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Drought Response of Young Apple Trees on Three Rootstocks: Growth and Development

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ABSTRACT. **'Imperial Gala' apple (*Malus domestica* Borkh.) trees, trained to two shoots, on M.9 EMLA, MM.111, and Mark rootstocks were subjected to two drought-stress and recovery periods in a rainshelter. Leaf growth rate, leaf area, leaf emergence, shoot length, and trunk cross-sectional area were measured during each stress and recovery period. Leaf growth rate was reduced during both stress periods but most consistently during the second drought stress. Length of the less-vigorous shoot was reduced most consistently due to drought stress but did not recover upon irrigation. Leaf emergence and trunk cross-sectional area increment were inconsistent in response to stress. Tree growth was reduced by drought stress to the greatest extent for trees on Mark, with MM.111 intermediate and M.9 EMLA least affected. At termination, the plants were separated into roots, current-season shoot growth, previous-season shoot growth, and rootstock, and dry weights were measured. Dry weights confirmed the growth measurements taken during the experiment with a 16%, 27%, and 34% reduction in total plant dry weight for drought-stressed trees on M.9 EMLA, MM.111, and Mark, respectively, compared to corresponding controls. It was concluded that Mark was the most sensitive of the three rootstocks followed by MM.111; M.9 EMLA was the most drought resistant.**

The effect of dwarfing rootstocks on apple growth and cropping is the subject of several reviews (Avery, 1970; Ferree and Carlson, 1987; Landsberg and Jones, 1981; Parry, 1977); however, the drought stress response is not as well understood. Landsberg and Jones (1981) cite several Russian publications (Misic and Gavrilovic, 1969; Moiseev et al., 1970; Razlivalova, 1974) that indicate that drought resistance of rootstocks is conferred to scions and that dwarfing rootstocks, especially M.9, are more drought resistant than vigorous rootstocks. Yet there is still contention regarding the capacity of dwarfing rootstocks, in general, to confer drought resistance to the scion. Ferree and Carlson (1987) and Tukey (1964) characterize dwarfing rootstocks, especially M.9, as intolerant of drought stress, while more vigorous rootstocks, particularly MM.111, are considered more drought resistant.

Irrigation practices and water availability are especially critical during establishment of young trees (Jackson et al., 1986; Proebsting et al., 1977). The initial care during plant establishment will strongly affect future performance of an orchard (Autio et al., 1991; Forshey, 1988; Proebsting et al., 1977). Rootstock selection in areas where irrigation is limiting or unavailable can be critical not only for the establishment period but for future performance as well.

This paper and that of Fernandez et al. (1997) analyzes the whole-plant response to drought stress in terms of plant growth and physiology of apple on two dwarfing rootstocks, M.9 EMLA and Mark, and one vigorous rootstock, MM.111, which are thought to differ in their response to drought. Specifically, the objective of this paper is to compare M.9 EMLA, MM.111, and Mark rootstock performance under drought conditions with respect to plant growth.

Materials and Methods

One-year-old 'Imperial Gala' apple trees (*Malus domestica* Borkh.) on M.9 EMLA, MM.111, and Mark rootstocks were planted with 45 cm in-row and 75 cm between-row spacing in a rainshelter on 17 and 22 May 1991 located at Kellogg Biological Station, Michigan State Univ, Hickory Corners, Mich. The rainshelter closed at a rate of 0.3 $m \cdot s^{-1}$ and was programmed to close after accumulation of 4 mm of rainfall. The rainshelter is described in detail by Martin et al. (1988). Soil was classified as a Kalamazoo loam (fine-loamy, mixed, mesic Typic Hapludolf). Due to size limitation of the plot, trees were planted in 30 cm wide ×40 cm deep trenches lined with a woven polypropylene geotextile (MM-8, AgriTex, Danbury, Conn.) to maintain roots within irrigation treatments and facilitate root excavation at termination of the project. Trees were planted on 15-cm-high raised beds to increase soil volume available to roots. Also, due to size limitations, plots had to be shared and the apples were interplanted with crab-apples (*Malus ×zumi* 'Indian Summer') and sweet cherry (*Prunus avium* L. 'Emperor Francis'). A split-plot design with two replicates of an irrigation main plot and six replicates per subplot (four subplots) of a rootstock subplot treatment for a total of 72 apple trees was used. Analysis of variance was conducted for a split plot using the PROC GLM and linear regression using the PROC REG procedures of the SAS statistical program (SAS Institute, Cary, N.C.). Mean separation was conducted using Tukey's test. The trees were trained and maintained at two shoots per tree. Trees were fertilized before each drought stress period with 14 g nitrogen as NH_4NO_3 per tree. The plots were kept weed free by either applying gramoxone (1,1'-dimethyl-4,4'-bipyridinium) or shallow tillage. Guthion (0,0-dimethyl *S*-4-oxo-1,2,3-benzotriazin-3(4*H*)ylmethyl phosphorodithioate) or malathion (0,0-dimethyl dithiophosphate of diethyl mercaptosuccinate) was applied weekly to suppress insect pests.

Two drought-stress periods lasting about 1 month each were imposed during 1991. The first stress period was from 2 July to 2 Aug., with a recovery period from 3 to 12 Aug. The second stress period was from 13 Aug. to 7 Sept., with a recovery period monitored until 17 Sept. Water was supplied to all trees by drip irrigation at 2 $L \cdot d^{-1}$ per tree before imposition of drought and during recovery periods. Emitters (1 $L \cdot h^{-1}$) were place 8 cm from

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the trunk of each tree. During the stress periods, water was withheld from one-half of the trees, control treatments were maintained at 2 $L \cdot d^{-1}$ per tree. A malfunction prohibited the shelter from closing on 9 July (day 6 of the first stress period), and 10 mm of rain fell on this date.

The following measurements were taken twice weekly at about the same time of day to reduce diurnal variation. Soil moisture content was determined using a time-domain reflectometer (TDR Tektronix 1053, Beaverton, Ore.) and 32-cm steel rods to give an average soil moisture content within the top 30 cm of soil (Topp and Davis, 1985; Topp et al., 1982). Measurements were made at seven locations within the root zone randomly determined within each subplot from 9:00 to 10:30 HR. Soil moisture content was converted to soil matric potential using the equations of McLean (1993). Length from the base of the shoot to the apical bud of each shoot was measured for all trees from 13:00 to 14:30 HR. Trunk diameter of all trees was measured from 14:00 to 15:00 HR with a digital micrometer (Fowler Max-Cal) at marked locations on the trunk 5 cm above the bud union. Trunk diameter was converted to trunk cross-sectional area. Trunk cross-sectional area increment (TCAI) from day 0 of the first stress period was calculated from trunk cross-sectional area. Daily leaf growth rate was determined for leaves on both shoots of four of the six replicates per plot by marking the first unfolded leaf, measuring the length of the lamina and width at the widest region of the leaf, and multiplying by 0.7 to determine leaf area (J.A. Flore, unpublished data), remeasuring during the next monitoring period and taking the difference divided by the number of days between measurements. Leaf growth measurements were taken from 8:00 to 10:30 HR. Leaf emergence rate was determined by counting the number of leaves between the leaf marked from the previous measurement period and the leaf marked in the current period and dividing by the number of days between measurements.

At the end of the first stress period, mature leaf area was estimated by measuring lamina length and width at the widest point and multiplying by 0.7 for three mature leaves per shoot for all trees. Plant leaf area was determined by counting the number of unfolded leaves of all trees and then multiplying the mature leaf area by the number of leaves. The trees were defoliated 8 Oct., and leaves were counted and dried to determine dry weight. Mature leaf area and plant leaf area were determined with the defoliated leaves by measuring three mature leaves per tree as described above and multiplying by the number of unfolded leaves. Four of the six replicates were excavated from 17 to 27 Oct. including roots inside and outside of the material lining the trenches. The other two replicates previously had been used for cold-hardiness evaluation (data not shown). Trees were separated into current-season scion growth (1-year-old wood), previous-season scion growth (2-year-old wood), rootstock wood, roots attached to the tree (attached roots), roots sifted from inside the material (inside roots), and roots sifted from outside the material (outside roots) and dried to determine dry weight.

Results

Soil matric potential within the top 30 cm of soil was lower for the drought-stressed treatments 14 and 3 d after imposition of the first and second stress, respectively, and remained lower for both stress periods until irrigation during the recovery periods (Fig. 1). The longer period of time for the difference to become apparent during the first stress period was due to the malfunction of the shelter 7 d into the first stress. Additionally, larger canopies achieved by the second stress period resulted in greater transpirational demand (Fernandez et al., 1997).

The two shoots did not grow at the same rate. The more-apically located shoot was usually more vigorous than the other. Regardless of location, the more-vigorous shoot was denoted as shoot 1 and the less-vigorous as shoot 2. Length of shoot 2 was affected first and was lower 7 and 24 d into the first stress and remained so until termination of the experiment for drought-stressed (D) 'Imperial Gala' trees on Mark (Mark) and 'Imperial Gala' trees on MM.111 (MM.111) compared to control (C) Mark and MM.111, respectively (Fig. 2A). Length of shoot 2 of 'Imperial Gala' on M.9 EMLA (M.9 EMLA) were different between control and drought-stressed treatments for only 3 d during the experiment. The length of shoot 2 initially was greater for Mark C than for MM.111 C, but was not different later in the experiment. Final shoot 2 length was 33% and 38% lower for MM.111 D and Mark D, respectively, compared to corresponding controls.

Differences in shoot 1 were not seen until day 7 of the first recovery period for Mark D compared to Mark C (Fig. 2B). Length of shoot 1 for Mark D remained lower than Mark C throughout the second stress period from day 7 until termination. Shoot 1 length was lower for MM.111 D compared to MM.111 C only at $P = 0.10$ from day 3 of the second stress until the end of the experiment except for day 14. No difference in shoot 1 length was found between M.9 EMLA C and any of the drought-stressed rootstocks. Shoot 1 length at termination of the project was reduced by 30% (significant at $P = 0.10$) and 35% (significant at $P = 0.05$) for MM.111 D and Mark D, respectively, compared to corresponding controls.

Growth of both shoots of MM.111 C and Mark C was linear when data were subjected to regression analysis (Fig. 2 A and B). A cubic pattern was apparent for M.9 EMLA C and the drought-stressed rootstocks with a change of inflection of the curves at about 14 and 10 days after imposition of the first stress for shoot 1 and 2, respectively. The curves for both shoots are depressed more for Mark D than MM.111 D compared to corresponding controls. The curves for shoot 1 and 2 length of M.9 EMLA C and the drought-stressed rootstocks were similar in shape and magnitude and shoot length was not different among them during the experiment.

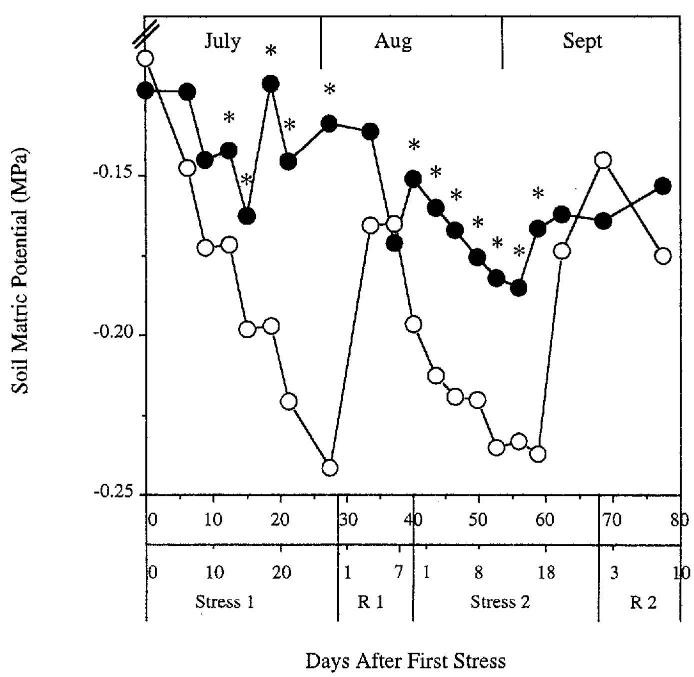

Fig. 1. Soil matrix potential for top 30 cm for drought (○) and control (●) treatments during both stress and recovery periods. *Significant at $P = 0.05$.

Differences in leaf growth rate of the drought-stressed trees versus corresponding controls were mainly found during the second drought stress (Table 1). Leaf growth rate during the first drought stress was lower during the 21- to 24-d measurement for MM.111 D and Mark D compared to MM.111 C and Mark C and during the 28- to 31-d measurement for all drought-stressed rootstocks compared to controls. Leaf growth rate of MM.111 D and Mark D was lower from the 7- to 10-d measurement until the 24- to 28-d measurement of the second drought stress when compared to corresponding controls. Leaf growth rate of M.9 EMLA D was lower than M.9 EMLA C for these same measurement periods during the second drought stress except for the 14- to 21-d measurement. Differences also were found between rootstocks. Leaf growth rate was lower for M.9 EMLA D and MM.111 D during the 3- to 7-d measurement of the first stress compared to Mark D but not the control rootstocks. Leaf growth rate also was lower for the 7- to 10-d measurement of the first drought stress for M.9 EMLA D compared with MM.111 C. Leaf growth rate of M.9 EMLA D was lower than MM.111 C and Mark C but not M.9 EMLA C for the 21- to 24-d and 28- to 31-d measurements during the first drought stress. During the first recovery period leaf growth rate for the drought stressed rootstocks returned to that of the controls by the 4- to 7-d measurement. For the 7- to 10-d measurement of the first recovery period there were not enough new leaves to estimate leaf growth rate for M.9 EMLA D nor were there enough new leaves to estimate leaf growth rate for MM.111 D and M.9 EMLA D for the 3- to 7-d measurement of the second drought stress. For the measurements taken between day 1 and 7 of the second recovery period leaf growth rate for the drought-stressed treatments had returned to the same rate as controls.

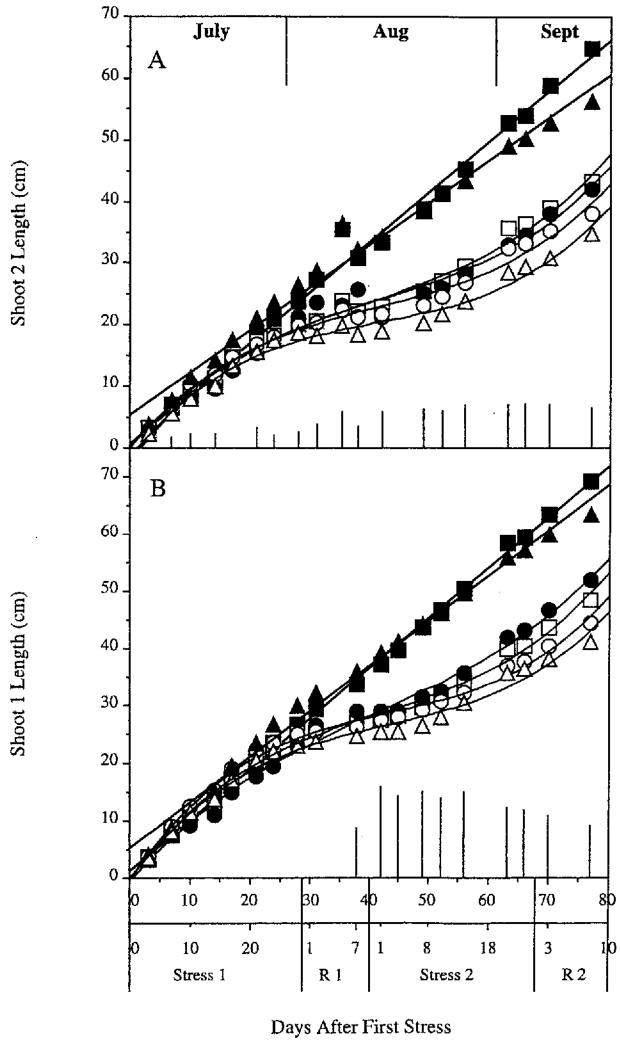

Fig. 2. Shoot length of the less vigorous shoot (shoot 2) for both stress and recovery periods (**A**). Equations for regression lines are as follows: MM.111 C (■), $y = 0.794 + 0.816x$, $R^2 = 0.99$; MM.111 D (□), $y = 0.261 + 1.102x - 0.019x^2 + 0.00016x^3$, $R^2 = 0.99$; M.9 EMLA C (●), $y = -2.127 + 1.280x - 0.023x^2 + 0.00019x^3$, $R^2 = 0.98$; M.9 EMLA D (○), $y = 0.091 + 1.153x - 0.023x^2 + 0.00018x^3$, $R^2 = 0.99$; Mark C (▲), $y = 5.468 + 0.689x$, $R^2 = 0.98$; Mark D (Δ), $y = -1.418 + 1.209x - 0.025x^2 + 0.00020x^3$, $R^2 = 0.98$. Shoot length of the more vigorous shoot (shoot 1) for both stress and recovery periods (**B**). Equations for regression lines are as follows: MM.111 C, $y = 1.156 + 0.885x$, $R^2 = 0.99$; MM.111 D, $y = -0.215 + 1.406x - 0.026x^2 + 0.00021x^3$, $R^2 = 0.99$; M.9 EMLA C, $y = -0.594 + 1.201x - 0.018x^2 + 0.00015x^3$, $R^2 = 0.99$; M.9 EMLA D, $y = -0.284 + 1.551x - 0.031x^2 + 0.00024x^3$, $R^2 = 0.99$; Mark C, $y = 5.134 + 0.796x$, $R^2 = 0.99$; Mark D, $y = -0.062 + 1.384x - 0.027x^2 + 0.00021x^3$, $R^2 = 0.99$. All regression equations are significant at $F < 0.05$. Vertical lines in **A** and **B** represent significant differences by Tukey's test at $P = 0.05$.

Differences in TCAI and leaf emergence rate rarely were seen and were inconsistent during the experiment. Leaf emergence rate was lower for Mark D compared to Mark C on days 14 and 28 of the first drought stress, both days of the first recovery period, and day 3 of the second stress period (Table 2). Leaf emergence rate was lower on day 28 of the first drought stress and day 3 of the second drought stress for MM.111 D and M.9 EMLA D compared to corresponding controls. Leaf emergence rate also was lower on day 7 of the first recovery period for M.9 EMLA D vs. M.9 EMLA C. Trunk cross-sectional area increment was lower for Mark D than Mark C from day 24 of the first drought stress until termination of the experiment (Fig. 3). At termination of the experiment TCAI was 52% lower for Mark D compared to Mark C. There were no differences between MM.111 D and M.9 EMLA D and corresponding controls. However, TCAI generally was highest for MM.111 C, MM.111 D, and Mark C during both stress and recovery periods, with Mark D usually exhibiting the lowest TCAI during the experiment and M.9 EMLA C and D exhibiting intermediate TCAI.

TCAI increased linearly for all treatments: MM.111 C had the greatest slope, Mark C and MM.111 D had intermediate slopes, and M.9 EMLA C and D and Mark D had the lowest slopes (Fig. 3). The slopes of the regression lines were 2%, 32%, and 52% lower for M.9 EMLA D, MM.111 D, and Mark D, respectively, compared to corresponding controls.

Dry weights for 1-year-old scion wood were lower for MM.111 D, Mark D, and M.9 EMLA C and D than MM.111 C and Mark C (Table 3). Dry weight of 1-year-old wood was 20% (nonsignificant), 49%, and 56% lower for M.9 EMLA D, MM.111 D, and Mark D, respectively, compared with corresponding controls. No differences were seen in dry weight of 2-year-old wood compared to corresponding controls, but rootstock wood had the highest dry weight for MM.111 C followed by MM.111 D, then Mark C, with Mark D, and M.9 EMLA C and D the lowest. Dry weights of attached roots were lower for MM.111 D and Mark D compared to corresponding controls. Dry weights of attached roots were similar for M.9 EMLA C and all drought-stressed trees. Differences in inside roots were due mainly to rootstock, although M.9 EMLA C was higher than M.9 EMLA D. Dry weights were higher for outside roots of M.9 EMLA D and Mark D compared to corresponding controls. The woven polypropylene geotextile used in this experiment to restrict the root zone was ineffective since up to 27% of root biomass escaped in one season. Total root dry weight was higher for Mark C than all other treatments, while M.9 EMLA D was lower than Mark D and MM.111 C, with no other differences apparent. Total root dry weights were reduced by 31% for

Table 1. Leaf growth rate (change in leaf area, $cm^2 \cdot d^{-1}$, over the range listed) during the first and second drought stress and recovery periods. Stress 1 was imposed on 2 July and released 2 Aug. 1991. Stress 2 was imposed on 13 Aug. and released 7 Sept. 1991.

	Days after stress 1									Days after recovery 1		
Treatment	0–3	3–7	7–10	10–14	14–17	17–21	21–24	24–28	28--31	1–4	4–7	7–10
MM.111 C	2.33	3.33 ab[z]	2.99 a	1.97	1.97	2.96	3.07 a	2.61	3.34 a	3.13 a	2.19	2.85
MM.111 D	2.57	2.78 b	2.64 ab	2.58	0.64	1.61	1.38 b	1.19	1.36 b	1.50 b	1.43	2.50
M.9 EMLA C	2.79	3.22 ab	2.69 ab	1.78	2.09	2.63	2.47 ab	3.25	3.24 a	3.14 a	1.49	2.66
M.9 EMLA D	2.55	2.65 b	2.20 b	2.69	1.37	1.63	1.54 b	1.38	1.54 b	1.57 b	1.43	---
Mark C	2.89	3.22 ab	2.79 ab	1.89	2.31	3.07	3.11 a	3.04	3.43 a	3.26 a	2.37	2.70
Mark D	2.25	3.70 a	2.63 ab	1.54	2.05	1.62	1.64 b	1.57	1.58 b	1.86 b	1.21	2.21
	Days after stress 2							Days after recovery 2				
	1–3	3–7	7–10	10–14	14–21	21–24	24–28	1–7				
MM.111 C	2.84	3.33	3.27 b	4.80 a	4.70 ab	2.09 a	4.53	3.62				
MM.111 D	2.01	---	2.56 c	2.08 b	2.50 c	1.14 b	3.49	3.79				
M.9 EMLA C	2.24	2.95	3.23 b	4.49 a	3.94 abc	2.32 a	4.59	3.80				
M.9 EMLA D	1.59	---	2.39 c	2.69 b	2.66 bc	1.28 b	3.55	3.20				
Mark C	2.84	3.43	3.66 a	4.85 a	4.79 a	2.05 a	3.91	2.98				
Mark D	1.70	2.15	1.85 d	2.12 b	2.09 c	1.29 b	3.08	3.67				

[z]Means followed by different letters within the same column are significantly different at $P < 0.05$ by Tukey's test. Missing data due to insufficient leaf emergence.

Mark D compared to Mark C. Root : shoot ratio was reduced only for M.9 EMLA D compared to M.9 EMLA C. Total dry weights of the trees were greatest for MM.111 C and Mark C, with MM.111 D lower than MM.111 C but similar to Mark C and Mark D, and M.9 EMLA C and D, which had the lowest dry weights. Total tree dry weight was reduced by 27% and 34% for MM.111 D and Mark D, respectively, compared with corresponding controls.

Dry weights of leaves from shoot 1 were lower for drought-stressed trees compared to corresponding controls and were lower for shoot 2 of MM.111 D and Mark D compared to corresponding controls but not for M.9 EMLA D (Table 4). Mature leaf area and number of leaves on shoot 1 were not affected by rootstocks or treatments at the end of either stress period. Number of leaves on shoot 2 was affected primarily by rootstock, although a response to drought stress was seen in a reduction for Mark D compared with Mark C at the end of the second stress period. M.9 EMLA had the fewest leaves regardless of treatment at the end of the first stress period, and Mark C had the most leaves on shoot 2 at the end of the second stress period, with no differences between the other treatments. Rootstock differences for dry weight measurements except leaf and 1-year-old wood dry weights may have been due to differences in weight at planting; however, differences within rootstock and between treatments were due to the drought stress.

Discussion

Conflicting reports exist concerning drought resistance of dwarfing rootstocks and few deal with Mark rootstock. Results of this experiment indicate a greater degree of drought resistance for M.9 EMLA, with MM.111 intermediate and Mark least drought resistant. There has been concern expressed recently by growers and researchers regarding Mark rootstock and callus-like proliferation of roots, commonly called root mass proliferation (RMP), near the soil line (NC-140, 1991; Waliser, 1994; Warner, 1993). Otero (1994) investigated the extent of occurrence of this phenomenon in Michigan and the anatomical structure of affected tissue to determine anomalies. It was found that RMP occurred at all locations surveyed in over 80% of trees on Mark rootstock but not

Table 2. Leaf emergence rate (leaves/day) during the first and second drought stress and recovery periods. Stress 1 was imposed on 2 July and released 2 Aug. 1991. Stress 2 was imposed on 13 Aug. and released 7 Sept. 1991.

	Days after stress 1									Days after recovery 1	
Treatment	0	3	7	10	14	17	21	24	28	1	7
IG/MM.111 C	1.23	0.88	1.16	1.50	0.91 ab[z]	1.46	1.03	1.25	0.88 b	0.92 a	0.30 a
IG/MM.111 D	1.23	1.17	1.03	1.75	0.81 abc	1.38	0.69	1.36	0.56 c	0.83 ab	0.21 ab
IG/M.9 EMLA C	0.95	0.96	0.91	1.21	0.69 cd	1.13	0.85	1.11	0.84 b	0.83 ab	0.25 a
IG/M.9 EMLA D	0.73	0.92	1.25	1.38	0.78 bcd	1.17	0.79	1.24	0.47 c	0.67 bc	0.07 c
IG/Mark C	1.27	1.29	1.03	1.50	0.94 a	1.33	1.13	1.08	1.09 a	0.79 ab	0.27 a
IG/Mark D	0.89	0.83	1.00	1.38	0.66 d	1.38	0.97	1.24	0.53 c	0.54 c	0.13 bc
	Days after stress 2							Days after recovery 2			
	1	3	7	10	14	21	24	3	10		
IG/MM.111 C	0.39	0.34 a	0.88	0.79 a	0.47	1.04	0.75	1.13	0.89		
IG/MM.111 D	0.26	0.11 b	0.19	0.38 a	0.35	1.29	0.75	0.91	0.71		
IG/M.9 EMLA C	0.27	0.32 a	0.50	0.71 ab	0.38	0.95	0.79	1.00	0.82		
IG/M.9 EMLA D	0.09	0.09 b	0.16	0.17 b	0.25	1.16	0.71	0.75	0.70		
IG/Mark C	0.41	0.38 a	0.59	0.92 a	0.50	0.96	0.63	0.81	0.66		
IG/Mark D	0.13	0.09 b	0.13	0.46 ab	0.22	1.30	0.75	0.69	0.54		

[z]Means followed by different letters within the same column are significantly different at $P < 0.05$ by Tukey's test.

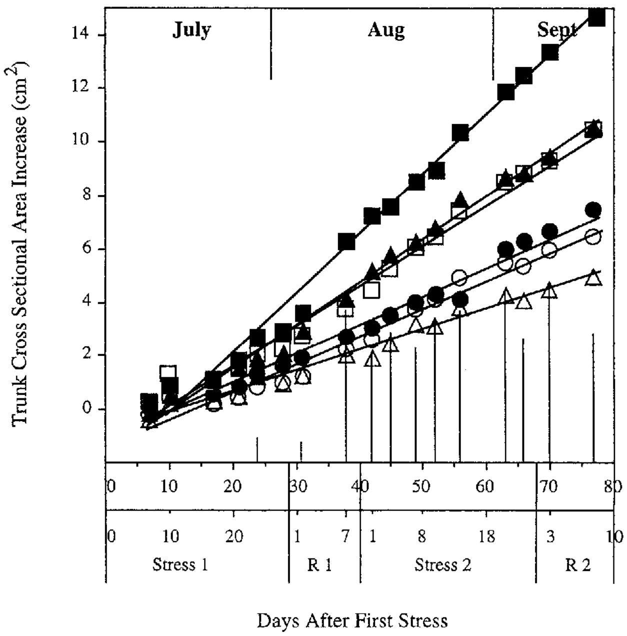

Fig. 3. Trunk cross-sectional area increment for both stress and recovery periods. Vertical lines represent significant differences by Tukey's test at P = 0.05. Equations for regression lines are as follows: MM.111 C (■), y = –2.343 + 0.222x, R^2=0.99; MM.111 D (□), y = –1.3615 + 0.151x, R^2=0.98; M.9 EMLA C (●), y = –1.115 + 0.107x, R^2 = 0.97; M.9 EMLA D (○), y = –1.429 + 0.104x, R^2 = 0.97; Mark C (▲), y = –1.656 + 0.161x, R^2 = 0.99; Mark D (Δ), y = –0.853 + 0.077x, R^2 = 0.98. All regression equations are significant at F < 0.05.

on other rootstocks. The anatomical study found swirling patterns in the xylem vessels and other anomalies in the xylem. This could be partially responsible for the sensitivity of Mark rootstock to drought stress by inhibiting water flow through the xylem. In a separate study, the anomalous growth was found to be greater for Mark rootstock when under stress (unpublished data).

Leaves and shoots of MM.111 and Mark were affected adversely by drought stress but the root : shoot ratio was not, and these rootstocks performed poorly under drought stress compared to M.9 EMLA. The root : shoot ratio was lower for M.9 EMLA D than M.9 EMLA C, indicating carbohydrate partitioning favoring the shoot system. There were more outside roots and fewer inside roots for M.9 EMLA D and Mark D than corresponding controls, indicating a change in root distribution pattern. The smaller mass of the root system and wider root distribution pattern of M.9 EMLA D compared to M.9 EMLA C may have resulted in slower depletion of soil water in the root zone. Root distribution patterns have been shown to be affected by adverse soil conditions (Beukes, 1984; Fernandez et al., 1995; Layne et al., 1986). Roots were found to have a greater ability to adjust osmotically and continue growth than leaves, stems, and silks of corn (Westgate and Boyer, 1985), which also may have occurred during this study since total root dry weight was lower only for Mark D than Mark C. Although the root system of Mark adapted to stress with regard to root distribution, root mass was lower for drought stressed trees unlike M.9 EMLA and MM.111. This could result in inadequate water uptake. Combined with anomalous growth of the xylem vessels, transport of water to the shoot system of Mark D may have been reduced greatly.

Differences in leaf growth rate occurred fairly early and returned to control levels upon irrigation during both recovery periods. There was no difference in mature leaf area, indicating that drought delayed leaf maturity rather than decreased leaf area. There were few differences in leaf area and number at the end of the second stress period; however, final leaf dry weights were lower for MM.111 D and Mark D than corresponding controls indicating other aspects of the leaf were affected, such as leaf thickness.

Growth of shoot 2 was the first parameter to respond to drought stress and showed the most consistent differences between drought and control; however, values for drought-stressed trees did not return to those of controls during the recovery periods. Growth of shoot 2 may be the most sensitive parameter to measure onset of a single stress event per growing season but it may not indicate when recovery or subsequent stress occurs. Length of a less vigorous shoot also may be a more difficult parameter to measure in complex canopies. Leaf emergence rates were inconsistent and did not return to control rates during either of the recovery periods. Differences in TCAI were not as consistent and did not occur between all treatments as was seen for leaf growth rate or length of shoot 2.

Regression analysis of shoot 1 and 2 length and TCAI vs. duration of stress was useful in understanding drought stress response; however, relying on this method to determine onset of stress may be misleading since various rootstocks, scions, and species have different growth curves (unpublished data) and models would have to be developed for each situation. The inflection points of the regression curves of the drought-stressed rootstocks occurred at dates similar to the more sensitive parameters, but curves could be calculated only after all data were collected.

An easily measured growth parameter that acts as a sensitive indicator of the water status of the plant would aid researchers studying water stress and orchardists interested in optimizing irrigation practices. Since plants respond differently to stress, even the same scion on a different rootstock, it would be more reliable to use a plant parameter for irrigation scheduling versus the various measures of soil water potential. This is especially true in situations with several rootstocks in the same orchard.

The most drought resistant of the three rootstocks in this study was M.9 EMLA, with MM.111 intermediate and Mark most

Table 3. Dry weights (g) of woody tissues at termination of the experiment.

	Wood			Roots				Root : shoot	Total
Treatment	(1-year)	(2-year)	Rootstock	Attached	Inside	Outside	Total	ratio	dry wt
IG/MM.111 C	23.90 a[z]	14.71	76.18 a	20.15 a	8.56[y] bc	4.67[y] c	33.97[y] b	0.30 b	183.31 a
IG/MM.111 D	12.10 b	13.47	61.66 b	14.20 b	6.26 c	5.13 bc	25.75 bc	0.32 b	132.25 bc
IG/M.9 EMLA C	11.90 b	12.49	34.69 d	10.28 b	15.09 a	3.23 c	28.33 bc	0.50 a	119.68 c
IG/M.9 EMLA D	9.51 b	12.02	36.90 d	8.30 b	7.71 b	6.65 b	21.98 c	0.39 b	101.03 c
IG/Mark C	23.49 a	23.72	46.42 c	26.54 a	14.95 a	5.14 bc	45.12 a	0.48 a	177.66 ab
IG/Mark D	10.30 b	15.06	39.06 d	12.17 b	10.88 ab	10.09 a	31.28 b	0.51 a	117.47 c

[z]Means followed by different letters within the same column are significantly different at P < 0.05 by Tukey's test.
[y]Means adjusted for missing data.

Table 4. Leaf dry weights at termination and leaf area and number at end of each stress cycle.

	Termination		Stress 1			Stress 2		
Treatment	Shoot 1 leaf dry wt (g)	Shoot 2 leaf dry wt (g)	Leaf area (cm^2)	Shoot 1 leaf no.	Shoot 2 leaf no.	Leaf area (cm^2)	Shoot 1 leaf no.	Shoot 2 leaf no.
IG/MM.111 C	18.84 a[z]	15.70 ab	25.94	31.50	31.13	36.35	41.00	36.58 ab
IG/MM.111 D	14.37 bc	10.04 c	23.13	32.25	28.50	30.02	40.00	35.92 ab
IG/M.9 EMLA C	17.48 ab	12.09 bc	28.47	29.38	24.50	33.64	38.42	33.10 b
IG/M.9 EMLA D	10.81 c	9.67 c	24.01	29.75	25.92	28.41	34.92	31.80 b
IG/Mark C	22.06 a	14.32 a	32.73	33.88	32.00	37.62	42.08	40.28 a
IG/Mark D	12.38 c	9.39 c	23.23	31.00	26.50	29.91	38.00	33.00 b

[z]Means followed by different letters within the same column are significantly different at $P < 0.05$ by Tukey's test.

sensitive, suggesting that M.9 EMLA would be the best choice for conventionally managed orchards subject to drought. Conversely, irrigated Mark was as vigorous as MM.111, indicating that Mark is sensitive to available water. The generalization that dwarfing rootstocks are drought resistant does not apply to Mark and, therefore, each dwarfing rootstock should be evaluated independently. The many similarities between M.9 EMLA C and all drought-stressed rootstocks may indicate that M.9 EMLA is always under stress, although more research is needed to determine this. The sensitivity of Mark to water stress and the widespread occurrence of RMP (NC-140, 1991; Otero, 1994) needs to be considered in management systems, especially in areas subject to drought conditions.

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