

Water Stress Affects Rhizosphere Respiration Rates and Root Morphology of Young ‘Mutsu’ Apple Trees on M.9 and MM.111 Rootstocks

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ABSTRACT. One-year-old potted ‘Mutsu’ apple [*Malus sylvestris* (L.) Mill. var. *domestica* (Borkh.) Mansf.] trees on scion invigorating Malling-Merton 111 (MM.111) and scion dwarfing Malling 9 (M.9) rootstocks were grown outdoors in containers under three levels of water availability (irrigated at –20, –80, and –200 kPa) to investigate the effects of soil water availability on combined soil/root (rhizosphere) respiration rates, and developmental morphology of root systems. Rhizosphere respiration was measured with a portable infrared gas analyzer, and root biomass was estimated by electrical capacitance. These nondestructive measurements were compared with final root dry weights of harvested trees, to determine their reliability for estimating relative differences in root biomass. Water stress reduced final biomass similarly for both rootstocks, but the relative reduction in shoot growth was greater for MM.111. Root to shoot ratios were higher and average specific root respiration was lower for M.9 rootstock compared with MM.111. M.9 appeared to be more tolerant of water stress than MM.111, due to reduced canopy transpiration relative to root system mass. Water stress increased root to shoot ratios, specific root length, and the carbohydrate costs of root maintenance as indicated by specific respiration rates. Root dry weight (DW) was better correlated to rhizosphere respiration than to root electric capacitance. The observed r^2 values between root capacitance and root DW were as high as 0.73, but capacitance measurements were also influenced by soil water content and rootstock type. Electrical capacitance estimated total root biomass more accurately for M.9 than for MM.111.

Modern apple (*Malus sylvestris* var. *domestica*) production relies upon clonal rootstocks to control tree size and optimize root responses to adverse soil conditions. Soil water availability greatly affects the growth and yield of fruit trees. Apple rootstocks can influence midday leaf water potential and root hydraulic conductivity (Giulivo et al., 1985; Olien and Lakso, 1986), but data on the relative tolerance and physiological responses of different rootstock genotypes to water stress are contradictory. Landsberg and Jones (1981) summarized evidence that dwarfing rootstocks, especially Malling 9 (M.9), are more tolerant to water stress than vigorous ones; but Ferree and Carlson (1987) ranked M.9 as less tolerant of water stress than Malling Merton 111 (MM.111). Fernandez et al. (1997a, 1997b) reported that shoot growth, net photosynthesis and water relations of ‘Gala’ apple trees were less affected by soil water deficits on M.9 than on MM.111 rootstocks.

Rooting depth, root density, specific root length, and changes in root to shoot ratios may be crucial in determining the relative tolerance of different rootstocks to water stress. Coker (1958) reported that rooting depth was controlled mostly by soil type and profile; only in deep and permeable soils was there an effect of rootstock genotype. Rooting density or depth may be higher for invigorating rootstocks (Rogers, 1939), but root to shoot ratios and morphology of the root system could be as important as the actual soil volume exploited by roots.

Water stress reportedly affects the carbon balance of fruit trees

by reducing net photosynthesis (Lakso, 1985), but its apparent effects on root and shoot respiration have been contradictory (Landsberg and Jones, 1981). Dark respiration reportedly increased or decreased slightly under water deficits, depending on the severity of stress (Jones and Fanjul, 1983). Amthor (1989) suggested that decreased photosynthetic rates and increased accumulation of organic solutes in water stressed plant tissues should increase respiratory activity. Nicolas et al. (1985) found that specific root respiration of herbaceous plants decreased under water stress, becoming more efficient due to reduced involvement of the alternative pathway. Effects of water deficits on specific root respiration of apple trees have apparently not been evaluated.

Development of nondestructive methods to provide information about rootstock form and function would improve understanding of root responses to environmental factors. Electrical capacitance and oxidative respiration of root systems have reportedly correlated well with root dry weight (DW) and root density per unit soil volume (Ben-Asher et al., 1994; Dalton, 1995). Our previous work with apple trees in sand culture showed that both methods were significantly, but loosely, correlated with different root parameters over a narrow range of root DWs (Psarras, 1999). Therefore, the objectives of the present study were to 1) investigate carbon partitioning or growth differences in early development of M.9 and MM.111 rootstocks in relation to water deficits, 2) study the effects of water stress on absolute and specific respiration rates of these root systems, and 3) evaluate root electrical capacitance and rhizosphere respiration measurements as nondestructive methods for estimating the size and function of apple-tree root systems.

Materials and Methods

PLANT MATERIAL. Thirty 1-year-old ‘Mutsu’ apple trees grafted on M.9 and MM.111 rootstocks were planted 30 Apr. 1997 in 28-L pots with a steam pasteurized medium of 1 field soil : 1 peat (v/

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v). To improve uniformity of root systems before planting, the root system of each tree was pruned radially to 20 cm from the rootstock shank (i.e., the central axis of each root system); the single shoot axis left to grow was also headed back to a lateral bud at 60 cm from the base of the rootstock shank. Trunk diameter at 20 and 30 cm height, fresh weight (FW) of each tree after pruning, root volume (by water displacement), and fresh and DWs of the pruned shoots were also measured.

GROWING ENVIRONMENT. Trees were grown in containers in an outdoor nursery near Ithaca, N.Y., Before planting, 20 g of 14N–4.2P–11.6K Osmocote fertilizer (Scotts Co., Columbus, Ohio) was uniformly mixed into the growing medium of each pot, and pots were surrounded by wood chips to keep soil temperatures comparable to orchard conditions. Rims of the pots were covered (but not sealed) with a conical silver tarp to exclude rainfall and reduce direct solar heating. An 0.8-mm diameter trickle tube was used for irrigating each tree. Two weeks after budbreak, all but six selected lateral shoots were removed from each tree.

TREATMENTS AND EXPERIMENTAL DESIGN. A randomized complete block design with five replications was used, with shoot vigor 5 weeks after planting as a blocking factor. Three levels of soil water potential were randomly assigned to trees within each block: control (CTL) trees irrigated whenever soil water potential was less than -20 kPa, low stress (LS) trees irrigated whenever soil water potential was less than -80 kPa, and high stress (HS) trees irrigated whenever soil water potential was less than -200 kPa.

Each block included one tree for each rootstock–irrigation treatment combination (i.e., six trees per block). Treatments were initiated 10 June, but since leaf area and evapotranspiration were limited, it took ≈ 15 d for the LS trees to attain the -80 kPa level, and ≈ 1 month for soil water potential of HS trees to reach the -200 kPa set point. Soil water potential was measured with tensiometers for the CTL and LS treatments, while for the HS treatment, moisture sensors (Watermark; Irrrometer Company, Inc., Riverside, Calif.) were used. All sensors were inserted to 15 cm in the container medium. Soil water potential was recorded every 3 or 4 d for all trees, and more often for CTL trees during the hotter part of the growing season. Whenever soil water potential dropped below the defined limit for each treatment, the trees were irrigated to the saturation point of 0 kPa.

Predawn leaf–stem water potential measurements were taken twice during the growing season. Two leaves per tree were enclosed in aluminum foil and placed in a plastic bag the previous evening; and early the following morning leaf water potential was measured with a pressure bomb.

GROWTH, RESPIRATION, AND ELECTRICAL CAPACITANCE MEASUREMENTS. Scion shoot growth was recorded weekly during the growing season, while measurements of soil and root respiration and root electrical capacitance were used as estimates of root growth. Soil and root respiration was measured through 10-cm-wide polyvinyl chloride collars permanently inserted in each pot to a depth of 6 cm, using a soil respiration chamber (LI-6000-09; LI-COR Inc., Lincoln, Nebr.) connected to an infrared gas analyzer (LI-6200). As controls for measuring respiration in soil without apple roots, four similar pots filled with the pasteurized growing medium but without trees, and irrigated within the CTL soil water potential range were used.

Electrical capacitance was measured by connecting the negative lead of a B&K Precision 810A capacitance meter (B&K Maxtec Intl. Corp., Chicago, Ill.) to a stainless steel needle inserted in each trunk 35 cm above the lower end of the rootstock,

and the positive lead to a stainless steel rod inserted at a 45° angle, 25 cm deep in the soil, 15 cm from the rootstock top (Psarras, 1999).

At the onset of leaf abscission in mid-October 1997, trees were harvested, total leaf area was determined with an AgVision pseudocolor image analysis system (Decagon Devices Inc., Pullman, Wash.), and shoot, scion-wood, and leaf DWs were measured. The roots (still attached to each rootstock) were then stored at 2° C in perforated plastic bags, in a barrel of 20% methanol solution. Due to time constraints, we only completed digital image analyses of root systems for three of the five replicates of each treatment combination. For image analysis, each root system was spread flat, and two 5 cm wide transect subsamples comprising about 10% of the total root system were excised 10 cm from both sides of the rootstock shank. Samples were dyed in a 0.5% solution of methylene blue, spread in a thin layer of water in 20×25 cm transparent plastic trays, and scanned with an HP ScanJet IIc desktop scanner (Hewlett-Packard Co., Palo Alto, Calif.) at a resolution of 300 dots per inch (dpi), against a white background. Images were analyzed with NIH Image 1.61, public-domain image processing and analysis software developed by the U.S. National Institute of Health, Bethesda, Md. An eight-bit monochrome scanned image (256 gray levels) of each root system was obtained, then converted to a binary (black and white) image with a minimum root diameter resolution of $42.5 \mu\text{m}$, to approximate root surface area. To estimate root length, binary images were converted to a 1-pixel wide image using the 'Skeletonize' function of NIH Image. A Euclidean distance map of each binary root image was then constructed, and each skeletonized image was inverted and subtracted from its Euclidean image. The resulting skeleton image was transformed mathematically to represent total root length and surface area within eight root-diameter classes. The resulting root-length values were validated by regression with similarly scanned images of bent metal wires of known total lengths in various positions ($r^2 = 0.999$). Root scanning and image processing methods used have been described previously (Psarras, 1999).

DWs of lateral roots and rootstock shank were measured after the scanning process was completed. Specific root length (meter of root length per gram of root DW) was calculated by dividing total root length by the DW of sampled roots. The average specific respiration rate was calculated as $R_{sp} = (RA/W_R) \times 1000$, where R_{sp} is the average specific root CO_2 respiration rate in $\text{nmol} \cdot \text{g}^{-1} \cdot \text{s}^{-1}$, R is the seasonal average CO_2 respiration rate in $\mu\text{mol} \cdot \text{m}^{-2}$ soil surface per s, where A is the total soil surface area per pot (in this case $A = 0.0856 \text{ m}^2$), and W_R is the final root DW in grams.

Statistical models used for data analysis included linear and polynomial regressions for correlations of root and shoot DW with soil water potential and rhizosphere respiration rates, and ANOVAs with block, rootstock genotype, watering treatment, and interaction between genotype and watering treatment as factors for all variables, and rootstock trunk volume at planting time as a covariate. When measured comparably over time, variables were treated as repeated measurements using the statistical software SuperAnova (Abacus Concepts, Inc., Berkeley, Calif.).

Results

SOIL AND LEAF WATER POTENTIAL. Water potential for the CTL trees occasionally fell below the -20 kPa set point during hot days (Fig. 1), because these pots contained the largest plants with the

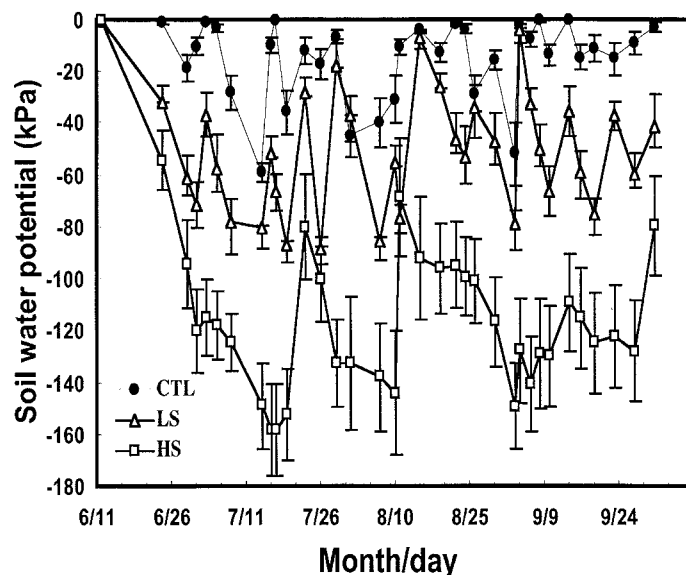


Fig. 1. Soil water potential at a 15 cm soil depth for fully watered control (CTL), low stress (LS = irrigated at -80 kPa), and high stress (HS = irrigated at -200 kPa) treatments applied to 'Mutsu' apple trees grown in 28-L pots during 1997. Each symbol represents the mean \pm SE for 10 replications.

greatest rates of respiration. However, there was a clear separation in soil water potential between treatments for most of the growing season. Leaf water potential was closely correlated with soil water potential of individual trees (data not presented).

ABOVEGROUND GROWTH. Shoot length of CTL trees was significantly higher for the more vigorous MM.111 rootstock (Fig. 2). Shoot biomass was reduced by water stress for both rootstocks, as were stem and leaf DWs (Table 1) and cumulative total leaf area; specific leaf area was greater under high water stress (Table 2).

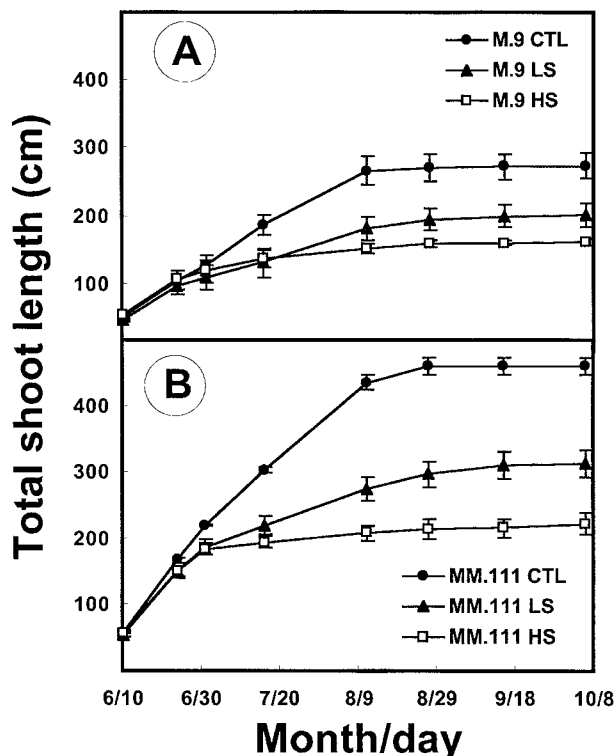


Fig. 2. Total shoot growth over time for 1-year-old 'Mutsu' apple trees on (A) M.9 and (B) MM.111 rootstocks, under three levels of irrigation: CTL = control, fully watered; LS = low stress, irrigated at -80 kPa, and HS = high stress, irrigated at -200 kPa. Each symbol represents the mean \pm SE of five trees.

Shoot DW was related to average soil water potential during the growing season (Fig. 3). Compared to CTL trees, shoot growth of M.9 was substantially less affected than MM.111 was

Table 1. Analysis of variance for effects of rootstock genotype and watering treatment on final dry weight (DW) means of different tissues of 1-year-old 'Mutsu' apple trees on M.9 and MM.111 clonal rootstocks.

Factor	DW (g)				
	Leaf	Current year extension shoot	Main stem	Rootstock shank	Lateral root
Rootstock					
M.9	44.5 a ^z	35.8	69.1 a	79.3	39.8
MM.111	53.4 b	71.6	43.7 b	88.2	43.3
Watering treatment ^y					
CTL	74.9 a	94.2	78.9 a	111.3	66.4 a
LS	46.2 b	47.6	54.2 b	81.0	36.4 b
HS	25.8 c	19.3	36.1 c	59.0	21.8 c
Rootstock \times water stress					
M.9 CTL		56.4 b		99.7 b	
M.9 LS		36.4 c		77.9 c	
M.9 HS		14.7 d		60.5 d	
MM.111 CTL		132.1 a		122.9 a	
MM.111 LS		58.8 b		84.2 c	
MM.111 HS		23.8 d		57.4 d	
Rootstock	*	**	**	*	NS
Water stress	**	**	**	**	**
Rootstock \times water stress	NS	**	NS	*	NS

^zMeans followed by different letters are significantly different at $P \leq 0.05$ (Fisher's protected LSD test).

^yCTL = fully watered trees, LS = low stressed trees, watered at -80 kPa, HS = high stressed trees watered at -200 kPa.

NS, *, ** Factor effects or interactions that are nonsignificant or significant at $P \leq 0.05$ or 0.01, respectively.

Table 2. Analysis of variance for effects of rootstock genotype and watering treatment on leaf area, specific leaf area, and root to leaf and root to stem dry weight (DW) ratios of 1-year-old 'Mutsu' apple trees on M.9 and MM.111 rootstocks.

Factor	Leaf area (cm ²)	Specific leaf area (cm ² ·g ⁻¹)	Root to leaf DW ratio	Root to stem DW ratio
Rootstock				
M.9	2922	63.3	0.94	1.17 a ^z
MM.111	4155	64.7	0.81	0.72 b
Watering treatment ^y				
CTL	5564	53.2 c	0.91	0.83 b
LS	3157	64.7 b	0.84	0.82 b
HS	1894	74.0 a	0.87	1.20 a
Rootstock × water stress				
M.9 CTL	4499 b			
M.9 LS	2622 c			
M.9 HS	1645 d			
MM.111 CTL	6630 a			
MM.111 LS	3691 b			
MM.111 HS	2144 cd			
Rootstock	**	NS	NS	**
Water stress	**	*	NS	**
Rootstock × water stress	*	NS	NS	NS

^zMeans followed by different letters are significantly different at $P \leq 0.05$ (Fisher's protected LSD test).

^yCTL = fully watered trees, LS = low stressed trees, watered at -80 kPa, HS = high stressed trees watered at -200 kPa.

NS,*,**Factor effects or interactions that are nonsignificant or significant at $P \leq 0.05$ or 0.01 , respectively.

by low soil water potential (Fig. 3). The DWs of shoot and root tissue also reflected the effects of water stress on growth. We attributed the higher final shoot DW of M.9 to the fact that at

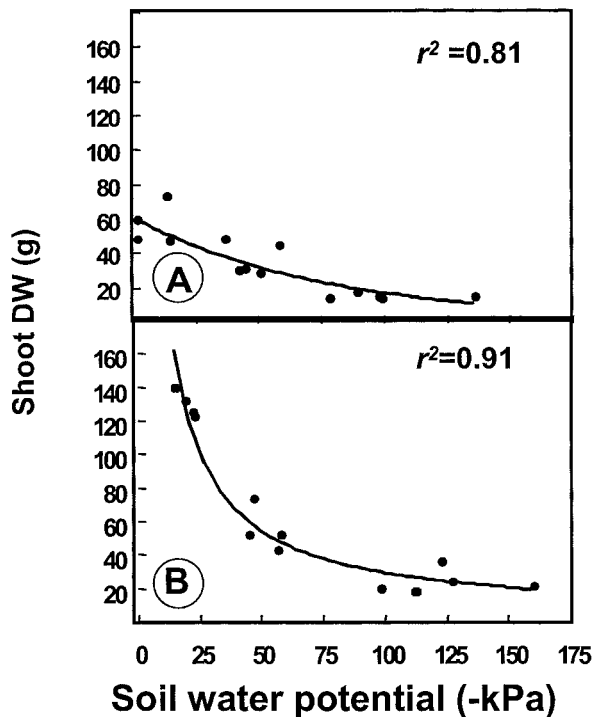


Fig. 3. Relationship between current-season's shoot dry weight (DW) of individual trees at the end of the experiment and average soil water potential over the growing period, for 1-year-old 'Mutsu' apple trees on (A) M.9 and (B) MM.111 rootstocks. Several data points were omitted in CTL and LS treatments due to questionable soil water potential values.

planting time, trees on M.9 had a greater initial mass of shoot tissue compared to trees on MM.111.

ROOT GROWTH. Despite its effect on above ground growth, rootstock genotype did not significantly affect root DW, which decreased substantially under water stress for both rootstocks (Table 1). The reduction of root DW was correlated with average soil water potential during the growing season, and was similar for both rootstocks (Fig. 4).

ROOT TO SHOOT GROWTH RATIOS. The root to stem DW ratios for M.9 were higher than for MM.111 in all watering treatments (Table 2). Root to stem DW ratios were similar in CTL and LS, and increased for both rootstocks in HS, while root to leaf DW ratios were equivalent in all watering treatments and both rootstocks (Table 2).

RHIZOSPHERE RESPIRATION. Respiration rates for both rootstocks began to differ among treatments in mid-June, increasing for CTL and LS trees, but remaining steady or decreasing for HS trees (Fig. 5). Trees on MM.111 had higher respiration rates than trees on M.9 in the CTL treatment, but rootstock respiration rates were similar in LS and HS treatments.

Rhizosphere respiration rates were weakly correlated with soil temperature (data not presented). Respiration and soil temperature both increased until mid July, but rhizosphere respiration then kept increasing despite a reduction in soil temperature. After August, soil and soil-plus-root respiration once again paralleled soil temperatures, although respiration rates were greater in soil with tree roots. Soil temperatures were often slightly higher in pots without trees, due to lack of canopy shade in those pots. Average specific root respiration rates were higher for MM.111 than M.9 under CTL and LS treatments, but similar for both rootstocks under HS, indicating that water stress increased the respiration per unit root DW (Table 3). Root biomass and respiration rates were closely correlated ($r^2 = 0.74$) for both rootstocks (Fig. 6).

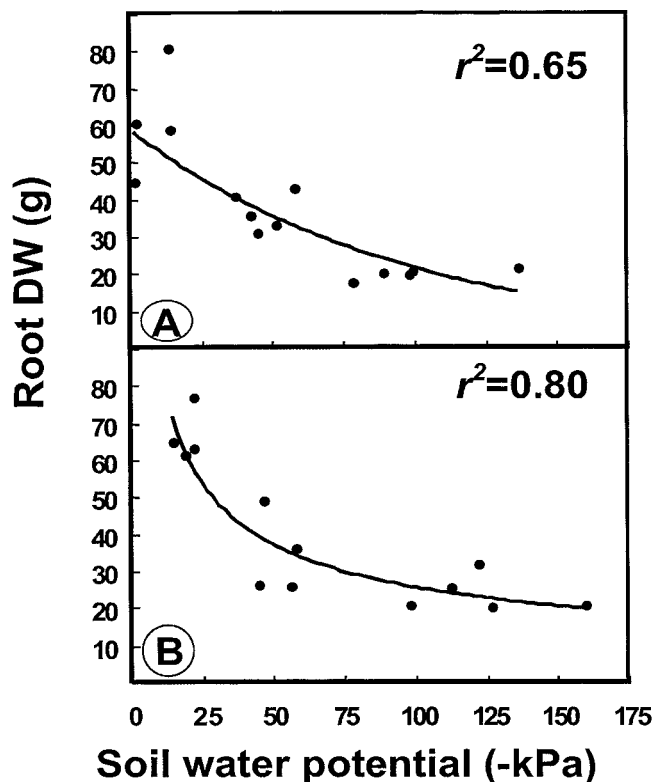


Fig. 4. Relationship between root dry weight (DW) of individual trees at the end of the experiment and average soil water potential over the growing period in 1-year-old Mutsu apple trees grown on (A) M.9 and (B) MM.111 rootstocks. Several data points were omitted in the CTL and LS treatments due to questionable soil water potential values.

ELECTRICAL CAPACITANCE. Electrical capacitance of M.9 root systems was greater than MM.111, despite the equivalent root biomass of these two genotypes (data not presented). After increasing during June, root capacitance declined during July for both rootstocks, except for M.9 in the CTL treatments. In a final measurement at the end of our experiment, with all leaves removed and the soil fully saturated, root capacitance and biomass were correlated for both rootstocks, but the relationship was stronger for M.9 ($r^2 = 0.73$) than MM.111 ($r^2 = 0.44$) (Fig. 7).

DIGITAL ROOT IMAGE ANALYSES. Root size distributions were similar for both genotypes, and $\approx 80\%$ of total root length was in the two smallest diameter classes from 0.042 to 0.38 mm (Fig. 8). Rootstock genotype and soil water treatments had no effect on most size categories, except that trees in HS treatments had more fine-feeder roots (0.042 to 0.212 mm diameter) than CTL trees, and a lower percentage of roots in other categories. This resulted in higher specific root length for HS trees, but rootstock genotype had no effect on specific root length (Table 3).

Discussion

PLANT GROWTH. Water stress reduced DWs of stems, leaves and roots for both rootstocks. The more vigorous MM.111 had greater stem and leaf DW, but not higher root DW compared to M.9 (Table 1). Other studies of young apple trees have also shown that despite its invigoration of scion growth, MM.111 did not have larger root DW than M.9, confirming that root to stem ratios may be higher on dwarf than semidwarf rootstocks under water stress (Atkinson et al., 1997). Genotypic differences in stem and leaf growth were most apparent under well watered conditions

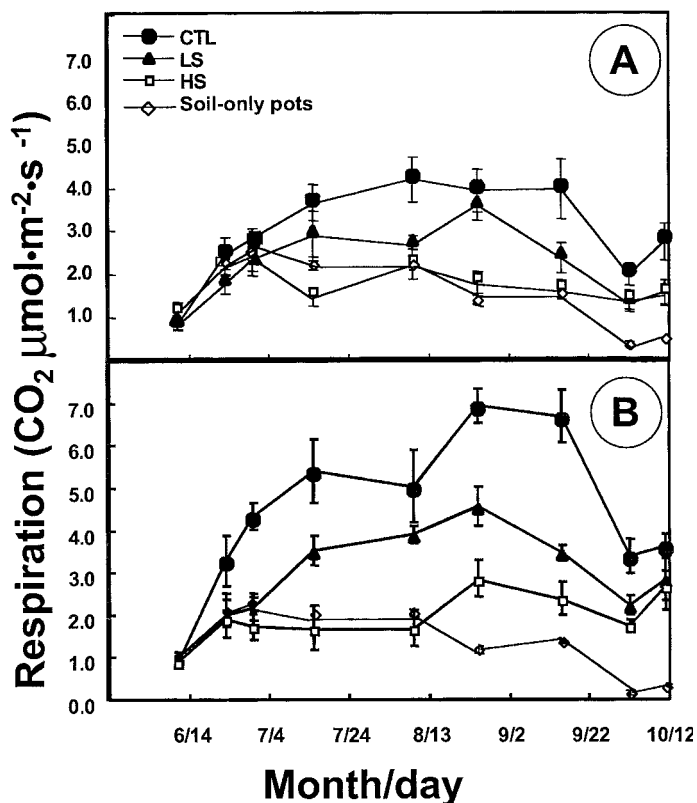


Fig. 5. Combined soil \pm root respiration rates in pots containing only a pasteurized soil: peat medium (soil-only pots), and pots containing 1-year-old 'Mutsu' apple trees on (A) M.9 or (B) MM.111 rootstocks. CTL = control, fully watered control; LS = low stress, irrigated at -80 kPa, and HS = high stress, irrigated at -200 kPa. Symbols represent means \pm SE of four replications.

Table 3. Analysis of variance for effects of rootstock genotype and watering treatment on specific root length, and specific soil and root respiration of 1-year-old 'Mutsu' apple trees on M.9 and MM.111 rootstocks.

Factor	Specific root length ($\text{m}\cdot\text{g}^{-1}$)	Avg specific respiration ($\text{CO}_2, \text{nmol}\cdot\text{g}^{-1}\cdot\text{s}^{-1}$)
Rootstock		
M.9	29.7	6.0 b ^z
MM.111	38.5	7.2 a
Watering treatment ^y		
CTL	28.3 b	5.2 b
LS	31.9 ab	6.7 a
HS	42.2 a	8.0 a
Rootstock	NS	*
Water stress	*	*
Rootstock \times water stress	NS	NS

^zMeans followed by different letters are significantly different at $P \leq 0.05$ (Fisher's protected LSD test).

^yCTL = fully watered trees, LS = low stressed trees, watered at -80 kPa, HS = high stressed trees watered at -200 kPa.

NS,*,**Factor effects or interactions that are nonsignificant or significant at $P \leq 0.05$ or 0.01, respectively.

(Table 1), while under water stress the potential for vigorous scion growth on MM.111 was suppressed (Fig. 3). Fernandez et al. (1997a) reported similar observations for young 'Gala' apple

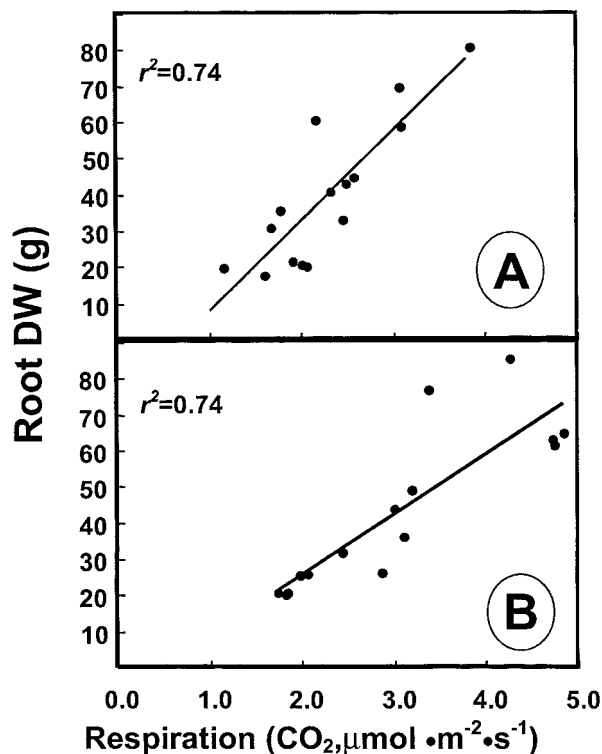


Fig 6. Relationship between final root dry weight (DW) and average rhizosphere respiration over the growing season for 1-year-old 'Mutsu' apple trees on (A) M.9 and (B) MM.111 rootstocks.

trees on M.9 and MM.111 rootstocks.

Landsberg and Jones (1981) reported that tolerance to water stress can be due to either avoidance or physiological adaptation. Limitation of scion growth by M.9 may reduce canopy transpiration relative to root water uptake, resulting in functional avoidance rather than physiological tolerance of water stress. This interpretation is supported by the study of Higgs and Jones (1990), where soil water depletion was generally related to scion-vigor limitation by rootstocks, and trees depleted soil water faster on MM.111 than on M.9. Research in Russia reviewed by Landsberg and Jones (1981) demonstrated better tree performance on dwarfing rootstocks, including M.9, under drought conditions. However, other studies have suggested that scion growth was less affected by water stress on MM.111 than on M.9 (Chandel and Chauhan, 1990; Ferree and Carlson, 1987).

Apart from differences in root to shoot DW ratios, specific root length (SRL) can also affect tree-soil water relations. Information about SRL of apple trees is limited and inconclusive. Atkinson et al. (1997) reported SRL values of 42 and 44 $\text{m} \cdot \text{g}^{-1}$ for M.9 and MM.111, respectively, but observed no differences that could be attributed to rootstock genotype or water stress for roots <2 mm in diameter, on apple trees in their first growing season after planting. In our study, SRL was greater under HS and smaller in CTL and LS treatments for both rootstocks, in comparison to values reported by Atkinson et al. (1997).

Higher SRL can represent either finer roots, or roots with lower tissue density (Eissenstat, 1991, 1992). In the present study, HS and LS trees had relatively more fine roots and fewer coarse roots than CTL trees (Fig. 8), and this may explain the greater SRL under HS (Table 3). Regardless of its underlying causes, higher SRL suggests lower carbohydrate costs for roots exploring a given soil volume, and may benefit trees under limited water supply (Eissenstat, 1991).

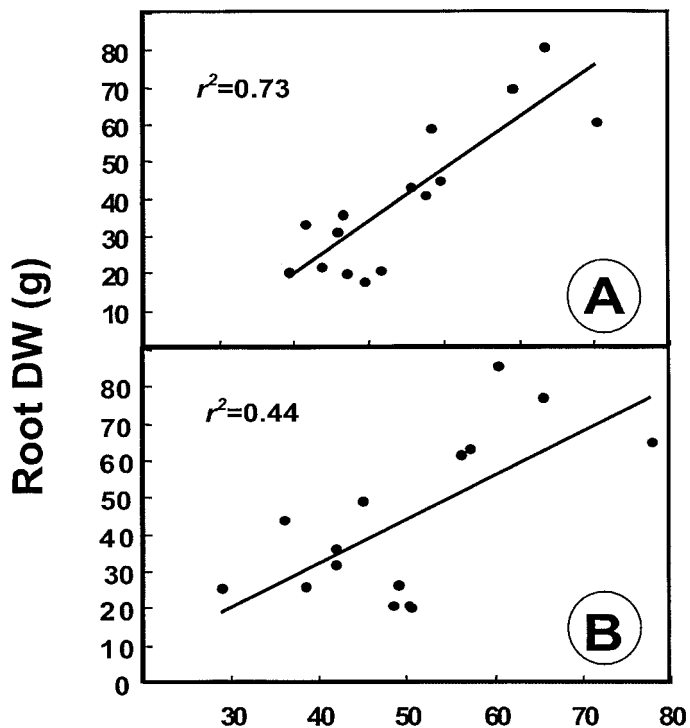


Fig. 7. Relationship between final root dry weight (DW) and final root electrical capacitance before destructive harvesting of 1-year-old 'Mutsu' apple trees on (A) M.9 and (B) MM.111 rootstocks.

The increased root to stem ratios under water stress in our study (Table 2) were similar to other reports (Buwalda and Lenz, 1992; Cripps, 1971; Maggs, 1961). In contrast to previous studies, the effects of water stress on root to stem DW ratios in our trees were asymmetric with its effects on root to leaf DW ratios, which did not differ among soil-water potentials or rootstocks (Table 2). Maggs (1961) reported that water stress reduced stem DW more than leaf DW, and our calculations based on Cripps (1971) data showed that irrigation increased the DW of stems, leaves and roots by factors of 17.3, 4.2, and 2.6, respectively, in a sandy loam soil, and by 9.4, 4.6, and 2.4 in a loamy soil. Fernandez et al. (1997a) also found that shoot extension of young apple trees was the growth parameter most affected by water stress. Evidently the DW allocations in apple stem and leaf tissue respond differently to water stress.

There are few published reports for rhizosphere respiration rates of apple trees. We observed CO_2 maxima of 4 and 7 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ for CTL trees on M.9 and MM.111, respectively (Fig. 5), which was comparable to observations of Proctor et al. (1976), who reported a maximum CO_2 rhizosphere respiration rate of 5.9 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. Soil CO_2 respiration rates in our pots without trees reached a maximum of 2.4 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ (Fig. 5), slightly higher than rates observed in a nearby undisturbed field soil (Psarras, 1999), but lower than previously reported rates of 3.8 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ in pots of peat under greenhouse conditions (Silvola et al., 1996).

Trees on MM.111 had higher specific root respiration rates than trees on M.9 (Table 3). Poorter et al. (1991) found that specific respiration was correlated with root growth potential of different species; more vigorous species had higher specific respiration rates. In the present study, MM.111 did not have a higher root DW (Table 1), but its greater shoot DW probably created more demand for nutrients on a root DW basis, which may

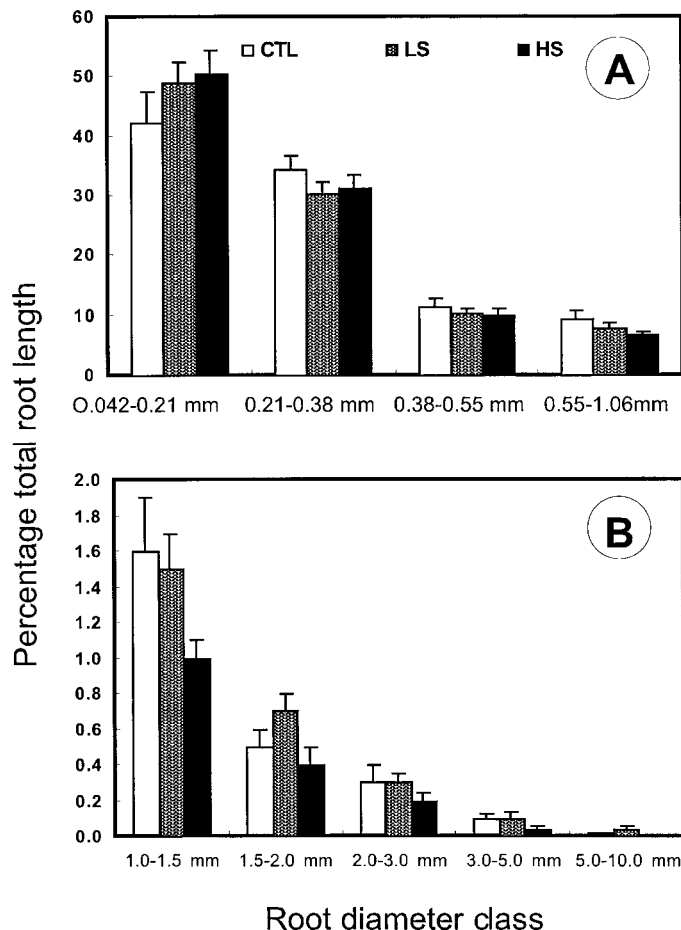


Fig. 8. Percent total root length comprised of various root-diameter classes in 1-year-old 'Mutsu' trees under three levels of soil water potential: CTL = control, fully watered trees; LS = low stress, irrigated at -80kPa , and HS = high stress, irrigated at -200kPa . (A) Roots $\leq 1\text{mm}$ in diameter, (B) roots $> 1\text{mm}$ diameter. Values represent means \pm SE of six trees.

explain the higher specific respiration rates observed for MM.111 relative to M.9. Water stress reduced absolute rhizosphere respiration rates for both rootstocks (Fig. 5), reflecting the reduction of root DW, despite increased specific root respiration rates in stressed roots (Table 3). Soil water content can affect rhizosphere respiration measurements by reducing soil pore volume for CO_2 and O_2 diffusion (Bouma et al., 1997). We observed that root DW and rhizosphere respiration were closely coupled (Fig. 6), and respiration rates increased in wetter soil treatments (Fig. 5), suggesting that differences in soil CO_2 permeability did not obscure the effects of water stress on root growth and respiration rates.

Decreased root respiration under drought stress (Fig. 5) may be linked to reduced carbohydrate supply from leaves and/or lower respiratory demand for root growth (Kosola and Eissenstat, 1994; Palta and Gregory, 1997). Since total root biomass was lower for drought stressed trees (Table 1), the increased specific root respiration observed in the present study probably reflected higher costs for root maintenance, osmoregulation, or ion absorption (Johnson 1983; Lakso, 1994; Wang et al., 1995).

ROOT ELECTRICAL CAPACITANCE. Electrical capacitance of roots on herbaceous plants has been correlated with several root parameters, but capacitance is also affected by soil moisture content (Box, 1996; Chloupek, 1977; Dalton, 1995). Since most

of our capacitance measurements were taken under different soil water potentials, it is not clear if the reduced capacitance observed under HS conditions was due to lower root biomass or lower soil water potential. At the end of the experiment, with leaves abscised and soil in all pots irrigated to 0kPa water potential, there was a strong correlation between root system electrical capacitance and root biomass for M.9, and a significant but weaker correlation for MM.111 (Fig. 7). Root capacitance was greater for M.9 than MM.111, despite the negligible differences in final root DW for these two genotypes. Anatomical or physiological characteristics may explain these rootstock differences in electrical capacitance per unit root DW.

In summary, root biomass of M.9 was less affected by water stress than MM.111, and root to shoot ratios were higher for M.9 than MM.111, suggesting that trees on M.9 may adapt better to drought stress, due to higher root to shoot ratios. Of the two nondestructive methods we used to estimate apple root biomass, combined soil/root respiration worked relatively well for both rootstocks, while electrical capacitance was more reliable for M.9, and was affected by soil water content during measurements.

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