Response of Container-grown Apple Trees to Soil Compaction

D.C. Ferree and J.G. Streeter

Department of Horticulture and Crop Science, Ohio State University/OARDC, Wooster, OH 44691

Y. Yuncong

Department of Horticulture, Beijing Agricultural College, Beijing 102206, China

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Abstract. Container-grown apple (*Malus ×domestica* Borkh.) trees were exposed to soil compaction created by changing soil bulk density (SBD) to determine the effect of compaction levels, rootstock, and moisture stress on mineral nutrition, leaf gas exchange, and foliar carbohydrate levels. With SBD of 1.0, 1.2, and 1.4 g·cm⁻³, there was no interaction of rootstock and soil compaction for growth of ‘Melrose’ trees on nine rootstocks. Trees grown in a SBD of 1.2 g·cm⁻³ had a greater dry weight than trees at 1.4 g·cm⁻³ bulk density. Increasing SBD to 1.5 g·cm⁻³ reduced shoot length, total leaf area, leaf size, and dry weight of leaves, shoots, and roots. The interaction between rootstock and SBD was significant and total dry weight of ‘B.9’, ‘G.16’, ‘G.30’, and ‘M.7 EMLA’ was less influenced by 1.5 g·cm⁻³ soil than trees on ‘M.26 EMLA’ and ‘MM.106 EMLA’. Withholding moisture for 10 days at the end of a 70-day experiment caused 8% to 25% reduction in growth in a non-compacted (1.0 g·cm⁻³) soil with much less effect in a compacted soil. Prior to imposing the moisture stress by withholding water, net photosynthesis (Pn) was reduced 13% and transpiration (E) 19% by increasing bulk density to 1.5 g·cm⁻³. Following 7 days of moisture stress in non-compacted soil, Pn and E were reduced 49% and 36%, respectively, with no such reductions in the compacted soil. Increasing SBD to 1.5 g·cm⁻³ caused a decrease in the leaf concentration of quinic acid, myoinositol, and sucrose and an increase in fructose and glucose. Trees growing in 1.5 g·cm⁻³ had reduced concentrations of N, Ca, Mg, Mn, Na, and Zn, and increased P, K, B, and Fe in leaves.

The profitable life of an apple orchard can be 10 to 20 years after fruiting begins and, as orchard planting density increases, equipment traffic follows nearly the identical track with each pass. In production areas with abundant rainfall, soil compaction can occur due to multiple passes of heavy sprayers during the growing season and fruit removal equipment at harvest. Soil compaction resulting from the use of heavy equipment in the field can become a serious problem, especially in soils that are not regularly tilled (Blackwell et al., 1985; Brereton et al., 1986). Compaction increases the bulk density and the mechanical impedance of soil and reduces soil conductivity, permeability, and diffusivity to water and air (Vepraskas, 1994).

Effects of compaction on annual plants include restriction of root growth and, as a consequence, decreased shoot growth, leaf area development, dry matter production, and stomatal conductance (Gross, 1977; Gross and Russell, 1980). Soil compaction can significantly reduce yields of many agronomic species (Andrade et al., 1993; Blackwell et al., 1985; Brereton et al., 1986). Soil mechanical impedance and resistance to root penetration

increase as soils dry and, therefore, even in non-compacted soils the plant response to soil mechanical impedance is important during drought (Andrade et al., 1993). Passioura and Gardner (1990) found that the decline in growth of wheat seedlings occurred at a higher soil water content in compacted and dense soil than in loose soil.

Most of the work on the influence of soil compaction on perennial woody species has involved the use of conifer seedlings (Conlin and van den Driessche, 1996; Duffy and McClurkin, 1974) or container-grown ornamental plants (Maupin and Struve, 1997). One of the few studies on apple trees indicated that compaction of two soil types decreased dry matter production, with root growth being more affected than shoot growth (Slowik, 1970). Bulbotko (1973) also reported that SBD of 1.6 to 1.7 g·cm⁻³ inhibited the spread of apple root systems.

Mechanisms underlying the response of roots to compaction probably involve hormones as primary signals. Kays et al. (1974) noted that impeded barley roots generated ethylene. More detailed studies have extended this observation to maize (Sarquis et al., 1991) and tomato (Hussain et al., 1999b). Other studies implicate abscisic acid (ABA) as a signal transported from roots to shoots in response to mechanical impedance (Hussain et al., 1999a; Mulholland et al., 1996a, 1996b). In the latter study, ABA concentration in the

xylem and stomatal conductance of barley plants were negatively correlated. For some crops, there appears to be genetic variation for improved root growth in compacted soils (Masle, 1992).

Drought stress can cause serious losses in yield and productivity of most crop plants, including apple in arid and sub-arid regions. The accumulation of solutes, such as polyols, sugars, proline, and glycine-betaine, is almost certainly an important component of the adaptation or osmotic adjustment of plants to water deficit (Daie, 1996). Transgenic plant studies have implicated carbohydrates as important osmolytes in plants subjected to water and salt stress—for example, increased drought resistance of sugar beet plants expressing a bacterial gene for fructan biosynthesis (Pilon-Smits et al., 1999); increased salt tolerance of tobacco plants expressing a bacterial gene for mannitol biosynthesis (Tarczynski et al., 1993); and increased tolerance to osmotic stress by yeast expressing a plant gene for sorbitol synthesis or a bacterial gene for mannitol biosynthesis (Shen et al., 1999).

There is accumulation of sorbitol in cherry and apple trees subjected to water deficit (Ranney et al., 1991; Wang and Stutte, 1992). Recently, this response has also been noted in peach (Lo Bianco et al., 2000). All of these studies indicate that sucrose plays a minor role in osmotic adjustment relative to sorbitol. The latter study also involved the analysis of enzymes of sucrose and sorbitol synthesis, and the combination of results indicates that sorbitol accumulation results primarily from a down-regulation of sorbitol use as opposed to up-regulation of sorbitol synthesis. Recently, a detailed study of the effects of drought on apple roots indicates higher respiration rates and greater carbohydrate costs in roots subjected to water deficit (Psarras and Merwin, 2000).

The effects of compaction on stomatal conductance of barley leaves have been noted (Hussain et al., 1999a). However, compaction of sunflower roots did not have a significant effect on photosynthesis of leaves (Andrade et al., 1993). Thus, the impact of compaction on carbon assimilation or solute accumulation in leaves is not known. To our knowledge, the interaction or combined effects of compaction and water deficit on apple trees have not been reported.

The objective of the present series of studies was to determine: 1) the level of soil bulk density that would cause a decrease in apple tree growth; 2) whether some apple rootstocks enable trees to avoid the negative effects on growth caused by soil compaction; 3) if an interaction exists between soil compaction and soil moisture stress; and 4) if the reductions in growth caused by soil compaction are related to photosynthesis transpiration, mineral nutrients, or carbohydrates in apple leaves.

Materials and Methods

Rootstock levels of compaction. In 1997, ‘Melrose’ apple scions were grafted on the following commercially purchased apple root-

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stocks: 'M.27 EMLA', 'M.9 EMLA', 'M.26 EMLA', 'M.7 EMLA', 'MM.111 EMLA', 'MM.106 EMLA', 'G.30', and 'B.118'. After growing from April to November in 5.6-L containers in a medium of equal parts of peat, perlite, and soil (Wooster silt loam—Fine loamy mixed mesic typic Fragiudalf), the trees were moved to refrigerated storage (7.0 °C) until removal on 19 Mar. 1998. The medium was washed from the roots and all roots trimmed to a length of 5 cm from the rootstock shank. Trees were planted in 5.6-L containers in Orville silt loam soil (20%, sand, 62% silt, 18% clay, fine-loamy, mixed, active, non-acid, mesic Fluvaquentic Endoaquepts). The same soil was used in all studies described here. The soil was placed in the pot in 2-cm layers and compressed with a mallet to establish bulk densities of 1.0 (control), 1.2, and 1.4 g·cm⁻³.

Treatments were arranged on the greenhouse bench in a randomized block design with three (levels of compaction) × nine (rootstock) factorial with six single-tree replications. Greenhouse temperatures were 21 ± 3 °C day/15 ± 3 °C night, and water was applied by weighing each pot regularly and returning the pot to its wet weight by submerging it briefly until the soil was saturated. Coarse pea gravel was applied to the pot surface to reduce water evaporation. Trees were trained to a single shoot and length measured monthly. Trees were harvested on 12 Aug. and divided into component parts of leaves, shoots, shank, and roots, which were dried in a forced draft oven at 70 °C and weighed.

Rootstock severe compaction. In Mar. 1999, 'Red Gala #42' trees were purchased from a commercial nursery on the following rootstocks: 'M.9 EMLA', 'G.16', 'M.26 EMLA', 'M.7 EMLA', 'G.30', and 'MM.106 EMLA'. Trees and soil were handled as previously described, except soil bulk densities were 1.0 (control) and 1.5 g·cm⁻³. In addition to the data recorded in the previous experiment, a soil penetrometer (Spectrum Technology, Plainfield, Ill.) was used to determine the level and consistency of soil compaction in containers 12 h after they were saturated with water. Treatments were arranged in a randomized block design with a two (levels of compaction) × six (rootstocks) factorial with six single-tree replications.

Compaction plus short-term moisture stress. On 1 June 2001, 'M.9 EMLA' apple rootstock liners were planted as previously described into soil bulk densities of either 1.0 (control) or 1.5 g·cm⁻³. The trees were trained to a single shoot and grown as previously described. We chose M.9 because it is the most widely planted dwarfing rootstock worldwide and provides a simple plant system without the complications of a graft union. On 31 July 2001, the soil in containers was saturated by submersion in water, and then no further water was provided to half of the trees. The design was a randomized complete-block design with treatments arranged as a two (bulk densities of 1.0 or 1.5 g·cm⁻³) × two (water control or moisture stress) factorial with 10 single-tree replications. Net photosynthesis and E were measured on the most recent fully expanded

leaf after water was withheld for 7 and 10 d, with a portable infrared gas analyzer equipped with a 6.25-cm² leaf chamber (Model LCA 2, Analytical Development Co., Hoddesdon, England). Air flow was regulated at 300 mL·min⁻¹, with the air intake outside the greenhouse. Ambient CO₂ concentration, humidity of the air entering and leaving the leaf chamber, the chamber temperature and incidence level of photosynthetically active radiation (PAR) were recorded with each measurement. All measurements were taken with PAR above 800 μmol to attain light saturation of photosynthesis.

Following measurement of Pn and E, the leaf was removed and immediately frozen at -20 °C. The tissue was freeze-dried and ground using a Wiley mill to pass through a 20-mesh screen. Ground tissue was stored in tightly sealed vials at room temperature. Dried, ground tissue was simultaneously extracted and derivatized for analysis of carbohydrates by gas-liquid chromatography using an automated injector as described by Streeter and Strimbu (1998). Because the use of an internal standard gives high precision in these analyses, each sample was analyzed only once.

The major unknown peak in chromatograms was tentatively identified as quinic acid based on a retention time difference of 12 s between standard and sample (retention times using an automated injector are highly reproducible) and based on the lack of shoulders on the putative quinic acid peak when a proportional amount of standard was added to the samples.

The whole trees were harvested on 10 Aug. 2001, and separated into component parts and dried as previously described. The dried leaves were ground and passed through a 20-mesh screen and submitted to the Ohio State Univ. STAR Laboratory for nutrient analyses using an inductively coupled plasma (ICP) spectrophotometer (Watson and Isaac, 1990).

Compaction plus extended moisture stress. Rootstock liners of 'M.9 EMLA' were planted 8 Mar. 2000, and handled as previously described with half in at 1.0 g·cm⁻³ SBD and the other half in 1.5 g·cm⁻³ SBD. On 22 Apr. 2000, pots were submerged in water until the soil volume was thoroughly saturated. This was the final water given to the trees in the drought treatment. The statistical design was a randomized complete block with treatments arranged as a two (SBD at 1.0 or 1.5 g·cm⁻³) by two (watered-control or non-watered-stressed) factorial with 10 single-tree replications.

In addition to the measurements previously described in the short-term moisture stress study, relative water content was determined by removing a fully expanded leaf from each of the 10 replicate plants (different from the leaves for Pn or E measurements) weekly, beginning with the third lowest leaf on the stem. On subsequent sampling dates the 5th, 7th, 9th, etc., leaf was collected for relative water content (RWC) analysis so that the last leaves sampled were approximately in the center of each stem. The samples were taken beginning at 9:00 AM. Four leaf disks 0.8-cm diameter from each leaf were cut and weighed immediately in the greenhouse to the nearest 0.2 mg and then

floated on distilled water for 4 h in a covered petri dish at 4 °C to allow the disks to become fully turgid. The remainder of the test leaf was immediately placed in a plastic vial and frozen for later use to analyze for carbohydrates. The turgid disks were blotted dry and weighed; the disks were then dried overnight at 70 °C and weighed. RWC was calculated as:

$$[(\text{fresh weight} - \text{dry weight}) / (\text{turgid weight} - \text{dry weight}) \times 100].$$

Results

Rootstocks level of compaction. Rootstocks are listed in Table 1 from smallest to largest based on their performance in long-term replicated field trials. Tree size in containers generally followed this order, except for trees on 'B.118', which were similar in size to the most dwarfing rootstock 'M.27 EMLA'. Trees on 'M.7 EMLA' were large relative to tree size in field trials and had a larger amount of small roots (<2-mm diameter) than all other rootstocks. Shoot length of trees grown in containers with a SBD of 1.4 g·cm⁻³ was less than shoot length of trees grown in less compacted soil. However, in other measurements of growth, trees in soil at 1.2 g·cm⁻³ were slightly larger than trees in soil with 1.0 or 1.4 g·cm⁻³. There was no interaction for any measure of growth between rootstock and the three levels of SBD.

Rootstock severe compaction. Rootstocks are again listed in order of their tree size in field trials for Table 2. Trees on 'M.7 EMLA' in this greenhouse study were small, while trees on 'G.16' large, relative to their expected trees size in the field. Trees on 'M.7 EMLA' had 17% of their dry weight in roots, which was higher than most of the other rootstocks. Soil compaction caused a significant reduction in all growth parameters except the shank. The interaction between rootstock and SBD was significant for shoot length, shank and total dry weight (Fig. 1). Shoot length of trees on 'G.16' and 'B.9' were less affected by a bulk density of 1.5 g·cm⁻³ than shoot length of trees on other rootstocks. Shank dry weight of trees on 'M.26 EMLA' was reduced and on 'G.30' increased in trees growing in containers with 1.5 g·cm⁻³ SBD. When considering total dry weight trees on 'M.26 EMLA' and 'MM.106 EMLA' were significantly lighter than on other rootstocks on compacted (1.5 g·cm⁻³) soil. Total dry weight of trees on 'B.9', 'G.16', and 'M.7 EMLA' was not affected by a 1.5 g·cm⁻³ SBD.

Compaction plus short-term moisture stress. The interaction between SBD and moisture stress was significant for all measures of growth of 'M.9 EMLA' apple trees except rootstock shank (Table 3). Compacting soil to a bulk density of 1.5 g·cm⁻³ caused a 32% to 68% reduction in various growth parameters measured at the end of the 70-d experiment. While a short-term (10 d) moisture stress at the end of the growth period caused growth reductions of 8% to 25% in non-compacted soil (1.0 g·cm⁻³) and had much less effect on compacted soil (1.5 g·cm⁻³). Total dry weight in compacted soil was 13% higher in trees exposed to a moisture stress compared to those

Table 1. Growth and tissue dry weight distribution of 'Melrose' apple trees on nine rootstocks grown in containers with soil at three bulk densities.

Rootstock	Shoot length (cm)	Total leaf area (cm ²)	Avg leaf area (cm ²)	Dry wt distribution (g)					
				Leaves	Shoot	Root diam (mm)		Shank	Total
						<2	>2		
M.27 EMLA	81.8 cd ^z	1671 b	37.2 bc	15.3 d	14.2 e	4.3 bc	1.3 de	17.5 e	52.8 d
M.9 T337	84.2 b-d	1861 ab	40.1 ab	17.5 a-c	15.9 c-e	4.6 bc	2.6 bc	21.1 c-e	61.8 bc
B.9	86.3 a-d	1756 b	38.9 ab	16.7 b-d	16.4 b-e	4.0 c	1.8 cd	18.9 e	58.0 cd
M.26 EMLA	85.8 b-d	1828 ab	38.2 a-c	17.4 a-c	16.8 b-e	3.9 cd	3.1 b	25.5 a-c	66.9 ab
M.7 EMLA	93.4 a	1986 a	40.3 ab	18.5 ab	17.2 a-d	6.9 a	3.4 b	24.0 b-d	70.1 ab
G.30	90.5 ab	1971 a	40.7 a	19.2 a	19.0 ab	2.6 d	5.5 a	22.0 c-e	60.5 ab
MM.106 EMLA	89.9 ab	2029 a	40.3 ab	18.5 ab	19.6 a	5.6 b	1.2 de	29.6 a	74.6 a
MM.111 EMLA	88.9 a-c	1840 ab	38.6 a-c	16.2 cd	18.9 a-c	4.2 bc	0.5 e	27.1 ab	66.6 ab
B.118	80.1 d	1710 b	35.6 c	15.0 d	15.5 de	3.6 cd	1.0 de	20.4 de	55.7 cd
Soil bulk density (g·cm ⁻³)									
1.0	87.3 a	1828 b	39.2 ab	16.8 b	16.7 b	4.6	2.1	23.6	64.0 ab
1.2	90.0 a	1933 a	39.7 a	18.6 a	18.5 a	4.6	2.4	23.4	67.7 a
1.4	83.0 b	1783 b	37.9 b	15.9 b	15.6 b	4.1	2.3	21.9	59.9 b
F Significance									
Rootstock (RS)	**	**	*	**	**	**	**	**	**
Bulk density (BD)	**	*	NS	**	**	NS	NS	NS	**
RS × BD	NS	NS	NS	NS	NS	NS	NS	NS	NS

^zMean separation for main effects of rootstock and bulk density by Duncan's multiple range, $P < 0.05$.

NS, *, **Nonsignificant or significant at $P < 0.05$ or 0.01, respectively.

Table 2. Growth and dry weight distribution of 'Red Gala 42' apple trees on six rootstocks grown in containers with soil at two bulk densities.

Rootstock	Shoot length (cm)	Total leaf area (cm ²)	Avg leaf area (cm ²)	Dry wt distribution (g)				
				Leaves	Shoot	Roots	Shank	Total
B.9	93.9	2363 ab ^z	47.2 a	20.8 a	23.3 ab	16.0 bc	92.2 b	152.5 c
G.16	95.9	2177 a-c	41.3 a-c	18.2 ab	25.8 a	19.4 ab	123.2 a	186.7 a
M.26 EMLA	93.0	2169 a-c	43.4 ab	17.8 ab	20.5 b	13.0 c	115.9 a	197.3 bc
M.7 EMLA	93.1	1804 c	36.4 c	14.4 b	18.2 b	22.2 a	74.3 c	129.2 d
G.30	84.2	2516 a	47.4 a	20.6 a	26.1 a	19.0 ab	109.1 a	174.9 ab
MM.106	100.0	2005 bc	39.1 bc	17.4 ab	23.1 ab	12.1 c	54.1 d	106.9 e
Soil bulk density (g·cm ⁻³)								
1.0	111.9	2738	50.4	22.5	27.3	18.4	93.8	162.2
1.5	73.6	1584	34.4	13.7	18.2	15.1	95.7	142.8
F Significance								
Rootstock (RS)	*	*	**	**	**	**	**	**
Bulk density (BD)	**	**	**	**	**	*	NS	**
RS × BD	*	NS	NS	NS	NS	NS	**	**

^zMean separation for main effects of rootstock and bulk density by Duncan's multiple range test, $P < 0.05$

NS, *, **Nonsignificant or significant at $P < 0.05$ or 0.01, respectively.

with no moisture stress.

Trees grown for 60 d in compacted soil had a 13% reduction in Pn and a 19% reduction in E prior to imposing a moisture stress (Table 4). In the compacted soil, moisture stress had no significant influence on Pn or E. After 10 d of withholding water, Pn and E were significantly reduced in both compacted and non-compacted soil, but the reduction was greatest in the latter. After 7 d of withholding water, Pn of trees in the non-compacted soil was reduced 49% and E 36%.

Increasing SBD to 1.5 g·cm⁻³ caused a decrease in leaf quinic acid, myo-inositol and sucrose, and an increase in fructose and glucose (Table 5). The response was similar after 7 or 10 d of water stress, except sucrose concentration was not different after 10 d. After 7 d of moisture stress, leaf concentrations of quinic acid and sorbitol were reduced, while after 10 d of moisture stress all carbohydrate fractions, except quinic acid, were reduced. The significant interaction with sorbitol after 7 d of moisture stress was due to stable concentrations at 1.5 g·cm⁻³, but a 17% increase associated with water stress in leaves from trees on non-compacted (1.0 g·cm⁻³) soil.

Increasing SBD to 1.5 g·cm⁻³ resulted in a significant decrease in leaf concentrations of N, Ca, Mg, Mn, Na, and Zn and significant increases in P, K, B, and Fe (Table 6). The 10 d of moisture stress caused an increase in iron. The only other leaf nutrient affected by the moisture stress was B, which was not affected in non-compacted soil (1.0 g·cm⁻³), but decreased 10% in trees grown in compacted (1.5 g·cm⁻³) soil.

Compaction plus extended moisture stress. Soil compaction (1.5 g·cm⁻³) on well-watered plants reduced height by 43%, stem diameter by 15%, number of leaves 32%, and leaf area 34% to 49% compared to controls depending on what portion of the tree was sampled (Table 7). Stressing the trees by withholding moisture for 32 d caused the following reductions in growth: height 31%, stem diam 7%, number of leaves 23%, and leaf area 15% to 68% with the greatest effect on upper leaves. A significant interaction occurred between compaction and moisture stress, as moisture stress had less effect on growth in the compacted soil. Measuring the rate of water loss from the pots by weighing showed that loss from the compacted pots was half that of the

non-compacted during the first week of withholding water. This trend continued until 17 May when rate of water loss in the stressed treatments was near zero for trees in both compacted and non-compacted soils. Plants on all treatments had similar RWC 1 week after the initiation of moisture treatments (Fig. 2). However, 2 weeks later, the trend toward lower RWC in stressed plants was apparent. By 22 May, RWC in moisture-stressed trees was much lower than the controls. Analysis of variance (ANOVA) for 1 and 15 May indicated highly significant effects of both stress and compaction. The most striking difference was between moisture-stressed trees growing in compacted and non-compacted soil. That is, because of a substantially greater rate of water loss from trees growing in non-compacted soil, leaves on these trees had very low RWC. In the week following re-watering (24 May), RWC in all leaves was similar.

Photosynthesis and transpiration were lower in moisture-stressed plants for essentially all of the sampling dates and this was true regardless of compaction (Fig. 3). Thus, moisture stress and non-compaction of soil had the most significant impact on these parameters.

ANOVA indicated a statistically significant effect of compaction on transpiration only for the 3 and 10 May sampling dates. There was a tendency for trees growing in compacted soil to have slightly higher rates of photosynthesis and transpiration on 17 May and 1 June, and this trend was much clearer for the well-watered plants. The photosynthetic activity of moisture-stressed trees did not fully recover following rewatering. A positive correlation ($r = 0.76^{**}$) was noted between P_n and RWC for the moisture-stressed/non-compacted treatment, but the coefficient for moisture-stressed plants in compacted soil was nonsignificant. Correlations between transpiration and RWC were significant for moisture-stressed trees in both compacted ($r = 0.58^*$) and non-compacted ($r = 0.69^{**}$) treatments.

Results for the carbohydrate composition in trees with the moisture-stressed non-compacted treatment on 22 May were erratic and may not be valid. Trees were severely stressed on this date, having an extremely low RWC of 38% (Fig. 2), and photosynthetic and transpiration rates of near zero (Fig. 3). That plants in this treatment were more severely stressed than plants in the moisture-stressed one, and compacted treatment is probably due to more rapid withdrawal of water from the root volume of non-compacted plants.

For the sample on 6 May, collection of leaf samples had to be delayed until 1:00 PM. RWC values were unusually low, and data for carbohydrates that are relatively rapidly metabolized (e.g., glucose and fructose) were also low in well-watered plants. Rather than select certain data to report for this sampling, all of the data were considered atypical and are not presented. The major difference in results caused by a 4-h delay in sampling emphasizes the importance of consistency in the time of day when samples are obtained, especially for RWC.

For well-watered trees in compacted soil, leaf sucrose concentrations were very high relative to non-compacted plants (Fig. 4A). Also, whereas sucrose concentration in the well-watered 1.5 g·cm⁻³ treatment increased slightly and then declined sharply, sucrose in the well-watered 1.0 g·cm⁻³ treatment was flat over time. For trees subjected to soil compaction, sucrose concentration tended to be higher in leaves of moisture-stressed trees, but there was an anomalous switch in this relationship for the leaves sampled on 22 May, probably due to the severe stress level in the moisture-stressed non-compacted trees, as noted above. Results of ANOVA for the 1 and 15 May dates indicated significant effects for both the moisture stress and compaction treatments.

Glucose concentration in leaves of trees not moisture stressed showed random variations over time, but no clear trends (Fig. 4B). In contrast, glucose in leaves of moisture-stressed plants showed a weak trend toward increasing concentrations over time. For neither group of trees did there appear to be an effect of compaction. Similar trends were seen for fructose concentration (Fig. 4D), although the concentration of fructose in leaves was much less than the concentration of either sucrose or glucose.

Fig. 1. Interaction of 'Gala' on six apple rootstocks and container SBD on (A) shoot length, (B) shank dry weight, and (C) total dry weight.

Table 3. Growth and tissue dry weight distribution of 'M.9 EMLA' trees grown in containers in soil at two bulk densities with and without a moisture stress.

Soil bulk density (g·m ⁻³)	Shoot length (cm)	Leaf area (cm ²)	Dry wt distribution (g)				
			Leaves	Shoot	Shank	Root	Total
1.0 Control	61.8	1512	10.65	8.45	29.1	13.44	61.69
Moisture stress	56.7	1210	9.00	6.73	31.2	10.07	57.00
1.5 Control	33.4	483	3.50	2.27	27.7	8.46	41.99
Moisture stress	34.9	534	3.72	2.46	30.9	11.15	48.30
LSD _{0.05}	4.2	123	0.36	0.71	NS	2.72	5.42
F Significance							
Bulk density (BD)	**	**	**	**	NS	*	**
Moisture stress (MS)	NS	**	*	**	NS	NS	NS
BD × MS	*	*	**	**	NS	**	**

NS, *, ** Nonsignificant or significant at $P < 0.05$ or 0.01 , respectively.

Table 4. Net photosynthesis (Pn) and transpiration (E) of leaves of 'M.9 EMLA' apple trees grown in containers in soil at two bulk densities with and without a moisture stress.

Soil bulk densities (g·cm ⁻³)	Pn (μmol·CO ₂ ·m ⁻¹ ·s ⁻¹ and E (μg·H ₂ O·s ⁻¹)					
	31 July		7 Aug.		10 Aug.	
	Pn	E	Pn	E	Pn	E
1.0 W ^z	19.5	15.5	18.6	13.2	14.6	10.8
S	19.7	15.6	9.6	8.5	3.4	3.1
1.5 W	16.9	12.6	15.4	9.4	12.2	9.0
S	18.0	13.4	13.4	8.8	6.7	5.0
LSD _{0.05}	NS	NS	2.6	1.2	2.4	1.6
F Significance						
Bulk density (BD)	**	**	NS	**	NS	NS
Moisture stress (MS)	NS	NS	**	**	**	**
BD × MS	NS	NS	**	**	**	**

^zMoisture withheld after the measurements on 31 July (S) and compared to well-watered trees (W) with 7 and 10 Aug. measurements after 7 and 10 d of withholding moisture.

NS, *, ** Nonsignificant or significant at $P < 0.05$ or 0.01 , respectively.

Table 5. Leaf carbohydrate concentration (mg·g⁻¹ dry wt.) of 'M.9 EMLA' apple trees grown in soil at two bulk densities with and without a moisture stress.

Soil bulk density (g·cm ⁻³)	After 7 d of moisture stress						After 10 d of moisture stress					
	Quinic acid	Sorbitol	Fructose	Glucose	Myoinositol	Sucrose	Quinic acid	Sorbitol	Fructose	Glucose	Myoinositol	Sucrose
1.0	129	379	9.1	68	6.3	114	153	470	10.3	69	6.8	88
1.5	110	256	13.7	94	5.6	79	128	475	14.1	97	6.0	77
Moisture stress												
Control	126	349	11.6	77	6.1	100	144	433	8.7	56	6.8	107
Stress	113	386	11.2	85	5.8	93	136	512	15.7	110	6.0	58
F Significance												
Bulk density (BD)	**	NS	*	*	**	**	**	NS	*	**	**	NS
Stress (S)	*	**	NS	NS	NS	NS	NS	**	**	**	**	**
BD × S	NS	**	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS

NS, *, ** Nonsignificant or significant at $P < 0.05$ or 0.01 , respectively.

Table 6. Minimal nutrient concentrations in leaves of 'M.9 EMLA' apple trees grown in containers in soil at two bulk densities with and without a moisture stress of 10 d.

Soil bulk density (g·cm ⁻³)	% Dry wt					μg·g ⁻¹ Dry wt				
	N	P	K	Ca	Mg	B	Fe	Mn	Na	Zn
1.0	2.62	0.16	1.48	1.63	0.43	19.9	56.6	79.4	639	29.5
1.5	2.52	0.18	1.66	1.16	0.30	26.7	62.1	40.2	114	23.1
Water stress										
Control	2.58	0.17	1.59	1.40	0.37	23.9	55.6	59.0	12	427.7
Stress	2.58	0.17	1.55	1.39	0.37	22.7	63.1	60.7	125	24.9
F Significance										
Bulk density (BD)	*	**	**	**	**	**	**	**	**	*
Stress (S)	NS	NS	NS	NS	NS	*	**	NS	NS	NS
BD × S	NS	NS	NS	NS	NS	**	NS	NS	NS	NS

NS, *, ** Nonsignificant or significant at $P < 0.05$ or 0.01 , respectively.

Table 7. Effect of container soil bulk density and moisture stress on growth of 'M.9 EMLA' apple trees over 77 d.

Soil bulk density (g·cm ⁻³)	Moisture ^z stress	Plant ht (m)		Stem diam (mm)	No. of leaves		Avg. leaf area (cm ²)		
		24 May	Change		24 May	Change	Lower	Middle	Upper
			22 Apr.–24 May			22 Apr.–24 May			
1.0	W	94.5	23.9	8.8	42.1	13.8	34.2	33.2	69.9
1.5	W	53.7	15.7	7.5	28.6	9.3	19.2	22.1	36.2
1.0	S	65.4	5.6	8.2	32.6	5.7	28.9	28.3	22.2
1.5	S	50.2	6.2	7.4	24.7	4.5	20.9	21.2	19.9
LSD _{0.05}		6.3	3.9	0.4	3.1	2.2	1.1	1.0	2.5
F Significance									
Bulk density (BD)		**	**	**	**	**	**	**	**
Stress (S)		**	**	**	**	**	**	**	**
BD × S		**	**	NS	**	**	NS	NS	NS

^zTrees planted 8 Mar. and watered as needed until the soil was saturated on 22 Apr. and following that date, half were watered as needed (W), and half were not watered (S) until soil in all pots was saturated 24 May.

NS, *, ** Nonsignificant or significant at $P < 0.05$ or 0.01 , respectively.

Fig. 2. Effect of container SBD and water stress (W = watered; S = not watered) on relative water content of 'M.9 EMLA' apple leaves. Soil was saturated with water just prior to 19 Apr. and just after 23 May.

As expected, the major carbohydrate in leaves was sorbitol. Effects of treatments on sorbitol concentration were complex, but in general, trees in non-compacted soil had higher sorbitol concentrations (Fig. 4C). ANOVA confirmed the highly significant effect of compaction on sorbitol concentration on 1 and 15 May. Note that, for the period from 15 to 29 May, the sucrose and sorbitol concentrations in the moisture-stressed non-compacted treatment were mirror images in terms of concentration changes. Except for the well-watered non-compacted controls, the general trend in leaf sorbitol concentration during the period of moisture stress was an increase, the increase being particularly large in the compacted + moisture-stressed plants. Sorbitol concentration in leaves was significantly correlated with photosynthetic activity for the well-watered non-compacted treatment ($r = 0.50^*$) and the moisture-stressed compacted treatment ($r = 0.90^{**}$), but not for the other two treatments.

The concentration of myoinositol in apple leaves was low ($1\text{--}6\text{ mg}\cdot\text{g}^{-1}$ dry weight) relative to other compounds at all sampling times. Quinic acid ranged from $60\text{--}95\text{ mg}\cdot\text{g}^{-1}$ dry weight. Although ANOVA indicated some significant treatment effects at a few dates for these compounds, the plotted data revealed no meaningful trends across time (data not shown).

In view of the lack of significant effect of compaction on photosynthesis (Fig. 3 and ANOVA results), it is curious that there were large and statistically significant effects of compaction on sorbitol (Fig. 4C and ANOVA results). In the leaves of well-watered and moisture-stressed trees, the average decrease in sorbitol concentration for the samples taken during the onset of moisture stress was 151 and 116 $\text{mg}\cdot\text{g}^{-1}$ dry weight, respectively. These amounts represent 33% of the sorbitol concentration found in leaves on non-compacted plants, so

the effect of compaction was substantial. The decline in sorbitol was accompanied by an increase in sucrose concentration in leaves, although the quantitative increase in sucrose cannot account for the decline in sorbitol. Also, the increase in sucrose in moisture-stressed plants in response to compaction was only about half that in the well-watered controls. Effects of compaction on the concentration of glucose and other carbohydrates were either small or inconsistent. In contrast, the reciprocal effects of compaction on sucrose and sorbitol were very consistent across time. This suggests that hexose was diverted from sorbitol synthesis to sucrose synthesis, but how this might be caused by soil compaction is difficult to explain.

Discussion

Although it is not possible to extrapolate to field conditions from these greenhouse studies, this work indicates that a wide range of apple rootstocks are tolerant of SBD to $1.4\text{ g}\cdot\text{cm}^{-3}$ in silt loam soils (Table 1). Increasing bulk density to $1.5\text{ g}\cdot\text{cm}^{-3}$ (Table 2) caused 80% (771 vs. 3720 kPa for $1.5\text{ g}\cdot\text{cm}^{-3}$) greater resistance measured by a penetrometer compared to $1.0\text{ g}\cdot\text{cm}^{-3}$ soil, and this caused significant reductions in shoot growth, with greater effects on some rootstocks than others. Work of Slowik (1970) with apple also reported no compaction effect below $1.4\text{ g}\cdot\text{cm}^{-3}$. Work with red oak (*Quercus rubra* L.) in Wooster silt loam soil (25% sand, 60% silt, 15% clay) indicated growth was not influenced by 1.5, but was reduced at $1.75\text{ g}\cdot\text{cm}^{-3}$ bulk density (Maupin and Struve, 1997). With pine seedlings, the tallest seedlings occurred at the highest compaction levels in a loam soil (46% sand, 47% silt, 7% clay), but compaction above $1.7\text{ g}\cdot\text{cm}^{-3}$ caused decreased needle length and root dry weight (Conlin and van den Driessche, 1996). Although it is not possible to make direct comparisons among

these studies because bulk density depends on soil types, apple trees appear similar or slightly more sensitive to soil compaction than these other tree species.

The greater sensitivity of some rootstocks to soil compaction of $1.5\text{ g}\cdot\text{cm}^{-3}$ confirms work of Slowik (1970), who studied a more limited range of rootstocks. He found 'M.26' and 'M.4' more sensitive than 'Antonovka' seedlings, and 'M.26' was also sensitive in our study (Table 2). Tree size in the field does not seem like the determining factor in sensitivity, as both 'M.26' (dwarfing) and 'MM.106' (semi-standard) were sensitive. 'B.9' (dwarfing), 'M.7 EMLA', and 'G.30' (semi-standard) were tolerant based on total dry weight, and the new 'G.16', which is similar to 'M.9' in tree size, was also reasonably tolerant (Fig. 1). Masle (1992) has suggested that growth responses to soil compaction vary considerably between plant species and also between genotypes within species. Genotypes with lower growth rates in non-compacted soils will respond less to soil compaction than genotypes with high growth rates. The relative growth rates of root systems of apple rootstocks is not known, but may be linked with the difference in response. A field comparison will be required to confirm that these dwarfing rootstocks, which are promising for modern intensive orchards, have some tolerance to soil compaction. However, soil compaction should be avoided if possible because shoot length of trees on all rootstocks was reduced by a SBD of $1.5\text{ g}\cdot\text{cm}^{-3}$.

One of the most interesting and surprising results is that, although compaction had major effects on plant growth (Tables 2 and 3; Fig. 1), there was relatively little effect of compaction on photosynthesis (Table 4; Fig. 3), suggesting that carbon supply was not the major factor limiting growth under compacted soil conditions. Similar effects of compaction on growth of barley (*Hordeum vulgare* L.) plants have been reported (Gross, 1977; Gross and Russell, 1980; Hussain et al., 1999a). Reports on the effect of soil compaction on wheat (*Triticum aestivum* L.) (Masle and Farquhar, 1988) and sunflower (*Helianthus annuus* L.) (Andrade et al., 1993) show that the rate of photosynthesis was equal to or, in some cases, higher than in plants growing in non-compacted soil even though total photosynthetic leaf area had been reduced by soil compaction. However, photosynthesis of *Pinus contorta* was decreased by soil compaction (Conlin and van den Driessche, 1996).

Soil compaction had major effects on transpiration and RWC, and often the response was positive in trees growing in compacted soil. These effects of compaction were small relative to the effects of moisture stress (Table 4; Figs. 2 and 3). Increasing soil compaction had little effect on the water relations of red oak (Maupin and Struve, 1997), barley (Mulholland et al., 1996a, 1996b), sunflower (Andrade et al., 1993), and wheat (Masle and Farquhar, 1988) under conditions of adequate soil moisture. A bulk density of $1.5\text{ g}\cdot\text{cm}^{-3}$ had no effect on transpiration under adequate soil moisture. However, this level of soil compaction resulted in higher transpiration rates compared to trees

Fig. 3. Effect of container SBD and water stress (W = watered; S = not watered) on (A) net photosynthesis and (B) transpiration of 'M.9 EMLA' apple leaves. Soil was saturated with water just prior to 19 Apr. and just after 23 May.

growing in 1.0 g·cm⁻³ soil when water was withheld, due to more rapid loss of water from the non-compacted soil. Thus, the data suggest that if water is available, moderate compaction does not greatly affect the ability of the plant to take up water. Compaction appears to slow soil water loss as moisture stress develops, thus permitting these trees to maintain a higher level of transpiration. On fine-textured soils (as used in our studies), soybean yields were higher in dry years on compacted soils than in wet years, while the reverse was evident on coarse-textured soil (Vepraskas, 1994).

'M.9 EMLA' rootstock was selected as the plant material for these studies because it is the most widely planted dwarfing apple

rootstock and was reportedly more tolerant of soil moisture deficit (Fernandez et al., 1997) and soil compaction (Ferree and Schmid, 2001) compared to other rootstocks. In a study of root distribution, 'M.9 EMLA' had a higher root density than 'Mark' at all soil depths from 59 to 132 cm in a soil with bulk densities of 1.5 g·cm⁻³ (Fernandez et al., 1995).

In apple, sorbitol is the major product of photosynthesis and is the major translocated form of carbon (Loescher et al., 1982). Sorbitol is also an important reserve carbohydrate in apple leaves (Chong and Taper, 1971). Soil compaction had no effect on sorbitol in one of our studies (Table 5) and caused a 33% reduction in sorbitol (Fig. 4C) in another.

These results in the second study occurred in the absence of statistically significant effects of compaction on CO₂ assimilation rates. The depression of sorbitol concentration occurred in concert with a marked depression of shoot growth (Table 3), so it is possible that the relative lack of sorbitol availability in compacted plants plays a role in reducing plant growth. The increase in sorbitol concentration in apple leaves in response to moisture stress has been reported previously (Wang and Stutte, 1992). Compaction increased sucrose concentrations in leaves (Fig. 4A), suggesting diversion of hexose from sorbitol to sucrose, but the mechanism underlying this phenomenon could not be deduced from the analyses carried out in this study. In the short-term moisture study (Table 5), compaction caused a decrease in sucrose 7 d after initiation of moisture stress, but had no effect at 10 d.

Soil compaction caused a large reduction in tree height, number of leaves, stem diameter, and leaf area (Tables 3 and 7). The interaction between compaction and moisture stress for height and number of leaves was statistically significant in both studies. For all the growth variables, the effect of moisture stress was smaller for trees growing in compacted soil than for trees in non-compacted soil. The sensitivity of shoot length and leaf development to soil compaction has also been shown for barley (Mulholland et al., 1996a) and sunflower (Andrade et al., 1993). These previous studies also showed that root growth was generally less affected than shoot growth, and that was confirmed in Table 3.

Alteration of nutrient uptake could provide a partial explanation for the reduction in growth caused by soil compaction, since leaf levels of N, Ca, Mg, Mn, Na, and Zn were significantly reduced (Table 6). However, other elements, such as P, K, B, and Fe, were increased in leaves of trees growing in compacted soil. Shierlaw and Alston (1984) suggested that inhibition of root elongation is not necessarily correlated with inhibited uptake of mineral nutrients because contact between roots and soil increases in compacted soils. Higher rates of P uptake per unit root length in compacted soils have been reported (Cornish et al., 1984). Krannitz et al. (1991) proposed that the increased uptake of P could be the expression of a higher demand placed by the shoot on a smaller root system or brought about by root-induced changes in the rhizosphere. In our study, the concentrations of most of the mineral elements were in the sufficient range for apple; except for Ca concentration, which was 11% below the sufficiency range (Cahoon, 1985). A review of the effects of deficient Ca on apple tree growth indicates the greatest effect is on root growth (Boynton and Oberly, 1996). However, root dry weight in the present study was reduced less than shoots or leaves (Table 3); thus, nutrient deficiency caused by soil compaction was probably not responsible for the large growth reduction that occurred.

Sievers and Hensel (1991) suggested that the root cap is the site of perception of chemical and physical signals for the root. Thus, the root cap is likely the sensor of soil compaction. Sev-

Fig. 4. Effect of container SBD and water stress (W = watered; S = not watered) on (A) sucrose, (B) glucose, (C) sorbitol, and (D) fructose concentration in 'M.9 EMLA' apple leaves. Soil was saturated with water just prior to 19 Apr. and just after 23 May.

eral investigators (Hussain et al., 1999a; Masle and Passioura, 1987; Mulholland et al., 1996a) suggested that root-derived hormonal signals were likely responsible for the growth reductions caused by soil compaction. Although we did not measure plant hormones, we did demonstrate that under greenhouse container conditions, a wide range of rootstocks were very tolerant of increasing soil compaction up to a bulk density of 1.4 g·cm⁻³. Trees on a wide range of rootstocks had significant reduction in growth when bulk density was increased to 1.5 g·cm⁻³ with 'B.9', 'M.7 EMLA', 'G.16', and 'G.30' being relatively tolerant and 'M.26

EMLA' and 'MM.106 EMLA' having greater reductions in total dry weight. Soil compaction that affected growth had little effect on photosynthesis but did alter carbohydrates in the leaves. Soil compaction slowed the decline in leaf RWC and transpiration under conditions of water stress. Soil compaction significantly altered leaf mineral concentrations, but the changes were unlikely to be responsible for the reduction in growth. Additional research is needed to see if the growth responses for soil compaction at a bulk density of 1.5 g·cm⁻³ or higher in these greenhouse studies will resemble responses to compaction in the field.

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