This is to certify that the

dissertation entitled

MECHANISMS OF DROUGHT TOLERANCE IN APPLE AS INFLUENCED BY ROOTSTOCK

presented by

Rodney Thomas Fernandez

has been accepted towards fulfillment
of the requirements for

Ph.D. degree in Horticulture

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Date Nov. 16, 1992

MECHANISMS OF DROUGHT TOLERANCE IN APPLE AS INFLUENCED BY ROOTSTOCK

By

Rodney Thomas Fernandez

A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Horticulture

1992

ABSTRACT

MECHANISMS OF DROUGHT TOLERANCE IN APPLE AS INFLUENCED BY ROOTSTOCK

By

Rodney Thomas Fernandez

Root distribution patterns of 'Starkspur Supreme Red Delicious' apple (*Malus domestica* Borkh.) propagated on MAC 9, MAC 24, M.7 EMLA, M.9, M.9 EMLA, M.26 EMLA, M.27 EMLA OAR 1 and Ottawa 3 rootstocks were characterized at Michigan and Ohio sites with substantially different soil types. The number of roots/dm^2 was highest for the more vigorous rootstocks and lowest for the most dwarfing rootstock. Roots were distributed evenly throughout the soil profile in Michigan except the more dwarfing rootstocks had fewer roots deeper in the soil profile. Roots were restricted to the soil profile above 60 cm in Ohio due to a fragipan and high soil bulk densities. Trees on M.9 EMLA had more roots/dm^2 in Michigan than Ohio while MAC 9 had more roots/dm^2 in Ohio than Michigan.

Root hydraulic conductance (L_p) as determined by pressure induced flow for the apple rootstocks in order from greatest to least was M.9 EMLA, M.26 EMLA, Mark, MM.106 and MM.111. Root system size was considered important in L_p since the absolute flow (L_p without considering root system size) was almost twice that of the next highest for Mark.

Translocation of ^{14}C assimilates and gas exchange parameters were not affected by pressurizing the roots in the chamber system used for L_p determination. These findings demonstrate that the pressure chambers could be used for whole plant studies without disrupting shoot to root translocation.

'Imperial Gala' apple on Mark, M.9 EMLA and MM.111 rootstocks were subjected to two drought stresses, each followed by an irrigated recovery period. Trees on Mark rootstock were found to be most sensitive to drought stress showing significant differences first in 21 of the 27 growth and physiological parameters measured, MM.111 intermediate with differences first for 6 of the 27 parameters and M.9 EMLA were most drought tolerant with differences first for 5 of the 27 parameters. Reductions in growth of up to 56%, 49% and 20% were found for drought stressed trees on Mark, MM.111 and M.9 EMLA, respectively. Leaf growth rate and leaf water potential were considered to be the most sensitive parameters to drought stress, showing differences early and consistently and returning to control levels during recovery.

DEDICATION

This dissertation is dedicated to my parents, Louis and Gail Fernandez, whose love and support has always encouraged me to fulfill my goals.

ACKNOWLEDGEMENTS

I would like to express my sincere gratitude to Dr. Ronald Perry, my major professor, for the support, advice, and mostly, the friendship that he has generously given during my doctoral program. The interest and encouragement he has given to our projects provided motivation for their completion.

I also would like to thank the members of my guidance committee, Dr. Kurt Pregitzer and Dr. Alvin Smucker, for their encouragement, interest and suggestions with the dissertation projects and curriculum; Dr. Robert Schutzki for his advice and interest and his active participation in one of the dissertation projects as well as his friendship; and especially Dr. James Flore for watching after my program during Dr. Perry's sabbatic, for the many good ideas and great enthusiasm and for his valued friendship.

I would like to thank my good friend, Dr. Fred S. Davies of the University of Florida, for encouraging me to pursue a graduate course at Michigan State University, advice of which I am very grateful.

Appreciation is extended to Dr. David C. Ferree of Ohio State University for the opportunity to conduct cooperative work with him that was an essential part of this dissertation.

I would like to especially thank Kenneth Gordon and Daniel Kort for their invaluable assistance with these projects as well as the friendships we made. Joan Runkel, Mark Longstroth, David Costolo and Lynne Sage also provided assistance and camaraderie for many of the projects. Gloria Blake, Jane Waldron and Sherry Mulvaney of the secretarial staff provided much assistance and good friendship as well.

The support and assistance of my friends Mike McLean, Bill Evans, Des Layne and the many others in the department made my experiences at M.S.U. much easier and pleasant.

The love, support and encouragement of my parents, brothers and sisters, grandparents and the rest of my family has led to the successful completion of my goals in graduate school and will continue to inspire me in the future.

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Guidance Committee:

The journal-article format was adopted for this dissertation in accordance with departmental and university requirements. Each section was prepared as a self-standing manuscript so there is some duplication in the Materials and Methods portion of some sections of the dissertation. Section I, III and IV were prepared for publication in the *Journal of the American Society of Horticultural Science*. Section II was prepared for publication in *HortScience*.

INTRODUCTION

Mechanisms of plant tolerance and avoidance of water stress are not well understood. Many studies have demonstrated the effects of drought on apple grafted to different rootstocks but little has been done to determine the mechanisms of stress tolerance. One hypothesis is that rooting depth is involved in water stress avoidance (Parker, 1968). Many plants adapted to arid conditions form root systems as deep as 30 m. Deep rooted plants may be more drought tolerant because they can utilize water at greater depths in the soil profile while plants with roots distributed nearer the surface may be more drought susceptible because water in this region is depleted first and is influenced by evaporation.

Root hydraulic conductance has been shown to decrease under water stress as does photosynthesis, transpiration and stomatal conductance (Davies and Flore, 1986; Syvertsen et al., 1984). Root resistance, the inverse of conductance, is considered the greatest resistance to water flow in plants, ranging from 40% to 80% of the total resistance for apple (Landsberg and Jones, 1981; Davies and Lakso, 1979; Olien and Lakso, 1986). It has been suggested that root hydraulic conductance is involved in regulation of stomata either directly or by limiting the transport of water, hormones or nutrients (Davies and Flore, 1986).

Drought stress affects growth and physiology of plants. In the case of apples and other crops that are commonly grafted, the effects of stress can be minimized by the use of drought tolerant rootstocks. Understanding how rootstocks adapt and respond to drought stress is essential in selecting the proper rootstock for situations where drought stress is a likely occurrence. A measurable growth or physiological parameter that is sensitive to drought stress could be used to evaluate stress tolerance of various apple rootstocks and as a tool for irrigation management to alleviate stress and minimize water inputs.

The overall objectives of this dissertation were to characterize the root distribution patterns of apple clonal rootstocks and determine adaptation to different soil environments of the rootstocks, evaluate the root hydraulic conductance of several apple clonal rootstocks and determine the drought tolerance and adaptation to drought of three apple clonal rootstocks and evaluate the sensitivity of growth and physiological parameters in detecting onset of drought stress.

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SECTION I. ROOT DISTRIBUTION PATTERNS OF NINE APPLE ROOTSTOCKS AT MICHIGAN AND OHIO 1980 NC-140 TRIAL LOCATIONS

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Received for publication . Acknowledgement is made to the Michigan Agricultural Experiment Station, the Ohio Agricultural Experiment Station and the Michigan Apple Research Committee for their support of this research. The authors also wish to thank Mark Longstroth, Joan Runkel, Daniel Kort and Kenneth Gordon for their assistance with this project.

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Production and Culture

Root Distribution Patterns of Nine Apple Rootstocks at Michigan and Ohio 1980 NC-140 Trial Locations

Additional Index Words: *Malus domestica*, root distribution

Abstract. Root distribution of 'Starkspur Supreme Red Delicious' on nine apple rootstocks at the Michigan and Ohio sites for a 1980 NC-140 Uniform Apple Regional Rootstock Trial was determined using the trench profile method. The two locations differed greatly in soil type, a Marlette fine sandy loam at Michigan and a Canfield silt loam with a fragipan at Ohio. Roots were counted and separated into three size categories: less than 2 mm in diameter, 2 to 5 mm in diameter and greater than 5 mm in diameter. Number of roots counted per tree could be separated into 5 rootstock groups for the Michigan location: MAC.24 with the most roots/dm^2 per tree; OAR 1 with the second most; M.26 EMLA and M.9 EMLA with the third most; and M.7 EMLA, Ottawa 3, M.9 and MAC.9 with the fourth most; and M.27 EMLA with the least. In Ohio three groups were apparent with MAC.24 again having the most roots/dm^2 per tree; OAR 1, MAC.9 and M.7 EMLA intermediate and M.26 EMLA, Ottawa 3, M.9 EMLA and M.9 with the least. Depth of rooting could be separated into basically the same rootstock groupings as for total roots/dm^2. Root distribution pattern by depth was affected by soil type with roots fairly well

distributed throughout the Michigan soil but restricted to above the fragipan in the Ohio soil. Two rootstocks appeared to differentiate from others in adaptation to soil conditions at the different sites. MAC.9 had the second lowest number of roots/dm^2 at the Michigan location yet the second most at the Ohio location while M.9 EMLA had the fewest roots/dm^2 at the Ohio location and the fourth most at the Michigan location.

Soil bulk density, texture, water content and strength have substantial influence on root growth (Taylor and Gardner, 1963). High bulk densities and hardpans restrict root penetration and alter root distribution patterns (Eavis and Payne, 1968, Greacen et al., 1968). Adaptation of apple rootstock root systems to soil conditions is an important component in determining orchard performance and identifying and correcting possible problems such as drought or flooding by rootstock selection.

Characterization of root distribution patterns and adaptations to soil limitations are important to aid in rootstock selection. The objective of this study was to describe the root distribution pattern of nine clonal apple rootstocks at two NC-140 trial locations with highly different soil characteristics and determine adaptation to soil environment.

Materials and Methods

The 1980 NC-140 Uniform Apple Regional Rootstock Trial consisted of 'Starkspur Supreme Red Delicious' scion (*Malus domestica* Borkh.) propagated on 9 rootstocks: M.7 EMLA, M.9 EMLA, M.26 EMLA, M.27 EMLA, M.9, MAC 9, MAC 24, OAR 1 and Ottawa 3. Of the 15 cooperators, the sites located at Michigan State University, East Lansing, MI and Ohio State University, Ohio Agricultural Research and Development Center, Wooster, OH were used for this study. Trees were planted with a 3.5 m within-row and 5.5 m between-row spacing with North to South row orientation in a randomized complete block with 5 replications. Trees were trained to a central leader and received similar management practices at both sites.

The soil type at the Michigan location is a Marlette fine sandy loam (Fine-loamy, mixed, mesic Glossoboric Hapludalfs) with a reported bulk density of approximately 1.4 g/cm^3 (Anon, 1979). This soil is described as moderately well drained with moderate to moderately slow permeability (Anon, 1979). The soil type at the Ohio site is a Canfield silt loam (Fine-loamy, mixed, mesic Aquic Fragiudalfs), described as a moderately well drained soil with a fragipan (Anon., 1981). The fragipan was observed to be between 50 and 70 cm below the soil surface. Permeability is moderate above the fragipan but poor through the fragipan. The bulk density above the fragipan is between 1.3 and 1.5 g/cm^3 and greater than 1.7 g/cm^3 below the fragipan (Anon., 1981).

The profile wall method (Oskamp and Batjer, 1932) was used to determine the number of roots. Excavation began 9 Oct. 1989 and 30 Apr. 1990 for the Ohio and Michigan sites, respectively. Since the highest proportion of roots are found within 1 m from the center of the trunk of apple trees (Atkinson, 1980) trenches were excavated parallel to tree rows 0.8 m from the center of the trunks on both sides. The most common range for depth of rooting of apple is from 1 to 2 m (Atkinson, 1980), therefore, the trenches were 1.5 to 2 m deep. A frame was constructed at 1.2 m deep X 1.8 m wide and divided with cotton string into mapping grid squares of 15 cm deep X 30 cm wide. The soil on the face of the trench was loosened an additional 5 cm deep perpendicular to the soil profile with and washed with a high pressure water gun to expose roots. Grids were placed over the washed profiles and roots were counted and sized on corresponding paper grids as described by Layne et al. (1986). Roots were classified into 3 size categories: less than 2 mm (small), 2 to 5 mm (medium), and greater than 5 mm in diameter (large).

Subsequent to recording root numbers, roots were spray painted white to contrast with the soil and horizon interfaces were denoted with an orange painted line. Photographs were taken to illustrate the distribution pattern *in situ*.

The analysis of variance for the root mapping indicated little to no effect on root numbers due to the east or west profile of the tree or due to distance from the center of the trunk (data not shown), therefore, both profiles and all distances were combined for analysis. Data was analyzed to determine the relationship between number and size of roots at each depth by rootstock and presented as numbers of roots/dm^2 soil surface area. Differences in number of roots/dm^2 by depth also was analyzed for each rootstock.

Results

At the Michigan location, MAC 24 and OAR 1 were distinct in number of roots/dm^2 per tree from all other rootstocks. MAC 24 produced the greatest number of roots/dm^2 per tree in all size categories except for medium roots/dm^2 where MAC 24 was second to OAR 1 (Tables 1-3). OAR 1 had the second highest number of roots in all but the above mentioned size category. The other rootstocks showed some variation in number of roots/dm^2 per tree due to root size category.
M.26 EMLA and M.9 EMLA had the third highest number of small roots/dm^2 per tree followed by M.9 EMLA, M.7 EMLA, Ottawa 3, M.9 and MAC 9, with M.27 EMLA having the least roots/dm^2 per tree in this size category (Table 1). For medium roots/dm^2 per tree, M.26 EMLA, M.9 EMLA, M.7 EMLA and Ottawa 3 were third highest in number of roots/dm^2 per tree and M.9, MAC 9 and M.27 EMLA had the fewest number of roots/dm^2 per tree (Table 2). M.26 EMLA, M.9 EMLA and M.7 EMLA had the third highest number of large roots/dm^2 per tree followed by Ottawa 3 and M.9 with MAC 9 and M.27 EMLA having the least roots in this size category (Table 3).

M.27 EMLA was not included in the root mapping of the Ohio site since all but one replicate died before excavation due to severe frost heaving exposing the root system and resulting in root injury (Warmund et al., 1991). Again, MAC 24 was distinct from the other rootstocks in number of roots/dm^2 per tree for the Ohio location. MAC 24 always had the highest number of roots/dm^2 per tree for all size categories (Tables 4-6). OAR 1 still had the second highest number of small roots/dm^2 per tree in Ohio but shared this position with MAC 9 and M.7 EMLA (Table 4). The remaining rootstocks had the least roots/dm^2 per tree for this size category. For medium roots/dm^2, OAR 1 had the second most; M.7 EMLA, Ottawa 3 and MAC 9 had the third most; and M.9 EMLA, M.9 and M.26 EMLA had the fewest roots/dm^2 per tree at the Ohio location (Table 5). Rankings for large roots/dm^2 were the same as those for small roots/dm^2 except Ottawa 3 was included in the OAR 1 group for the Ohio site (Table 6).

Depth of rooting also was affected by rootstock (Table 1-6). Basically, rootstocks followed the same ranking for each depth as for roots/dm^2 per tree for each size category with MAC 24 having the highest number of roots/dm^2 counted at both locations and M.27 EMLA or M.9 and M.9 EMLA having the lowest at the Michigan or Ohio location, respectively.

Root distribution throughout the depth of the profile showed different patterns for rootstocks and locations (Tables 1-6). For the Michigan site MAC 24 and M.7 EMLA had the most consistent number of small roots/dm^2 throughout the profile (Table 1). MAC 24 showed no difference in number of small roots/dm^2 by depth except from 105 to 120 cm where there were fewer roots than the other depths (Table 1). M.7 EMLA had more small roots/dm^2 in the 15 to 30 cm depth than all other depths and fewer roots/dm^2 at the deepest depth with no difference in other depths (Table 1). OAR 1, M.9 EMLA, Ottawa 3, M.9 and M.27 EMLA at the Michigan location had more small roots/dm^2 for the 15 to 30 cm depth than the 0 to 15 cm depth and often more than the other depths (Table 1). This group of rootstocks also exhibited a gradual decline in number of small roots/dm^2 from the 30 to 45 cm depth to the 105 to 120 cm depth. M.26 EMLA displayed a steady decline in number of small roots/dm^2 from the 0 to 15 cm depth throughout the profile except for the 90 to 105 cm depth which was similar to the upper depths (Table 1). The greatest differences in root distribution of small roots due to depth at the Michigan location was seen for MAC 9 which showed a constant decrease in the number of roots/dm^2 below 30 cm (Table 1).

The most consistent distribution of medium roots/dm^2 throughout the profile in Michigan was seen for M.9 EMLA, M.9 and M.7 EMLA with very few differences in number of roots by depth (Table 2). The number of medium roots/dm^2 was higher in the 0 to 15 cm, 15 to 30 and 30 to 45 cm depths than the lower depths for MAC 9; higher in the 10 to 15 cm depth than the lower depths for M.26 EMLA; and higher in the 10 to 15 cm depth than the 15 to 30 cm depth which was higher than the remaining depths for MAC 24 at the Michigan location. OAR 1 had a similar number of roots/dm^2 in Michigan for the 0 to 15 cm and 15 to 30 cm but the 15 to 30 cm depth had more roots than the 30 to 45 cm depth with a sharp decrease in number of medium roots for subsequent depths. Ottawa 3 at the Michigan location had a pattern similar for medium roots/dm^2 to OAR 1, with comparable numbers for the 0 to 15 and 15 to 30 cm depths but a large decrease in numbers for subsequent depths. There was an increase in number of medium roots/dm^2 from the 15 to 30 cm depth to the 30 to 45 cm depth but a decrease at lower depths for M.27 EMLA in Michigan.

The number of large roots/dm^2 at the Michigan location was higher in the 0 to 15 cm and 15 to 30 cm depths with a rapid decrease at all other depths for MAC 24, OAR 1, M.7 EMLA, Ottawa 3, M.9 and MAC 9 (Table 3). This same trend was apparent for M.27 EMLA and M.9 EMLA except M.27 EMLA had more large roots/dm^2 only at the 15 to 30 cm depth and M.9 EMLA had more large roots/dm^2 for the 30 to 45 cm depth as well as the other two depths. M.26 EMLA had a more even distribution of large roots/dm^2 at deeper depths than the other rootstocks.

The root distribution pattern for small roots/dm^2 at the Ohio location was much more consistent across rootstocks. All rootstocks showed a gradual decrease in number of small roots/dm^2 from the 0 to 15 cm depth to the 45 to 60 cm depth with a considerable decrease subsequently. There was up to an order of magnitude difference in roots in the upper depths compared to the depths below 60 cm. The depths below 60 cm roughly correspond with the location of the fragipan in the Ohio soil (Anon., 1981).

In Ohio, the same root distribution pattern was seen for medium and large roots/dm^2 as for small roots/dm^2 except for each larger root size category roots were restricted to higher depths. For medium roots/dm^2 there were virtually no roots below 75 cm for most rootstocks and for large roots/dm^2 almost no roots were found below 60 cm in most instances. MAC 24 typically maintained a higher number of roots/dm^2

to a greater depth than the other rootstocks while M.26 EMLA, M.9 EMLA, M.9 and MAC 9 usually had very sparse rooting below 45 cm.

Discussion

There was little difference in ranking of rootstocks in number of roots/dm^2 per tree for all root diameters combined and small roots/dm^2. And since 90% to 96% of the roots counted were less than 2 mm in diameter (Fernandez et al., 1991), this size category will be used to describe total roots/dm^2 per tree in further discussion.

Although statistical comparison between the two sites cannot be made, relative performance of the rootstocks at each site show that adaptation to soil conditions has occurred. MAC 9 and M.9 EMLA virtually switched ranking at the two locations. MAC 9 had the second lowest number of roots/dm^2 per tree at the Michigan location, ahead of M.27 EMLA only, yet the second most at the Ohio location, similar to OAR 1. M.9 EMLA was in the third highest grouping of number of roots/dm^2 per tree behind OAR 1 at the Michigan location but had the fewest roots/dm^2 per tree in Ohio.

Scion vigor and the intensity and extensiveness of the root system has been shown to be positively correlated for many apple rootstocks (Atkinson, 1980; Avery, 1970; Coker, 1958; Rogers and Vyvyan, 1934). Rootstock performance with respect to scion vigor and yield parameters was similar for both locations (NC-140, 1991). For the Michigan location, trunk cross sectional area (TCA), tree height and spread

(NC-140, 1991) were similar in ranking by rootstock to number of roots/dm^2 per tree for all rootstocks except M.9 EMLA. The same was also the case for the Ohio location except MAC 9 instead of M.9 EMLA was the anomaly. However, the apparent differences in the size of the root systems of M.9 EMLA and MAC 9 at the two locations had no relationship to the 10-year cumulative yield/TCA (NC-140, 1991).

Although rootstock affected number of roots/dm^2 and depth of rooting, the site had more influence on the root distribution pattern by depth. Depth of rooting was restricted by the fragipan in Ohio and most roots were in soil layers above 60 cm. There was no such restriction to root distribution in Michigan and roots were distributed fairly evenly throughout the soil profile with a moderate decrease in roots/dm^2 with depth and in some cases no decrease until the lowest depth measured. Several authors have found a rootstock soil interaction for various tree crops with rootstocks performing differently under the diverse soil types (Cockroft and Wallbrink, 1966; Greacen et al., 1968; Irizarry et al., 1981; Mikhail and El-Zeftawi, 1978; Oskamp, 1932; Rogers and Vyvyan, 1934) confirming the observation in this study regarding MAC 9 and M.9 EMLA adaptation to soil environment. Rogers and Vyvyan (1934) found an increase in total weight of four Malling apple rootstock roots system from a heavy clay to a light sand to a loam.

Soil physical conditions affect root growth, especially mechanical impedance which is related to soil bulk density (Eavis and Payne, 1968; Greacen et al., 1968). Cemented or highly compacted pans present a physical barrier that severely limits root penetration (Eavis and Payne, 1968, Greacen et al., 1968). This would explain the limitation of the root system to the upper layers of the Ohio soil while no restriction of the root system is seen at the Michigan location.

The distribution pattern of M.9 EMLA and MAC 9 at both locations are shown in Figure 1. Most of the roots at the Ohio site are confined to the top 60 cm while they are well distributed through the profile in Michigan. M.9 EMLA has roots well distributed in all layers of the soil profile at the Michigan location (Figure 1A) while there are few roots in the lower horizon at the Ohio site (Figure 1B). Root distribution of MAC 9 at the Michigan location (Figure 1C) is more sparse than the Ohio location (Figure 1D). This indicates adaptation of MAC.9 to heavy soils with M.9 EMLA performing better in Michigan with the other rootstocks not affected by soil type as far as total number of roots although root distribution was altered.

The percent of small roots was between 92% to 96% and 88% to 95% for the Michigan and Ohio site, respectively. The percent of medium roots was generally 3% or 4% at the Michigan location while usually 5% or greater at the Ohio location. The percent of large roots was from 1% to 2% at the Michigan site and typically 3% to 4% at the Ohio location. The percent of small roots and large roots was greater at the Ohio site except for M.26 EMLA for the former and MAC.9 for both size categories. Of the nine rootstocks, M.26 EMLA, M.7 EMLA and MAC.9 showed little to no change in percent of roots in each size category between the two locations. The rootstocks MAC 24, M.9 EMLA, OAR 1 and Ottawa 3 showed the greatest effect by site in percent roots in each size category. These results agree with a report by

Beukes (1984) showing an effect of soil type on percent of roots in different size categories.

In this study, rootstock had the greatest effect on number of roots per tree. Rootstocks were similar at both locations with respect to total number of roots counted and roots less than 2 mm with only three rootstocks with differences in the other size categories. Percent of roots in each size category was affected by location with more roots larger than 2 mm at the Ohio location. Roots appeared to be restricted to the upper 60 cm at the Ohio site but were more evenly distributed at all depths at the Michigan site.

Many aspects of tree root systems are similar, yet soil environment causes modifications moderated by genotype. The distribution pattern and size of root systems is integral to the understanding of stresses perceived by the root system. Characterizing the root systems of different genotypes under different soil environments is necessary to understand how these two factors affect adaptation of plants to soil stresses under different conditions and locations.

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Caption for Figure

Figure 1. Root distribution of two rootstocks at the Michigan and Ohio locations. (A) M.9 EMLA rootstock at the Michigan site. (B) M.9 EMLA rootstock at the Ohio site. (C) MAC 9 rootstock at the Michigan site. (D) MAC 9 rootstock at the Ohio site. Roots were spray painted white. Top, bottom and side orange lines denote area of grid for **A** and **C**, the middle two orange lines from top to bottom separate the A and B horizons and the B and Bt horizons. The top orange line in **B** and **D** denotes the soil surface and the second line separates the A and B horizons. The black and white sections of the bar in **B** and **D** are 30 cm each.

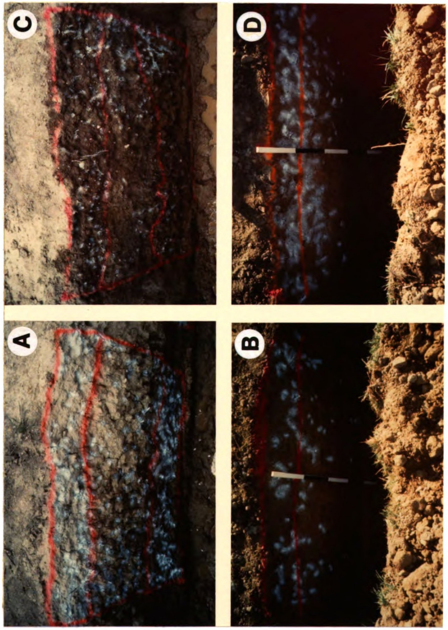

Figure 1

Table 1. Number of roots/dm^2 less than 2 mm in diameter for each depth and per tree (All depths) for the Michigan location.

	Rootstock									
Depth (cm)	MAC 24	OAR 1	M.26 EMLA	M.9 EMLA	M.7 EMLA	Ottawa 3	M.9	MAC 9	M.27 EMLA	Rootstock LSD^z
0-15	5.4	3.7	3.9	2.7	2.3	1.8	1.9	2.6	1.7	0.9
15-30	5.7	5.2	3.6	3.6	2.9	2.7	2.6	2.7	2.3	0.9
30-45	4.6	3.9	2.9	3.2	2.1	2.8	2.1	2.0	1.7	0.8
45-60	4.7	3.6	2.6	3.1	2.1	2.4	2.0	1.6	1.5	0.8
60-75	4.4	3.0	2.6	3.0	1.8	2.1	1.7	1.5	1.4	0.7
75-90	5.3	2.7	2.1	2.4	1.8	1.5	1.8	1.1	1.3	0.7
90-105	4.8	3.1	3.1	2.0	1.5	1.2	1.3	1.0	0.8	0.9
105-120	3.0	1.8	2.7	1.4	1.8	0.8	0.9	0.9	0.6	0.7
Depth LSD^y	1.2	0.8	0.9	0.7	0.5	0.5	0.5	0.5	0.4	
All depths	4.8	3.4	2.9	2.7	2.0	1.9	1.8	1.7	1.4	0.3

^{z}LSD at 5% comparing rootstock for each depth.

^{y}LSD at 5% comparing depth for each rootstock.

Table 2. Number of roots/dm^2 from 2 to 5 mm in diameter for each depth and per tree (All depths) for the Michigan location.

	Rootstock									
Depth (cm)	MAC 24	OAR 1	M.26 EMLA	M.9 EMLA	M.7 EMLA	Ottawa 3	M.9	MAC 9	M.27 EMLA	Rootstock LSD^z
0-15	0.34	0.29	0.21	0.14	0.10	0.13	0.10	0.11	0.09	0.09
15-30	0.26	0.39	0.11	0.13	0.13	0.16	0.11	0.15	0.15	0.09
30-45	0.11	0.24	0.07	0.07	0.11	0.04	0.07	0.11	0.06	0.07
45-60	0.11	0.13	0.10	0.06	0.06	0.08	0.05	0.05	0.02	0.06
60-75	0.09	0.16	0.06	0.08	0.06	0.06	0.10	0.04	0.05	0.06
75-90	0.10	0.09	0.07	0.05	0.04	0.05	0.03	0.03	0.03	0.04
90-105	0.07	0.11	0.11	0.07	0.08	0.06	0.02	0.02	0.03	0.05
105-120	0.13	0.09	0.05	0.06	0.06	0.05	0.03	0.02	0.01	0.06
Depth LSD^y	0.07	0.10	0.07	0.06	0.06	0.06	0.06	0.05	0.04	
All depths	0.15	0.19	0.10	0.08	0.08	0.08	0.06	0.07	0.05	0.02

^{z}LSD at 5% comparing rootstock for each depth.

^{y}LSD at 5% comparing depth for each rootstock.

Table 3. Number of roots/dm^2 greater than 5 mm in diameter for each depth and per tree (All depths) for the Michigan location.

	Rootstock									
Depth (cm)	MAC 24	OAR 1	M.26 EMLA	M.9 EMLA	M.7 EMLA	Ottawa 3	M.9	MAC 9	M.27 EMLA	Rootstock LSD[z]
0-15	0.22	0.15	0.09	0.08	0.15	0.10	0.10	0.04	0.03	0.07
15-30	0.27	0.25	0.06	0.08	0.15	0.10	0.10	0.04	0.07	0.07
30-45	0.10	0.12	0.03	0.07	0.03	0.02	0.03	0.01	0.03	0.04
45-60	0.08	0.06	0.06	0.02	0.01	0.01	0.02	0.01	0.01	0.03
60-75	0.05	0.07	0.02	0.03	0.02	0.01	0.01	0.00	0.01	0.03
75-90	0.04	0.03	0.03	0.01	0.02	0.01	0.00	0.01	0.01	0.03
90-105	0.09	0.04	0.03	0.00	0.00	0.01	0.00	0.00	0.00	0.03
105-120	0.06	0.01	0.01	0.01	0.02	0.01	0.00	0.01	0.00	0.02
Depth LSD[y]	0.06	0.06	0.04	0.04	0.05	0.04	0.04	0.02	0.03	
All depths	0.11	0.08	0.04	0.04	0.05	0.03	0.03	0.01	0.01	0.02

[z] LSD at 5% comparing rootstock for each depth.

[y] LSD at 5% comparing depth for each rootstock.

Table 4. Number of roots/dm^2 less than 2 mm in diameter for each depth and per tree (All depths) for the Ohio location.

	Rootstock								
Depth (cm)	MAC 24	OAR 1	M.26 EMLA	M.9 EMLA	M.7 EMLA	Ottawa 3	M.9	MAC 9	Rootstock LSD[z]
0-15	10.7	6.8	4.8	3.2	4.7	3.4	4.0	6.4	2.2
15-30	8.9	6.8	5.4	4.1	5.9	4.7	4.2	7.0	1.4
30-45	4.9	3.2	3.3	2.4	3.4	3.3	2.0	3.6	0.8
45-60	3.9	2.3	1.6	1.3	1.8	2.1	1.1	2.1	0.7
60-75	1.4	0.9	0.6	0.5	0.9	0.7	0.4	0.9	0.4
75-90	0.6	0.3	0.3	0.2	0.4	0.3	0.1	0.4	0.2
90-105	0.4	0.1	0.1	0.1	0.2	0.3	0.1	0.1	0.1
105-120	0.4	0.04	0.1	0.1	0.2	0.1	0.1	0.1	0.1
Depth LSD[y]	1.5	0.8	0.8	0.7	0.6	0.6	0.6	0.7	
All Depths	3.9	2.6	2.0	1.5	2.2	1.9	1.5	2.6	0.5

[z] LSD at 5% comparing rootstock for each depth.

[y] LSD at 5% comparing depth for each rootstock.

Table 5. Number of roots/dm^2 from 2 to 5 mm in diameter for each depth and per tree (All depths) for the Ohio location.

	Rootstock								
Depth (cm)	MAC 24	OAR 1	M.26 EMLA	M.9 EMLA	M.7 EMLA	Ottawa 3	M.9	MAC 9	Rootstock LSD^z
0-15	1.16	0.68	0.26	0.18	0.30	0.19	0.19	0.34	0.22
15-30	0.54	0.47	0.14	0.26	0.43	0.32	0.24	0.32	0.15
30-45	0.20	0.24	0.12	0.18	0.20	0.21	0.12	0.11	0.10
45-60	0.21	0.19	0.04	0.10	0.09	0.13	0.09	0.06	0.08
60-75	0.13	0.09	0.02	0.05	0.03	0.06	0.04	0.03	0.06
75-90	0.02	0.01	0.00	0.03	0.01	0.01	0.01	0.01	0.02
90-105	0.02	0.01	0.00	0.01	0.00	0.01	0.01	0.01	0.02
105-120	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02
Depth LSD^y	0.17	0.10	0.06	0.11	0.09	0.08	0.07	0.07	
All Depths	0.29	0.21	0.07	0.10	0.14	0.12	0.08	0.11	0.05

^{z}LSD at 5% comparing rootstock for each depth.

^{y}LSD at 5% comparing depth for each rootstock.

Table 6. Number of roots/dm^2 greater than 5 mm in diameter for each depth and per tree (All depths) for the Ohio location.

	Rootstock								
Depth (cm)	MAC 24	OAR 1	M.26 EMLA	M.9 EMLA	M.7 EMLA	Ottawa 3	M.9	MAC 9	Rootstock LSD^z
0-15	0.45	0.34	0.09	0.11	0.18	0.22	0.12	0.09	0.12
15-30	0.47	0.21	0.19	0.26	0.35	0.26	0.11	0.16	0.12
30-45	0.19	0.10	0.05	0.03	0.13	0.13	0.03	0.05	0.07
45-60	0.16	0.05	0.01	0.01	0.06	0.06	0.02	0.02	0.05
60-75	0.08	0.02	0.00	0.00	0.00	0.02	0.01	0.00	0.03
75-90	0.04	0.00	0.00	0.02	0.00	0.01	0.00	0.00	0.02
90-105	0.01	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.01
105-120	0.02	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.02
Depth LSD^y	0.09	0.07	0.04	0.07	0.07	0.07	0.04	0.04	
All depths	0.18	0.09	0.04	0.05	0.09	0.09	0.04	0.04	0.03

^{z}LSD at 5% comparing rootstock for each depth.

^{y}LSD at 5% comparing depth for each rootstock.

SECTION II. ROOT HYDRAULIC CONDUCTANCE OF FIVE APPLE ROOTSTOCKS AND CARBON TRANSLOCATION IN ROOT SYSTEMS UNDER PRESSURE

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Received for publication . Acknowledgment is made to the Michigan Agricultural Experiment Station and the Michigan Apple Research Committee for their support of this research. The cost of publishing this paper was defrayed in part by the payment of page charges. Under postal regulation, this paper must be hereby marked *advertisement* solely to indicate this fact.

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Cellular and Whole Plant Physiology

Root Hydraulic Conductance of Five Apple Rootstocks and Carbon Translocation in Root Systems Under Pressure

Additional index words. Malus domestica, root hydraulic conductance

Abbreviations: L_p, root hydraulic conductance

Abstract. Root hydraulic conductance was determined by pressure induced flow in 23 liter pressure chambers for the apple rootstocks M.9 EMLA, M.26 EMLA, MM.106, MM.111 and Mark. There appeared to be an inverse relationship between root hydraulic conductance and reported vigor of the rootstock, with the dwarfing M.9 EMLA having the greatest root hydraulic conductance, followed in decreasing order by M.26 EMLA and Mark, MM.106, and MM.111, the most vigorous rootstock, having the least. Effects of pressurizing the root system on ^{14}C translocation and assimilation, transpiration and leaf conductance were analyzed to determine whether the system could be used to measure root hydraulic conductance of intact plants without disruption of root to shoot communication. No effects of pressurization were found on ^{14}C translocation with equal amounts of ^{14}C found in the root system and apical regions of the plant for pressurized and unpressurized controls. There were a few differences in plant gas exchange but they were inconsistent. This

indicated that the system can be used with intact plants without disrupting root to shoot translocation of carbon in the phloem.

Movement of water through the soil-plant-atmosphere-continuum is considered analogous to flow in an electric system described by Ohm's Law (Cowan, 1972). Many studies have quantified the conductances through the shoot system and are the subject of several reviews (Cowan, 1977; Hsiao, 1973; Landsberg and Jones, 1981; Raschke, 1979; Sharkey, 1985). Relatively few studies have dealt with hydraulic conductance through the root system of perennial plants, the major resistance (inverse of conductance) to water flow in plants (Kramer, 1940; Landsberg and Jones, 1981; Olien and Lakso, 1986). In a recent review of water relations in apple, Landsberg and Jones (1981) state that they could find no *in vivo* estimates of apple root resistances. The most reliable information they could find were estimates by Landsberg et al. (1976) for MM.106 rootstock and Davies and Lakso (1979) for MM.111 rootstock. Two papers have been published subsequent to their review that estimate root hydraulic conductance (L_p) for several apple rootstocks (Olien and Lakso, 1984, 1986) and a paper by Baxter and West (1977) was found that directly measured apple L_p but only one rootstock was measured. This dearth of information lead to the first half of this study. The objective was to compare the L_p of a range of vigor controlling apple rootstocks.

The second part of this study arose from the desire to include the regulatory effects of the shoot system on the root system when measuring L_p. In a previous experiment (unpublished) it was determined that L_p could be evaluated with intact plants by measuring the exudation rate under pressure through a leaf petiole with the lamina excised. This would provide an ideal system for measuring L_p without disrupting shoot regulatory effects providing there was no alteration in translocation. The objectives of the second part of the experiment were to determine if pressurizing the root system had an effect on translocation of carbon assimilates in plants.

Materials and Methods

Root hydraulic conductance. The apple (*Malus domestica* Borkh.) rootstocks Mark, M.9 EMLA, M.26 EMLA, MM.106 and MM.111 were used to compare root hydraulic conductance over a range of size controlling rootstocks in Sept. 1989. Four 23-liter pressure chambers with heating/cooling coil connected to a water bath were used. The rootstocks were rooted layers, approximately 17 months old grown in a greenhouse and planted in a 7 field soil:1 sand:1 peat (v/v) soil mixture. Soil was gently washed from the root system and pressure chambers were filled with water and brought to 25 C. Plants were assigned chambers in a split plot design with main plots being day and subplot pressure chamber so that all rootstocks could be compared. Plants were prepared and placed in the pressure chambers at the same time of day each day to eliminate diurnal variations. Root systems were submerged and sealed in the pressure chambers and the stems were excised 15 cm above the soil line. An air stone in the pressure chambers allowed aeration when pressurized. The pressure chambers were pressurized to 0.345 MPa. Plants were allowed to equilibrate for 1 h before measurement. The conductivity through the excised stems was measured by connecting them to a horizontally positioned 1 ml graduated pipette, allowing the pipette to fill with exudate, injecting an air bubble with a syringe into the pipette and timing the rate of movement through the pipette. Rate of flow through the pipettes was measured at least four times for each plant. Subsequent to L_p measurement, plants were removed from the chambers, separated into roots and remaining shoot material and dry weights were determined.

Carbon translocation. 'Imperial Gala' apple on Mark rootstock was used to determine the effect of pressurizing the root system on carbon translocation patterns. Trees were potted in Apr. 1990 in a 7 field soil:1 sand:1 peat (v/v) soil mixture. In Aug. 1990 eight well-watered trees were brought into the laboratory and placed in a large fume hood. Four trees were placed in the pressure chambers described above and four were used as unpressurized controls. In this case the pressure chambers were not filled with water and the shoot system was not excised. One 400 watt high-pressure sodium lamp was placed over a pressurized and unpressurized pair of trees providing approximately 900 μmol m^{-2} s^{-1} photosynthetic photon flux at mid-canopy for a 12 h photoperiod for the duration of the experiment. The chambers were pressurized to 0.345 MPa and trees were allowed to equilibrate for 4 h before $^{14}CO_2$ treatment. A fully expanded mature leaf 12 leaves from the apex was pulsed with $^{14}CO_2$ using the method of Quinlan (1965) modified by Kappes and Flore (1989) and the leaf was allowed to assimilate the $^{14}CO_2$ for 30 min. After 30 min had elapsed the bag was removed and two 0.31 cm^2 leaf discs were taken immediately and frozen in liquid nitrogen from the treated leaf to determine the initial quantity of $^{14}CO_2$ assimilated. The trees remained in the hood for 72 hr and the pressure was maintained for this time. After 72 hr trees were removed from the pressure chambers and treated and control trees were dried and pressed. Autoradiographies were made to determine where the ^{14}C had been translocated by placing dried plants in contact with Kodak X-Omat AR film for 6 weeks. Samples were taken from the root system, the apical leaves and the source leaf to quantify the amount of ^{14}C present by combustion of samples as described by Kappes and Flore (1989). The process was repeated for two additional groups of eight plants.

Carbon assimilation (A), leaf (g_l), mesophyll (g_m) and stomatal (g_s) conductance, transpiration (E), water use efficiency (WUE) and internal CO_2 concentration (C_i) were determined using a portable CO_2 analyzer (Analytical Development Corp. Model LCA-2) equipped with a Parkinson broad leaf chamber. Gas exchange parameters were calculated as described by Moon and Flore (1986). Gas exchange parameters were measured on the 13th leaf of each plant daily three hours into the photoperiod for all three groups of eight plants.

Results and Discussion

Root hydraulic conductance. Plant dry weight and L_p are shown in Table 1. The reported vigor of the rootstocks used in this study are from most to least dwarfing: M.9 EMLA and Mark, M.26 EMLA, MM.106 and MM.111 (Ferree and Carlson, 1987), which appears to be inversely related to the L_p found in this study. The greatest L_p was found for M.9 EMLA followed by M.26 EMLA and Mark, MM.106 was third greatest and MM.111 had the slowest L_p. Although M.9 EMLA had the highest L_p, it had one of the lowest root dry weights. Mark, however, had a somewhat slower L_p than M.9 EMLA but a much larger root dry weight. The absolute flow through the plant, L_p times root dry weight, was 30% greater for Mark than M.9 EMLA and was almost 5 times greater for Mark than MM.111, the rootstock with the slowest L_p.

These results are contrary to the indirect measurements of L_p by Olien and Lakso (1984, 1986). They derived L_p from stem water potential data and found higher conductances for trees grafted on more vigorous rootstocks. However, they did not account for the size difference in the root system which were found to have a large effect on L_p in this study. Plant size also has been shown to have an effect on L_p with smaller bean plants (*Phaseolus vulgaris* L. 'Ouray') having lower L_p than larger ones (Fiscus and Markhart, 1979) and this may explain the difference in results since the trees were of different size for Olien and Lakso (1984, 1986) but similar size for this study. Studies on citrus rootstocks were inconclusive regarding the relationship between rootstock vigor and L_p (Syvertsen, 1981, Wilcox and Davies, 1981)

Carbon translocation. The shoot system also may have contributed to the different results due to a regulatory effect related to transpirational demand and canopy water relations (Kaufmann and Fiscus, 1985). In a previous study with *Populus sp.* (unpublished data) it was determined that the pressure chambers described above could be used to measure root conductance through a leaf petiole with the lamina excised and the remaining shoot system intact.

Autoradiographies indicated that ^{14}C had been translocated from the source leaf to the apex and root system similarly for controls and pressurized plants. It was determined that 25.8% and 26.5% of the initial $^{14}CO_2$ assimilated remained in the source leaf; 1.1% and 0.8% of the initial ^{14}C was translocated to the apical most leaf; and 0.5% and 0.4% of the initial ^{14}C occurred in samples taken from the root system for control and pressurized plants, respectively, with no statistical differences for any of the locations. This indicates that translocation patterns are not affected by pressurizing the root system for an extended time period.

Gas exchange was taken to insure that assimilation was not altered thus affecting translocation patterns (Flore and Lakso, 1989). Gas exchange also was used as an indicator of plant physiological status. Lower A was found only once during the first 72 h measurement and once during the third 72 h measurement for the pressurized plants versus the control plants (Figure 1A). Differences were seen in g_l only on the first day of the first 72 h measurement where the pressurized plants had higher g_l than control plants (Figure 1B). Lower E was found on day three of the last 72 h measurement for pressurized plants compared to controls (Figure 1C). The few differences in gas exchange found during the pressurization treatments indicated little difference in physiological status of the plants.

Pressurization of the root system had no effect on translocation patterns. Minor differences were noted in gas exchange of the plants while pressurized. These results indicate that this system can be used to measure L_p of intact plants without interfering with root to shoot communication. There are many other potential uses of the system as well such as artificially increasing the water potential of root systems under water stress or determining the effects of various soil gas concentrations on the root system and whole plant.

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Caption for Figure

Figure 1. Gas exchange of control and pressurized plants for the three 72 h measurement periods. Dates are for the month of Aug. (A) CO_2 assimilation (A), (B) leaf conductance (g_l) and (C) transpiration (E). *Means significantly different at the 5% level.

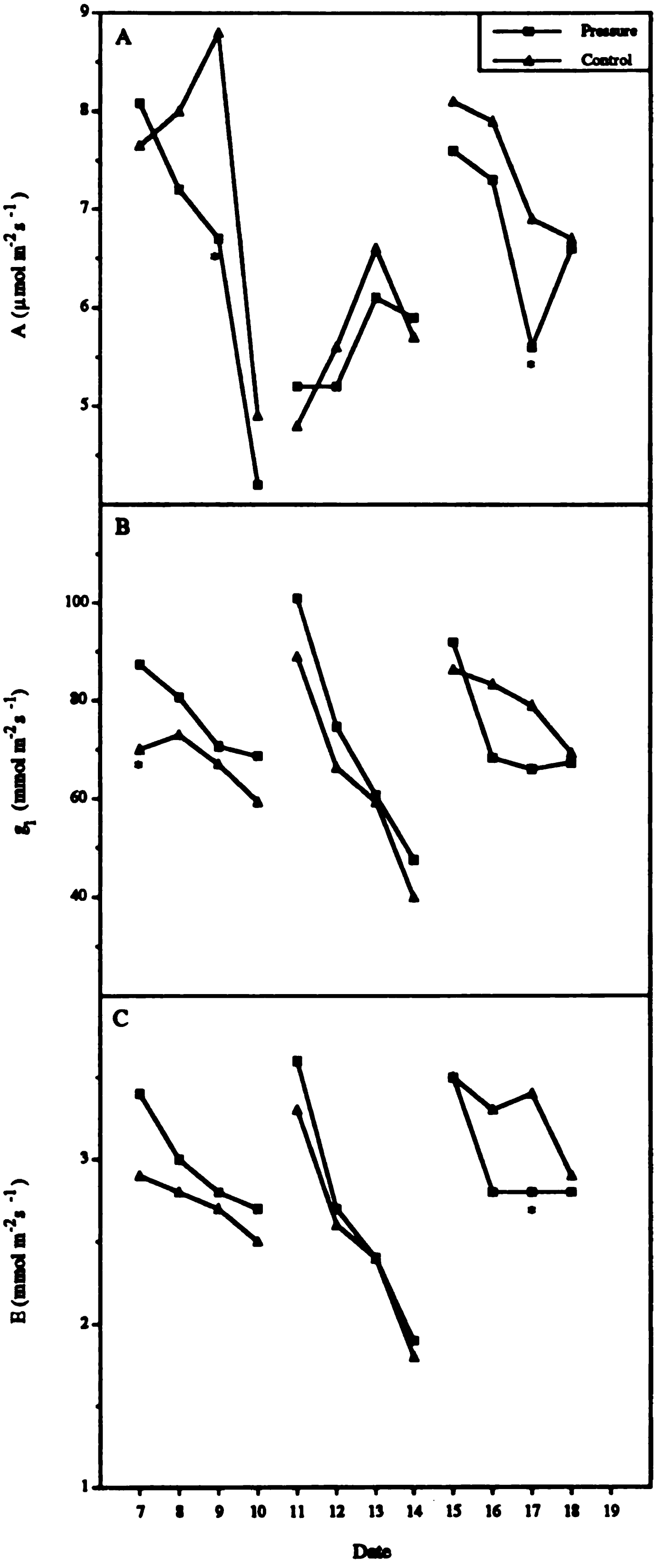
A
B
C
Pressure
Control
A (µ mol m-2 s -1)
gl (mmol m-2 s -1)
E (mmol m-2 s -1)
9
8
7
6
5
100
80
60
40
3
2
1
*
7
8
9
10
11
12
13
14
15
16
17
18
19
Date

Figure 1

Table 1. Root hydraulic conductance and plant and root dry weight of five apple rootstocks. Means followed by different letters are significantly different at the 5% level as determined by Duncan's multiple range test.

Rootstock	L_p (ml Pa^{-1} s^{-1} x 10^{-1})	Plant dry wt (g)	Root dry wt (g)
M.9 EMLA	3.43 a	24.69 d	7.45 cd
M.26 EMLA	2.45 b	24.22 d	6.74 d
Mark	1.95 bc	39.75 a	20.43 a
MM.106	1.22 cd	35.09 b	11.90 b
MM.111	0.98 d	27.50 c	8.30 c

SECTION III: DROUGHT RESPONSE OF YOUNG APPLE TREES ON THREE ROOTSTOCKS I. WATER RELATIONS, CHLOROPHYLL FLUORESCENCE, LEAF ABSCISIC ACID AND GAS EXCHANGE

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Received for publication . Acknowledgment is made to the Michigan Agricultural Experiment Station and the Michigan Apple Research Committee for their support of this research. The authors wish to thank Kenneth Gordon, Daniel Kort, David Costolo, James Kalishek and Wendy Wilkins for their assistance with this project. The cost of publishing this paper was defrayed in part by the payment of page charges. Under postal regulation, this paper must be hereby marked *advertisement* solely to indicate this fact.

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Cellular and Whole Plant Physiology

Drought Response of Young Apple Trees on Three Rootstocks

I. Water Relations, Chlorophyll Fluorescence, Leaf Abscisic Acid and Gas Exchange

Additional index words. abscisic acid, chlorophyll fluorescence, photosynthesis, leaf conductance, water stress

Abbreviations: A, net CO_2 assimilation per leaf area; A', net CO_2 assimilation per tree; ABA, leaf abscisic acid content; E, transpiration per leaf area; E', transpiration per tree; g_l, leaf conductance per leaf area; g_l', leaf conductance per tree; F_m, maximal chlorophyll fluorescence; F_o, non-variable chlorophyll fluorescence; F_t, terminal chlorophyll fluorescence; F_q, fluorescence quenching; F_v, variable chlorophyll fluorescence; F_v/F_m, photosystem II photochemical efficiency; IG/M.9 EMLA C, 'Imperial Gala' on control M.9 EMLA; IG/M.9 EMLA D, 'Imperial Gala' on drought stressed M.9 EMLA; IG/Mark C, 'Imperial Gala' on control Mark; IG/Mark D, 'Imperial Gala' on drought stressed Mark; IG/MM.111 C, 'Imperial Gala' on control MM.111; IG/MM.111 D, 'Imperial Gala' on drought stressed MM.111; WUE', water use efficiency per tree

Abstract. 'Imperial Gala' apple trees (*Malus domestica* Borkh.) on M.9 EMLA, MM.111 and Mark rootstocks were subjected to two drought stress periods in a rainshelter. Water relations, gas exchange parameters per unit area and per tree, chlorophyll fluorescence and leaf abscisic acid were determined throughout each stress period. Leaf water potential was the most sensitive indicator of drought the experiment, stress being consistently reduced during drought and returning to control values upon irrigation. Gas exchange per tree was the best integrator of plant response to drought stress with consistent reductions in CO_2 assimilation, transpiration and leaf and stomatal conductance and water use efficiency. Variable and maximal chlorophyll fluorescence and fluorescence quenching were not as sensitive to stress but demonstrated the cumulative effects of stress. Other fluorescence parameters showed little difference. The most consistent decreases due to stress for gas exchange per unit area were in transpiration and leaf and stomatal conductance with few differences in CO_2 assimilation and fewer for mesophyll conductance and water use efficiency. M.9 EMLA was least affected by drought stress with MM.111 intermediate and Mark showing the greatest sensitivity with reduced values due to drought stress.

Recent reviews by Ferree and Carlson (1987) and Landsberg and Jones (1981) have demonstrated the rootstock influence on the drought response of apple, however, conclusions were often contradictory especially concerning dwarfing rootstocks. Many studies only deal with the growth aspects or the physiological aspects and do not integrate responses. This and the following paper are an attempt to analyze the whole plant response to drought stress in terms of plant growth and physiology and determine mechanisms of stress tolerance for three different rootstocks; M.9 EMLA, MM.111 and Mark, which are thought to differ in their response to drought (Ferree and Carlson, 1987; Landsberg and Jones, 1981).

The objectives of this study were to determine which physiological parameter was most sensitive to drought stress, compare M.9 EMLA, MM.111 and Mark rootstock performance under drought conditions and determine methods of adaptation to drought stress. Growth parameters also were measured during this experiment and the integration of growth and physiological parameters with respect to the objectives is discussed in the subsequent paper (Section IV).

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 mobile rainshelter on 17 and 22 May 1991. The rainshelter, upon closing, traveled at a rate of 0.3 m/s and was programmed to close after accumulation of 4 mm of rainfall. The rainshelter is described in detail by Martin et al. (1988). The trees were planted in 30 cm wide X 40 cm deep trenches lined with a spun bound polypropylene material to restrict root volume and mounded to 15 cm high raised beds. Soil was classified as a Kalamazoo loam (fine-loamy, mixed, mesic Typic Hapludolf). The trees were interplanted with crab-apples (*M.* x *zumi* 'Indian

Summer') and sweet cherries (*Prunus avium* L. 'Emperor Francis') in a split plot design with two replicates of main plots of irrigation and 6 replicates of subplots of rootstock for a total of 72 apple trees. The trees were trained to have 2 shoots per tree. Trees were fertilized prior to each drought stress 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(4H)ylmethyl phosphorodithioate) or malathion (0,0-dimethyl dithiophosphate of diethyl mercaptosuccinate) was applied weekly due to infestations of Japanese beetles.

Water was supplied by drip irrigation at 2 liters per day per tree before and after each drought period while water was withheld from one half of the trees during the drought stresses. Two drought stress periods lasting approximately one month each were imposed during 1991. The first drought stress was from 2 July through 2 Aug. with a recovery period from 3 to 12 Aug. The second drought stress lasted from 13 Aug. through 7 Sept. Recovery from the second drought stress was monitored through 17 Sept. A malfunction prohibited the shelter from closing on 9 July (day 7 of the first stress period) and 10 mm of rain fell on this date. Soil moisture content was determined using a time domain reflectometer and 32 cm steel rods to give an average soil moisture content within the top 30 cm of soil (TDR Tektronix 1053) (Topp and Davis, 1985; Topp et al., 1982).

Leaf water relations and abscisic acid content. Predawn leaf water potential (ψ_l) was determined using a pressure bomb (Plant Moisture Stress Instrument Co.) on

1, 10, 17, 24, 28, 31 Aug. and 11 Sept. and diurnal ψ_l was measured 30 Aug. Leaf samples were cut and measured within 40 sec. Leaves were placed on dry ice immediately subsequent to measurement and afterward transferred to a -20 C freezer. Later the leaves from 1, 10, 17, 31 Aug. and 11 Sept. were cut in half longitudinally in a 1 C cold room. One half was used to determine leaf osmotic potential (ψ_s) and the other half for leaf abscisic acid (ABA) content determination. Leaf osmotic potential was determined by placing the leaf sample into a 3 cc syringe and applying pressure to exude 10 μl of solution which was measured with a vapor pressure osmometer (Wescor model 5500 vapor pressure osmometer). Leaf turgor potential (ψ_t) was calculated from ψ_l and ψ_s. Free (S)-ABA content was determined using a mouse monoclonal antibody to ABA and a radioimmunoassay method described by Vernieri et al. (1989).

The following measurements were taken twice weekly at the same time of day to reduce diurnal variation:

Gas exchange. Carbon assimilation (A), leaf (g_l), mesophyll (g_m) and stomatal (g_s) conductance, transpiration (E), water use efficiency (WUE) and internal CO_2 concentration (C_i) were determined using a portable CO_2 analyzer (Analytical Development Corp., Model LCA-2) equipped with a Parkinson broad leaf chamber (Analytical Development Corp., Model PLC-B). Measurements were made between 1000 and 1200 HR on a single leaf per plant receiving at least 900 μmol m^{-2} s^{-1} photosynthetic photon flux (PPF) on a mature recently (3 weeks old) fully expanded leaf for 4 of the 6 replicates and allowed to equilibrate before taking the measurements. Diurnal measurements were taken on 31 July, 10, 20, 23, 27, 31 Aug. and 2 Sept. Gas exchange parameters were calculated as described by Moon and Flore (1986). Since the trees were trained to only 2 shoots per tree and the trees were in the first leaf, canopy shading was considered negligible and the gas exchange parameters per leaf area A, E, g_l, and WUE were extrapolated for the entire canopy, designated A', E', g_l', g_s' and WUE', for each measurement period. Canopy gas exchange parameters were estimated by multiplying by the canopy leaf area on the day of measurement calculated from leaf emergence data taken biweekly and the leaf area estimates determined at the end of each stress period for this plot (Section IV).

Chlorophyll fluorescence kinetics. Chlorophyll *a* fluorescence parameters of photosystem II (PS II) were determined using a CF-1000 chlorophyll fluorescence measurement system (P.K. Morgan Instruments, Inc.). Parameters measured were non-variable (F_o), maximal (F_m), variable (F_v) and terminal (F_t) chlorophyll fluorescence and photochemical efficiency (F_v/F_m), fluorescence quenching (F_q) and half rise time from F_o to F_m ($t_{1/2}$). Measurements were taken between 900 and 1300 HR. Dark acclimation cuvettes with a shutter-gate to eliminate ambient light when inserting the fiber optic light source were affixed to the same leaf used for gas exchange measurements for a minimum of 15 min before measurements were taken. The light source was inserted into the cuvette from the abaxial side of the leaf and a pulse of 1000 μmol m^{-2} s^{-1} 680 nm actinic light was applied for 60 sec.

Results

Soil moisture was lower for the drought stressed treatments 14 and 3 days after imposition of the first and second stress, respectively, and remained lower for both stress periods until irrigation during the respective recovery periods (Figure 1). The longer period of time for the difference to become apparent for the first stress period was due to the malfunction of the shelter 7 days into the first stress. Additionally, a larger canopy achieved in the second stress period resulted in a greater transpirational demand resulting in a more rapid depletion of soil water.

Leaf water relations. Leaf water potential was not measured during the first stress period until the last day of treatment (day 30) since there were an inadequate number of leaves initially and several authors have indicated that ψ_l is one of the least sensitive parameters to measure drought stress (Landsberg and Jones, 1981; Higgs and Jones, 1991). However, ψ_l was reduced on this date by 60%, 68% and 71% for drought stressed 'Imperial Gala' on MM.111 (IG/MM.111 D), on M.9 EMLA (IG/M.9 EMLA D) and on Mark (IG/Mark D), respectively, compared to corresponding controls (Figure 2A). All drought stressed rootstocks were lower than all control rootstocks while there was no difference within treatments in regard to rootstocks (Figure 2A). Recovery was noted for ψ_l for the next measurement period, 8 days into the first recovery period. During the second drought stress ψ_l was monitored at least once a week and differences from control were noted upon the first measurement after reimposing treatments (day 4) and subsequently until stress was relieved. On day 4 of the second stress IG/MM.111 D and IG/Mark D had the lowest ψ_l compared to all other treatments while IG/M.9 EMLA D was similar to control 'Imperial Gala' on MM.111 (IG/MM.111 C) and on Mark (IG/Mark C) but more negative than control 'Imperial Gala' on M.9 EMLA (IG/M.9 EMLA C). Eleven days into the second stress ψ_l for IG/MM.111 D and IG/Mark D was lower than all controls but IG/M.9 EMLA D was not different from the controls or drought treatments. On days 15 and 18 of the second stress ψ_l was lower for all drought stress treatments compared with all controls. Leaf water potential for IG/Mark D usually was reduced most during stress 2 with an 89%, 71%, 156% and 124% reduction compared to IG/Mark C, IG/MM.111 D was intermediate with a 50%, 78%, 117% and 88% reduction compared to IG/MM.111 C and IG/M.9 EMLA D was affected least with a 44%, 16%, 100% and 141% reduction compared to IG/M.9 EMLA C on days 4, 11, 15 and 18 of the second stress, respectively. Values for ψ_l were not different for any treatment 4 days after irrigating during the second recovery period.

Differences occurred for ψ_s and ψ_t only for the measurement taken during the first stress period (Figure 2B and C). For this measurement, leaf osmotic potential was more negative for the drought stressed rootstocks compared with corresponding controls, although IG/MM.111 D and IG/Mark D were not different from IG/M.9 EMLA C. Leaf turgor potential was lower for IG/Mark D compared with all controls, IG/M.9 EMLA D was lower than IG/M.9 EMLA C and IG/Mark C and IG/MM.111 D was lower than IG/M.9 EMLA C and IG/Mark C but not IG/MM.111 C.

Diurnal ψ_l was measured during day 17 with a predawn measurement on day 18 of the second stress period (Figure 3). For the 1030 HR measurement, ψ_l for IG/M.9 EMLA C was less negative than all other treatments except IG/MM.111 C which was less negative than IG/MM.111 D and IG/Mark D but not IG/M.9 EMLA D while IG/Mark C was not different from IG/MM.111 C or the drought stressed rootstocks. At the 1430 HR measurement ψ_l for all control rootstocks was less negative than all drought stressed rootstocks with IG/M.9 EMLA C less negative than IG/MM.111 C and IG/Mark C and IG/MM.111 D more negative than IG/M.9 EMLA D and IG/Mark D. During the 1600 HR measurement, values were significantly less negative at the 10% level only for IG/M.9 EMLA C and IG/Mark C compared with IG/M.9 EMLA D and IG/MM.111 D, all other treatments showing no differences. Predawn ψ_l was less negative for all control rootstocks than all drought stressed rootstocks.

Leaf abscisic acid content. Generally, ABA was higher in drought stressed than control treatments. ABA was higher for IG/M.9 EMLA D than the control treatments with IG/Mark D higher than IG/M.9 EMLA C and IG/MM.111 C but not IG/Mark C and IG/MM.111 D higher than IG/MM.111 C but not the other controls on day 30 of stress 1 (Table 1). During the first recovery period ABA was not different for IG/MM.111 C and IG/MM.111 D or IG/Mark C and IG/Mark D but IG/M.9 EMLA D was still greater than IG/M.9 EMLA C and IG/Mark D was higher than IG/M.9 EMLA C and IG/MM.111 C. No difference in ABA content was seen for any treatment for the first measurement of the second stress period (day 4) but by day 18 IG/Mark D and IG/M.9 EMLA D were greater than all controls and IG/MM.111 D was greater than IG/M.9 EMLA C. Levels of ABA for drought treatments had returned to those of the controls 4 days after irrigating.

Gas exchange. Gas exchange parameters began to differ between stressed and control treatments 14 days into stress 1. Assimilation was decreased for all drought stressed rootstocks compared to corresponding controls on this date (Figure 4A) with IG/MM.111 D lowest and IG/Mark C lower than IG/MM.111 C and IG/M.9 EMLA C but not different from IG/M.9 EMLA D or IG/MM.111 D. Assimilation consistently was reduced for IG/M.9 EMLA D with lower values on days 14, 21, 24 and 28 of stress 1 and also day 29 at the 10% level compared with IG/M.9 EMLA C and all but day 28 versus IG/MM.111 C. Assimilation was lower for IG/MM.111 D than IG/MM.111 C on days 14 and 24 and was lower than IG/M.9 EMLA C on days 14, 24 and 28 during the first stress period. During stress 1, IG/Mark C often had A similar to IG/Mark D and the other drought stressed rootstocks but was lower on day 14 and days 14, 28 and 29 compared to IG/MM.111 C and IG/M.9 EMLA C, respectively. All drought stressed treatments had returned to control levels 8 days into the first recovery period. During the second stress period, A showed few differences between controls and drought stressed rootstocks. Three days into the second drought stress IG/Mark D had the lowest A versus IG/MM.111 C, IG/M.9 EMLA C and IG/M.9 EMLA D but not compared with IG/Mark C. Assimilation for IG/MM.111 D was lower than IG/MM.111 C but similar to the other treatments on day 3 of stress 2. The only other difference in A was at the 10% level 14 days into stress 2 where IG/MM.111 D and IG/M.9 EMLA D were lower than IG/M.9 EMLA C with no difference in the other treatments.

As was the case with A, g_l for M.9 EMLA was affected more than the other rootstocks during the first drought stress. Leaf conductance for IG/MM.111 D was affected first, 14 days after imposition of stress, but g_l for IG/MM.111 D was lower than IG/MM.111 C only twice during the first drought stress period (Figure 4B). From day 21 through day 8 of the first recovery period g_l was lower for IG/M.9 EMLA D than IG/M.9 EMLA C and usually IG/MM.111 C and IG/Mark C as well. The other rootstock treatment combinations had similar g_l with drought stressed rootstocks occasionally lower than IG/M.9 EMLA C and less frequently than IG/MM.111 C or IG/Mark C. No difference in g_l was noted for any treatments during recovery 1 except IG/M.9 EMLA D remained lower than IG/M.9 EMLA C at the 10% level. Differences in g_l were seen on day 1 of stress 2. During stress 2 g_l for IG/MM.111 D and IG/Mark D were reduced more consistently due to the drought than IG/M.9 EMLA D compared to their corresponding controls. Lower g_l was found on day 14 for IG/M.9 EMLA D, days 1, 7, 10 and 14 for IG/MM.111 D, days 1, 10, 14 and 17 for IG/Mark D compared to corresponding controls. Differences in g_l due to rootstock alone generally were not found during stress 2. 'Imperial Gala' on Mark D often had lower g_l than IG/MM.111 C and IG/M.9 EMLA C and g_l for IG/M.9 EMLA D occasionally was lower than IG/MM.111 C and IG/Mark C but not

IG/M.9 EMLA C while g_l was usually similar between IG/MM.111 D and IG/M.9 EMLA C and IG/Mark C.

Transpiration was reduced for IG/MM.111 D compared to IG/MM.111 C and IG/Mark C on day 14 of stress 1 with all other treatments similar (Figure 4C). During the next measurement period, E for IG/MM.111 C was higher than all treatments except IG/MM.111 D. During measurements taken from 21 through 29 days after the beginning of stress 1, E was lower to at least the 10% level for IG/MM.111 D and IG/M.9 EMLA D versus IG/MM.111 C and IG/M.9 EMLA D was lower than IG/M.9 EMLA C on these days except day 29. Transpiration for IG/Mark D was often lower than IG/MM.111 C but similar to the other treatments during this time. E for all treatments was the same after 8 days of recovery except IG/Mark D was lower than IG/MM.111 C and IG/M.9 EMLA C. Few differences between drought stressed rootstocks and corresponding control rootstocks were seen during the second stress period. 'Imperial Gala' on Mark D usually had the lowest E between rootstocks when differences were noted and was lower than all other treatments 1 and 17 days into the second stress period.

Differences in g_m occurred only during the first stress period and only on 3 of the 18 days measurements were taken (data not shown). Ten days after imposition of stress 1, g_m for all rootstock treatment combinations was similar except IG/M.9 EMLA C was lower than IG/Mark D. On days 14 and 24 all drought stressed rootstocks were lower than IG/MM.111 C and IG/M.9 EMLA C but not IG/Mark C. The few and inconsistent differences in g_m indicate little effect on A. Differences in

WUE also were rare occurring on day 14 of stress 1 for IG/MM.111 and on days 14 and 21 of stress 1 for IG/Mark and did not contribute to drought tolerance (data not shown).

A typical diurnal response during the drought stress is shown in figure 5 A-C for A, g_l, and E on day 29 of the first stress period. WUE and g_m are not shown since no differences were noted. 'Imperial Gala' on M.9 EMLA C was the only treatment that showed differences for A with higher rates compared to IG/M.9 EMLA D and IG/Mark C and D at the 0900 HR measurement and higher rates than all drought stressed treatments at the 1700 HR measurement, no differences were noted for the 1400 HR measurement. During the 0900 HR measurement, E was lower for the drought stressed rootstocks than IG/M.9 EMLA C and IG/MM.111 C and lower for IG/M.9 EMLA D and IG/MM.111 D than IG/Mark C, but IG/Mark C and IG/Mark D were not different. During the 1400 HR measurement, all drought stressed rootstocks had lower E than IG/MM.111 C but no other differences were observed. By the 1700 HR measurement all drought stressed treatments had lower E than all control treatments except IG/Mark C was not different from IG/MM.111 D or IG/M.9 EMLA D. Results for g_l were similar to A with drought stressed rootstocks having lower g_l than IG/M.9 EMLA C for the 0900 HR, 1400 HR and 1700 HR measurements except IG/MM.111 D was not lower during the 1400 HR measurement. No differences were found in g_l between IG/MM.111 C and D and IG/Mark C and D except IG/Mark D was lower than IG/MM.111 C during the 0900 HR measurement.

Results for gas exchange parameters calculated on a per tree basis were much different than on a per m^2 basis. Gas exchange parameters per tree usually were reduced for the drought stressed rootstocks compared to corresponding controls 14 or 17 days into stress 1, often 3 to 4 days sooner for IG/Mark D (Figure 6A-D). 'Imperial Gala' on Mark C usually had the highest A', E', g_l' and WUE' of all rootstock treatment combinations while IG/Mark D usually had the lowest.

Differences in A' were first seen in IG/Mark by day 10 with IG/Mark D lower than IG/Mark C (Figure 6A). This difference in A' between IG/Mark C and D was seen for all subsequent measurements during stress 1, recovery 1 and stress 2 except on days 17 and 29 of stress 1 and day 17 of stress 2. A' for IG/MM.111 D was lower than IG/MM.111 C only on day 14 and 21 of stress 1, day 8 of recovery 1 and day 3, 14 and 18 of stress 2. 'Imperial Gala' on M.9 EMLA D had lower A' than IG/M.9 EMLA C on days 14, 21, 24, 28 and 29 of stress 1, was similar during recovery 1 and higher again on days 3, 14 and 20 of stress 2. During recovery 1, A' did not return to control levels for IG/Mark D or IG/MM.111 D but did for IG/M.9 EMLA D. 'Imperial Gala' on Mark C had higher A' on 5, 9, 12 and 15 days out of 18 days measurements were taken compared to IG/MM.111 C, IG/M.9 EMLA C, IG/MM.111 D and IG/M.9 EMLA D, respectively.

Again IG/Mark showed differences first for g_l' by day 14 of the first stress period (Figure 6B). 'Imperial Gala' on Mark D g_l' remained lower than IG/Mark C throughout both stress periods and recovery 1 except for day 20 of stress 2. 'Imperial Gala' on MM.111 and IG/M.9 EMLA responded by day 17 with reductions in g_l' for the drought stressed treatments. On days 17, 21 and 28 of stress 1 g_l' for IG/MM.111 D was lower than IG/MM.111 C and IG/M.9 EMLA D was lower than IG/M.9 EMLA C. Recovery for g_l' occurred for IG/MM.111 D but not IG/M.9 EMLA D during recovery 1. On days 1, 7, 10, 14, 17 and 24 of stress 2 g_l' again was lower for IG/MM.111 D than IG/MM.111 C and IG/M.9 EMLA D was lower than IG/M.9 EMLA C. From day 10 of the first stress until termination of the experiment IG/Mark C had higher g_l' than IG/M.9 EMLA D except on day 20 of stress 2, higher than IG/MM.111 D except on day 29 of stress 1 and days 18 and 20 of stress 2, higher than IG/M.9 EMLA C except for days 24 and 29 of stress 1 and days 18, 20 and 24 of stress 2 and higher than IG/MM.111 C except on days 24, 28 and 29 of stress 1 and days 3, 17, 18, 20 and 24 of stress 2. Differences in g_l' were noted between IG/MM.111 C and IG/M.9 EMLA C only on days 7, 10, 14 and 17 of stress 2 and differences between the drought stressed rootstocks were rare.

Reductions due to drought stress for E' occurred on day 14 of stress 1 for IG/Mark D and IG/MM.111 D compared with IG/Mark C and IG/MM.111 C, respectively (Figure 6C). 'Imperial Gala' on Mark D continued to have lower E' than IG/Mark C throughout stress 1, recovery 1 and stress 2 except for day 20 of stress 2. Differences in E' were not as consistent for IG/MM.111 as IG/Mark with lower values for IG/MM.111 D than IG/MM.111 C on all days except 24, 28 and 29 of stress 1, day 8 of recovery 1 and days 18 and 20 of stress 2. 'Imperial Gala' on M.9 EMLA D showed no reduction in E' versus IG/M.9 EMLA C during stress 1 except for day 21. E' for IG/M.9 EMLA C and D was similar during recovery 1 but was lower for IG/M.9 EMLA D by day 1 of stress 2 and remained so except for day 18. 'Imperial Gala' on Mark C had higher E' for all measurements from day 10 of stress 1 until termination of the experiment compared to IG/M.9 EMLA D and higher than IG/MM.111 D for the same measurements except days 18 and 20 of stress 2. E' for IG/Mark C was higher than IG/M.9 EMLA C except on days 7, 24, 28 and 29 of stress 1 and days 18 and 20 of stress 2. Higher E' was measured on days 14, 17 and 21 of stress 1 and days 1, 7, 14 and 24 of stress 2 for IG/Mark C compared to IG/MM.111 C. Differences in E' between drought stressed rootstocks were infrequent.

Reduced WUE' was first noticed for IG/M.9 EMLA D compared with IG/M.9 EMLA C on day 7 of stress 1 (Figure 6D). The only other differences in WUE' between IG/M.9 EMLA C and D were on days 14 and 24 of stress 1 and day 8 of recovery 1 where IG/M.9 EMLA D was lower. 'Imperial Gala' on Mark D had the most days where WUE' was lower than IG/Mark C with differences on days 14, 21 and 24 of stress 1, day 8 of recovery 1 and for all measurements of stress 2 except days 17, 20 and 24. WUE' was lower only on day 24 of stress 1, day 8 of recovery 1 and days 3 and 18 of stress 2 for IG/MM.111 D versus IG/MM.111 C. 'Imperial Gala' on Mark C usually had the highest WUE' than all other treatments on days differences were significant while the other treatments had very few differences except those mentioned above.

The diurnal response on day 29 of stress 1 for gas exchange per tree for A', g_l' and E' is shown in Figure 7 A-C. Lower A' was seen for IG/M.9 EMLA D and

IG/Mark D compared to IG/M.9 EMLA C at the 1000 HR measurement with no difference in the other treatments. There was no difference in A' during the 1400 HR measurement but during the 1700 HR measurement all drought treatments were lower than all control treatments. For g_l', IG/Mark D and IG/M.9 EMLA D were lower than IG/Mark C during the 1000 HR measurement but no differences occurred for other treatments. During the 1400 HR measurement, all drought treatments were lower than IG/Mark C but no other differences were noted. For the 1700 HR measurement, all drought stressed treatments had lower g_l' than all control treatments. E' responded as g_l' except the differences for the 1400 HR measurement were significant to only the 10% level. Gas exchange generally decreased during the midday measurement and remained at this level during the late afternoon measurement regardless of rootstock or treatment with the exception of E' which remained at nearly the same level for the morning and midday measurements for the control rootstocks and decreased in the late afternoon for IG/Mark C and IG/MM.111 C but not IG/M.9 EMLA C.

Chlorophyll fluorescence kinetics. Chlorophyll fluorescence parameters began showing differences between drought and control 17 days into the first stress for all parameters at the 10% level and 10 days into the second stress period for all parameters except F_v/F_m (Table 2-7) at the 5% level. Of these, F_v, F_q and F_m gave the most consistent results.

During stress 1, F_v was lower for IG/Mark D compared to IG/Mark C and IG/MM.111 C at the 10% level on day 17 (Table 2). F_v was lower for IG/MM.111 D than IG/MM.111 C from day 21 of stress 1 through day 7 of recovery 1 and on day

10 of stress 2. Differences were not seen between IG/M.9 EMLA C and D except on day 24 of stress 1 when IG/M.9 EMLA D was higher than IG/M.9 EMLA C. 'Imperial Gala' on Mark D had lower F_v on days 17 and 21 of stress 1, day 7 of recovery 1 and days 10 and 21 of stress 2 but had higher F_v on day 24 of stress 1 when compared to IG/Mark C. F_v for IG/M.9 EMLA D was often similar to controls, while, when IG/Mark D and IG/MM.111 D were lower than corresponding controls, generally they were lower than the other controls as well. Differences in F_v occurred earlier during stress 2, 10 days after imposing stress, but were not consistently different as in the first stress period. Neither IG/MM.111 D or IG/Mark D returned to similar levels of F_v as corresponding controls during recovery 1, but did during recovery 2. 'Imperial Gala' on M.9 EMLA D was never lower than IG/M.9 EMLA C at any time during the experiment. F_q responded similarly to F_v except no differences were found for any treatments on day 24 of stress 1, day 7 of recovery 1 or day 10 of recovery 2 and IG/M.9 EMLA D and IG/Mark D were lower than IG/MM.111 C on day 3 of recovery 2 (Table 3). Basically the results were identical for F_m as F_v although drought stressed treatments were never higher than corresponding controls. 'Imperial Gala' on M.9 EMLA D was lower than IG/M.9 EMLA C on day 10 of stress 2 and there were no differences due to treatment during recovery 1 or day 21 of stress 2 (Table 4).

Differences were inconsistent for the remaining chlorophyll fluorescence parameters. 'Imperial Gala' on Mark D was lower than all controls for F_t on days 17 and 21 of stress 1, IG/MM.111 D was lower than IG/MM.111 C on day 21 of stress

1 and day 10 of stress 2 and IG/M.9 EMLA D was lower than IG/M.9 EMLA C on day 14 of stress 2 and day 10 of recovery 2 with few other differences observed (Table 5). For F_o, drought stressed rootstocks were lower than corresponding controls only on day 17 of stress 1 (Table 6). On day 10 of stress 2, F_o was lower for all drought stressed rootstocks than IG/MM.111 C with the other treatments showing no differences. On day 14 of stress 2 and day 3 of recovery 2, F_o was lower for IG/MM.111 D than IG/MM.111 C and IG/M.9 EMLA D was lower than IG/M.9 EMLA C. All rootstock treatments had higher F_v/F_m than IG/MM.111 C except IG/Mark D on day 17 of stress 1. 'Imperial Gala' on MM.111 D and IG/M.9 EMLA D were higher than IG/Mark C on day 14 of stress 2 with no other differences observed (Table 7). Differences in $t_{1/2}$ were found only on day 17 of stress 1 with IG/Mark D higher than IG/Mark C and IG/MM.111 C and D (data not shown).

Discussion

During this experiment ψ_l usually was much lower for drought stressed rootstocks compared to control rootstocks except during recovery periods. Lower ψ_l is an indication of decreased water flow into leaves which has implications with regard to growth and physiological processes (Boyer, 1988; Hsiao, 1973; Jones et al., 1985; Lakso, 1979). Threshold values for ψ_l at which stomata begin to close have been reported for a number of crops with values for apple reported to range from -1.8 to below -3.0 MPa depending on environment before and during measurement and time of year (Lakso, 1979; West and Gaff, 1976). During the diurnal ψ_l measurement on day 17 of stress 2 values were -1.8, -1.5 and -1.7 MPa at the 1030 HR measurement for IG/MM.111 D, IG/M.9 EMLA D and IG/Mark D, respectively, while above -1.5 MPa for the controls. Lower g_s and g_l were noticed on this date and time for IG/MM.111 D and IG/Mark D than their respective controls at the 10% level. The correlation between ψ_l and g_s appears to hold for this study. The sensitivity of Mark rootstock to drought stress was exemplified by stomatal response at a higher ψ_l than MM.111.

Differences in ψ_t and ψ_s were found only on day 30 of stress 1 when ψ_t was lower for IG/M.9 EMLA D and IG/Mark D compared to corresponding controls and ψ_s was more negative for all drought stressed rootstocks than corresponding controls. The more negative ψ_s indicates osmotic adjustment has occurred although it was not sufficient to maintain ψ_t for IG/M.9 EMLA D or IG/Mark D. The lack of difference in ψ_t for IG/MM.111 D on this day probably was due to a slightly lower ψ_t for IG/MM.111 in general and not a greater ability to osmotically adjust since ψ_t was slightly, but not significantly, lower for IG/MM.111 C than the other controls and ψ_t for IG/MM.111 D was lower than IG/M.9 EMLA C and IG/Mark C. Stress 2 was not maintained as long as stress 1 thus differences in water relations were not as great as seen on day 30 of stress 1. Maintenance of ψ_t during stress 2 most likely was due to osmotic adjustment as ψ_s, although not significantly different, tended to be more negative during stress 2 and ψ_l was lower for the drought stressed rootstocks while ψ_t

was not. Osmotic adjustment is reported as common for apple (Davies and Lakso, 1979b; Goode and Higgs, 1973; Jones et al., 1985).

Osmotic adjustment is beneficial in that it allows turgor maintenance for cell expansion and adequate g_l for gas exchange. It also requires retention of solutes or mobilization of solutes, photosynthates being the primary solutes (Acevedo et al., 1979; Michelena and Boyer, 1982), into the region where turgor is to be maintained (Jones et al., 1985; Westgate and Boyer, 1985) resulting in a new or at least stronger sink for photosynthates. Osmotic adjustment may not occur similarly for all organs of a plant. Shoot tips of apple were found not to osmotically adjust while leaves did (Lakso, 1983; Lakso et al., 1984) which may account for the large reductions in shoot growth but little difference in individual leaf area found during this study for the drought stressed rootstocks (Section IV).

Reductions in A were infrequent during either stress period for the drought stressed rootstocks, however, growth parameters were substantially reduced for IG/MM.111 D and IG/Mark D and to some extent for IG/M.9 EMLA D when compared to corresponding controls (Section IV). Increases in sink strength have been shown to result in higher A for several fruit crops (Flore and Lakso, 1989). During this study a slight reduction due to drought stress was found for leaf dry weight, leaf area and leaf number resulting in a smaller canopy area for the production of photosynthates while the sink demand, if anything, increased due to the need for more solutes for osmotic adjustment and the greater loss of carbohydrates to root respiration and turnover (see Section IV for further discussion). With a similar to higher sink demand and smaller photosynthetic production area, sink strength per leaf area would increase resulting in increased A. This is apparent particularly for IG/Mark since A was lower only once for IG/Mark D compared to IG/Mark C but growth parameters were reduced by as much as 52%, more than the other drought stressed rootstocks. Some of the effect of sink strength was offset by the reduced g_s, F_v and F_m near the end of each stress period leading to lower A. Differences in g_m and WUE occurred infrequently and had little effect on gas exchange per unit area.

Stomata usually function to optimize CO_2 intake while reducing water loss especially under water limited conditions (Farquhar and Sharkey, 1982; Raschke, 1979). The levels of internal CO_2 concentration and ψ_l exert control over stomata by feedback and feed-forward loops and ABA seems to be involved (Raschke, 1979; Turner et al., 1984). No differences were found in internal CO_2 concentration during this study. Changes in ψ_l affect g_s by altering water flow into leaves and by modification of the ψ_t component of ψ_l which is essential for stomatal opening. Lower ψ_l was found for drought stressed treatments but may not have been a factor since ψ_t was only affected late in stress 1. In a study comparing ψ_l and ψ_t to g_s for apple leaves, a significant relationship was found for ψ_t but not ψ_l (Davies and Lakso, 1978) demonstrating that ψ_t may be more important in stomatal regulation.

Initial reductions in ψ_t have been linked to increased synthesis of ABA (Davies and Lakso, 1978; Pierce and Raschke, 1980) and ABA was found to greatly increase invertase activity in sugar cane (Gayler and Glaziou, 1969) which may provide an additional mechanism for osmotic adjustment by conversion of sucrose to glucose and fructose negating the initial reduction in turgor (Jones et al., 1985). In addition many studies have shown that higher ABA concentrations result in lower g_l (Davies and Lakso, 1978; Davies et al., 1986; Schulte and Hinckley, 1987; Zhang and Davies, 1989, 1990) exhibiting that ABA has multiple roles in drought stress response. The most consistent reduction in g_l during this study was for IG/M.9 EMLA D which had the largest relative increase in ABA, IG/MM.111 D was intermediate in response with respect to both g_l and ABA and IG/Mark D was least responsive for g_l and had the lowest relative increase in ABA when compared with corresponding controls. The contrasting role of ABA in ψ_t and stomatal regulation needs further study.

The lower ψ_l found during the drought stress periods reflects a decrease in water flow to the leaves since the water potential gradient between soil and leaf is the driving force for water flow (Jones et al., 1985) moderated by internal conductance to flow. This combined with lower g_l resulted in reduced E for the drought stressed rootstocks. Although g_l was most consistently reduced for IG/M.9 EMLA D followed by IG/MM.111 D and lastly IG/Mark D, IG/M.9 EMLA D and IG/MM.111 D switched order for E. This can be attributed to a more consistent and sometimes greater reduction in ψ_l for IG/MM.111 D than IG/M.9 EMLA D and a low rate of root hydraulic conductance for MM.111 rootstock and faster rate for M.9 EMLA rootstock (Section II) while as IG/Mark D consistently had a lower ψ_l, g_l was rarely different and root hydraulic conductance for Mark has been found to be very high (Section II).

The primary cause for lower A' for drought stressed trees was the reduced canopy growth of the drought stressed rootstocks compared to controls. While A was decreased on only 1, 3 and 6 of the 18 measurements A' was reduced on 14, 7 and 8 of the 18 measurements for IG/Mark D, IG/MM.111 D and IG/M.9 EMLA D, respectively, compared to corresponding controls. The proposed increase in sink strength for the drought stressed treatments was enough to maintain A at rates similar to controls but could not make up the decrease in photosynthetic production areas by drought stress. Dry weight of leaves and shoots grown during the experiment was reduced by 47%, 26% and 22% for IG/Mark D, IG/MM.111 D and IG/M.9 EMLA D, respectively, compared with corresponding controls. The largest reduction in dry weight corresponds with the largest number of days differences were found in A'. The combination of reduced A and leaf area, number and dry weight for drought stressed rootstocks, although often not significantly different separately, resulted in much more frequent reductions in A'. This also explains reductions in E' and g_l' since there were fewer stomata and less transpiring surface in addition to lower E and g_l for the drought stressed treatments.

Usually WUE is found to increase, if anything, for plants under water stress and is considered a mechanism for drought tolerance (Davies and Lakso, 1979a; Flore et al., 1985). During this study few differences were noted in WUE, however, WUE' was lower for drought stressed trees than controls. This indicates, contrary to many results that rely on WUE per unit area, that the whole plant uses water less efficiently under drought situations. Calculations for WUE' were based upon measurements of mature 3 week old leaves and extrapolated for the entire canopy including young and old leaves that respond differently to water relations (Lakso et al., 1984; Syvertsen, 1985). This raises some concerns over extrapolating WUE for the whole plant from measurements based upon leaves of one particular age. Syvertsen (1985) found an increase in WUE for citrus as leaves matured peaking at 28 days old and then a decline as leaves grew older. Immature leaves of apple, unlike mature leaves, were found to be incapable of osmotic adjustment (Lakso et al., 1984) thus they would be expected to close stomata in response to water deficits faster than mature leaves resulting in lower water loss. Despite these problems, results indicate that WUE on a whole plant basis should be evaluated when considering drought stress response.

Whole tree gas exchange is a difficult parameter to calculate for developed canopies but integrates several parameters including leaf area and number and shoot growth and is useful in understanding prolonged effects of drought stress and recovery from drought stress in relation to overall tree growth. Conclusions made based on physiological parameters without integration as a whole plant response may be misleading. For example, the different response of A and A' for Mark rootstock would lead to contradictory conclusions regarding the sensitivity of the rootstock to drought, however, when considered in conjunction with the results of most of the other parameters it is apparent that the whole plant parameter A' correlates best with the other results.

Lloyd et al. (1986) contend that chlorophyll fluorescence reflects cumulative stress in regard to water deficits and salt stress and is a sensitive tool in detecting water stress. Chlorophyll fluorescence was more sensitive to drought stress than gas exchange per unit area and did reflect cumulative stress during this experiment for F_v, F_m and F_q with differences occurring later in the stress periods but few differences were noted in the other fluorescence parameters. During this experiment whole tree gas exchange was found to be a better measure of cumulative stress. F_v reflects the rate of reduction of the electron acceptor Q_A and gives an estimate of the PS II fluorescence quantum yield (Karukstis, 1991; Krause and Weis, 1984) F_v is considered one of the most sensitive chlorophyll fluorescence parameter to drought stress (Downton, 1983; Krause and Weis, 1984; Lloyd et al., 1986). This was reflected in F_v being the most consistently reduced fluorescence parameter for the drought stressed rootstocks. Lower F_v is an indication of a slower reduction rate of Q_A and a decrease in PS II quantum yield. F_m occurs when all available Q_A is in a reduced state and has been found to be very responsive to water stress (Downton, 1983; Krause and Weis, 1984; Lloyd et al., 1986). F_q and F_t are related to the transfer of electrons from Q_A to photosystem I (PS I). The reduction in chlorophyll fluorescence from F_m to F_t is a result of F_q. F_q is comprised of photochemical quenching (q_p) caused by oxidation of Q_A as a result of changes in the rate of noncyclic electron transport and nonphotochemical quenching (q_E) caused by increases in the magnitude of the transthylakoid proton gradient, depletion of cations, phosphorylation of PS II light harvesting complex and reduction of pheophytin (Karukstis, 1991). The mechanism responsible for changes in q_E is not known. Measurements taken during this experiment do not allow separation of F_q into q_p and

q_E but inhibition of q_p has been determined to be a valuable indicator of drought resistance for Durum wheat (Havaux and Lannoye, 1985). Steady-state chlorophyll fluorescence is F_t and this represents electron transport through PS II upon saturation of electron acceptors. F_o represents the emission by excited chlorophyll *a* antenna molecules and usually is the last parameter affected by drought stress and indirectly so since reduction of F_o is a result of structural damage of PS II pigments (Bjorkman et al., 1981; Fork et al., 1981; Karukstis, 1991; Krause and Weis, 1984).

Physiological parameters for IG/Mark D usually showed the first and most consistent reductions due to drought stress compared to IG/Mark C. When compared to corresponding controls, IG/Mark D was the first treatment to be significantly lower for 17 of the 21 physiological parameters measured or calculated, IG/MM.111 D was first for 5 of the 21 (similar to IG/Mark D for two) and IG/M.9 EMLA D was first for 4 of the 21 (similar to IG/MM.111 D for three and IG/Mark D for one) when compared to corresponding controls. Physiological parameters for IG/Mark D were reduced by a greater percentage with IG/MM.111 D intermediate and IG/M.9 EMLA D least when compared with corresponding controls.

There were differences mainly in whole tree gas exchange parameters between control treatments demonstrating rootstock effects on scion even under non-stressed conditions. 'Imperial Gala' on Mark C was often highest for gas exchange parameters per tree with IG/MM.111 C slightly lower and IG/M.9 EMLA C lowest. This corresponds with the results for growth parameters that occurred during the experiment.

Sensitivity of physiological parameters to drought stress was ranked by considering when a significant difference between drought and control was first seen, the consistency of the difference and whether the parameter returned to control values during the recovery periods. To determine sensitivity, the number of days in each stress period was divided by three and one point was given to parameters in which differences were seen in the first third of the stress period, two points for parameters in which differences were seen in the second third and three points to parameters in which differences were seen in the last third. To determine consistency, one point was given for parameters in which differences for treatments were significantly different from corresponding controls 67 % to 100 % of the days measured, two points for parameters with differences for 34 % to 66 % of the days measured and three points for parameters with differences for 0 % to 33 % of the days measured. One point was given for parameters that returned to the same level as corresponding controls during recovery, 1.5 points if measurements were not taken for the parameter during recovery, two points for parameters that did not show recovery and three points for parameters that did not differ from controls during the previous drought stress. This was done for each of the three rootstocks and the points were summed. Parameters with the lowest sum were considered most sensitive to drought stress. Parameters were grouped by taking the difference between the highest and lowest rank and dividing by the number of parameters with different sums. If the sum of a parameter differed by this amount from another parameter it was placed into a different grouping. Sensitivity ranking of the parameters was as follows:

1. leaf water potential
2. E', leaf growth rate
3. A', g_l', shoot 2 length
4. g_l, leaf emergence rate
5. A, F_o, F_m, F_q, WUE'
6. E, F_t, leaf osmotic potential, leaf turgor potential
7. F_v, leaf ABA content
8. shoot 1 length, TCAI
9. C_i, g_m, F_m/F_v, $t_{1/2}$, WUE

Although ψ_l was measured only once late into stress 1, the large differences for that measurement, the rapid resurgence during recovery 1 and subsequent reduction during stress 2 demonstrates sensitivity to drought. Leaf growth rate was found to be one of the most sensitive parameters and also was easily measured compared with physiological parameters. Whole tree gas exchange showed the best integration of growth (Section IV) and physiological parameters for detecting and understanding the drought stress response although values did not recover upon irrigation. ABA was slightly less sensitive than ψ_l showing a lag effect during recovery 1 and stress 2. Chlorophyll fluorescence demonstrated cumulative effects of each drought stress for the parameters F_v, F_m and F_q while other parameters were insensitive to stress. Gas exchange per unit area was less sensitive than some of the chlorophyll fluorescence parameters indicating the effect of those parameters on gas exchange. Gas exchange per unit area also was misleading when considering the whole plant response to drought stress indicating M.9 EMLA as most sensitive and Mark as least sensitive to drought stress, contrary to the results for most other parameters.

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Captions for Figures

Figure 1. Percent soil moisture content for drought and control treatments during both stress and recovery period. *LSD significant at the 5% level.

Figure 2. Predawn water relations for stress 1, recovery 1, stress 2 and recovery 2. (A) leaf turgor potential (ψ_t), (B) leaf osmotic potential (ψ_s) and (C) leaf water potential (ψ_l). Solid vertical lines represent LSD at 5%.

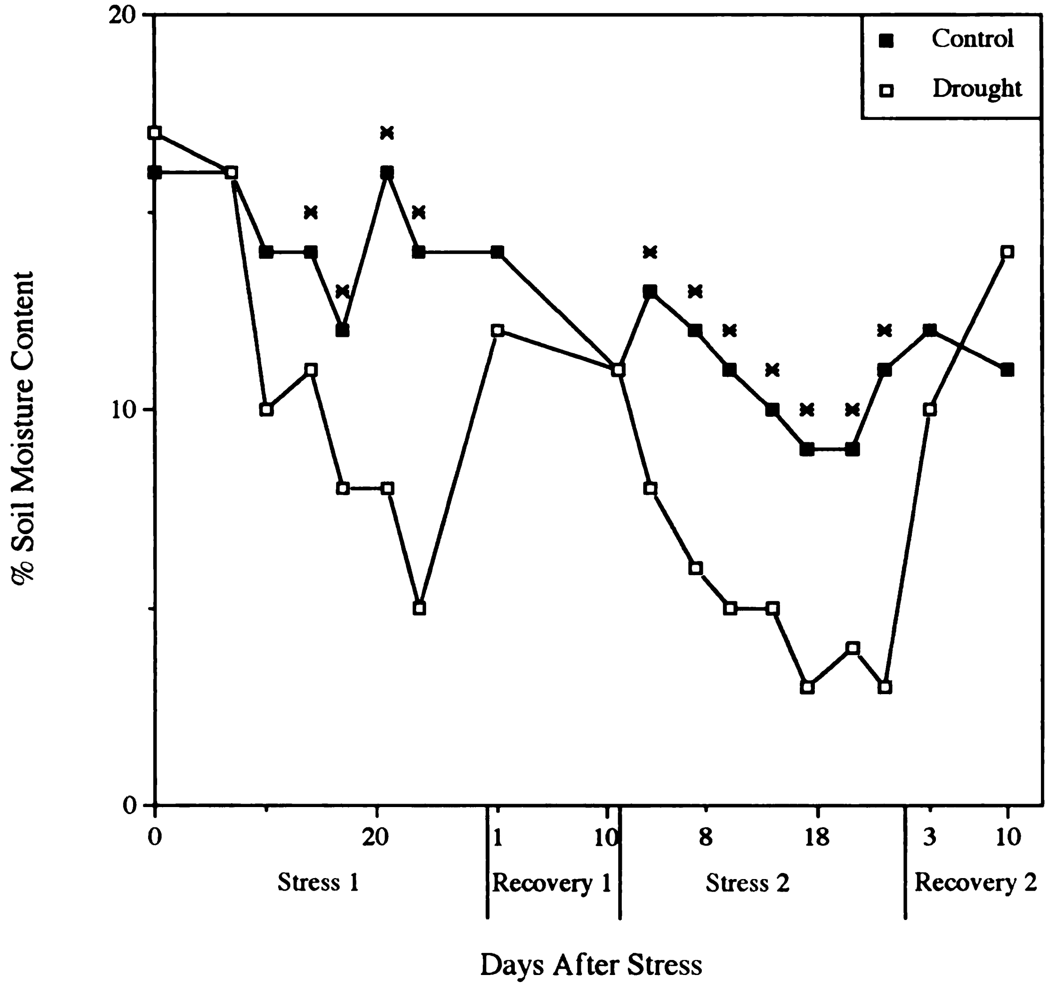
Figure 3. Diurnal leaf water potential (ψ_l) for day 17 and predawn ψ_l for day 18 of stress 1. Solid and dashed vertical lines represent LSD at 5% and 10%, respectively.

Figure 4. Gas exchange per unit area for stress 1, recovery 1 (R1), stress 2 and recovery 2 (R2). (A) CO_2 assimilation (A), (B) leaf conductance (g_l) and (C) transpiration (E). Solid and dashed vertical lines represent LSD at 5% and 10%, respectively.

Figure 5. Diurnal gas exchange per unit area for day 29 of stress 1. (A) CO_2 assimilation (A), (B) leaf conductance (g_l) and (C) transpiration (E). Solid and dashed vertical lines represent LSD at 5% and 10%, respectively.

Figure 6. Gas exchange per tree for stress 1, recovery 1 (R1), stress 2 and recovery 2 (R2). (**A**) CO_2 assimilation (A'), (**B**) leaf conductance (g_l'), (**C**) transpiration (E') and (**D**) water use efficiency (WUE'). Solid vertical lines represent LSD at 5% and 10%, respectively.

Figure 7. Diurnal gas exchange per tree for day 29 of stress 1. (**A**) CO_2 assimilation (A'), (**B**) leaf conductance (g_l') and (**C**) transpiration (E'). Solid and dashed vertical lines represent LSD at 5% and 10%, respectively.



■ Control
□ Drought
20
10
0
% Soil Moisture Content
0
20
1
10
8
18
3
10
Stress 1
Recovery 1
Stress 2
Recovery 2
Days After Stress

Figure 1

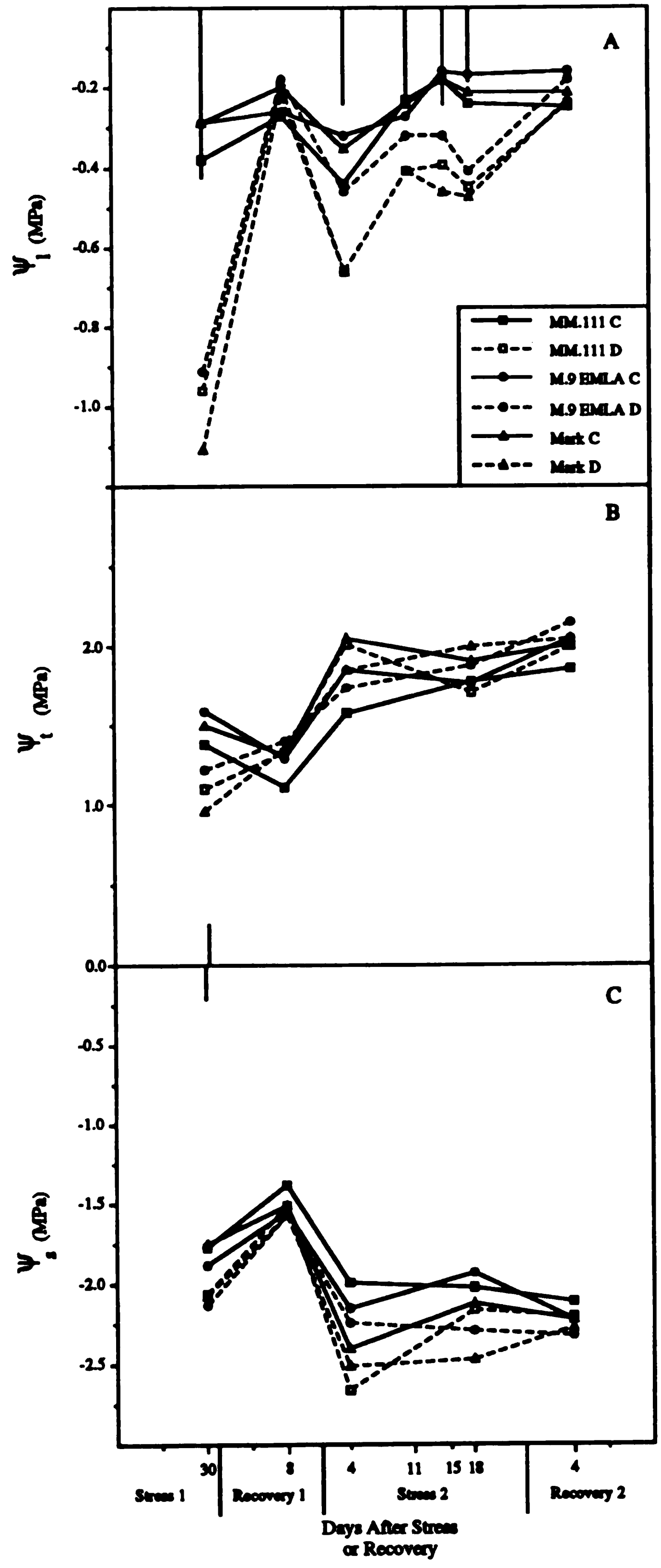
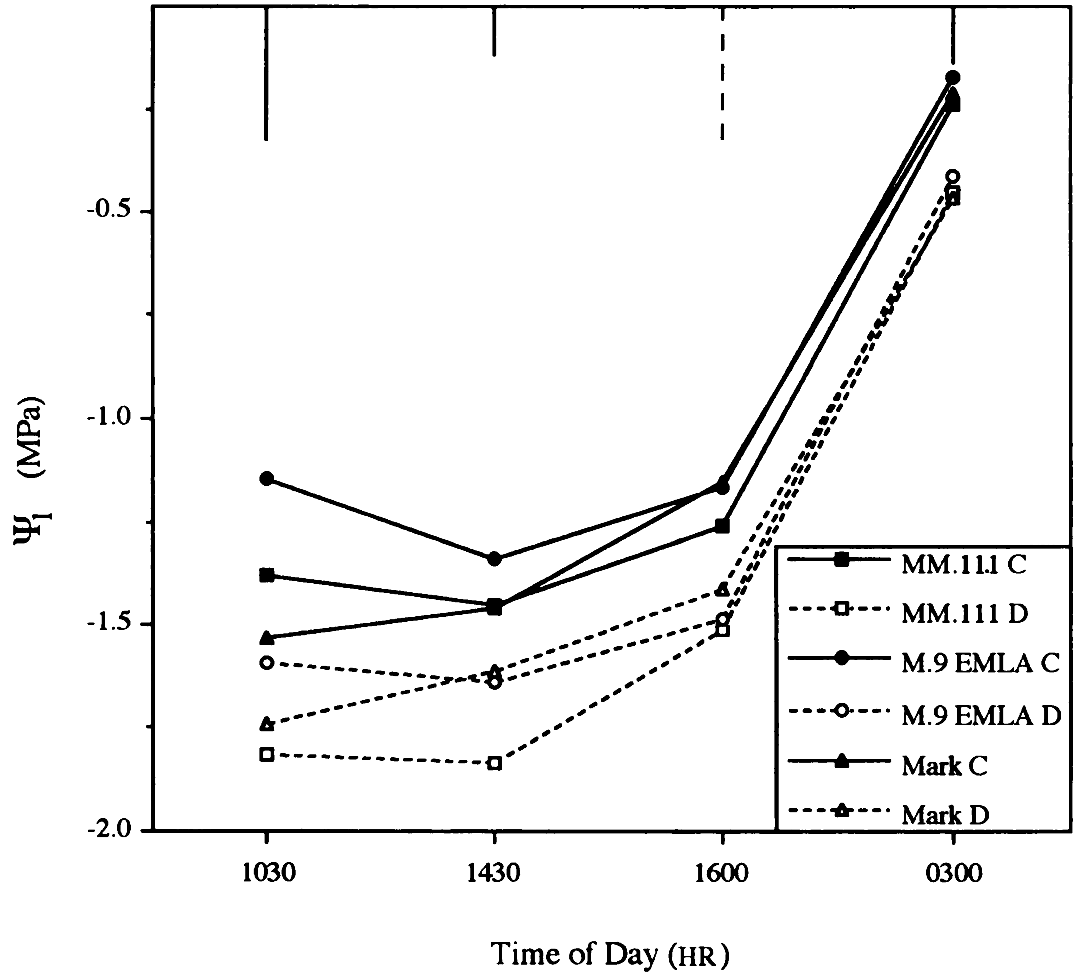

A
-0.2
-0.4
-0.6
-0.8
-1.0
Ψ l (MPa)
MM.111 C
MM.111 D
M.9 EMLA C
M.9 EMLA D
Mark C
Mark D
B
2.0
1.0
0.0
Ψ t (MPa)
C
-0.5
-1.0
-1.5
-2.0
-2.5
Ψ s (MPa)
30
8
4
11
15
18
4
Stress 1
Recovery 1
Stress 2
Recovery 2
Days After Stress
or Recovery

Figure 2



Ψ_l (MPa)
-0.5
-1.0
-1.5
-2.0
1030
1430
1600
0300
Time of Day (HR)
MM.111 C
MM.111 D
M.9 EMLA C
M.9 EMLA D
Mark C
Mark D

Figure 3

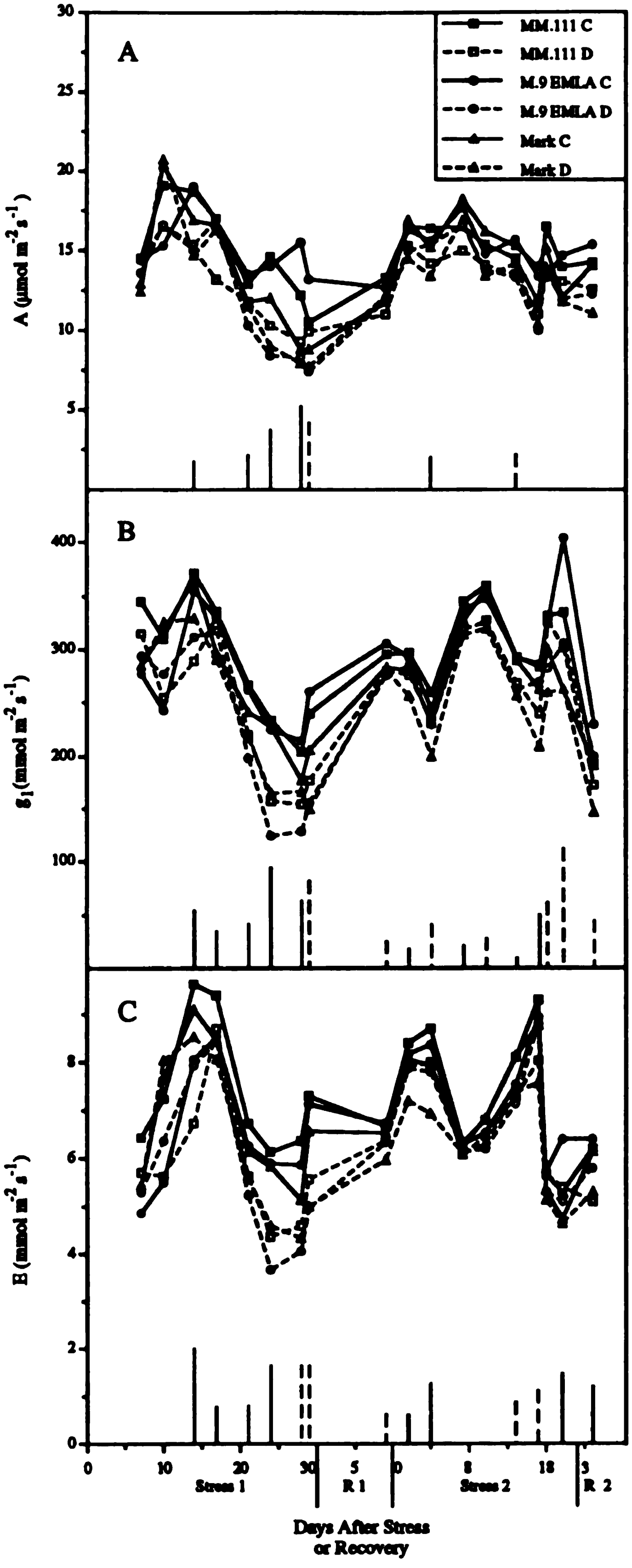

A
B
C
MM.111 C
MM.111 D
M.9 EMLA C
M.9 EMLA D
Mark C
Mark D
A (μmol m^{-2} s^{-1})
g$_1$ (mmol m^{-2} s^{-1})
E (mmol m^{-2} s^{-1})
0
5
10
15
20
25
30
100
200
300
400
2
4
6
8
0
10
20
30
5
0
8
18
3
Stress 1
R 1
Stress 2
R 2
Days After Stress or Recovery

Figure 4

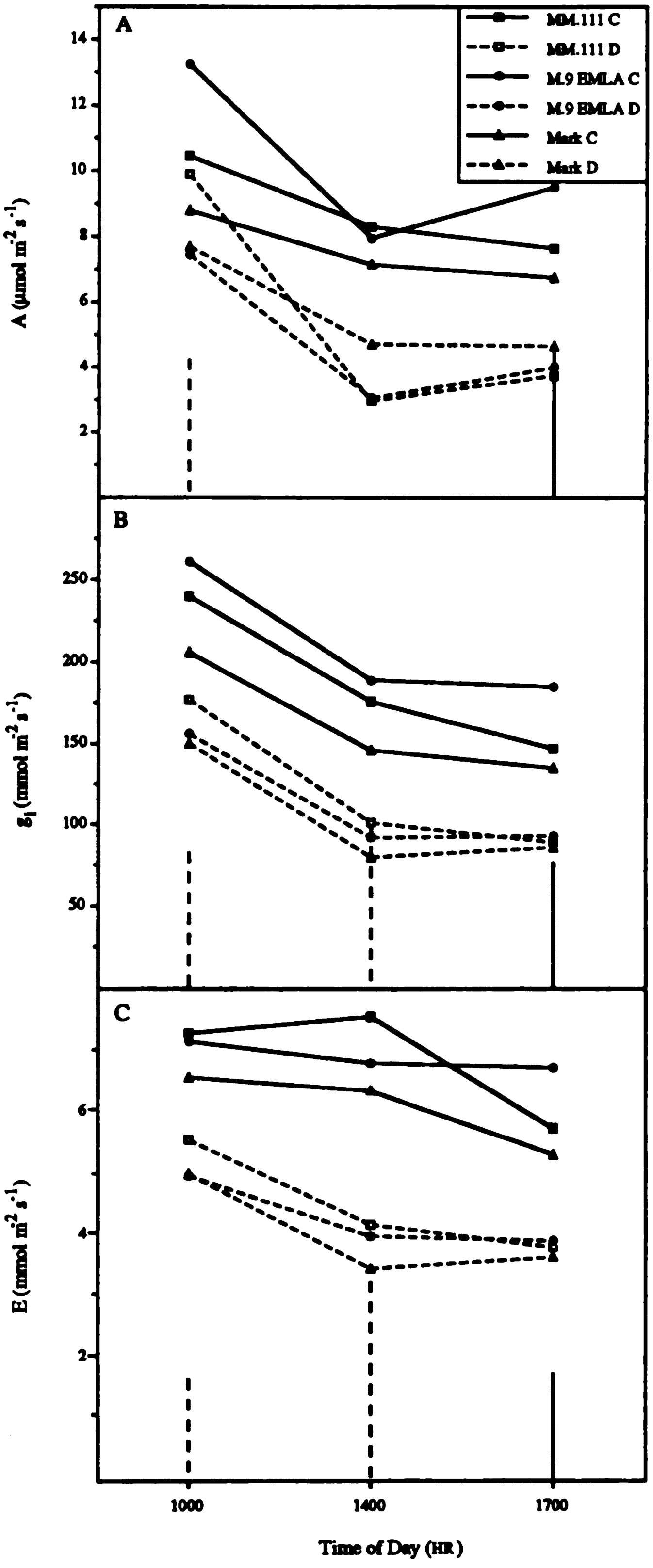

A
B
C
MM.111 C
MM.111 D
M.9 EMLA C
M.9 EMLA D
Mark C
Mark D
A (μmol m⁻² s⁻¹)
2
4
6
8
10
12
14
g_l (mmol m⁻² s⁻¹)
50
100
150
200
250
E (mmol m⁻² s⁻¹)
2
4
6
1000
1400
1700
Time of Day (HR)

Figure 5

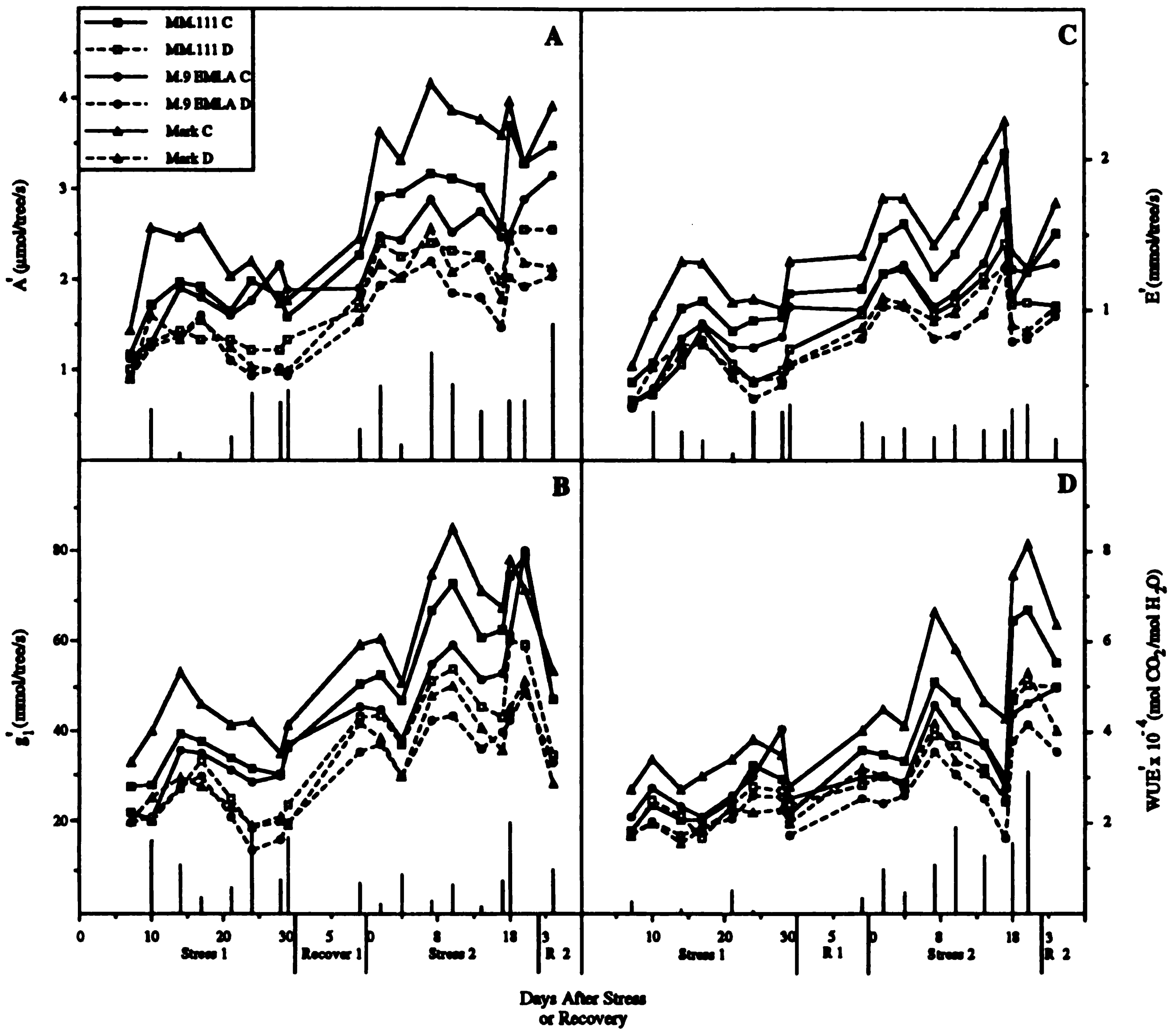

MM.111 C
MM.111 D
M.9 EMLA C
M.9 EMLA D
Mark C
Mark D
A
B
C
D
A′ (μmol/tree/s)
g′l (mmol/tree/s)
E′ (mmol/tree/s)
WUE′ x 10⁻⁴ (mol CO2/mol H2O)
1
2
3
4
20
40
60
80
0
10
20
30
5
8
18
3
Stress 1
Recover 1
Stress 2
R 2
R 1
Days After Stress
or Recovery

Figure 6

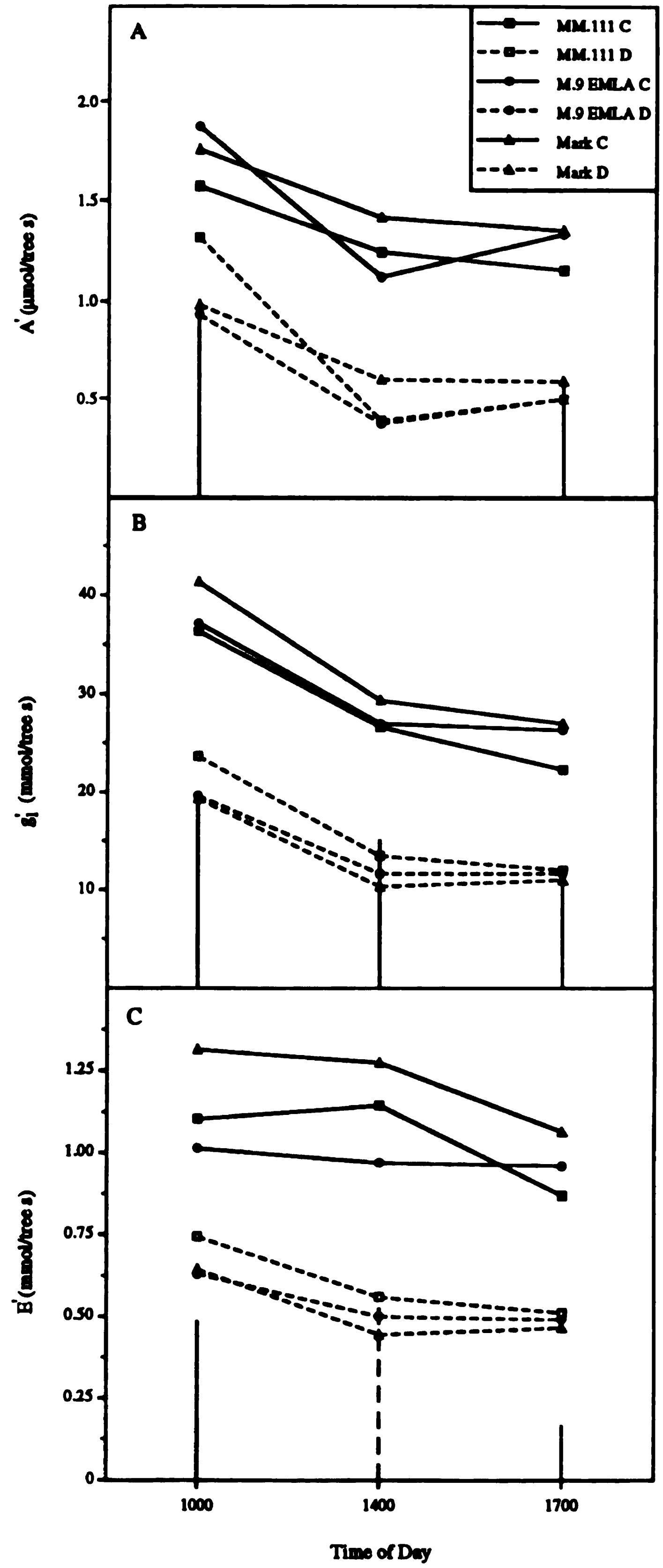

A
MM.111 C
MM.111 D
M.9 EMLA C
M.9 EMLA D
Mark C
Mark D
A' (µmol/tree s)
2.0
1.5
1.0
0.5
B
g_i' (mmol/tree s)
40
30
20
10
C
E' (mmol/tree s)
1.25
1.00
0.75
0.50
0.25
0
1000
1400
1700
Time of Day

Figure 7

Table 1. Leaf abscisic acid content (ng/g dry weight) during the first and second drought stress cycles and recovery. Stress 1 was imposed on 2 July and released 2 August 1991. Stress 2 was imposed on 13 August and released 7 September 1991. Treatment means followed by different letters are significantly different at the 5% level.

	Days After Stress 1	Days After Recovery 1	Days After Stress 2		Days After Recovery 2
Treatment	30	8	4	18	4
MM.111 C	59 d	189 c	369	123 bc	91
MM.111 D	145 abc	322 bc	375	162 ab	99
M.9 EMLA C	80 cd	232 c	359	62 c	70
M.9 EMLA D	193 a	548 a	380	207 a	102
Mark C	98 bcd	312 bc	363	115 bc	88
Mark D	163 ab	434 ab	279	206 a	83

Table 2. Variable chlorophyll fluorescence (relative units) during the first and second drought stress cycles and recovery. Stress 1 was imposed on 2 July and released 2 August 1991. Stress 2 was imposed 13 August and released 7 September 1991. Treatment means followed by different letters are significantly different at the 5% level unless indicated at the column head.

	Days After Stress 1							Days After Recovery 1
Treatment	3	7	10	14	17	21	24	7
					10%			
MM.111 C	1.46	1.55	2.23	1.99	1.68 a	1.97 a	2.08 a	2.11 a
MM.111 D	1.48	1.73	2.19	1.91	1.61 ab	1.63 b	1.94 b	1.80 c
M.9 EMLA C	1.57	1.84	2.16	1.72	1.65 ab	2.08 a	1.99 b	1.93 bc
M.9 EMLA D	1.38	1.55	1.94	1.77	1.45 ab	2.06 a	2.13 a	1.84 c
Mark C	1.55	1.66	2.16	1.89	1.75 a	2.11 a	1.92 b	2.08 ab
Mark D	1.47	1.74	2.18	1.79	1.32 b	1.78 b	2.08 a	1.85 c

	Days After Stress 2						Days After Recovery 2	
	1	3	10	14	21	24	3	10
MM.111 C	1.79	1.82	1.83 ab	2.18 a	1.41 a	1.25	1.38	1.21 ab
MM.111 D	1.87	1.82	1.60 c	1.96 ab	1.34 ab	1.13	1.44	1.33 a
M.9 EMLA C	1.87	1.70	1.82 ab	2.13 ab	1.43 a	1.38	1.32	1.18 ab
M.9 EMLA D	1.75	1.66	1.77 b	1.91 b	1.28 ab	1.27	1.22	1.05 b
Mark C	1.82	1.88	1.94 a	2.17 ab	1.39 a	1.26	1.32	1.15 ab
Mark D	1.69	1.82	1.74 bc	2.05 ab	1.18 b	1.10	1.23	1.19 ab

Table 3. Chlorophyll fluorescence quenching (relative units) during the first and second drought stress cycles and recovery. Stress 1 was imposed on 2 July and released 2 August 1991. Stress 2 was imposed on 13 August and released 7 September 1991. Treatment means followed by different letters are significantly different at the 5% level unless otherwise indicated at the column head.

	Days After Stress 1							Days After Recovery 1
Treatment	3	7	10	14	17	21	24	7
					10%			
MM.111 C	1.80	2.03	2.38	2.62	2.10 a	2.12 ab	2.52	2.48
MM.111 D	1.81	2.27	2.33	2.49	1.93 abc	1.85 c	2.38	2.19
M.9 EMLA C	1.85	2.24	2.45	2.24	1.99 ab	2.26 ab	2.34	2.24
M.9 EMLA D	1.70	2.03	2.00	2.26	1.75 bc	2.32 a	2.53	2.19
Mark C	1.84	2.19	2.34	2.45	2.07 ab	2.31 a	2.36	2.47
Mark D	1.76	2.20	2.25	2.35	1.63 c	2.04 bc	2.59	2.17

	Days After Stress 2						Days After Recovery 2	
	1	3	10	14	21	24	3	10
MM.111 C	2.16	2.04	2.05 b	2.48 a	1.49 a	1.44	1.55 a	1.26
MM.111 D	2.20	2.05	1.81 c	2.12 bc	1.26 b	1.21	1.44 ab	1.33
M.9 EMLA C	2.20	1.92	2.01 b	2.26 abc	1.40 a	1.54	1.39 ab	1.14
M.9 EMLA D	2.03	1.88	1.90 c	2.03 c	1.16 bc	1.38	1.29 b	1.13
Mark C	2.10	2.09	2.15 a	2.44 ab	1.44 a	1.41	1.46 ab	1.17
Mark D	2.08	2.09	1.90 c	2.21 abc	1.10 c	1.25	1.27 b	1.16

Table 4. Maximal chlorophyll fluorescence (relative units) during the first and second drought stress cycles and recovery. Stress 1 was imposed on 2 July and released 2 August 1991. Stress 2 was imposed on 13 August and released 7 September 1991. Treatment means followed by different letters are significantly different at the 5% level unless otherwise indicated at the column head.

	Days After Stress 1							Days After Recovery 1
Treatment	3	7	10	14	17	21	24	7
					10%			
MM.111 C	2.18	2.48	3.31	3.21	2.56 a	3.02 a	3.40 ab	3.06
MM.111 D	2.20	2.74	3.28	3.08	2.35 abc	2.45 b	3.14 c	2.66
M.9 EMLA C	2.24	2.92	3.28	2.79	2.44 ab	3.14 a	3.23 abc	2.80
M.9 EMLA D	2.04	2.48	2.88	2.78	2.13 bc	2.97 a	3.42 a	2.65
Mark C	2.21	2.66	3.20	3.01	2.55 a	3.18 a	3.16 bc	3.04
Mark D	2.09	2.68	3.24	2.87	1.99 c	2.60 b	3.27 abc	2.66
	Days After Stress 2						Days After Recovery 2	
	1	3	10	14	21	24	3	10
MM.111 C	2.66	2.56	2.65 b	3.08 a	2.04	1.86	2.00 a	1.82
MM.111 D	2.66	2.52	2.30 f	2.68 ab	1.90	1.63	1.99 a	1.91
M.9 EMLA C	2.69	2.38	2.58 c	3.00 ab	2.02	2.04	1.89 ab	1.73
M.9 EMLA D	2.48	2.30	2.46 d	2.58 b	1.80	1.85	1.72 b	1.51
Mark C	2.61	2.58	2.72 a	3.11 a	1.97	1.84	1.89 ab	1.70
Mark D	2.49	2.52	2.43 e	2.86 ab	1.68	1.62	1.78 ab	1.71

Table 5. Terminal chlorophyll fluorescence (relative units) during the first and second drought stress cycles and recovery. Stress 1 was imposed on 2 July and released 2 August 1991. Stress 2 was imposed on 13 August and released 7 September 1991. Treatment means followed by different letters are significantly different at the 5% level unless otherwise indicated at the column head.

	Days After Stress 1							Days After Recovery 1
Treatment	3	7	10	14	17	21	24	7
					10%			
MM.111 C	0.38	0.46	0.93	0.59	0.46 ab	0.91 a	0.88	0.58
MM.111 D	0.38	0.47	0.95	0.58	0.41 abc	0.60 b	0.76	0.46
M.9 EMLA C	0.39	0.68	0.83	0.55	0.45 ab	0.88 ab	0.89	0.57
M.9 EMLA D	0.34	0.45	0.88	0.52	0.38 bc	0.66 abc	0.89	0.46
Mark C	0.37	0.47	0.86	0.56	0.48 a	0.87 ab	0.80	0.57
Mark D	0.34	0.48	0.98	0.53	0.36 c	0.56 c	0.69	0.49

	Days After Stress 2						Days After Recovery 2	
	1	3	10	14	21	24	3	10
MM.111 C	0.50	0.52	0.61 a	0.60 b	0.55	0.42	0.45	0.56 ab
MM.111 D	0.46	0.47	0.49 c	0.57 b	0.64	0.42	0.55	0.58 a
M.9 EMLA C	0.50	0.46	0.57 ab	0.74 a	0.62	0.50	0.50	0.58 a
M.9 EMLA D	0.45	0.42	0.56 ab	0.55 b	0.64	0.47	0.42	0.38 b
Mark C	0.51	0.49	0.58 ab	0.67 ab	0.53	0.43	0.44	0.52 ab
Mark D	0.41	0.43	0.53 bc	0.65 ab	0.58	0.37	0.51	0.55 ab

Table 6. Non-variable chlorophyll fluorescence (relative units) during the first and second stress cycles and recovery. Stress 1 was imposed on 2 July and released 2 August 1991. Stress 2 was imposed on 13 August and released 7 September 1991. Treatment means followed by different letters are significantly different at the 5% level.

	Days After Stress 1							Days After Recovery 1
Treatment	3	7	10	14	17	21	24	7
MM.111 C	0.72	0.94	1.08	1.22	0.89 a	1.06	1.32	0.95
MM.111 D	0.72	1.01	1.10	1.16	0.73 bc	0.82	1.21	0.86
M.9 EMLA C	0.67	1.08	1.11	1.07	0.79 b	1.06	1.24	0.87
M.9 EMLA D	0.66	0.93	0.95	1.02	0.67 c	0.91	1.29	0.81
Mark C	0.66	1.00	1.03	1.12	0.80 b	1.07	1.23	0.96
Mark D	0.63	0.94	1.06	1.08	0.67 c	0.83	1.19	0.81

	Days After Stress 2						Days After Recovery 2	
	1	3	10	14	21	24	3	10
MM.111 C	0.87	0.74	0.83 a	0.91 a	0.62	0.61	0.62 a	0.61
MM.111 D	0.79	0.69	0.70 b	0.72 bc	0.56	0.50	0.54 b	0.59
M.9 EMLA C	0.83	0.69	0.76 ab	0.87 ab	0.60	0.66	0.57 ab	0.55
M.9 EMLA D	0.73	0.64	0.70 b	0.68 c	0.52	0.58	0.49 c	0.45
Mark C	0.79	0.70	0.79 ab	0.94 a	0.58	0.58	0.58 ab	0.54
Mark D	0.80	0.70	0.69 b	0.81 abc	0.50	0.52	0.55 bc	0.53

Table 7. Chlorophyll efficiency (F_{var}/F_{max}) during the first and second drought stress cycles and recovery. Stress 1 was imposed on 2 July and released 2 August 1991. Stress 2 was imposed on 13 August and release 7 September 1991. Treatment means followed by different letters are significantly different at the 5% level unless otherwise indicated at the column head.

	Days After Stress 1							Days After Recovery 1
Treatment	3	7	10	14	17	21	24	7
					10%			
MM.111 C	0.67	0.62	0.67	0.61	0.65 b	0.64	0.61	0.69
MM.111 D	0.67	0.63	0.67	0.62	0.69 a	0.66	0.61	0.68
M.9 EMLA C	0.70	0.63	0.66	0.62	0.68 a	0.66	0.62	0.69
M.9 EMLA D	0.68	0.62	0.68	0.63	0.68 a	0.69	0.62	0.69
Mark C	0.70	0.61	0.68	0.63	0.69 a	0.66	0.61	0.68
Mark D	0.70	0.65	0.67	0.63	0.66 ab	0.68	0.63	0.70

	Days After Stress 2						Days After Recovery 2	
	1	3	10	14	21	24	3	10
MM.111 C	0.67	0.71	0.69	0.71 ab	0.69	0.67	0.69	0.67
MM.111 D	0.70	0.72	0.69	0.73 a	0.71	0.69	0.72	0.70
M.9 EMLA C	0.69	0.71	0.70	0.71 ab	0.71	0.68	0.70	0.68
M.9 EMLA D	0.71	0.73	072	0.74 a	0.71	0.69	0.71	0.70
Mark C	0.68	0.73	0.71	0.70 b	0.71	0.68	0.70	0.68
Mark D	0.67	0.72	0.71	0.72 ab	0.71	0.68	0.69	0.69

SECTION IV. DROUGHT RESPONSE OF YOUNG APPLE TREES ON THREE ROOTSTOCKS II. GROWTH AND DEVELOPMENT

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Received for publication . Acknowledgment is made to the Michigan Agricultural Experiment Station and the Michigan Apple Research Committee for their support of this research. The authors wish to thank Kenneth Gordon, Daniel Kort, David Costolo, Joan Runkel and Gail Byler for their assistance with this project. The cost of publishing this paper was defrayed in part by the payment of page charges. Under postal regulation, this paper must be hereby marked *advertisement* solely to indicate this fact.

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Cellular and Whole Plant Physiology

Drought Response of Young Apple Trees on Three Rootstocks

II. Growth and Development

Additional index words. ***Malus domestica***, growth, water stress

Abbreviations: IG/M.9 EMLA C, 'Imperial Gala' on control M.9 EMLA; IG/M.9 EMLA D, 'Imperial Gala' on drought stressed M.9 EMLA; IG/Mark C, 'Imperial Gala' on control Mark; IG/Mark D, 'Imperial Gala' on drought stressed Mark; IG/MM.111 C, 'Imperial Gala' on control MM.111; IG/MM.111 D, 'Imperial Gala' on drought stressed MM.111; TCAI, trunk cross sectional area increase

Abstract. 'Imperial Gala' apple trees (*Malus domestica* Borkh.) on M.9 EMLA, MM.111 and Mark rootstocks were subjected to two drought stress periods and two recovery periods in a rainshelter. Leaf growth rate, leaf area, leaf emergence, shoot length and trunk cross sectional area were measured throughout each stress and recovery period. Leaf growth rate was the best indicator of drought stress being consistently reduced during drought periods and returning to control levels during recovery periods. Length of the less vigorous shoot also was sensitive to stress but did not recover upon irrigation. Leaf emergence and trunk cross sectional area increase were inconsistent in response to stress. Growth of trees on Mark rootstock was

reduced to the greatest extent for all parameters by drought stress followed by MM.111 and M.9 EMLA. At termination of the experiment 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 34%, 27% and 16% reduction in total plant dry weight for drought stressed trees on Mark, MM.111 and M.9 EMLA, respectively. It was concluded that Mark was the most sensitive of the three rootstocks followed by MM.111 with M.9 EMLA being fairly drought tolerant.

The effect of dwarfing rootstocks on apple growth and cropping is the subject of several reviews (Avery, 1970; Ferree and Carlson, 1987; Parry, 1977); however, the drought stress response is not as well understood. Landsberg and Jones (1981) cite several Russian publications (Misic and Gavrilovic, 1960; Moiseev et al., 1970; Razlivalova, 1974) that demonstrate conferance of drought resistance of dwarfing rootstocks to scions and that indicate M.9 is one of the most drought tolerant rootstocks. Yet there is still contention regarding the capacity of dwarfing rootstocks, in general, to confer drought resistance or tolerance to the scion. Some authors have characterized dwarfing rootstocks, especially M.9, as intolerant of drought stress while more vigorous rootstocks, particularly MM.111, are considered more drought tolerant (Ferree and Carlson, 1987; Tukey, 1964).

Debate also exists regarding the most sensitive plant parameter to drought stress (Higgs and Jones, 1991; Hsiao, 1973; Olien and Flore, 1990). An easily measured growth parameter would be ideal for detecting drought stress both for researchers as well as orchardists who might want to use it for detection of drought stress and irrigation management.

The objectives of this study were to determine growth parameter sensitivity to drought stress, compare M.9 EMLA, MM.111 and Mark rootstock performance under drought conditions, and determine methods of adaptation to drought stress. This paper also will address the relationship between the growth response to drought stress and the physiological changes reported in the previous paper (Section III) and summarize vegetative and physiological responses.

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. The rainshelter, upon closing, traveled at a rate of 0.3 m/s and was programmed to close after accumulation of 4 mm of rainfall. The rainshelter is described in detail by Martin et al. (1988). The trees were planted in 30 cm wide X 40 cm deep trenches lined with a spun bound polypropylene material to restrict root volume and mounded to 15 cm high raised beds. The trees were interplanted with crab-apples (*Malus* x *zumi* 'Indian Summer') and sweet cherry (*Prunus avium* L. 'Emperor Francis') in a split plot design with two replicates of main plots of irrigation and six replicates of subplots of rootstock for a total of 72 apple trees. The trees were trained to have two shoots per tree. Soil was classified as a Kalamazoo loam (fine-loamy, mixed, mesic Typic Hapludolf). Trees were fertilized prior to each drought stress period with 14 g nitrogen as NH_4NO_3 per tree. The plots were kept weed free by either applying paraquat or shallow tillage. Guthion or malathion was applied weekly to suppress infestation of Japanese beetles.

Water was supplied by drip irrigation at 2 liters per day per tree before and after each drought period while water was withheld from one half of the trees during the drought stresses. Two drought stress periods lasting approximately one month each were imposed during 1991. The first drought stress was from 2 July through 2 Aug with a recovery period from 3 to 12 Aug. The second drought stress lasted from 13 Aug through 7 Sept. Recovery from the second drought stress was monitored through 17 Sept. A malfunction prohibited the shelter from closing on 9 July (day 7 of the first stress period) and 10 mm of rain fell on this date.

The following measurements were taken twice weekly at approximately the same time of day to reduce diurnal variation:

Trunk diameter of all trees was measured with a digital micrometer (Fowler Max-Cal) at marked locations 5 cm above the bud union. Cumulative trunk cross sectional area increase (TCAI) from the beginning of the first stress was calculated from trunk diameters. Length from the base to the apical bud of each shoot also was measured for all trees. 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, remeasuring during the next monitoring period and taking the difference divided by the number of days between measurements. 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. Soil moisture content was determined using a time domain reflectometer and 32 cm steel rods to give an average soil moisture content within the top 30 cm of soil (TDR Tektronix 1053) (Topp and Davis, 1985; Topp et al., 1982).

Following each stress period an estimate of plant leaf area was calculated by measuring leaf area as described above for three mature leaves per shoot and counting the number of unfolded leaves per shoot for all trees. The trees were defoliated 8 Oct and leaves were counted and dried to determine dry weight. Trees that were not removed for cold hardiness evaluation (unpublished data) were excavated from 17 to 27 Oct. including roots inside and outside of the material lining the trenches. The 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 (roots off tree), roots sifted from inside the material (roots inside) and roots sifted from outside the material (roots outside) and dried to determine dry weight.

Results

Soil moisture within the top 30 cm of soil was lower for the drought stressed treatments 14 and 3 days after imposition of the first and second stress, respectively, and remained lower for both stress periods until irrigation during the respective recovery periods (Figure 1). The longer period of time for the difference to become apparent for the first stress period was due to the malfunction of the shelter 7 days into the first stress. Additionally, a larger canopy achieved in the second stress period resulted in a greater transpirational demand.

Shoot length for the less vigorous shoot (shoot 2) was reduced 7 days into the first stress for 'Imperial Gala' on drought stressed Mark (IG/Mark D) compared to 'Imperial Gala' on control Mark (IG/Mark C) and remained lower during both stress and recovery periods except day 17 of the first stress period (Figure 2). Shoot 2 length did not differ for 'Imperial Gala' on control MM.111 (IG/MM.111 C) or drought MM.111 (IG/MM.111 D) until day 24 of the first stress when IG/MM.111 D remained lower than IG/MM.111 C for the duration of the experiment. There was no difference between IG/M.9 EMLA C and D during the study except for the first stress period on days 10 and 14 where shoot extension on IG/M.9 EMLA D was greater than IG/M.9 EMLA C and day 7 of the first recovery period where IG/M.9 EMLA C was greater than IG/M.9 EMLA D. Shoot 2 length was greater for IG/Mark C than IG/MM.111 C on days 7, 10, 14, 17, 24 and 28 of the first stress period but the same subsequently until termination of the experiment; greater than

IG/M.9 EMLA D for all measurements except days 7, 10 and 17 of stress 1; greater than IG/MM.111 D on all days except day 7 and 17 of the first stress and greater than IG/M.9 EMLA C on all days except day 17 of the first stress. Shoot 2 length of IG/MM.111 C was greater than IG/M.9 EMLA C and the drought stressed rootstocks from day 24 of the first stress period throughout the duration of the project while IG/M.9 EMLA C and the drought stressed rootstocks were not different except for a few occasions. Final shoot 2 length was 10%, 33% and 38% lower for IG/M.9 EMLA D, IG/MM.111 D and IG/Mark D, respectively, compared to corresponding rootstock controls. Shoot 2 length was lower for three out of the 20 measurements for IG/M.9 EMLA D than IG/M.9 EMLA C, 13 out of the 20 measurements for IG/MM.111 D than IG/MM.111 C and 18 out of the 20 measurements for IG/Mark D than IG/Mark C.

Differences in shoot length of the more vigorous shoot (shoot 1) were not seen until day 7 of the first recovery period at which time shoot length was reduced only for IG/Mark D compared with IG/Mark C at the 10% level (Figure 3). Shoot 1 length for IG/Mark D remained lower than IG/Mark C throughout the second stress period and differences were significant at the 5% level from day 7 of the second stress until termination. Shoot 1 length was lower for IG/MM.111 D compared to IG/MM.111 C at the 10% level from day 3 of the second stress until the end of the experiment except for day 14. No difference in shoot 1 length was seen between IG/M.9 EMLA C and D. Shoot 1 length was similar for all control rootstocks during the first stress and recovery periods while shoot 1 length for IG/Mark D was reduced most compared to IG/Mark C and IG/MM.111 C with IG/MM.111 D and IG/M.9 EMLA D lower than IG/Mark C but not different from IG/MM.111 C, IG/M.9 EMLA C or IG/Mark D. During the second stress period shoot 1 length for IG/Mark D always was lower than IG/Mark C and usually lower than IG/MM.111 C. Shoot 1 length for IG/MM.111 D and IG/M.9 EMLA D was not different from IG/M.9 EMLA C but was lower than IG/MM.111 C and IG/Mark C for most dates. From day 21 through 35, IG/M.9 EMLA C was lower than IG/MM.111 C and IG/Mark C but similar to the drought stressed rootstocks. Shoot 1 length at termination of the project was reduced by 14%, 30% and 35% for IG/M.9 EMLA D, IG/MM.111 D and IG/Mark D, respectively, compared to corresponding controls. Shoot 1 length was lower for six out of 20 measurements for IG/MM.111 D than IG/MM.111 C and 10 out of 20 measurements for IG/Mark D than IG/Mark C with no differences between IG/M.9 EMLA C and D.

Shoot length of both shoots showed a linear pattern for IG/MM.111 C and IG/Mark C when data was subjected to regression analysis (Figs. 2, 3). A sigmoidal pattern was apparent for IG/M.9 EMLA C and the drought stressed rootstocks. Regression curves for IG/Mark D, IG/MM.111 D and IG/M.9 EMLA C and D depart from linearity with a change in inflection of the curves at approximately 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 IG/Mark D than IG/MM.111 D with IG/M.9 EMLA D intermediate compared to corresponding controls. The curves for shoot 1 and 2 of IG/M.9 EMLA C and the drought stressed rootstocks are similar in shape and magnitude as shoot length was not different among them during the experiment.

Reduction in leaf growth rate occurred for IG/M.9 EMLA D and IG/MM.111 D 7 days after imposition of the first stress compared to IG/Mark D but not the control rootstocks (Table 1). Leaf growth rate also was lower 10 days into the first drought stress for IG/M.9 EMLA D when compared with IG/MM.111 C. No differences were noted for the next two measurement periods; however, from day 21 of the first stress and subsequently until the recovery period a reduction in leaf growth rate for the drought stressed rootstocks was detected. Leaf growth rate for IG/MM.111 D and IG/Mark D were most consistently reduced compared with IG/MM.111 C and IG/Mark C. 'Imperial Gala' on M.9 EMLA D also was lower than IG/MM.111 C and IG/Mark C but not for IG/M.9 EMLA C until 31 days into the first drought stress. Leaf growth rate was not different for any drought stressed rootstock compared with IG/M.9 EMLA C until late in the first stress period (day 31). As the stress progressed, leaf growth rate for all drought stressed rootstocks was lower than all control rootstocks. During the first recovery period leaf growth rate for the drought stressed rootstocks returned to that of the controls by day 7. For the measurement on day 10 of the first recovery period there were not enough leaves to estimate leaf growth rate for IG/M.9 EMLA D. Results were similar for the second stress period although more rapid. Leaf growth rate was lower for all drought stressed rootstocks versus IG/MM.111 C and IG/Mark C on day 3 of the second stress period at the 10% level. During the following measurement period, day 7, there was an inadequate number of new leaves for the drought stressed rootstocks to make statistical comparisons; however, for all subsequent measurements until recovery leaf growth rate for all drought stressed rootstocks was lower than controls at the 5% level except day 21 when IG/M.9 EMLA D was not different from IG/M.9 EMLA C or IG/MM.111 C. By day 3 of the second recovery period leaf growth rate for the drought stressed treatments had returned to the same rate as controls.

Reductions in TCAI were first seen on day 7 of the first stress period for IG/M.9 EMLA D compared to IG/M.9 EMLA C; however, no other reductions for IG/M.9 EMLA D occurred except for day 7 of the first recovery period (Figure 4). TCAI was reduced for IG/Mark D compared to IG/Mark C on days 21 and 28 of the first stress period, day 1 of the first recovery period, day 24 of the second stress period and day 10 of the second recovery period. Lower TCAI for IG/MM.111 D compared to IG/MM.111 C was seen only on day 1 of the first recovery period. TCAI was lower at the 10% level for IG/Mark D compared to IG/Mark C for all measurements during the second stress and recovery periods, no other rootstocks showed differences at the 10% level. Differences did occur due to rootstock with TCAI generally highest for IG/MM.111 C, IG/MM.111 D and IG/Mark C during both stress and recovery periods, IG/Mark D usually exhibiting the lowest TCAI during the experiment and IG/M.9 EMLA C and D intermediate. During the first stress period IG/M.9 EMLA D and IG/Mark D had the lowest TCAI compared with IG/MM.111 C, IG/Mark C and IG/MM.111 D. IG/M.9 EMLA C rarely was different from IG/M.9 EMLA D or IG/Mark D but lower than IG/MM.111 C 7, 21, 28, and 31 days after imposition of the first stress and IG/Mark C and IG/MM.111 D 7, 21 and 31 days into the stress. In the first recovery period no differences were seen in TCAI except on day 1 when all control rootstocks were higher than corresponding drought stressed rootstocks and IG/MM.111 C and IG/Mark C were higher than IG/M.9 EMLA C and D and IG/Mark D. The difference in IG/MM.111 C compared to IG/M.9 EMLA C, IG/M.9 EMLA D and IG/Mark D was seen throughout the second stress period. The only other difference at the 5% level was a lower TCAI for IG/Mark D compared with all other treatments except IG/M.9 EMLA C and IG/M.9 EMLA D 24 days after the beginning of the second stress and day 10 of the second recovery period. TCAI at termination of the experiment was 16%, 30% and 52% lower IG/M.9 EMLA D, IG/MM.111 D and IG/Mark D, respectively, compared to corresponding controls. Of the 19 measurements of TCAI, IG/M.9 EMLA D was lower than IG/M.9 EMLA C only twice, IG/MM.111 D was lower than IG/MM.111 C only once and IG/Mark D was lower than IG/Mark C five times.

When subjected to regression analysis TCAI exhibited a linear pattern for all treatments with IG/MM.111 C having the greatest slope, IG/Mark C and IG/MM.111 D intermediate and IG/M.9 EMLA C and D and IG/Mark D having the flattest slopes (Figure 4). The slopes of the regression lines were 2%, 32% and 52% lower for IG/M.9 EMLA D, IG/MM.111 D and IG/Mark D, respectively, compared to corresponding rootstock controls.

A reduction in leaf emergence during the first drought stress was apparent 14 days after imposition of stress where IG/Mark D was lowest compared to IG/Mark C and IG/MM.111 C and D but similar to IG/M.9 EMLA C and D (Table 2). No difference was noticed for the next three measurements at the 5% level. Leaf emergence again was affected on day 28 with all three drought stressed rootstocks being lower than the control treatments, of which IG/Mark C leaf emergence was greater than IG/MM.111 C and IG/M.9 EMLA C. On day 1 of the first recovery period IG/Mark D was lower than all other treatments except IG/M.9 EMLA D, at this time, IG/M.9 EMLA D was lower than IG/MM.111 C with no other differences between treatments. By day 7 of the first recovery period leaf emergence was lowest for IG/M.9 EMLA D followed by IG/Mark D compared to control rootstocks with no other differences between treatments. During the second stress period, leaf emergence was reduced for all drought stressed rootstocks compared to control rootstocks by day 3. On day 10 IG/M.9 EMLA D was lower from IG/MM.111 C and IG/Mark C with all other comparisons showing no difference. No differences were seen for leaf emergence from day 14 of the second stress period through the second recovery. 'Imperial Gala' on Mark D had the most consistently reduced leaf emergence rate with five measurement periods lower than IG/Mark C, IG/M.9 EMLA D had three measurement periods lower than IG/M.9 EMLA C and IG/MM.111 D was lower for two measurement periods than IG/MM.111 C.

Dry weights for 1-year-old wood (current season scion growth) were lower for IG/MM.111 D, IG/Mark D, IG/M.9 EMLA C and D than IG/MM.111 C and

IG/Mark C (Table 3). One-year-old wood was 20%, 49% and 56% lower for IG/M.9 EMLA D, IG/MM.111 D and IG/Mark D, respectively, compared with corresponding controls. No differences were seen in dry weight of 2-year-old wood (previous season scion growth) compared to corresponding controls but rootstock wood was highest for IG/MM.111 C followed by IG/MM.111 D then IG/Mark C with IG/Mark D, IG/M.9 EMLA C and D lowest with a total reduction of 19% and 16% for IG/MM.111 D and IG/Mark D, respectively, and a 6% increase for IG/M.9 EMLA D compared to corresponding controls. No differences were noted for roots off tree (roots removed directly from the tree) except IG/Mark C was higher than IG/M.9 EMLA D. Differences in roots inside (roots sifted from inside the material) were mainly due to rootstock with IG/M.9 EMLA C, IG/Mark C and D highest followed by IG/M.9 EMLA D and IG/MM.111 C with IG/MM.111 D lowest. Roots sifted from outside the material showed no differences in dry weight due to either rootstock or treatment. Total root dry weight was higher for IG/Mark C than any of the other rootstock/treatment combinations and IG/M.9 EMLA D was lower than IG/Mark D and IG/MM.111 C with no other differences apparent. Reductions of 22%, 24% and 31% were noted for IG/M.9 EMLA D, IG/MM.111 D and IG/Mark D, respectively, compared to corresponding controls for total root dry weight. The gross root distribution of IG/M.9 EMLA D was affected as evidenced by no difference in total root dry weight but fewer roots inside than IG/M.9 EMLA C and more roots outside, although not significantly different. Dry weights of the trees were highest for IG/MM.111 C and IG/Mark C, with IG/MM.111 D lower than

IG/MM.111 C but similar to IG/Mark C as well as IG/Mark D, IG/M.9 EMLA C and D, which had the lowest dry weights. Total tree dry weight was reduced by 16%, 27% and 34% for IG/M.9 EMLA D, IG/MM.111 D and IG/Mark D, respectively, compared with corresponding controls.

Dry weights for leaves from shoot 2 were lower for IG/MM.111 D, IG/Mark D and IG/M.9 EMLA C and D than IG/MM.111 C and IG/Mark C and dry weights for leaves from shoot 1 were lower for IG/Mark D and IG/M.9 EMLA D than IG/Mark C, all other comparisons showing no difference (Table 4). 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 IG/Mark D compared with IG/Mark C at the end of the second stress period. 'Imperial Gala' on M.9 EMLA had the fewest leaves regardless of treatment at the end of the first stress period and IG/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 at planting but differences within rootstock and between treatments were due to the drought stress.

Discussion

Many authors have found drought stress to affect the growth parameters reported in this experiment but few have measured them with the intent to determine the most sensitive. This was done by Olien and Flore (1990) for peach who ranked parameter sensitivity to stress in order of occurrence of significant differences. They found leaf growth rate and leaf emergence to be the most sensitive parameters and water relations and gas exchange to be the least sensitive parameters to drought. Parameter sensitivity to drought in this study was ranked by considering when a significant difference between drought and control treatments first occurred, consistency of the difference and whether the values for drought stressed treatments returned to those of controls during recovery. Parameters are discussed in order from most to least sensitive to drought stress: Leaf growth rate was considered to be the most sensitive parameter to water stress since differences were consistent between drought and control, occurred fairly early and returned to control levels upon irrigation during both recovery periods. Significant differences were seen by day 7 and 3 of the first and second drought stress, respectively. Consistent differences were found from day 21 and day 3 of the first and second drought stress, respectively, until day 7 and 10 of the first and second recovery period, respectively. Leaf growth rate was the only growth parameter that had shown a difference during both drought stress periods to have returned to control levels during both of the recovery periods. Shoot 2 length was the first parameter to respond to drought stress and showed the most consistent differences between drought and control from day 7 of the first stress period until termination of the experiment, however, values for drought stressed trees did not return to those of controls during the recovery periods. Shoot 2 length 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. Shoot length of a less vigorous shoot also may be a more difficult parameter to measure in complex canopies with several competing shoots. Leaf emergence was reduced by the drought stress by day 14 of the first stress period but differences were inconsistent and did not return to control rates during either of the recovery periods. TCAI was the next most sensitive growth parameter differing 7 and 1 days after imposition of the first and second stress, respectively. Differences for TCAI were not as consistent and did not occur between all treatments as was seen for leaf growth rate or shoot 2 length. TCAI returned to that of controls during the first recovery period but not the second recovery period for treatments showing differences. Shoot 1 length did not show significant differences until day 8 of the first recovery period after which differences were consistent throughout the second stress period and did not show recovery upon irrigation during the second recovery period.

Regression analysis of shoot 1 and 2 length and TCAI 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 only be calculated after all data was collected. The similarity of the curves for the drought stressed rootstocks and IG/M.9 EMLA C mirrored the results of the other growth parameters measured.

Several researchers have proposed the use of spun-bound polypropylene material such as was used in this experiment for the purpose of restricting the root zone. However, after one seasons growth up to 27% of the root system had escaped the material. This material does not seem appropriate for such uses.

Physiological parameters also were measured during this study and are discussed in detail in Section III. These parameters were CO_2 assimilation μmol m^{-2} s^{-1} (A) ; transpiration mmol m^{-2} s^{-1} (E); leaf (g_l), stomatal (g_s) and mesophyll (g_m) conductance mmol m^{-2} s^{-1}; water use efficiency (WUE); internal CO_2 concentration (C_i); leaf water (ψ_l), turgor (ψ_t) and osmotic (ψ_s) potential; abscisic acid content (ABA); non-variable (F_o), variable (F_v), maximal (F_m) and terminal (F_t) chlorophyll fluorescence; fluorescence quenching (F_q); efficiency of photosystem II (F_v/F_m); and half-time-rise from F_o to F_m ($t_{1/2}$). Whole tree gas exchange parameters (A', E', g_l', g_s', g_m', WUE') were calculated using gas exchange, leaf area and leaf emergence data and expressed as μmol tree^{-1} s^{-1} for A' or mmol tree^{-1} s^{-1} for the other gas exchange parameters. To determine sensitivity, the number of days in each stress period was divided by three and one point was given to parameters in which differences were seen in the first third of the stress period, two points for parameters in which differences were seen in the second third and three points to parameters in which differences were seen in the last third. To determine consistency, one point was given for parameters in which differences for treatments were significantly different from corresponding controls 67 % to 100 % of the days measured, two points for parameters with differences for 34 % to 66 % of the days measured and three points for parameters with differences for 0 % to 33 % of the days measured. One point was given for parameters that returned to the same level as corresponding controls during recovery, 1.5 points if measurements were not taken for the parameter during recovery, two points for parameters that did not show recovery and three points for parameters that did not differ from controls during the previous drought stress. This was done for each of the three rootstocks and the points were summed. Parameters with the lowest sum were considered most sensitive to drought stress. Parameters were grouped by taking the difference between the highest and lowest rank and dividing by the number of parameters with different sums. If the sum of a parameter differed by this amount from another parameter it was placed into a different grouping. Sensitivity ranking of growth and physiological parameters to drought stress are as follows:

1. leaf water potential
2. E', leaf growth rate
3. A', g_l', shoot 2 length
4. g_l, leaf emergence rate
5. A, F_o, F_m, F_q, WUE'
6. E, F_t, leaf osmotic potential, leaf turgor potential

7. F_v, leaf ABA content

8. shoot 1 length, TCAI

9. C_i, g_m, F_m/F_v, $t_{1/2}$, WUE

Parameters were ranked according to the criteria listed above and discussion of the ranking of physiological parameters can be found in Section III.

Factors contributing to growth reductions include water relations (Boyer, 1988; Hsiao, 1973; Westgate and Boyer, 1985), ABA (Bunce, 1990; Davies et al., 1986; Zhang and Davies, 1990) and photosynthesis. The changes in water relations, ABA and photosynthesis due to the drought stress are discussed in Section III. Reduced water availability as demonstrated by lower soil moisture content and ψ_l during the drought stresses would lead to reduced growth (Boyer, 1988). The increased leaf ABA concentrations for drought stressed trees found during this experiment also have been linked to reduced leaf growth (Bunce, 1990; Myers and Landsberg, 1989; Zhang and Davies, 1990). Reduction in A' during the drought stress was due to a combination of lower A, reduced number of leaves and smaller leaf area as well as physiological changes caused by the drought such as increased leaf ABA concentration and reduced g_l. Although these parameters may not have shown a significant difference individually, the combined effect resulted in lower A'. Lower A' resulted in further decreases in growth creating a feedback loop. A' may have been reduced further by a delay in maturity of leaves as evidenced by a slower growth rate but no difference in final leaf area. Immature leaves have been shown to respond to ABA and environmental conditions to a greater extent than mature leaves with respect to A and g_s (Zhang and Davies, 1989; Zimmermann, 1983) and a delay in maturity could further decrease A'.

Reductions in growth parameters due to drought stress appear to be related to the lower whole tree gas exchange of the drought stressed treatments as well as carbohydrate reallocation. Evidence for carbohydrate reallocation include the differential response of shoot 1 and 2 to drought stress, a larger percent reduction for 1-year-old wood compared to the root system and for IG/M.9 EMLA D a significantly lower root to shoot ratio at the 10% level compared to IG/M.9 EMLA C. Osmotic adjustment also accounts for carbohydrate reallocation since the primary solutes involved are photoassimilates (Acevedo et al., 1979) that otherwise would be used for growth. ABA also could be involved in carbohydrate movement. Bunce (1990) found increased export of carbohydrates from soybean leaves when treated with either a drought stress or ABA. As there were no differences in dry weights of the root system for IG/MM.111 C and D or IG/Mark C and D it is believed that more carbohydrates were exported to the root system and carbohydrates were lost to increased root respiration or root turnover as has been found in other instances of soil stress (Jones et al., 1985; Klepper et al., 1973; Landsberg, 1980; Smucker, 1984). The diversion of assimilates for osmotic adjustment and to the root system resulted in decreased shoot growth for the drought stressed rootstocks.

Conflicting reports exist concerning drought tolerance of dwarfing rootstocks and few deal with Mark rootstock. In a review, Landsberg and Jones (1981) state that dwarfing rootstocks, especially M.9, usually are more tolerant to drought stress conditions than vigorous rootstocks while Ferree and Carlson (1987) state that M.9 is intolerant of drought conditions and MM.111 is one of the most tolerant rootstocks. Although some growth and physiological parameters for IG/M.9 EMLA D were reduced compared to the other controls, the similarities to IG/M.9 EMLA C indicate a greater degree of drought tolerance for M.9 EMLA with MM.111 intermediate and Mark least drought tolerant. When compared to corresponding controls IG/Mark D was first to be significantly lower for 21 of the 27 growth and physiological parameters measured or calculated, IG/MM.111 D was first for six of the 27 (similar to IG/Mark D for three) and IG/M.9 EMLA D was first for five of the 27 (similar to IG/Mark D for two and IG/MM.111 D for three). 'Imperial Gala' on Mark D was reduced by a greater percentage for most parameters with IG/MM.111 D intermediate and IG/M.9 EMLA D least when compared with corresponding controls. The assumption that dwarfing rootstocks are drought tolerant does not apply to Mark and should be evaluated for other dwarfing rootstocks as well.

The large reductions in scion and rootstock growth due to drought for Mark rootstock may be beneficial to managing canopy vigor in intensive systems. A rootstock sensitive to drought such as Mark may be useful in a system that utilizes the regulated deficit irrigation techniques described for peach and pear (Chalmers et al., 1981, 1986; Mitchell and Chalmers, 1982; Mitchell et al., 1984, 1989) and being attempted for apple, especially in areas receiving high rainfall.

Adaptation by IG/M.9 EMLA D resulted from a decrease in carbohydrate allocation to the root system evidenced by a lower root to shoot ratio. This allowed continued shoot growth at approximately the same rates as IG/M.9 EMLA C leading to limited reduction in A' (Section III) which in turn provided assimilates for continued growth. While leaves and shoots of IG/MM.111 and IG/Mark were affected by drought stress, the root to shoot ratio was not and these rootstocks performed poorly under drought stress. The smaller root system and wider root distribution pattern of IG/M.9 EMLA D compared to IG/M.9 EMLA C also 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 (Fernandez et al., 1991; Beukes, 1984; Layne et al., 1986; Section I). Roots were found to have a greater ability to osmotically adjust and continue growth than leaves, stems and silks for corn (Westgate and Boyer, 1985) which may also have been the case during this study since root dry weight was lower only for IG/Mark D than IG/Mark C . Reduced allocation of carbohydrates from the shoot to the root system for IG/M.9 EMLA D resulted in minimal reductions in growth and most physiological parameters (Section III) and no differences in final dry weight at termination of the experiment.

M.9 EMLA and MM.111 also imparted a lower transpirational demand per tree to the scion which may have resulted in slower depletion of soil water which was reflected in ψ_l remaining similar to controls for a longer duration for IG/M.9 EMLA D than the other drought stressed treatments (Section III). Differences in E' between IG/M.9 EMLA C and D occurred on only 8 of the 18 days for which measurements were taken, whereas IG/M.9 EMLA was always lower than IG/Mark C regardless of treatment and IG/M.9 EMLA C was lower than IG/MM.111 C on five of the 18 days measurements were taken (Section III). Transpiration per tree for IG/MM.111 C was lower than IG/Mark C on 8 of the 18 measurements while similar to IG/MM.111 D for the same number of days (Section III).

Studies quantifying the carbon allocation patterns, root respiration and root turnover rate are needed to determine how these parameters are affected for these and other rootstocks under drought stress. ABA has been implicated as a moderator of drought stress by eliciting several of the drought stress responses found in this experiment as well as carbohydrate partitioning. The role that ABA plays needs further study as well as other growth regulators that may be involved.

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Captions for Figures

Figure 1. Percent soil moisture content for drought and control treatments during both stress and recovery period. *LSD significant at the 5% level.

Figure 2. Shoot length of the less vigorous shoot (Shoot 2) for stress and recovery periods 1 and 2. Vertical lines represent LSD at 5%. Equations for regression lines and R^2 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, $y=-1.418+1.209x-0.025x^2+0.00020x^3$, $R^2=0.98$.

Figure 3. Shoot length of the more vigorous shoot (Shoot 1) for stress and recovery periods 1 and 2. Solid and dashed vertical lines represent LSD at the 5% and 10% level, respectively. Equations for regression lines and R^2 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, $y=-0.062+1.384x-0.027x^2+0.00021x^3$, $R^2=0.99$.

Figure 4. Trunk cross sectional area increase from the beginning of stress 1 until termination of the experiment. Solid and dashed vertical lines represent LSD at the 5% and 10% levels, respectively. Equations for regression lines and R^2 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, $y=-0.853+0.077x$, $R^2=0.98$.

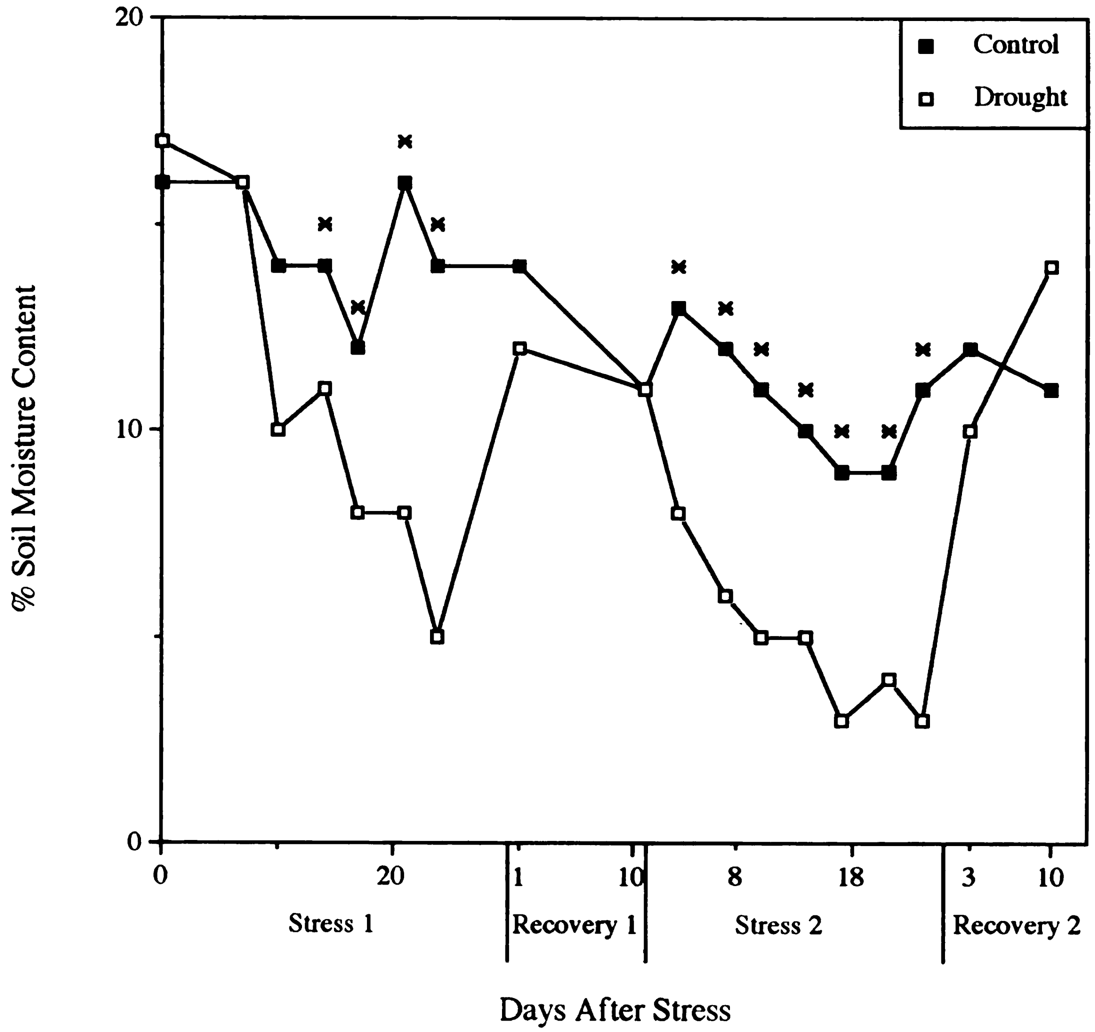
20
10
0
% Soil Moisture Content
■ Control
□ Drought
0
20
1
10
8
18
3
10
Stress 1
Recovery 1
Stress 2
Recovery 2
Days After Stress

Figure 1

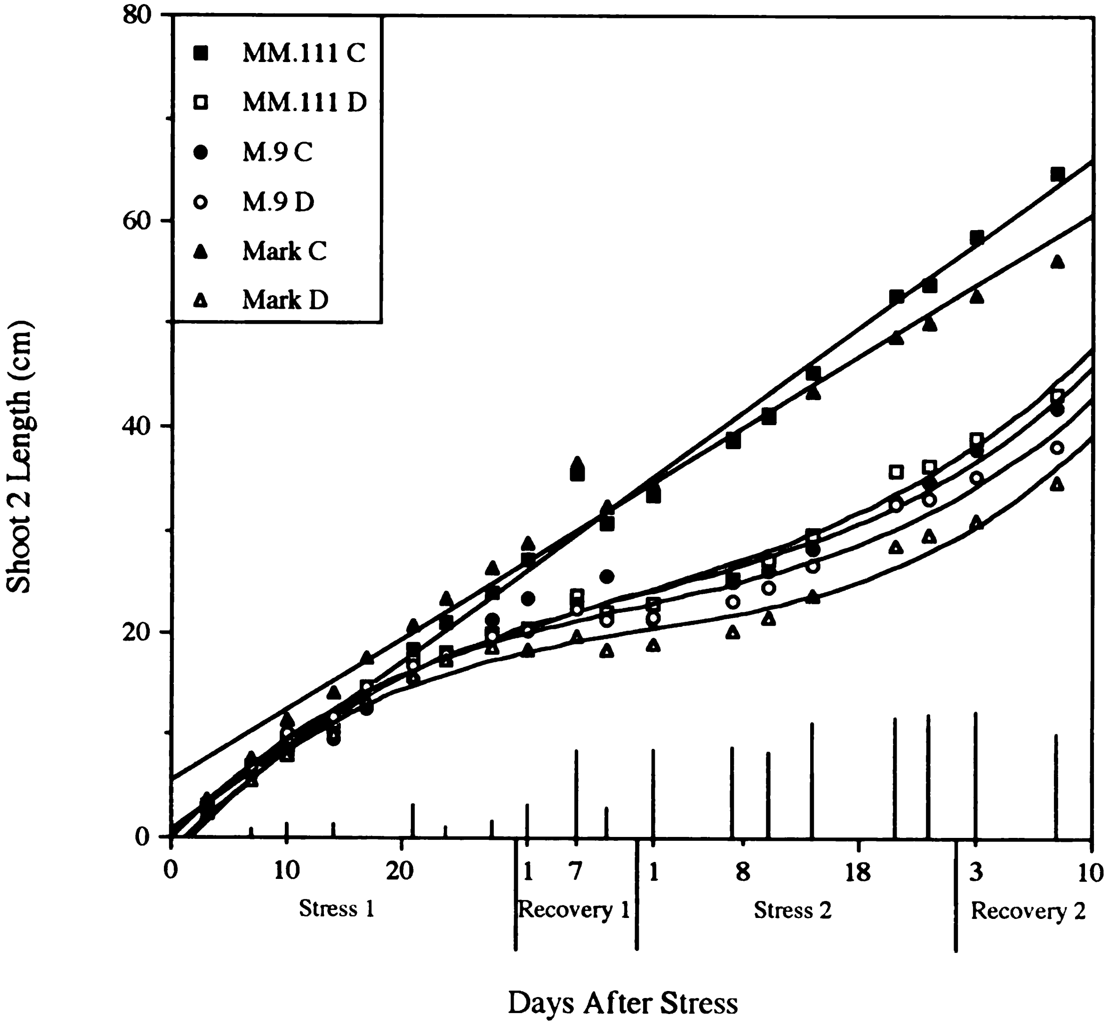
80
60
40
20
0
Shoot 2 Length (cm)
■ MM.111 C
□ MM.111 D
● M.9 C
○ M.9 D
▲ Mark C
△ Mark D
0
10
20
1
7
1
8
18
3
10
Stress 1
Recovery 1
Stress 2
Recovery 2
Days After Stress

Figure 2

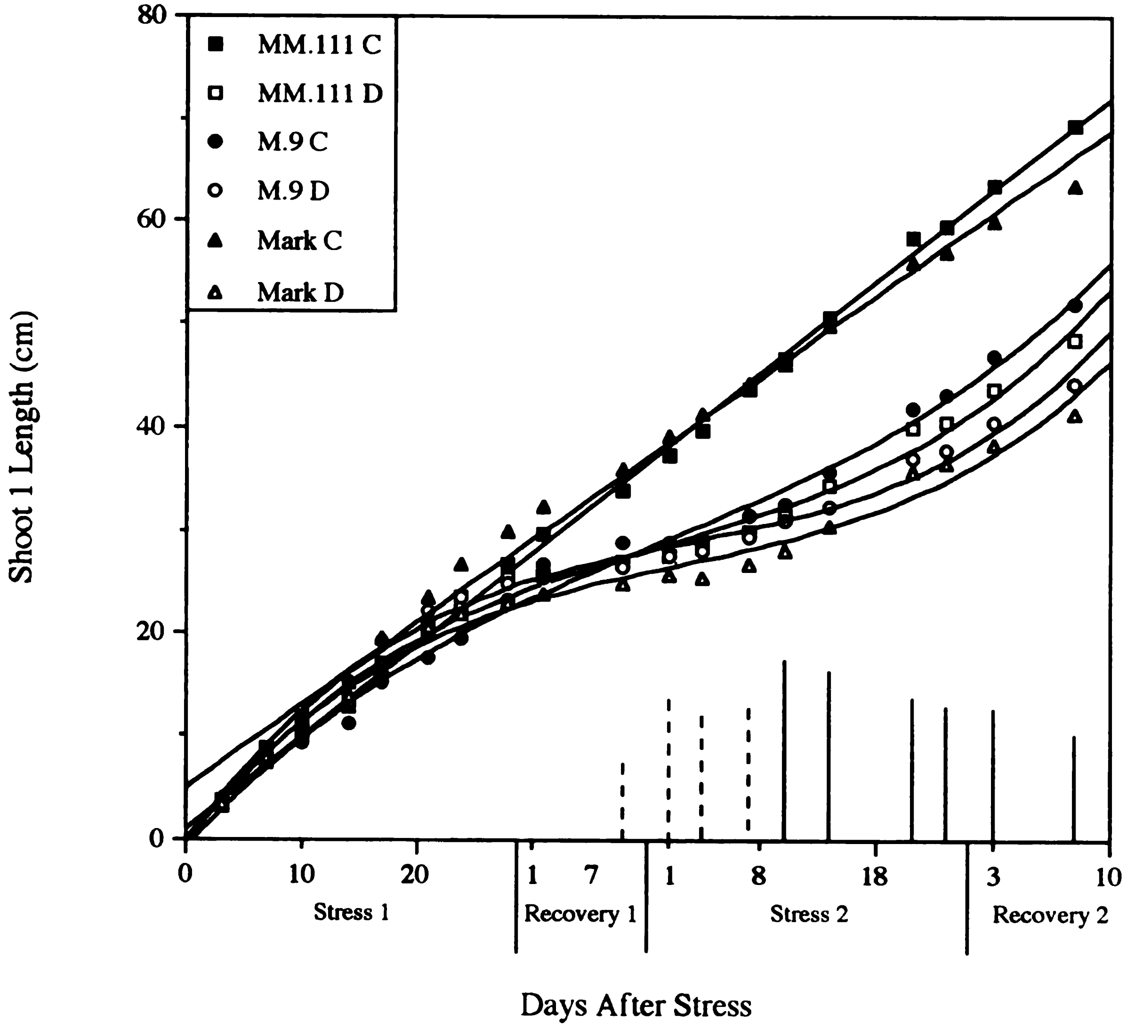
80
60
40
20
0
Shoot 1 Length (cm)
■ MM.111 C
□ MM.111 D
● M.9 C
○ M.9 D
▲ Mark C
△ Mark D
0
10
20
1
7
1
8
18
3
10
Stress 1
Recovery 1
Stress 2
Recovery 2
Days After Stress

Figure 3

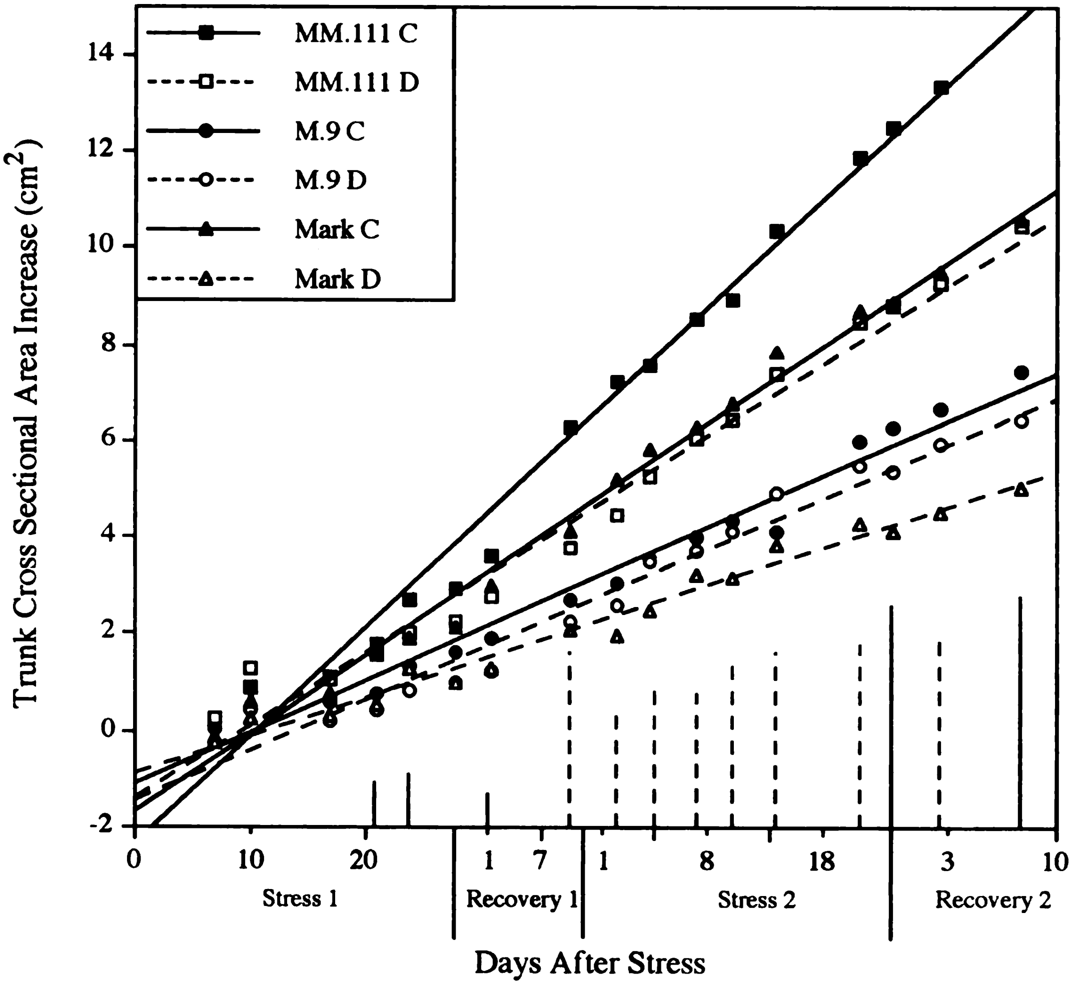
MM.111 C
MM.111 D
M.9 C
M.9 D
Mark C
Mark D
Trunk Cross Sectional Area Increase (cm^2)
14
12
10
8
6
4
2
0
-2
0
10
20
1
7
1
8
18
3
10
Stress 1
Recovery 1
Stress 2
Recovery 2
Days After Stress

Figure 4

Table 1. Leaf growth rate (change in leaf area cm^2 per day) during the first and second drought stress cycles and recovery. Stress 1 was imposed on 2 July and released 2 August 1991. Stress 2 was imposed on 13 August and released 7 September 1991. Treatment means followed by different letters are significantly different at the 5% level unless otherwise indicated at the column head.

	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
						10%		10%				
IG/MM.111 C	2.33	3.33 ab	2.99 a	1.97	1.97	2.96 a	3.07 a	2.61 ab	3.34 a	3.13 a	2.19	2.85
IG/MM.111 D	2.57	2.78 b	2.64 ab	2.58	0.64	1.61 b	1.38 b	1.19 b	1.36 b	1.50 b	1.43	2.50
IG/M.9 EMLA C	2.79	3.22 ab	2.69 ab	1.78	2.09	2.63 ab	2.47 ab	3.25 a	3.24 a	3.14 a	1.49	2.66
IG/M.9 EMLA D	2.55	2.65 b	2.20 b	2.69	1.37	1.63 b	1.54 b	1.38 ab	1.54 b	1.57 b	1.43	.
IG/Mark C	2.89	3.22 ab	2.79 ab	1.89	2.31	3.07 a	3.11 a	3.04 a	3.43 a	3.26 a	2.37	2.70
IG/Mark D	2.25	3.70 a	2.63 ab	1.54	2.05	1.62 b	1.64 b	1.57 ab	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
	10%						10%	
IG/MM.111 C	2.84 a	3.33	3.27 b	4.80 a	4.70 ab	2.09 a	4.53 a	3.62
IG/MM.111 D	2.01 b	.	2.56 c	2.08 b	2.50 c	1.14 b	3.49 ab	3.79
IG/M.9 EMLA C	2.24 ab	2.95	3.23 b	4.49 a	3.94 abc	2.32 a	4.59 a	3.80
IG/M.9 EMLA D	1.59 b	.	2.39 c	2.69 b	2.66 bc	1.28 b	3.55 ab	3.20
IG/Mark C	2.84 a	3.43	3.66 a	4.85 a	4.79 a	2.05 a	3.91 ab	2.98
IG/Mark D	1.70 b	2.15	1.85 d	2.12 b	2.09 c	1.29 b	3.08 b	3.67

Table 2. Leaf emergence (leaves/day) for both shoots during the first and second drought stress cycles and recovery. Stress 1 was imposed on 2 July and released 2 August 1991. Stress 2 was imposed on 13 August and released 7 September 1991. Treatment means followed by different letters are significantly different at the 5% level unless otherwise indicated at the column head.

	Days After Stress 1									Days After Recovery 1	
Treatment	0	3	7	10	14	17	21	24	28	1	7
								10%			
IG/MM.111 C	1.23	0.88	1.16	1.50	0.91 ab	1.46	1.03	1.25 ab	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 a	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 b	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 ab	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 b	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 ab	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
	10%		10%					10%	10%
IG/MM.111 C	0.39 a	0.34 a	0.88 a	0.79 a	0.47	1.04	0.75	1.13 a	0.89 a
IG/MM.111 D	0.26 ab	0.11 b	0.19 b	0.38 a	0.35	1.29	0.75	0.91 bc	0.71 abc
IG/M.9 EMLA C	0.27 ab	0.32 a	0.50 ab	0.71 ab	0.38	0.95	0.79	1.00 ab	0.82 ab
IG/M.9 EMLA D	0.09 b	0.09 b	0.16 b	0.17 b	0.25	1.16	0.71	0.75 cd	0.70 abc
IG/Mark C	0.41 a	0.38 a	0.59 ab	0.92 a	0.50	0.96	0.63	0.81 bcd	0.66 bc
IG/Mark D	0.13 b	0.09 b	0.13 b	0.46 ab	0.22	1.30	0.75	0.69 d	0.54 c

Table 3. Dry weights (g) at termination of second drought stress. Treatment means followed by different letters are significantly different at the 5% level.

Treatment	1-year-wood	2-year-wood	Rootstock	Roots off tree	Roots inside	Roots outside	Total Roots	Root to shoot ratio	Total Dry Weight
IG/MM.111 C	23.90 a	14.71	76.18 a	20.15 ab	8.56 bc	5.26	33.97 b	0.30 b	183.31 a
IG/MM.111 D	12.10 b	13.47	61.66 b	13.72 ab	6.26 c	5.11	25.75 bc	0.32 b	132.25 bc
IG/M.9 EMLA C	11.90 b	12.49	34.69 d	10.28 ab	15.09 a	2.96	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	5.97	21.98 c	0.39 ab	101.03 c
IG/Mark C	23.49 a	23.72	46.42 c	25.58 a	14.95 a	4.59	45.12 a	0.48 a	177.66 ab
IG/Mark D	10.30 b	15.06	39.06 d	12.67 ab	10.88 ab	8.27	31.28 b	0.51 a	117.47 c

Table 4. Dry weights at termination of second drought stress and leaf area and number at end of each stress cycle. Treatment means followed by different letters are significantly different at the 5% level.

	Termination			Stress 1			Stress 2	
Treatment	Shoot 1 Leaf Dry Weight (g)	Shoot 2 Leaf Dry Weight (g)	Leaf Area (cm^2)	Shoot 1 Leaf Number	Shoot 2 Leaf Number	Leaf Area (cm^2)	Shoot 1 Leaf Number	Shoot 2 Leaf Number
					10%			10%
IG/MM.111 C	18.19 ab	14.38 ab	25.94	31.50	31.13 ab	36.35	41.00	36.58 ab
IG/MM.111 D	13.97 ab	9.97 c	23.13	32.25	28.50 abc	30.02	40.00	35.92 ab
IG/M.9 EMLA C	17.17 ab	12.03 bc	28.47	29.38	24.50 c	33.64	38.42	33.10 b
IG/M.9 EMLA D	12.38 b	10.00 c	24.01	29.75	25.92 bc	28.41	34.92	31.80 b
IG/Mark C	22.06 a	16.48 a	32.73	33.88	32.00 a	37.62	42.08	40.28 a
IG/Mark D	13.06 b	9.44 c	23.23	31.00	26.50 abc	29.91	38.00	33.00 b

SUMMARY AND CONCLUSIONS

The overall rooting intensity of apple seemed to be related to scion vigor and was found to be fairly consistent even at two diverse soil types. However, adaptation to soil type and condition was apparent as demonstrated by MAC 9 and M.9 EMLA rootstocks. The ranking of MAC 9 with respect to number of roots/dm^2 was second to last at the Michigan location but second highest at the Ohio location. The ranking for M.9 EMLA was third highest in number of roots/dm^2 in Michigan but second lowest in Ohio. Also, the restriction of the root system to the top 60 cm above the fragipan at the Ohio location while remaining fairly consistent at most depths in Michigan demonstrated the ability of root systems to adapt to soil restrictions.

Root hydraulic conductance of apple rootstocks also was found to be related to rootstock vigor with dwarfing rootstocks having greater L_p than more vigorous rootstocks. The importance of the relationship between root system size and absolute flow of water through the root system was illustrated by Mark rootstock which had the second greatest L_p but the greatest absolute flow rate by far when compared to the other four rootstocks tested. The combination of a large root system and rapid L_p would result in rapid depletion of soil water, unless moderated by physiological changes in L_p, and would be undesirable in most situations where drought stress is common.

Translocation of carbon in the phloem was not affected by pressurization of apple root systems. The infrequent and inconsistent differences in gas exchange of apples with root systems under pressure indicated that the physiology was not affected. These results demonstrate that this pressure chamber system can be used with intact plants to determine root hydraulic conductance without interrupting phloem translocation or removing the regulatory effects of the shoot system. Pressurizing plant root systems also could be used for many other types of studies such as investigating the Münch pressure-flow hypothesis (Münch, 1927, 1930 cited by Salisbury and Ross, 1985) or altering water potentials without increasing the amount of water available.

Growth and physiological parameters were reduced consistently and to a greater percent by the drought stressed treatment compared to the control treatment for 'Imperial Gala' on Mark rootstock than MM.111 or M.9 EMLA. 'Imperial Gala' on M.9 EMLA had few differences between drought and control treatments. Leaf water potential, leaf growth rate, whole tree gas exchange and shoot 2 length were the most sensitive of the 27 growth and physiological parameters measured and were considered good indicators of the onset and recovery of stress. Whole plant gas exchange parameters were good indicators of the cumulative effects of drought stress and reflected the decreases in shoot and trunk growth and plant dry weights. Gas exchange per unit leaf area showed few differences between drought and control treatments and did not reflect differences in growth and dry weights. Variable and maximal chlorophyll fluorescence and fluorescence quenching parameters were more sensitive to drought stress than assimilation per unit leaf area which indicates that photosystem II plays an important role in regulating drought stress response. A relationship between increased ABA concentration and decreased leaf conductance was found during this study indicating the role of ABA in controlling stomatal aperture. The effects of ABA on ψ_t and carbohydrate partitioning needs further study since these appear to be important parameters involved in the adaptation of apple rootstocks to drought stress.

Adaptation of drought stressed 'Imperial Gala' on M.9 EMLA was due to a reduction in root system growth and no decrease in shoot growth, neither of which occurred for drought stressed Mark or MM.111. A smaller mass of roots would result in diminished water flow to the canopy leading to slower depletion of soil water. The maintenance of shoot growth for drought stressed trees on M.9 EMLA similar to shoot growth of control trees allowed similar rates of whole plant CO_2 assimilation. This was not the case for drought stressed trees on MM.111 or Mark rootstocks with reductions in shoot growth of over 30% compared to controls. The slower L_p found for MM.111 probably contributed to the better drought tolerance compared to Mark rootstock since the slower L_p would result in slower depletion of soil water. In most situations where drought stress is a consideration M.9 EMLA would be the best of the three rootstocks.

The combination of a large root system, which is the case for Mark under certain soil conditions, a rapid L_p and sensitive response of growth and physiological parameters to drought stress suggest that Mark rootstock is not suited for situations where drought stress is a common occurrence without proper management. Although M.9 EMLA also can have a large root system under optimum soil conditions and does have a rapid L_p, its response to drought stress is to limit root mass. While root dry weight was lower for drought stressed M.9 EMLA, the rapid L_p could supply adequate water despite the decreased root mass. No difference in root dry weight was found for trees on Mark rootstock during the study described in Sections III and IV, and unless there were physiological changes in L_p water was more rapidly depleted from the soil due to the rapid L_p found for Mark rootstock reported in Section II. Under certain circumstances, however, Mark may be desirable, even in dry climates, where irrigation management techniques such as reduced deficit irrigation are employed to manage canopy vigor. Rapid response to short term drought stress resulting in reduced canopy growth without affecting yield is the goal of reduced deficit irrigation in intensive orchard systems and Mark might be the best rootstock for this situation.

More research is needed to determine the effects of drought stress on source-sink relationships. Indirect evidence was found in the drought stress studies for carbohydrate reallocation to the root system at the expense of the shoot system for Mark and MM.111 rootstocks resulting in poor tree performance. There was little reduction in assimilation on a leaf area basis yet the final dry weights indicate less carbon was retained by the drought stressed rootstocks. This suggests a loss of carbon due to increased respiration and/or senescence of plant material, which was not observed for the shoot system. Root respiration and root turnover should be measured to determine how the root systems adapt to drought stress. Long term studies need to be implemented in order to assess the effects of drought stress on bearing trees. The additional competition for water, carbohydrates and nutrients of fruit may exacerbate the drought stress response of the more sensitive rootstocks.

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