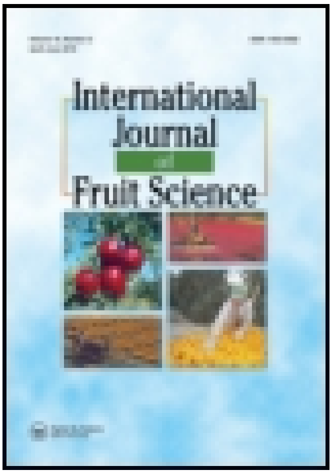

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T. Tworkoski[a] & G. Fazio[b]

[a] Appalachian Fruit Research Station, ARS, USDA, Kearneysville, West Virginia, USA

[b] Plant Genetics Resources Unit, ARS, USDA, Cornell University, Geneva, New York, USA

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T. TWORKOSKI[1] and G. FAZIO[2]
[1]*Appalachian Fruit Research Station, ARS, USDA, Kearneysville, West Virginia, USA*
[2]*Plant Genetics Resources Unit, ARS, USDA, Cornell University, Geneva, New York, USA*

Size-controlling rootstocks are required to attain trees with reduced stature that are necessary for modern orchard management, such as high density plantings. Apple cultivars can be grafted on commercially-available size-controlling rootstocks but new rootstocks are needed for both size-controlling efficacy and improved tolerance of abiotic and biotic stress. This research was designed to determine the consistency of Geneva and Malling rootstocks for size-control with scions of different growth potentials. Hydraulic conductivity (HC) and abscisic acid (ABA) in xylem exudates were measured in selected scions grafted to Malling (from least-to-most size control M.7, M.9, and M.27) and Geneva (from least-to-most size control, G.935, G.5087, G.41, and G.11) rootstocks. Regardless of scion vigor, trees with G.935 and G.41 rootstocks had the most height and diameter growth and the highest HC, whereas trees with M.27 rootstocks had the least. Lower ABA was measured in xylem exudate of 'Fuji' grown on G.935 and G.41 than G.5087 and G.11 rootstocks. Regardless of scion vigor, tree growth was less when grown on G.11 and G.5087, which were associated with less HC and elevated ABA in 'Fuji' scion. Tree heights of the scion were similar when grown on G.11, G.5087, and M.7. It is proposed that trees grafted to G.11 and G.5087 may be better adapted to dry environments based upon their size and elevated ABA.

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Address correspondence to T. Tworkoski, USDA-ARS Appalachian Fruit Research Station, 2217 Wiltshire Rd, Kearneysville, WV 25430. E-mail: tom.tworkoski@ars.usda.gov

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INTRODUCTION

Efficient modern apple orchards rely on size-controlling rootstocks to attain trees with reduced stature that provide superior yield in high density plantings. Desired scions of apple cultivars can be grafted on commercially-available size-controlling rootstocks, but new rootstocks are needed for tree size management under a variety of environmental conditions, including reduced irrigation and drought. To assist in developing new rootstocks, improved knowledge is needed of rootstock processes that may affect dwarfing and stress tolerance. The processes that regulate size in rootstocks are not fully known but may include hydraulic and hormone communication between root and shoot.

Reduced growth in dwarfed apple trees has been attributed to altered shoot concentrations of endogenous hormones, including auxin, gibberellin, abscisic acid (ABA), and cytokinin (Grochowska et al., 1984; Jaumein and Faust, 1984; Kamboj et al., 1999; Looney et al., 1988; Steffens and Hedden, 1992). Elevated levels of ABA and limited hydraulic conductivity (HC; the ratio of water flow to pressure) of vascular systems have been found in some dwarfing rootstocks, and these factors may be part of the size-controlling process (Kamboj et al., 1999; Kamboj and Quinlan, 1998; Tworkoski and Fazio, 2011; Yadava and Dayton, 1972). Reduced movement of water and minerals from rootstocks could dwarf the scion (Hussein and McFarland, 1994; Rogers and Booth, 1960). In addition, ABA has been shown to be a root-produced message that regulates shoot tolerance to drying soils (Davies et al., 2005). High ABA concentrations in xylem exudate of trees grown on dwarf rootstock may be significant because of its role in both growth control and drought tolerance. One possibility is that aberrant xylem configuration at the graft union may also reduce HC and increase ABA in the xylem stream (Atkinson et al., 2003; Tworkoski and Fazio, 2011). Comparison of the effect of different length dwarfing and non-dwarfing interstems on scion growth suggests that part of the mechanism for dwarfing might be related to specific conductivity of active compounds (hormones, nutrients, metabolites, water, etc.) being shuttled in the vascular tissues (Carlson and Oh, 1975). The dwarfing effect of Malling 9 and related rootstocks has been attributed to two main genetic factors (Dw1 and Dw2) located on chromosomes 5 and 11, respectively (Fazio et al., 2014; Pilcher et al., 2008). Therefore, it is possible that the dwarfing effect might be the combination of two independent physiological systems that interact to produce the dwarfing effect that we observe in Malling 9 related rootstocks.

Improved understanding of dwarfing processes, particularly in new rootstocks, will help select and develop rootstocks that provide trees with targeted sizes and that are adapted to warmer, dryer environments. In this greenhouse experiment scions of different vigor were used to assess rootstock-associated HC and ABA signals from a range of size-controlling, well-established Malling and newer Geneva rootstocks. The objective was to compare growth, ABA, and HC of genetically different apple scions and rootstocks.

MATERIALS AND METHODS

In this experiment scions of different vigor (i.e., from size-controlling rootstocks and two cultivars) were grafted on size-controlling rootstocks. Tree height and weight distribution were measured and xylem exudate was collected to determine HC. ABA concentrations were measured in 'Fuji' grafted to Geneva rootstocks.

Trees

Malling rootstocks (M.7 EMLA, M.9 EMLA, M.27 EMLA), were purchased from Willamette Nurseries, Canby, OR, USA. Geneva rootstocks (G.11, G.41, G.5087, and G.935) were obtained from the USDA/Cornell Apple Rootstock Breeding Program, Geneva, NY, USA. Rootstock G.5087 may also be designated CG.5087 (the CG prefix indicating that the rootstock has not been commercially released). In Mar. 2008, 100 trees of each rootstock were planted in 4-L pots with soil-less media (Metromix 360/fine sand, 2.8/1, v/v) at the Appalachian Fruit Research Station. In previous work we determined that buds from M.7, M.9, and M.27 that were grafted to a variety of rootstocks provided consistently long, intermediate, and short scion growth, respectively (unpublished data). We, therefore, used them as scions in this experiment to evaluate Geneva rootstock effects on scion with known growth capacity and on two scion cultivars 'Fuji' and 'Gala'. In July 2008, buds of 'Gala', 'Fuji', M.7, M.9, and M.27 were 'T' budded onto the three Malling and four Geneva rootstocks. To avoid confusion where Malling rootstocks were used as scion the letter 'S' will precede the rootstock designation; thus, SM.7, SM.9, and SM.27. There were at least five trees of each scion/rootstock combination.

Trees in the greenhouse were allowed to cool to 1 to 5°C, with a natural photoperiod from Oct. 2008 to Apr. 2009. Rootstock shoots of all grafted trees were removed in May 2009. In 2009 all scion/rootstock combinations were grown in the greenhouse. During the growing season, trees in the greenhouse were fertilized (1.75 g of 20N-8.8P-16.6K w/w/w per tree) on a weekly basis. Trees were grown for one full season and again maintained over winter in the greenhouse as described above.

In the greenhouse during June 2010 growth was measured, including height, diameter above and below the graft, number of nodes on the main stem from apex to graft union, number and length per tree of individual short (<3cm) and long (>3cm) branches, and dry weights of dissected trees (stems and leaves, root, and rootstock shank). The rootstock shank was the stem component of the rootstock to which scion buds were grafted.

Xylem Exudate and Tree Harvest

After 1 month of growth in 2010 five trees of each scion/rootstock combination were evaluated for HC and for ABA concentration in xylem exudate of 'Fuji' grafted to Geneva rootstocks. Roots were well watered the evening prior to collecting exudate and predawn leaf water potential (ψ_w) of two distal leaves was measured (Soil Moisture Equipment Corp., Santa Barbara, CA, USA). Trees were placed in root pressure chambers, pruned to 1 m above the graft union and 3 cm of green bark (assumed to include the phloem) was stripped. In general, trees began to produce xylem exudate from tree cuts when root pressure was 0.34 MPa. Xylem exudate was collected, the volume and collection time were recorded, and the exudate from each tree was quickly frozen and lyophilized (Tworkoski and Fazio, 2011). Hydraulic conductivity was calculated as:

$$\text{HC} = \text{xylem exudate (mL)/leaf } \psi_w \text{ (MPa)} - \text{soil } \psi_w \text{ (MPa)/hr/trunk length (cm) or trunk cross-sectional area (mm}^2\text{)}.$$

After collecting exudates, plant parts were dried at 80°C for 7 days and dry weights were measured of all shoots above the graft (stem and leaf), the rootstock shank below the graft, and roots.

Hormone Analysis

Abscisic acid was measured in xylem exudates of 'Fuji' on Geneva rootstocks using methods described previously (Tworkoski and Fazio 2011; Tworkoski and Miller 2007).

Experimental Design

The experimental design was completely randomized. There were five reps for greenhouse growth measurements in Oct. 2010 of scions on Malling and Geneva rootstock. Rootstock effects on growth, HC, and ABA in xylem were analyzed by SAS Proc GLM followed by Duncan's New Multiple Range Test.

Scion, rootstock, and their interaction were the main effects in the analysis. Relationships among continuous variables were tested by Proc Corr and Proc Reg in SAS. All statistical tests were considered significant if the $P > F$ was at the 0.05 level or lower (SAS system for Windows. Release 9.1. SAS Institute Inc., Cary, NC, USA).

RESULTS

Height and Diameter

Scions were consistently tallest on rootstocks G.935 and G.41 and were shortest on M.27 (Table 1). The other rootstocks provided intermediate height control and generally did not differ very much from each other (Table 1). However, trees on Malling rootstocks were numerically shorter than trees on Geneva rootstocks. Taller trees had more long and short branches (Table 1). Diameter growth of scion generally followed patterns found with height (Table 1). Malling selections (SM.9 and SM.27) that were used as scions tended to be smaller than other scions. Only SM.7 was as tall as or taller than 'Fuji' and 'Gala'. Analysis of height and diameter using weight of the rootstock shank as a covariate did not alter results.

TABLE 1 Rootstock Effects on Scion Height, Diameter above the Graft Union, and Branching in Apple Trees after One Growing Season in the Greenhouse

	Scion height[y] (cm)					Scion diameter (mm)	Branches (no.)	
Rootstock[z]	Fuji	Gala	SM.7	SM.9	SM.27		Long[x]	Short
G.935	197a[w] BC[v]	206a AB	231a A	174a CD	150a D	16.5b	6.3a	4.8a
G.5087	152b B	Miss	179bc A	121b C	133b BC	12.3d	1.0bc	2.0bc
G.41	195a B	196a B	234a A	134b C	134b C	18.5a	1.9b	3.1b
G.11	152b B	129b C	185b A	102c D	131b BC	14.5c	2.0b	3.1b
M.7	150b A	130b B	163bc A	99c D	112c C	11.3de	0.6bc	1.6cd
M.9	143b AB	128b B	151c A	103c C	98c C	11.8de	0.5c	1.0cd
M.27	102c A	95c A	113d A	74d B	90c A	10.8e	0.1c	0.3d

[z]Rootstock prefixes 'G' and 'M' designate Geneva and Malling, respectively. Scion prefixes 'SM' designate buds from Malling rootstocks were used as scion.
[y]Scion heights for each scion-rootstock combination are presented because there was a scion-by-rootstock interaction. The main effects of rootstock only are provided for diameter and long and short branches as there were no interactions.
[x]Long branches were >3 cm and short branches were <3 cm.
[w]Comparisons for rootstock effects are made within a column and means followed by the same lower case letter do not differ at the 0.05 level of significance.
[v]Comparisons for scion effects are made within a row and means followed by the same upper case letter do not differ at the 0.05 level of significance.

HC and ABA

Hydraulic conductivity reflects the capacity for water movement within the tree. We measured the volume of water movement over stem length and cross-sectional area and normalized for time and for the pressure differential between root and leaf (Table 2). In general, the tallest trees (G.935 and G.41) had the highest HC per unit length, and height was correlated with HC ($r = 0.49$ Pearson correlation coefficient, $P > F = 0.05$). Rootstock M.27 supported the smallest trees and also the lowest HC. Xylem exudate from more vigorous rootstocks (G.41 and G.935) contained lower ABA concentrations than from the more dwarfing rootstocks (G.5087 and G.11) (Fig. 1).

TABLE 2 Rootstock and Scion Effects on Hydraulic Conductivity (HC) in Apple Trees after One Growing Season in the Greenhouse

	Rootstock HC[y]			Scion HC	
Rootstock[z]	(mL/cm stem/hr/MPa)	(mL/mm^2 stem/hr/MPa)	Scion	(mL/cm stem/hr/MPa)	(mL/mm^2 stem/hr/MPa)
G.935	0.96a[x]	1.45b	Fuji	0.48cd	0.98bc
G.5087	0.51b	0.99cd	Gala	0.73a	1.39ab
G.41	0.99a	1.98a	SM.7	0.54bc	0.98bc
G.11	0.60b	1.35bc	SM.9	0.68ab	1.68a
M.7	0.33c	0.81de	SM.27	0.31d	0.67c
M.9	0.28cd	0.83de			
M.27	0.14d	0.48e			

[z]Rootstock prefixes ‘G’ and ‘M’ designate Geneva and Malling, respectively. Scion prefixes ‘SM’ designate buds from Malling rootstocks were used as scion.
[y]The main effects for rootstock and scion are presented because there were no scion-by-rootstock interactions.
[x]Comparisons for rootstock and scion effects are made within a column and means followed by the same letter do not differ at the 0.05 level of significance.

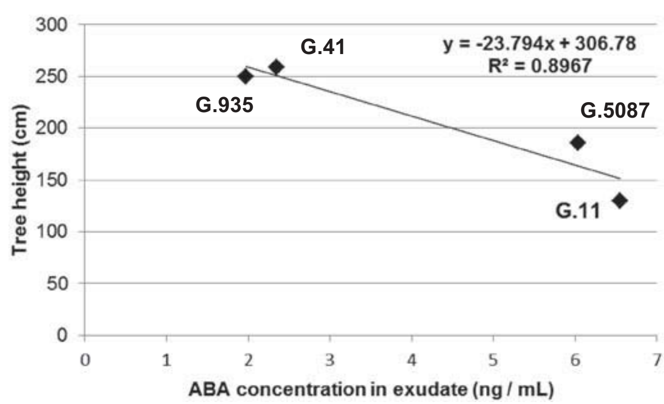

FIGURE 1 Relationship between tree height and abscisic acid (ABA) in xylem exudate of Fuji on four Geneva rootstocks.

Weight

Rootstock significantly affected dry weights and dry weight distribution between scion, rootstock shank, and root (Tables 3 and 4). Scion weight, as with height, was greatest in trees grafted to G.935 and G.41 (Table 3). Dry weight distribution to roots and rootstocks were generally greatest in

TABLE 3 Rootstock Effects on Tree Weight in Apple Trees after One Growing Season in the Greenhouse

	Scion wt (g)							
Rootstock[z]	Fuji[x]	Gala	SM.7	SM.9	SM.27	Root wt[y] (g)	Rootstock shank wt (g)	Total wt (g)
G.935	92.9a[w]	106.2a	107.4a	61.5a	64.8a	20.0a	27.0b	136a
G.5087	44.2b	Miss	64.9c	40.1bc	52.5b	12.6b	12.2c	76c
G.41	83.5a	82.7b	92.7b	48.9ab	49.8b	19.2a	33.3a	125b
G.11	48.9b	43.5c	57.2c	30.4cd	39.3c	13.0b	21.8c	79c
M.7	37.5bc	34.0c	38.5d	23.0de	30.1cd	11.5b	13.9c	57d
M.9	38.2bc	36.6c	34.7d	24.4de	30.2cd	9.2c	11.9c	56d
M.27	18.2c	14.2d	17.2e	11.5e	20.7d	8.9c	11.3c	37e

[z]Rootstock prefixes 'G' and 'M' designate Geneva and Malling, respectively. Scion prefixes 'SM' designate buds from Malling rootstocks were used as scion.
[y]Main effects are presented only for root weight and rootstock weights because no scion-by-rootstock interactions were found.
[x]Scion weights for each scion are presented because there was a scion-by-rootstock interaction.
[w]Comparisons for rootstock effects are made within a column and means followed by the same letter do not differ at the 0.05 level of significance.

TABLE 4 Rootstock Effects on Dry Weight Distribution in Apple Trees after One Growing Season in the Greenhouse

	Scion wt[z] (% of total weight)							
Rootstock[y]	Fuji	Gala	SM.7	SM.9	SM.27	Root wt[x] (% of total weight)	Rootstock shank wt (% of total weight)	R/S dw ratio
G.935	66a[w]	64a	68ab	56ab	61b	14d	19d	0.25c
G.5087	61ab	Miss	69a	61a	70a	16cd	16e	0.29c
G.41	59ab	59ab	63abc	46abc	52c	15cd	27b	0.29c
G.11	56bc	55b	61bc	42cd	58bc	16cd	27b	0.32bc
M.7	55bc	55b	60c	46bc	57bc	19b	23c	0.40b
M.9	61ab	61ab	60c	53ab	62b	17bc	22c	0.27c
M.27	44d	40c	42d	35d	55bc	23a	30a	0.67a

[z]Scion weight distribution for each scion are presented because there was a scion-by-rootstock interaction.
[y]Rootstock prefixes 'G' and 'M' designate Geneva and Malling, respectively. Scion prefixes 'SM' designate buds from Malling rootstocks were used as scion.
[x]Main effects are presented only for root weight and rootstock weight distribution because no scion-by-rootstock interactions were found.
[w]Comparisons for rootstock effects are made within a column and means followed by the same letter do not differ at the 0.05 level of significance.

M.27 rootstocks (23 and 30%, respectively) (Table 4). Dry weight distribution to scion was usually least in M.27 resulting in the greatest R/S ratio (Table 4).

DISCUSSION

New rootstocks are needed for size management of apple trees under a variety of environmental stresses including dehydration. In the current research our goal was to confirm the size-controlling effects of four Geneva rootstocks and to determine HC in these rootstocks and ABA in 'Fuji' grafted to these rootstocks with an aim to future use of these or similar rootstocks in dry environments. Three Malling rootstocks were included in this work to facilitate comparisons of Geneva rootstocks with long-studied Malling rootstocks. Effects of scion on roots and rootstock shank are finally considered.

Based on previous work, the heights and diameters of scions were expected to be similar for M.9 and the four Geneva rootstocks. Scions generally were taller on Geneva than Malling rootstocks (Table 1). The possibility of rootstock size affecting scion growth was eliminated by using rootstock shank weight as a covariate in the GLM. Hydraulic conductivity, however, was greater in the scions on Geneva than Malling rootstock (Table 2).

In this study, the same three Malling selections were used as both rootstock and scion. The HC was consistently greater when Malling selections were used as scion rather than rootstock (Table 2). This suggests that a factor associated with the rootstock, such as the root or graft union, limits HC. Previously, when the Malling selections were grafted to their own rootstock, no differences in height or HC were found (Tworkoski, manuscript under review). In that work HC was 0.31 mL/cm stem/hr/MPa for both ungrafted and grafted selections grown on their own root. The lack of a graft effect from that previous study and the HC results from the current one suggests that some manifestation of inadequate genetic graft affinity or a difference in specific conductivity of a growth factor is associated with the dwarfing mechanism. The graft union has been identified to be a possible site where functional xylem may be affected by modified cell diameters or cell disorganization between genetically different scions and rootstocks (Atkinson et al., 2003; Tworkoski and Fazio, 2011). In previous works root morphology of Geneva rootstocks differed markedly from the dwarfing Malling rootstocks in the level of root branching, new roots produced, and root half-life (Atucha et al., 2013; Emmet et al., 2014). Such morphological differences may in turn affect HC, generation of root hormones, or nutrient transport and explain the differences in growth.

Xylem exudate contained less ABA from the more vigorous rootstocks (G.41 and G.935) than from the more dwarfing rootstocks (G.5087 and G.11) (Fig. 1). This agrees with previous research where ABA was up to 10 times greater in xylem flow of 'Fuji' scion on dwarfing than vigorous size-controlling rootstocks that were grown for one growing season in a greenhouse (Tworkoski and Fazio, 2011). In that study, seasonal height growth of 'Fuji' scion was inversely proportional to ABA in xylem exudates of size-controlling rootstocks: 128 cm height with 3.1 ng ABA/mL and 98 cm height with 32.6 ng ABA/mL with M.7 and M.27, respectively. Elevated abscisic acid (ABA) from roots may play a role in the dwarfing capacity of apple rootstocks (Kamboj et al., 1999; Kamboj and Quinlan, 1998; Tworkoski and Miller, 2007; Yadava and Dayton, 1972). Also, ABA has been shown to be a root-produced message that regulates shoot growth and development in drying soils (Davies et al., 2005).

In addition to size-control, apple rootstocks may improve tree tolerance to drought and ability to absorb and translocate minerals from the soil to scion (Fazio et al., 2013).

Vigorous rootstocks may avoid drought because of large root systems and high hydraulic conductivity and fewer xylem embolisms (Atkinson et al., 1999; Bauerle et al., 2011). Conversely, a smaller tree on dwarfing rootstock, such as M.9 and M.27 in the current experiment, may be able to better tolerate drought if water requirements are less. Atkinson et al. (2000) found that fewer leaves and reduced leaf conductance on trees on dwarfing rootstocks (M.9) show less drought stress compared with vigorous rootstocks (MM.111). Fernandez et al. (1997) found elevated ABA in apple leaves on M.9 EMLA in comparison to MM.111. However, an associated decline in root dry weight may make trees on M.9 EMLA more susceptible to drought. Experimental evidence from the field is needed to clarify the relationship between size control and drought tolerance of apple rootstocks.

Scion weight, as with height, was greatest in trees grafted to G.935 and G.41 (Table 3). These rootstocks had the greatest root and rootstock shank weight. Absolute and relative root weight may significantly affect rootstock anchorage and the ability to absorb nutrients and water. Rootstock M.27 had the least root weight (8.9 g) but this comprised significantly more dry weight distribution (23% of the total dry weight) than other rootstocks (Tables 3 and 4). Lower weights of roots likely reflect smaller root systems and smaller soil volume exploited by the root system. Susceptibility to water deficits may result under drying conditions. It is also possible that trees with relatively high dry weight distribution to the root system may reflect a root-to-shoot balance that improves drought tolerance.

Scion affected rootstock characteristics. The scions 'Gala', SM.9, and SM.27 reduced rootstock diameter of G.41 and G.11 compared with 'Fuji' scion (Table 5). This was not surprising, since 'Fuji' was a robust scion that could likely provide more abundant resources, such as carbohydrates, than SM.27 or SM.9. This implies that some rootstocks are affected differently by specific scions and, in turn, rootstocks may affect scion. The significance of such a feedback loop is unknown. In some cases the diameter of rootstocks were not affected (e.g., M.27, G.5087, G.935) (Table 5).

TABLE 5 Apple Tree Rootstock Diameters below the Graft Union after One Growing Season in the Greenhouse

	Rootstock diameters associated with scions[y] (mm)				
Rootstock[z]	Fuji	Gala	SM.7	SM.9	SM.27
G.935	11.7A[x]	9.8A	10.8A	9.6A	9.8A
G.5087	9.6A	Miss	10.0A	7.9A	8.5A
G.41	12.3A	9.5BC	10.5AB	9.8BC	8.5C
G.11	10.5A	8.1C	9.4B	8.6BC	7.8C
M.7	9.4A	7.8B	8.1AB	8.3AB	7.9B
M.9	9.8A	8.2B	7.2B	8.0B	8.7AB
M.27	6.9A	6.3A	7.1A	6.5A	6.2A

[z]Rootstock prefixes ‘G’ and ‘M’ designate Geneva and Malling, respectively. Scion prefixes ‘SM’ designate buds from Malling rootstocks were used as scion.
[y]Rootstock diameters for each scion are presented because there was a scion-by-rootstock interaction.
[x]Comparisons for scion effects on rootstock diameter are made within a row and means followed by the same capital letter do not differ at the 0.05 level of significance.

TABLE 6 Effect of Scion on Rootstock Shank and Root Weight One Growing Season in the Greenhouse

Scion	G.935	G.5087	G.41	G.11	M.7	M.9	M.27
Rootstock shank weight[z] (g)							
Fuji	26.9c[y]	12.6b	34.6c	21.6d	17.1a	13.9a	12.4a
Gala	34.4a	Miss	35.6b	22.3c	14.3b	12.5c	10.8c
SM.7	27.5b	14.3a	36.4a	25.0b	13.8d	13.2b	12.3b
SM.9	23.4e	10.2d	32.7d	26.5a	14.0c	12.1d	12.3b
SM.27	24.1d	10.6c	32.2e	16.8e	11.3e	10.4e	9.3d
Root weight (g)							
Fuji	18.4a	14.8a	21.6a	15.9a	12.4a	9.9a	11.0a
Gala	22.6a	Miss	21.2a	13.3a	13.0a	10.7a	9.6a
SM.7	22.4a	14.5a	17.2ab	11.4a	11.2a	9.8a	9.7a
SM.9	24.8a	15.7a	23.5a	15.9a	12.3a	9.2ab	8.4a
SM.27	17.2a	11.4a	13.1b	11.2a	10.6a	7.3b	9.0a

[z]Rootstock shanks (stem component of the rootstock) and root weights for each scion are presented because there was a scion-by-rootstock interaction. Rootstock prefixes ‘G’ and ‘M’ designate Geneva and Malling, respectively. Scion prefixes ‘SM’ designate buds from Malling rootstocks were used as scion.
[y]Comparisons for scion effects on rootstock shank and root weights are made within a column and means followed by the same letter do not differ at the 0.05 level of significance.

Scion had little effect on root weight (Table 6). Only SM.27 reduced root weight and that was with rootstocks G.11 and M.9. However, rootstock shank dry weight was always least with scions SM.9 or SM.27. It is intuitively appealing that these scions that were grafted onto the most dwarfing rootstocks nearly always resulted in the lowest scion and total dry weight. Relatively few studies have considered how the rootstock interacts with and controls growth of the scion. For example, global gene expression is modified in the same scion variety depending on what rootstock it has been grafted onto (Jensen et al., 2003, 2011). But, as demonstrated here the scion may affect the rootstock. It has been demonstrated that dwarfing rootstocks on their own roots do not produce vigorous shoots (Fazio et al., 2014). This experiment indicates that the shoot of some dwarfing rootstocks are inherently slow growers, which is also in concordance with the interstem observations made by Carlson and Oh (1975). This brings an interesting question of whether a feedback loop between scion and rootstock may be part of the dwarfing process. In addition, rootstock-related size-control processes may entail age and stage of development of the tree, the ability to induce early bearing in the scion, and therefore partitioning photosynthates to fruit production instead of shoot, as well as weather, soil, and genetic control of scion growth.

We observed structural weakness of the graft union between G.935 and G.41 and the scions in this experiment. Occasionally scions would separate from these rootstocks during normal handling. Anecdotally, rootstock shanks of G.935 and G.41 felt brittle when cut. This may be attributed to hormonal differences, such as auxin accumulation above graft unions and alteration of xylem anatomy at the graft union (Aloni, 2007; Tworkoski and Fazio, 2011; Tworkoski, unpublished data).

The experimental approach of studying scion-rootstock interactions in a greenhouse has obvious limitations. One year in a pot does not reflect the effects of long-term tree development and environment that would affect scion and root growth. However, control and homogeneity of the environment can, arguably, allow evaluation of the growth potential of the trees. In the case of this experiment, tree root systems were substantial but not pot bound.

In the future, high demand for water for consumption, recreation, industry, and agriculture will almost certainly limit water availability for irrigation of fruit trees. New tools will be needed for sustainable fruit tree production, especially with concerns about climate change and the potential impact on precipitation. These tools may include trees that use water efficiently and are drought tolerant. Knowledge of mechanisms that impart stress tolerance in rootstocks is not clear but insights of mechanisms of size control can provide genetic-based approaches to addressing such problems.

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