) are thought to regulate growth and physiological processes depending on resource availability and environmental stresses (Weyers and Paterson 2001, Davies et al. 2002). The complexity of the interrelationships occurring between aboveground tree organs and roots has been demonstrated by artificial manipulation of different tree organs. For example, partial defoliation of kiwifruit (*Actinidia deliciosa* (A. Chev., C.F. Liang, A.R. Ferguson)) vines reduces root growth (Buwalda 1991) and drastic manipulation of peach (*Prunus persica* (L.) Batsch) root systems by artificial root restriction or root pruning reduces tree size (Geisler and Ferree 1984, Williamson et al. 1992, Rieger and Marra 1994). Further evidence of the interrelationships between aboveground and below-ground tree organs is the competition among growing organs. Buwalda (1991) found that most root growth of kiwifruit vines occurs after shoot and fruit growth is nearly completed. Head (1967) observed that root growth of apple (*Malus domestica* (Borkh)) decreased as shoot growth increased, and vice versa and Ben Mimoun and DeJong (2006) reported that the two primary periods of peach root growth occur in the spring and fall before and after major periods of fruit growth. Thus, the interdependence of roots and aboveground tree organs suggests that the continuous changes in the above- to belowground ratio occurring during tree growth tend to maintain equilibrium between roots and aboveground organs.

In fruit culture, specific rootstocks are used to control the

size and vigor of trees, a response referred to as dwarfing. Several theories have been developed to explain the dwarfing mechanism of size-controlling rootstocks for fruit trees, but this complex phenomenon is still not fully understood. One hypothesis to explain dwarfing invokes the effect of size-controlling rootstocks on tree water relations. Apple trees on dwarfing rootstocks have lower midday leaf (Giulivo and Bergamini 1982) and stem water potentials (Olien and Lakso 1986) than trees on invigorating rootstocks. Until recently, knowledge about dwarfing mechanisms in peaches has been limited by the lack of suitable dwarfing rootstocks for this species. Since 1986, an ongoing project of the University of California for the evaluation of peach rootstocks has led to the selection and characterization of several promising size-controlling rootstocks (DeJong et al. 2001, Weibel et al. 2003, DeJong et al. 2004). Peach trees on these rootstocks tend to have lower midday stem water potentials than trees on invigorating rootstocks (Basile et al. 2003*a*, Solari et al. 2006*a*); furthermore, the differences in plant water relations are strongly correlated with differences in shoot extension growth (Basile et al. 2003*a*, Weibel et al. 2003, Solari et al. 2006*a*). Some of these size-controlling peach rootstocks have lower leaf-specific hydraulic conductance than vigorous rootstocks (Basile et al. 2003*b*, Solari et al. 2006*b*). Root hydraulic resistance has also been implicated in the dwarfing mechanism for apple (Olien and Lakso 1986) and citrus (Syvertsen 1981).

Weibel et al. (2003) documented that most of the effect of dwarfing peach rootstocks on shoot extension growth of mature trees occurred early in the growing season. Basile et al. (2003*a*) measured lower midday stem water potential in mature peach trees grafted on dwarfing rootstocks compared to trees on vigorous rootstocks and related the differences in water relations with differences in shoot growth. The differences among rootstocks were clearer in the first part of the growing season than later on. A delay of several weeks after bud burst in the accumulation of root pressure in dwarfing compared with vigorous kiwifruit rootstocks has been observed (M.J. Clearwater, HFRI, New Zealand, personal communication). Therefore, a goal of this study was to determine if differences in scion growth behavior among trees on different rootstocks are associated with seasonal dynamics of fine root production, particularly in the first part of the growing season. Knowledge about the dynamics of root growth is relatively limited because root system dynamics are complex and difficult to study compared with growth dynamics of aboveground organs. Recently, the introduction of new techniques has allowed the quantification of root demography. In particular, the use of video imaging in minirhizotrons has improved knowledge about the phenology and physiology of small-diameter tree roots (Comas et al. 2000, Psarras et al. 2000, Wells and Eissenstat 2001). Fine roots (generally defined as roots with a diameter < 1 or 2 mm) are believed to play an important role in water and nutrient absorption (Eissenstat 1992), whole-plant carbon budgets, and ecosystem-level carbon and nutrient cycling (Eissenstat and Yanai 1997, Ruess et al. 2003). Most studies on root systems have considered fine roots as a single class of roots having similar structure and physiology, but

other studies have highlighted physiological differences among fine roots associated with differences in diameter (Pregitzer et al. 1998, Wells and Eissenstat 2001). "Thin" fine roots have been reported to have higher respiration rates (Pregitzer et al. 1998), nitrogen concentrations (Pregitzer et al. 1997), and risk of root mortality (Wells and Eissenstat 2001) than "thick" fine roots. Fine root morphology and anatomy (root diameter, cortical thickness, percent of non-suberized exodermal cells) have been related to hydraulic conductivity (Huang and Eissenstat 2000). It appears that fine root morphology may also play an important role in the relationship between rootstock and aboveground tree organs.

In this study, we compared the behavior of fine root systems of five peach rootstocks that impart differing degrees of tree vigor. We investigated seasonal patterns of fine root production, fine root distribution along the vertical soil profile, and fine root diameter. Our objectives were to determine if more dwarfing peach rootstocks exhibit delayed or reduced fine root production especially early in the growing season compared with less dwarfing and vigorous rootstocks, and if more dwarfing rootstocks are characterized by intrinsically different fine root morphological characteristics.

Materials and methods

Experimental site, plant material, and plot management

The study was carried out at the Kearney Agricultural Center of the University of California (Parlier, CA) during 2000 and 2001. Soil at the site was a Hanford fine sandy loam that was more than 3 m deep. However, a calcium carbonate hardpan layer confined most root growth to the upper 1.5 m of soil. The peach scion used in the field experiment was an early maturing clingstone processing cultivar, 'Loadel', grafted on five rootstocks: a vigorous control, Nemaguard (*Prunus persica* (L.) Batsch × *P. davidiana* Fr. hybrid), three intermediate vigor rootstocks, K119-50 (*Prunus salicina* Lindl. × *P. dulcis* (Mill) D.A. Webb hybrid), P30-135 (*Prunus salicina* × *P. persica* hybrid), and Hiawatha (open pollinated seedling of a *Prunus besseyi* Bailey × *P. salicina* hybrid), and a semi-dwarfing rootstock, K146-43 (*Prunus salicina* × *P. persica* hybrid). All rootstocks were vegetatively propagated from cuttings (except Nemaguard which was seed-propagated) and grown in a commercial nursery before being planted in the orchard in 1996. Trees were trained to a Kearney Agricultural Center perpendicular 'V' (KAC-V) (DeJong et al. 1994) system in a North-South orientation. Trees on Nemaguard and P30-135 rootstocks were spaced 4.88 × 1.98 m apart, whereas trees on K119-50, Hiawatha and K146-43 were spaced 4.88 × 1.83 m apart. Trees were planted in a randomized complete block design with four replications and five trees per replicate. Routine horticultural care was provided to trees according to commercial protocol for fruit production (LaRue and Johnson 1989). Trees were flood irrigated to replace 100% of the computed evapotranspiration throughout the growing season. A 3-m-wide herbicide strip was sprayed in the tree rows to control weed growth; space between rows was planted with a

grass cover crop and mowed regularly. Trees were winter-pruned on January 5, 2000 and January 23, 2001, and summer-pruned on August 2, 2000 and September 13, 2001. Fruit were thinned on April 24, 2000 and May 2, 2001, and fruits were harvested in three pickings between July 3 and 19, 2000, and between July 3 and 23, 2001.

Tree vigor

On March 5, 2000, November 15, 2000, and December 3, 2001, the trunk circumference of each tree was measured 20 cm above the ground and trunk cross-sectional area (TCSA) was computed assuming each trunk was circular.

Minirhizotron experiment

Eight trees per rootstock (two trees per replicate) were used for this experiment. One 1.5-m-long butyrate minirhizotron tube per tree was installed between February 22 and 29, 2000. The tubes were placed in the inter-row space at a distance of 1 m from the trunk at an angle of 60° from the horizontal. Digital pictures were captured at 22 fixed "windows" regularly spaced at different depths within the tubes by a minirhizotron digital camera system (BTC-2, Bartz Technology Co., Santa Barbara, CA). Each picture captured a tube–soil–interface surface of 19 × 14 mm (with 9.2× magnification power). The first location was just below the soil surface, and consecutive windows were 5 cm apart. The position of each window in the soil was defined by calculating its vertical distance from the soil surface. The first set of pictures was taken on April 19, 2000. Subsequent pictures were taken biweekly between April 19 and September 20, 2000, and between March 18 and October 15, 2001. Between September 20, 2000 and March 18, 2001, and between October 15 and December 19, 2001, pictures were captured monthly. Pictures were also captured monthly from January 28 to July 26, 2002.

Images were analyzed with RooTracker v. 2.0 software (Duke University, Durham, NC). The shallowest four windows (located between the soil surface and 17 cm of vertical depth) were omitted from the analysis to avoid the presence of weed roots, and the deepest three windows (located between 78 and 91 cm of vertical depth) were also excluded because of low visibility. Number, visible length, and diameter of new roots were recorded for each tube and window throughout the experiment. The surface area and volume of each root were estimated assuming they had a cylindrical shape and using measured root diameter and length. Pictures collected during 2002 were discarded because of the progressive decreasing visibility through the tubes that occurred in the third year of the experiment.

To avoid the effect of soil disturbance due to tube installation on root growth, comparisons among rootstocks were performed on only the data collected between December 20, 2000 and December 19, 2001. However, the data collected during 2000 were fully analyzed to compare them with the results of the second year of experiment.

In-growth core experiment

Cores were constructed from 0.1-m diameter PVC pipe cut into 0.2-m long pieces. Eight 5-cm diameter holes were drilled into the side of each core and covered with 2-mm nylon mesh glued to the outside of the core. Cores were filled with sieved soil collected at the site and capped with 1-mm mesh nylon screen on each end.

Two cores were buried 10-cm deep at 1 m from the center tree of each rootstock replicate and 0.3 m apart (a total of eight cores per rootstock). Cores were installed on April 18, July 9 and September 28, 2001 and removed 42 days after burial (on May 30, August 20, and November 9, 2001, respectively).

Roots were carefully washed and analyzed with an image analysis system, WinRHIZO (Regent Instruments Inc., Sainte Foy, Québec, Canada), that was used to measure the length and the diameter of each root. Root dry mass was measured after oven drying to constant mass at 60 °C. Specific root length was calculated by dividing total root length by total root dry mass per core, whereas root tissue density was calculated by dividing the inverse of specific root length by the mean root diameter. Root length density was calculated by dividing total root length by core volume.

Data analyses

Rootstock, time and time × rootstock effects on the seasonal pattern of new root production (expressed both as root number and length) and on the growth of trunk cross-sectional area were evaluated by repeated measures analysis procedures. The effects of rootstock, soil depth and soil depth × rootstock interaction on new root production (expressed as number of roots) was evaluated by two-way ANOVA. Differences among rootstocks in the other measured parameters were evaluated by one-way ANOVA with the Duncan test with a 95% confidence interval as a *post hoc* test for mean separation. All statistical analyses were performed with the SPSS software package (SPSS, Chicago, IL).

Results

Tree vigor

Repeated measures analysis of trunk cross-sectional area indicated significant ($P = 0.01$) effects of rootstock, time and rootstock × time on tree growth (Figure 1). During the experiment, trunk cross-sectional area was significantly less for trees grafted on K146-43 than for trees on Nemaguard (51 and 48% of trunk cross-sectional area of trees on Nemaguard at the beginning and end of the experiment, respectively). Trees on the other rootstocks had intermediate trunk cross-sectional areas.

Fine root production

There were significant ($P = 0.01$) effects of rootstock, time and rootstock × time on the seasonal patterns of new root production during 2001. The rate of new root accumulation was higher for K119-50 than for the other rootstocks throughout
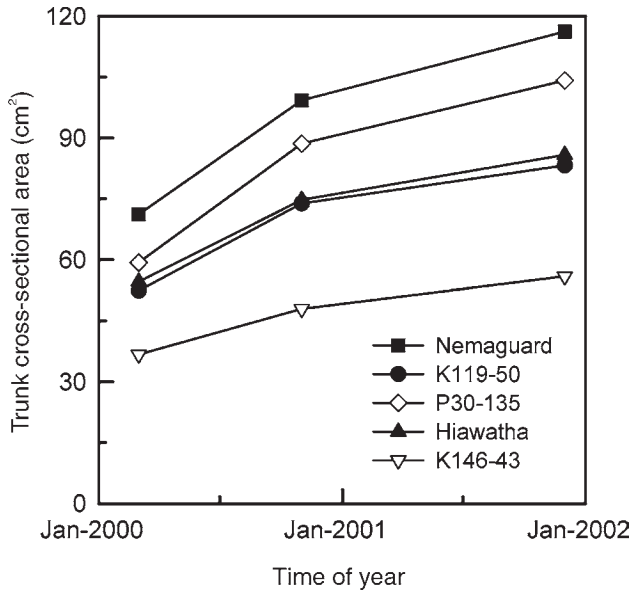
Figure 1. Trunk cross-sectional areas of trees on Nemaguard, K119-50, P30-135, Hiawatha and K146-43 rootstocks measured in March 2000, December 2000, and December 2001.

the season (Figure 2C), and total yearly root production was higher for K119-50 than for the other rootstocks. The ANOVA detected no significant differences among Nemaguard, P30-135, Hiawatha and K146-43 in the total number of new roots produced during the year.

Although the effect of rootstock × time was significant for the seasonal pattern of fine root production, the general shape of the seasonal pattern of new root production was similar for all rootstocks during both experimental years (Figure 2). A first flush of root growth occurred during spring followed by a decrease in root accumulation rate during the period before fruit harvest. This phase of decreased activity was shorter for K119-50 than for the other rootstocks. A second period of increased root growth occurred after fruit harvest in all rootstocks, as indicated by the increases in the slopes of the curves. Fine root production between June 27 and July 25, 2001 was 70–80% (depending on the rootstock) lower than in the previous month (May 15–June 27, 2001) and 75–95% lower than that measured in the month after fruit removal (July 25–August 21, 2001). Similar results were obtained when root growth was expressed in terms of root length (Figure 2D).

In 2001, fine root production of the most size-controlling rootstock K146-43 appeared to be low during spring and the pre-harvest period, with most root growth occurring after fruit removal (Figures 2C and 2D). However, this pattern was not evident in the first year of the experiment, perhaps because of the effect of soil disturbance on fine root production (especially on spring growth) (Figures 2A and 2B). Furthermore, this seasonal pattern was not consistent among the size-controlling rootstocks. For example, the increase in post-harvest root growth of Hiawatha (the next most size-controlling rootstock) was less than that of K146-43 (Figures 2C and 2D).

Total root production was 2–3 times (depending on the rootstock) higher during 2000 than during 2001. In all root-
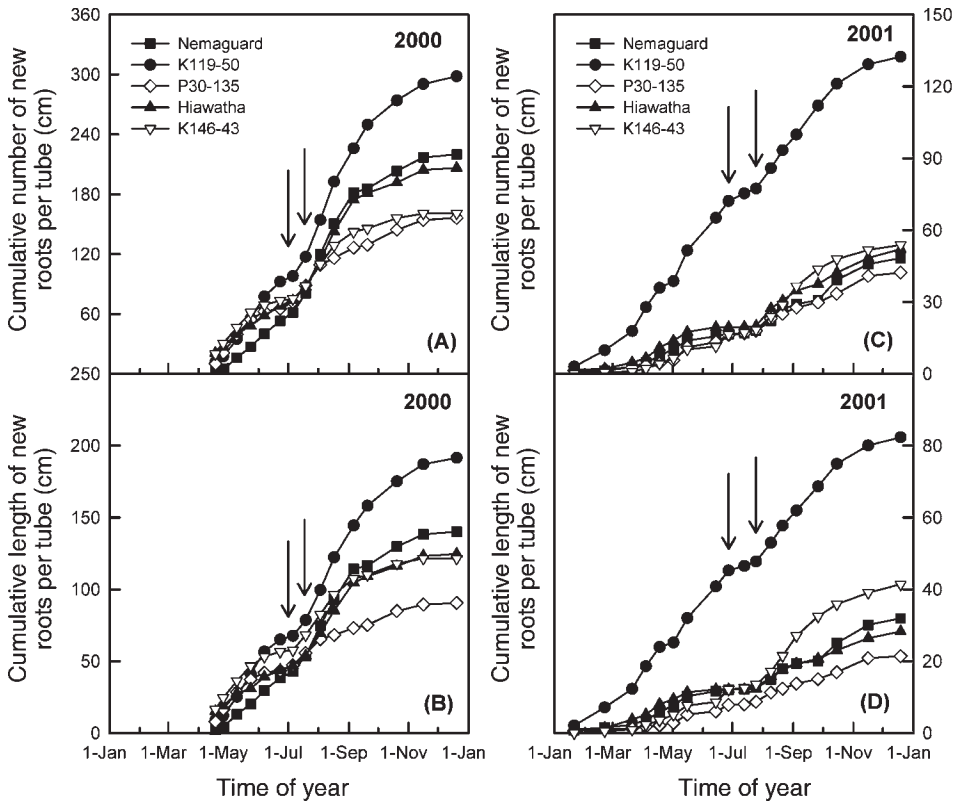

Figure 2. Cumulative number (A and C) and length (B and D) of new roots produced per minirhizotron tube between April 18, 2000 and December 20, 2000 (A and B) and between December 20, 2000 and December 19, 2001 (C and D) by trees on Nemaguard, K119-50, P30-135, Hiawatha and K146-43 rootstocks. Each value represents the mean of data from eight minirhizotron tubes. Arrows represent the beginning and the end of fruit harvest. Note the difference in scale between years.
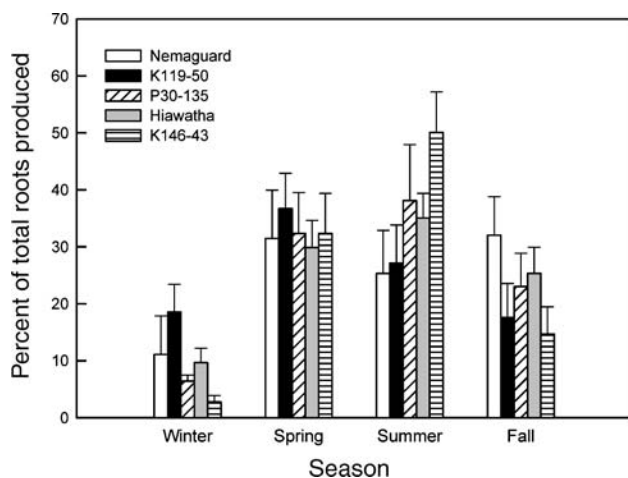
Figure 3. Percentage of the total annual production of new roots produced by trees on Nemaguard, K119-50, P30-135, Hiawatha and K146-43 rootstocks between December 20, 2000 and December 19, 2001 during different seasons: winter (from December 21, 2000 to March 19, 2001), spring (from March 20, 2001 to June 20, 2001), summer (from June 21, 2001 to September 21, 2001), and autumn (from September 22, 2001 to December 20, 2001). Each value represents the mean of data from eight minirhizotron tubes. Bars represent the standard errors of the means.
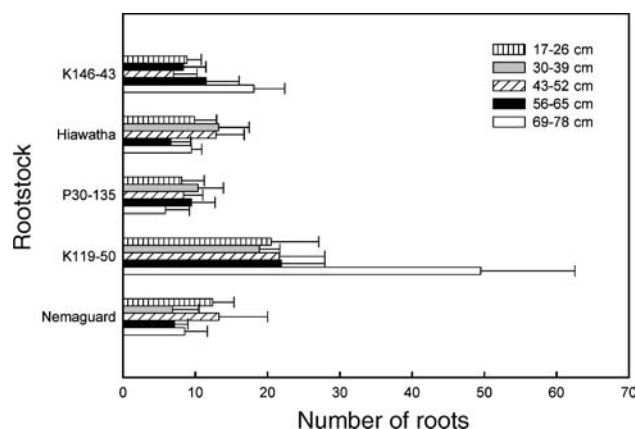

Figure 4. Number of new roots produced by trees on Nemaguard, K119-50, P30-135, Hiawatha and K146-43 rootstocks between December 20, 2000 and December 19, 2001 at different vertical depths in the soil (17–26, 30–39, 43–52, 56–65, and 69–78 cm). Each depth class represents the sum of three windows per minirhizotron tube. Each value is the mean of data from eight minirhizotron tubes. Bars represent the standard errors of the means.

stocks, most new roots were produced during spring and summer, and root production was lowest during winter (Figure 3); however, the percentage of roots produced in spring plus summer compared with winter did not differ significantly for Nemaguard or K119-50. For rootstocks K119-50, Nemaguard, P30-135 and Hiawatha, the percentage of roots produced did not differ significantly between spring and summer, whereas summer root production of K146-43 was significantly higher than spring root production.

Fine root distribution along the vertical soil profile

Rootstock and the soil depth × rootstock interaction had significant effects on the amount of new roots produced, whereas the effect of soil depth was not significant. The distribution of roots along the vertical soil profile differed among rootstocks (Figure 4). Nemaguard tended to produce more roots in the shallowest soil layer (17–26 cm), whereas 42% of K146-43 roots were at a soil depth of between 69 and 78 cm. The fine root system of K119-50 was produced mostly in the deepest soil layer (69–78 cm). The fine root systems of Hiawatha and P30-135 were fairly evenly distributed along the vertical soil profile (Figure 4).

Fine root thickness

In the minirhizotron experiment, all roots measured (independent of the rootstock) had diameters less than 2.0 mm (Figure 5). All rootstocks had similar distributions among root diameter classes with most roots having diameters between 0.2 and 0.4 mm (Figure 5). Significant differences among rootstocks in the percentage of roots in different diameter classes were detected only in the first four classes (0.0–0.2,

0.2–0.4, 0.4–0.6 and 0.6–0.8 mm) (Figure 5). Rootstocks P30-135 and K146-43 produced proportionally fewer roots with diameters between 0.0 and 0.2 mm than the other rootstocks (Figure 5). P30-135, Nemaguard and K146-43 had a higher percentage of roots with diameters between 0.2 and 0.4 mm than K119-50 (Figure 5). The percentage of roots produced by K146-43 in the third and fourth diameter classes (0.4–0.6 mm and 0.6–0.8 mm, respectively) was higher than for P30-135 and Hiawatha. Mean root diameter differed significantly among rootstocks (K146-43: 368 ± 10.5 μm;
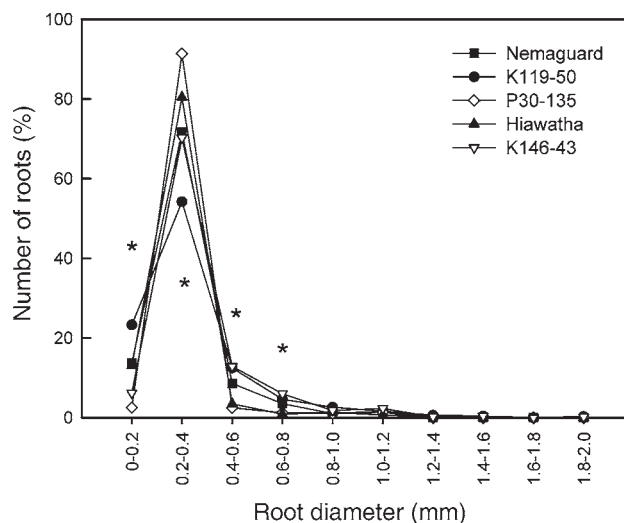

Figure 5. Percent distribution of new roots produced by trees on Nemaguard, K119-50, P30-135, Hiawatha and K146-43 rootstocks between December 20, 2000 and December 19, 2001 in ten diameter classes. Each value is the mean of data from eight minirhizotron tubes. Asterisks represent significant differences among rootstocks according to ANOVA ($P = 0.05$).

Table 1. Root diameter (measured in the minirhizotron and in-growth core experiments), specific root length, root tissue density and root length density of peach trees grafted on Nemaguard, K119-50, P30-135, Hiawatha and K146-43 rootstocks, measured in spring, summer and fall 2001. Roots were collected from in-growth cores. Each measurement represents the mean of eight in-growth cores (or eight minirhizotron tubes). Within a column, different letters indicate significant differences between means at $P \leq 0.05$ using Duncan's multiple range test.

Rootstock	Root diameter (µm)		Specific root length (mg root cm^{-3} root)	Root tissue density (cm root mg^{-1} root)	Root length density (cm root cm^{-3} soil)
	In-growth cores	Minirhizotrons			
Spring					
Nemaguard	332 a	328 ab	8.6 a	239 ab	0.11 b
K119-50	220 a	325 ab	19.5 a	183 ab	0.29 ab
P30-135	353 a	264 c	10.6 a	164 ab	0.29 ab
Hiawatha	210 a	289 bc	17.0 a	292 a	0.21 ab
K146-43	317 a	352 a	21.3 a	143 b	0.39 a
Summer					
Nemaguard	354 a	233 b	3.43 a	322 ab	0.10 a
K119-50	406 a	241 b	4.24 a	232 b	0.12 a
P30-135	375 a	261 b	3.88 a	288 ab	0.15 a
Hiawatha	409 a	227 b	3.49 a	250 ab	0.08 a
K146-43	360 a	354 a	3.45 a	355 a	0.11 a
Fall					
Nemaguard	571 ab	278 bc	3.87 ab	147 a	0.19 a
K119-50	671 a	325 b	2.60 b	127 a	0.17 b
P30-135	573 ab	306 bc	3.00 ab	150 a	0.15 b
Hiawatha	458 b	265 c	4.41 a	161 a	0.16 b
K146-43	663 a	414 a	2.72 b	128 a	0.10 b

K119-50: 317 ± 7.3 µm; Nemaguard: 303 ± 9.7 µm; P30-135: 281 ± 4.0 µm; Hiawatha: 269 ± 6.5 µm;) with K146-43 having significantly thicker roots than the other rootstocks and Hiawatha producing the thinnest fine root system.

Specific root length, root tissue density and root length density

Specific root length of all rootstocks was significantly higher in spring than in summer and fall, but there were no significant differences in this parameter between summer and fall (Table 1). Specific root length of fine roots produced during spring and summer did not differ significantly among rootstocks, whereas significant differences among rootstocks were detected in fall (Table 1). In the in-growth core experiment, significant differences among rootstocks were detected in root diameter only during fall, with K146-43 having the thickest fine roots (Table 1). Root tissue density did not differ significantly among rootstocks during fall, whereas some differences were found in spring and summer (Table 1).

Root length density of most rootstocks was higher in spring than in summer and fall (Table 1), except for Nemaguard, which had a root length density slightly, but significantly, higher in fall than in spring and summer (Table 1). During spring, root length density was higher in K146-43 than in Nemaguard, whereas root length density was higher in Nemaguard than in the other rootstocks during fall (Table 1). In summer, specific root length density was similar among rootstocks (Table 1).

Relationship between rootstock vigor, fine root production and root characteristics

In all rootstocks, specific root length of roots produced in spring was negatively correlated to TCSA growth rate during 2001 (Figure 6), whereas the correlation was not significant for specific root length of roots produced in summer and fall.
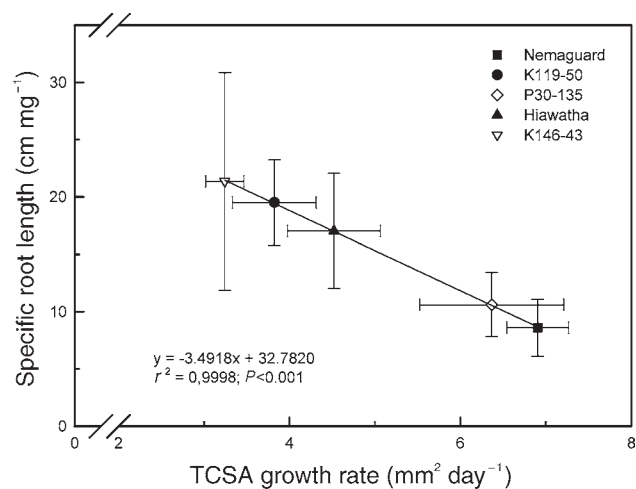

Figure 6. Relationship between specific root length measured in spring in the in-growth core experiments and the growth rate of trunk cross-sectional area of trees grafted on Nemaguard, K119-50, P30-135, Hiawatha and K146-43 rootstocks. Each value represents the mean value calculated for each rootstock. Vertical and horizontal bars indicate the standard errors of the means.

None of the other parameters measured (total amount of roots produced in 2001, percent of fine roots produced in the different seasons, root diameter, root tissue density) were significantly correlated to TCSA growth rate.

Discussion

Tree vigor

The rootstocks studied significantly affected scion vigor as confirmed by the large differences in trunk cross-sectional area among trees on the different rootstocks. K146-43 was the most size-controlling rootstock as reported previously (DeJong et al. 2001, 2004, Basile et al. 2003*a*, Weibel et al. 2003, Solari et al. 2006*a*), with the other size-reducing rootstocks imparting intermediate tree vigor between Nemaguard (the vigorous control) and K146-43.

Couvillon et al. (1989) reported that peach seedling trees are more vigorous than self-rooted trees particularly under dry conditions, but this finding was not confirmed in well-irrigated trees (Rieger 1992). Our study was carried out in an experimental plot that has been well irrigated every year since establishment and all measured trees were grafted on cutting-propagated (K119-50, K146-43, P30-135) or seed-propagated (Nemaguard) rootstock. Furthermore, all of our study trees were initially grown in a nursery and then transplanted to the experimental orchard. Because the roots were pruned in the transplanting process, it is unlikely that the root growth patterns we measured reflected differences carried forward from differences in the initial propagation methods.

Seasonal pattern of new fine root production

We detected no significant differences among peach rootstocks in seasonal patterns of fine root production that appeared to be directly associated with tree vigor. Fine root production of all rootstocks started synchronously at the beginning of the growing season. Although the most size-controlling rootstock (K146-43) produced a greater proportion of its total seasonal root production in the summer rather than in the spring, the next most size-controlling rootstock (Hiawatha) exhibited no such pattern. Thus, the initial hypothesis that the dwarfing phenomenon of peach rootstocks is associated with a delay in fine root production at the beginning of the growing season was not clearly supported.

In both study years and all rootstocks, the rate of new root production was highest during spring and after fruit harvest and lowest in the weeks before harvest and during winter. Fine root production by perennial fruit trees is often characterized by high production in the spring and fall (Eissenstat and Yanai 1997). Cockroft and Olsson (1972) reported that peach root production was higher in the spring than in the fall when trees were not irrigated after harvest. Richards and Cockroft (1975) presented evidence supporting the hypothesis that the summer depression in root production was a function of soil water availability. In contrast, Williamson and Coston (1989) reported that root growth peaked in well-irrigated peach trees

between fruit harvest and leaf senescence and demonstrated that the depression in root production that occurred during the growing season (between the spring and post-harvest growth peaks) was unrelated to water availability, but was associated with the presence of growing fruit. Glenn and Welker (1993) found that, independent of soil water availability, young non-fruiting peach trees had continuous white root production throughout the growing season, whereas the seasonal pattern of white root production became bimodal when the same trees started bearing fruit. This is consistent with the findings of Grossman and DeJong (1995*a*) who reported that stage III of fruit development is the phase of maximum fruit sink strength and can limit the availability of photosynthates for new root production. However, Ben Mimoun and DeJong (2006) presented evidence that summer root growth of mature trees can be depressed even when trees are defruited. It is likely that root growth recovers after fruit harvest because there is decreased competition between root and shoot growth during this period, though other soil environmental factors may also be important.

Weibel et al. (2003) reported that most shoots of 'Loadel' trees, grafted on the same rootstocks that we studied, ceased extension growth by early July (near harvest). In our study, K146-43 produced almost 50% of its fine root system during summer after fruit removal (Figure 3), indicating that competition between fruit and root growth may have been high in trees grafted on this rootstock, which was the most size-controlling. This finding implies that competition between growing organs may be stronger in dwarfed trees than vigorous trees, perhaps because of a relatively small available carbon pool (Lliso et al. 2004).

The bimodal pattern of root growth in peach treees observed in the present and previous studies (Williamson and Coston 1989, Glenn and Welker 1993) differs from the pattern reported for grape and apple (Eissenstat et al. 2005). This difference may reflect the longer fruit growth period in grape and apple trees compared with the early maturing peaches we studied, because the length of the fruit growth period strongly affects source–sink relationships in fruit trees (Grossman and DeJong 1995*a*, Grossman and DeJong 1995*b*, Basile et al. 2002).

Total fine root production

Total fine root production was not positively correlated with rootstock vigor. In the minirhizotron experiment, fine root production of a rootstock that conferred intermediate vigor (K119-50) was the highest, whereas no significant differences were detected among the other rootstocks. In addition, in the in-growth core experiment, Nemaguard (the most vigorous rootstock) had a root length density slightly higher than the other rootstocks only during fall, whereas its fine root production was similar to that of the other rootstocks in summer and much lower than that of K146-43 in spring. Trees on K146-43, the most size-controlling rootstock, had a trunk circumference that was 48–51% that of trees on Nemaguard, indicating that trees on K146-43 produce more fine roots relative to canopy size than trees on more vigorous rootstocks. This result was

supported by data from the soil core in-growth experiment showing that fine root production (expressed in terms of root length density) was more than three times higher in K146-43 than in Nemaguard. Similarly, Basile et al. (2003*b*) found that trees on K146-44 (a semi-dwarfing rootstock similar to K146-43) partitioned a greater proportion of dry mass to the root system than trees on Nemaguard. Furthermore, Solari et al. (2006*b*) found that trees on K146-43 and Hiawatha had higher root to shoot ratios than trees on Nemaguard and the ratios were proportionally related to rootstock differences in hydraulic conductance. Thus the evidence indicates that there is a tendency toward greater amounts of fine root production per unit canopy size with dwarfing rootstocks than with the more vigorous rootstocks.

Water stress decreases or inhibits root and shoot growth (Steinberg et al. 1990, Hipps et al. 1995, Kramer and Boyer 1995) depending on the severity and duration of the drought. In some studies, root growth appears to be stimulated by water deficit (Leuschner et al. 2001) but not in other studies (Steinberg et al. 1990). However, prolonged water stresses (both mild and severe) increase root to shoot ratio by enhancing carbon allocation to roots relative to shoots (Steinberg et al. 1990, Kramer and Boyer 1995). Peach (Basile et al. 2003*a*, Solari et al. 2006*a*) and apple (Olien and Lakso 1986) trees grafted on size-controlling rootstocks (K146-43 and Hiawatha, and M9; respectively) are reported to experience chronic mild water stress as a result of inefficient water transport through the root system (Basile et al. 2003*b*, Solari et al. 2006*b*). The relatively high fine root production of K146-43 and Hiawatha may be related to differences in water relations of trees on different rootstocks. Furthermore, greater proportional carbon partitioning to the root system of size-controlling rootstocks may reduce the carbohydrate pool available for shoot growth and strengthen the dwarfing effect. However, this does not appear to be the case for dwarfing rootstocks of apple, because Lo Bianco et al. (2003) found that apple trees on the dwarfing M9 had lower root to shoot ratios than trees on the semi-vigorous MM106.

Fine root distribution along the vertical soil profile

Root growth characteristics are genotype specific (Rom and Carlson 1987), and accordingly fine root distribution along the vertical soil profile differed significantly among rootstocks. In our study, K119-50, a *Prunus salicina* × *P. dulcis* hybrid, produced a large proportion of fine roots in deep soil layers (most of the differences in total root production between K119-50 and the other rootstocks were in the deepest soil layers), characteristics that were likely inherited from the almond parent. Almond seedlings are deeply rooted and adapted to resist drought (Rom and Carlson 1987). Tree root distribution is also strongly affected by soil environment characteristics such as soil type (Fernandez et al. 1995), temperature (Pregitzer et al. 2000), nutrient availability (Hodge 2004) and soil water availability (Dickmann et al. 1996). However, all our study trees were grown in the same orchard with a fairly uniform soil and because the complete randomized block design used in the

present study should control such variability, it is unlikely that any of these factors explain the observed differences among rootstocks. When a tree experiences a soil water deficit, its root system tends to grow more at greater depths where more water is generally available (Layne et al. 1986, Dickmann et al. 1996, Torreano and Morris 1998). Basile et al. (2003*a*) demonstrated that peach trees on the size-controlling K146-43 and Hiawatha rootstocks experience a mild water stress during midday but it is unlikely that this was related to differences in soil water availability associated with the different rootstocks because all the trees were irrigated in the same manner and the canopies of trees on K146-43 and Hiawatha rootstocks were smaller than the canopies of trees on more vigorous rootstocks. Thus water availability should have been relatively greater for the smaller trees.

Thickness of the fine root system

The distribution of fine roots among diameter classes differed significantly among the various size-controlling rootstocks. Total root hydraulic conductivity decreases with increasing fine root diameter (Rieger and Litvin 1999, Huang and Eissenstat 2000) and cortex width (Rieger and Litvin 1999). Huang and Eissenstat (2000) reported that a decrease in total root hydraulic conductivity could be explained by a decrease in radial hydraulic conductivity. In our study, the size-controlling rootstock, K146-43, had a thicker fine root system than the vigorous control, Nemaguard. This difference provides indirect support for the results of Basile et al. (2003*b*) and Solari et al. (2006*b*) showing that the dwarfing peach rootstocks, K146-44 and K146-43, have lower root hydraulic conductances than Nemaguard. However, the fine root system of Hiawatha, the next most size-controlling rootstock, did not fit the same patterns because it tended to have greater percentages of roots in the finer root categories. Consequently, the general relationship between fine root diameter and TCSA growth rate was not significant when all five rootstocks were considered in a regression analysis. Root hydraulic conductance is also a function of the hydraulic architecture of the root system (Tyree and Zimmermann 2002), but we did not evaluate these aspects.

Specific root length

According to the in-growth experiment, specific root length of all the rootstocks was greatest during spring when root length density was also greatest. This finding corroborates the reported positive relationship between root growth rate and root length density in *Citrus* species (Eissenstat 1991). Similarly, Comas et al. (2002) compared fine root characteristics of fast- and slow-growing species of the Aceraceae, Fagaceae and Pinaceae and reported that the fast-growing species had higher specific root lengths and smaller root diameters than the slow-growing species. Furthermore, Eissenstat 1992) concluded that the production of roots with high specific root length is a characteristic of opportunistic root growth (Eissenstat 1992). Although we did not assess root mortality, most tree species have low over-winter fine root survival

(Wells and Eissenstat 2001, Ruess et al. 2003). The high root growth rates and high specific root lengths that we measured in spring may reflect reconstruction of the fine root system in the spring.

The in-growth core data on specific root length and root diameter measured in summer and fall appeared to be unrelated to rootstock vigor. However, although specific root length of the roots produced in spring did not differ significantly among rootstocks, there was a strong negative linear relationship between mean specific root length from the in-growth core experiment and rootstock vigor (expressed as TCSA growth rate) (Figure 6). This relationship was not predicted. Instead, based on the differences among rootstocks in fine root diameter detected in the minirhizotron experiment (Figure 5), a corresponding positive relationship was predicted between specific root length measured in the in-growth core experiment and rootstock vigor. However, specific root length is a negative function of both root diameter and root tissue density. In the in-growth core experiment, the diameters of roots produced in spring did not differ significantly among rootstocks (Table 1), whereas root tissue density tended to increase progressively from the dwarfing rootstock, K146-43 (143 mg cm^{-3}), to the intermediate vigor rootstocks, P30-135 and K119-50 (164 and 183 mg cm^{-3}, respectively), and to the vigorous rootstock Nemaguard (239 mg cm^{-3}). The exception to this progression was Hiawatha, which had the highest root tissue density.

Fine root growth in spring has the important role of increasing the total surface of absorbing roots to support the growth of the aboveground organs, but at the same time it represents a large cost (Eissenstat 1992) that, in early spring, deciduous trees support with the stored carbohydrate pool. The negative relationship we found between rootstock vigor and specific root length of roots produced in spring suggests that peach trees grafted on rootstock with differing size-controlling potentials may follow different strategies when building new fine roots in spring. Trees on rootstock of low–intermediate vigor tended to invest less carbon per unit length of root produced in spring compared with trees on more vigorous rootstocks; however, specific root length of roots produced in summer and fall was unrelated to rootstock vigor. Another study (Solari et al. 2006c), using three of the rootstocks we studied, reported that specific root length decreased with decreasing rootstock vigor and the differences were related to differences in root diameter. In that experiment, root characteristics were determined at the end of an experiment with potted trees, whereas we measured specific root length in an in-growth core field experiment. The difference between our results and those reported by Solari et al. (2006c) may be related to an effect of soil disturbance during core installation. Soil disturbance may have caused the production of a thicker fine root system because root diameters measured in the second year of the minirizhotron experiment (undisturbed soil) were thinner than those measured in the in-growth core experiment (disturbed soil) (Table 1). Moreover, the roots produced in the first year of the minirhizotron experiment were significantly thicker than in the second year (data not shown).

Soil disturbance is a confounding issue in all root studies.

As reported previously for peach (Wells et al. 2002), soil disturbance probably accounted for a major part of the differences in fine root production observed in the minirhizotron experiment between 2000 and 2001 and in root thickness between the 2001 minirhizotron data and the in-growth root core experiment. These data demonstrate the importance of taking the effects of soil disturbance into account in root growth studies and highlight the difficulty of doing root growth studies that are free of experimental artifact. However, because the primary conclusions drawn from our research are based mainly on the second year of the minirhizotron experiment, the influence of soil disturbance should have been minimal. There is concern about the representativeness of minirhizotron data because only those parts of the root system growing along the soil tubes are measured and there may be long-term effects of the tubes on soil water penetration and nutrient movement as well as root penetrability. However, because we focused on a comparative study of rootstocks and there does not appear to be any reason why these factors would differentially effect root growth of the specific rootstocks used in this study, the primary conclusions of our study should be valid.

In conclusion, peach rootstocks differing in vigor had similar seasonal patterns of fine root production, with growth rate of the fine root system decreasing during the major period of fruit growth. Fine root production of K146-43 (the most size-controlling rootstock) was proportionally higher during summer (after fruit removal) than during early spring but this phenomenon was not consistent among all the size controlling rootstocks. Rootstock K119-50 had the deepest root system with production of fine roots in the soil profile between 69 and 78 cm, considerably deeper than the other rootstocks. Because of the deep fine root system of K119-50, there was a large difference in total fine root production of K119-50 compared with the other rootstocks. Independent of rootstock, fine roots produced during spring had a high specific root length, suggesting opportunistic root growth at the beginning of the growing season. Our results are consistent with the hypothesis that peach rootstocks control tree size by modifying tree water status (Basile et al. 2003a, 2003b, Solari et al. 2006a). The thicker fine root system of K146-43 may be related to its lower hydraulic conductance compared with Nemaguard (Solari et al. 2006b). However, anatomical studies are needed to better understand potential differences in the radial pathway of water in K146-43 fine roots compared with more vigorous rootstocks. Given the large differences in root growth characteristics of the moderately size-controlling K119-50 rootstock compared with the other rootstocks, further comparative studies of the water relations characteristics of this rootstock with more and less vigorous rootstocks should provide insight into whether different mechanisms underlie its modest size-controlling potential.

References

Basile, B., M.J. Mariscal, K.R. Day, R.S. Johnson and T.M. DeJong. 2002. Japanese plum (*Prunus salicina* L.) fruit growth: seasonal pattern of source/sink limitations. J. Am. Pomol. Soc. 56:86–93.

Basile, B., J. Marsal and T.M. DeJong. 2003*a*. Daily shoot extension growth of peach trees growing on roostocks that reduce scion growth is related to daily dynamics of stem water potential. Tree Physiol. 23:695–704.

Basile, B., J. Marsal, L.I. Solari, M.T. Tyree, D.R. Bryla and T.M. De-Jong. 2003*b*. Hydraulic conductance of peach trees grafted on rootstocks with differing size-controlling potentials. J. Hortic. Sci. Biotechnol. 78:768–774.

Ben Mimoun, M. and T.M. DeJong. 2006. Effect of fruit crop load on peach root growth. Acta Hortic. In press.

Buwalda, J.G. 1991. Root growth of kiwifruit vines and the impact of canopy manipulations. *In* Plant roots and their environment. Eds. B.L. McMichael and H. Persson. Elsevier, Amsterdam. pp 431–441.

Cockroft, B. and K.A. Olsson. 1972. Pattern of new root production in peach trees under irrigation. Aust. J. Agric. Res. 23:1021–1025.

Comas, L.H., D.M. Eissenstat and A.N. Lakso. 2000. Assessing root death and root system dynamics in a study of grape canopy pruning. New Phytol. 147:171–178.

Comas, L.H., T.J. Bouma and D.M. Eissenstat. 2002. Linking root traits to potential growth rate in six temperate tree species. Oecologia 132:34–43.

Couvillon, G.A., M. Rieger, R. Harrison, J. Daniell and J.G. Aparisi. 1989. Stress-mediated responses of own rooted peach cultivars. Acta Hortic. 243:221–230.

Davies, W.J., S. Wilkinson and B. Loveys. 2002. Stomatal control by chemical signaling and the exploitation of this mechanism to increase water use efficiency in agriculture. New Phytol. 153: 449–460.

DeJong, T.M., K.R. Day, J.F. Doyle and R.S. Johnson. 1994. The Kearney Agricultural Center perpendicular 'V' (KAC-V) orchard system for peaches and nectarines. HortTechnology 4:362–367.

DeJong, T.M., A. Weibel, W. Tsuji, J.F. Doyle, R.S. Johnson and D. Ramming. 2001. Evaluation of size controlling rootstocks for California peach production. Acta Hortic. 557:103–110.

DeJong, T.M., R.S. Johnson, J.F. Doyle, A. Weibel, L. Solari, J. Marsal, B. Basile, D. Ramming and D. Bryla. 2004. Growth, yield and physiological behavior of size-controlling peach rootstocks developed in California. Acta Hortic. 658:449–455.

Dickmann, D.I., P.V. Nguyen and K.S. Pregitzer. 1996. Effects of irrigation and coppicing on above-ground growth, physiology, and fine-root dynamics of two field-grown hybrid poplar clones. For. Ecol. Manage. 80:163–174.

Eissenstat, D.M. 1991. On the relationship between specific root length and the rate of root proliferation: a field study using Citrus rootstocks. New Phytol. 118:63–68.

Eissenstat, D.M. 1992. Costs and benefits of constructing roots of small diameter. J. Plant Nutr. 15:763–782.

Eissenstat, D.M. and R.D. Yanai. 1997. The ecology of root lifespan. Adv. Ecol. Res. 27:1–60.

Eissenstat, D.M., J.M. Withington, L.H. Comas, T. Bauerle, M. Goebel and A.N. Lakso. 2005. Misconceptions on seasonal patterns of root growth in woody plants. Proc. Ann. Meet. Ecol. Soc. Am., Montreal. http://abstracts.co.allenpress.com/pweb/esa2005/document/?ID=50933

Fernandez, R.T., R.L. Perry and D.C. Ferree. 1995. Root distribution patterns of nine apple rootstocks in two contrasting soil types. J. Am. Soc. Hortic. Sci. 120:6–13.

Geisler, D. and D.C. Ferree. 1984. Response of plants to root pruning. Hortic. Rev. 6:155–188.

Giulivo, C. and A. Bergamini. 1982. Effect of rootstock-scion combination on water balance of apple tree, cv Golden Delicious. 21st Int. Hor. Congress, Hamburg Federal Republic of Germany, Abstracts, p 1264.

Glenn, D.M. and W.V. Welker. 1993. Root development patterns in field grown peach trees. J. Am. Soc. Hortic. Sci. 118:362–365.

Grossman, Y.L. and T.M. DeJong. 1995*a*. Maximum vegetative growth potential and seasonal patterns of resource dynamics during peach growth. Ann. Bot. 76:473–482.

Grossman, Y.L. and T.M. DeJong. 1995*b*. Maximum fruit growth potential and seasonal patterns of resource dynamics during peach growth. Ann. Bot. 75:553–560.

Head, G.C. 1967. Effects of seasonal changes in shoot growth on the amount of unsuberized root on apple and plum trees. J. Hortic. Sci. 42:169–180.

Hipps, N.A., L. Pages, J.G. Huguet and V. Serra. 1995. Influence of controlled water supply on shoot and root development of young peach trees. Tree Physiol. 15:95–103.

Hodge, A. 2004. The plastic plant: root responses to heterogeneous supplies of nutrients. New Phytol. 162:9–24.

Huang, B. and D.M. Eissenstat. 2000. Linking hydraulic conductivity to anatomy in plants that vary in specific root length. J. Am. Soc. Hortic. Sci. 125:260–264.

Kramer, P.J. and J.S. Boyer. 1995. Water relations of plants and soils. Academic Press, San Diego, 495 p.

Layne, R.E.C., C.S. Tan and R.L. Perry. 1986. Characterization of peach roots in Fox sand as influenced by sprinkler irrigation and tree density. J. Am. Soc. Hortic. Sci. 111:670–677.

LaRue, J.H. and R.S. Johnson. 1989. Peaches, plums and nectarines—growing and handling for fresh market. Publication No. 3331. Univ. of California Div. of Agric. Nat. Resour., Oakland, CA, 252 p.

Leuschner, Ch., K. Backes, D. Hertel, F. Schipka, U. Schmitt, O. Terborg and M. Runge. 2001. Drought responses at leaf, stem and fine root levels of competitive *Fagus sylvatica* L. and *Quercus petraea* (Matt.) Liebl. trees in dry and wet years. For. Ecol. Manage. 149: 33–46.

Lliso, I., J.B. Forner and M. Talón. 2004. The dwarfing mechanism of citrus rootstocks F&A 418 and #23 is related to competition between vegetative and reproductive growth. Tree Physiol. 24: 225–232.

Lo Bianco, R, M. Policarpo and L. Scariano. 2003. Effects of rootstock vigour and in-row spacing on stem and root growth, conformation and dry-matter distribution of young apple trees. J. Hortic. Sci. Biotechnol. 78:828–836.

Olien, W.C. and A.N. Lakso. 1986. Effect of rootstock on apple (*Malus domestica*) tree water relations. Physiol. Plant. 67: 421–430.

Pregitzer, K.S., M.E. Kubiske, C.K. Yu and R.L. Hendrick. 1997. Root architecture, carbon and nitrogen in four temperate forest species. Oecologia 111:302–308.

Pregitzer, K.S., M.J. Laskowski, A.J. Burton, V.C. Lessard and D.R. Zac. 1998. Variation in sugar maple respiration with root diameter and soil depth. Tree Physiol. 18:665–670.

Pregitzer, K.S., J.S. King, A.J. Burton and S.E. Brown. 2000. Responses of tree fine roots to temperature. New Phytol. 147: 105–115.

Psarras, G., I.A. Merwin, A.N. Lakso and J.A. Ray. 2000. Root growth phenology, root longevity, and rhizosphere respiration of field grown 'Mutsu' apple trees on 'Malling 9' rootstock. J. Am. Soc. Hortic. Sci. 125:596–602.

Richards, D. and B. Cockroft. 1975. The effect of soil water on root production of peach trees in summer. Aust. J. Agric. Res. 26: 173–180.

Rieger, M. 1992. Growth, gas exchange, water uptake, and drought response of seedling- and cutting-propagated peach and citrus rootstocks. J. Am. Soc. Hortic. Sci. 117:834–840.

Rieger, M. and F. Marra. 1994. Responses of young peach trees to root confinement. J. Am. Soc. Hortic. Sci. 119:223–228.

Rieger, M. and P. Litvin. 1999. Root system hydraulic conductivity in species with contrasting root anatomy. J. Exp. Bot. 50:201–209.

Rom, R.C. and R.F. Carlson. 1987. Rootstocks for fruit crops. Wiley, New York, 494 p.

Ruess, R.W., R.L. Hendrick, A.J. Burton, K.S. Pregitzer, B. Svein-bjornssön, M.F. Allen and G.E. Maurer. 2003. Coupling fine root dynamics with ecosystem carbon cycling in black spruce forests of interior Alaska. Ecol. Monogr. 73:643–662.

Solari, L.I., S. Johnson and T.M. DeJong. 2006*a*. Relationship of water status to vegetative growth and leaf gas exchange of peach (*Prunus persica*) trees on different rootstocks. Tree Physiol. 26: 1333–1341.

Solari, L.I., S. Johnson and T.M. DeJong. 2006*b*. Hydraulic conductance characteristics of peach (*Prunus persica*) trees on different rootstocks are related to differences in biomass production, distribution and vegetative growth. Tree Physiol. 26:1343–1350.

Solari, L.I., F. Pernice and T.M. DeJong. 2006*c*. The relationship of hydraulic conductance to root system characteristics of peach (*Prunus persica*) rootstocks. Physiol. Plant. In press.

Steinberg, S.L., J.C. Miller, Jr. and M.J. McFarland. 1990. Dry matter partitioning and vegetative growth of young peach trees under water stress. Aust. J. Plant Physiol. 17:23–36.

Syvertsen, J.P. 1981. Hydraulic conductivity of four commercial citrus rootstocks. J. Am. Soc. Hortic. Sci. 106:378–381.

Torreano, S.J. and L.A. Morris. 1998. Loblolly pine root growth and distribution under water stress. Soil Sci. Soc. Am. J. 62:818–827.

Tyree, M.T. and M.H. Zimmermann. 2002. Xylem structure and the ascent of sap. 2nd Edn. Springer-Verlag, New York, 283 p.

Weibel, A., R.S. Johnson and T.M. DeJong. 2003. Comparative vegetative growth responses of two peach cultivars grown on size-controlling versus standard rootstocks. J. Am. Soc. Hortic. Sci. 28: 463–471.

Wells, C.E. and D.M. Eissenstat. 2001. Marked differences in survivorship among apple roots of different diameters. Ecology 82: 882–892.

Wells, C.E., D.M. Glenn and D.M. Eissenstat. 2002. Changes in the risk of fine-root mortality with age: a case study in peach, *Prunus persica* (Rosaceae). Am. J. Bot. 89:79–87.

Weyers, J.D.B. and N.W. Paterson. 2001. Plant hormones and the control of physiological processes. New Phytol. 152:375–407.

Williamson, J.G. and D.C. Coston. 1989. The relationship among root growth, shoot growth, and fruit growth of peach. J. Am. Soc. Hortic. Sci. 114:180–183.

Williamson, J.G., D.C. Coston and J.A. Cornell. 1992. Root restriction affects shoot development of peach in a high-density orchard. J. Am. Soc. Hortic. Sci. 117:362–367.