Using Rootstocks to Optimize Fruit Tree Water Use

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The effective use of irrigation has become a key component in the reliable production of high quality crops. The benefits of applying water to fruit trees are now generally well known. However, there are many situations where growers do not have access to irrigation water or, alternatively, cannot afford to apply it. Even the top fruit growing regions of the UK, which are predominantly in southern England, are frequently subject to dry summer periods, and irrigation has been shown to increase fruit size.

There are several ways in which a plant can change the efficiency with which it uses water. These adjustments can generally be grouped into changes in either the capacity of the plant to capture or regulate the loss of water, or the efficiency with which it is used. As the soil dries the rate at which leaves are produced can decline. Under more severe conditions of soil drying leaf area may decline as a result of leaves being shed. Plant water loss also can be controlled at the leaf level by the process which influences transpiration; the rate at which leaves transpire is influenced by the degree to which the stomatal pores on the leaf are open.

A decrease in stomatal conductance is frequently cited as a mechanism by which plants are able to adapt to drying soil by reducing water loss. Considerable interest has been shown in the potential to breed plants with stomatal characteristics that enable them to grow in drought-stressed environments (Jones, 1974, 1987). However, stomatal closure reduces not only water loss by transpiration but also the rate of photosynthesis and, ultimately, the rate of plant growth.

Stomatal characteristics for breeding drought tolerance into plants have been the subject of much research. Selections have been made for low maximum stomatal conductance, low minimum stomatal conductance and for stomatal responsiveness to drought stress, including stomatal sensitivity to relative humidity and the level of leaf stress (leaf water potential) (Jones, 1979, 1987). Many attempts to understand the plants' responses to drought have focused on interpreting the nature of the relationship between stomatal conductance and leaf water potential (see Lakso, 1979). It appears that there are sensitive genotypes with a high leaf water potential threshold for stomatal closure and insensitive genotypes that show gradual stomatal closure over a range of leaf water potential (Jones, 1974). Variations in the responsiveness of stomata to leaf water potential highlight the control that stomatal conductance can have on the extent and the rate at which the plant becomes stressed.

Modern high-density fruit orchards use composite plants that are made up of an above ground part (the "scion" cultivar) grafted on to a clonally produced root system ("rootstock"). There are considerable advantages in doing this as a rootstock can alter the behavior of the scion in many ways, i.e., flower numbers, flowering time and crop yield (Lockard and Schneider, 1981; Tubbs, 1973; Vyvyan, 1955). More importantly the rootstock can influence the rate and amount of vegetative growth made by a grafted shoot. As yet, we have no complete mechanistic understanding of how this control of vegetative growth occurs (Castle and Krezdon, 1975; Giulivo et al., 1985; Lockard and Schneider, 1981; Olien and Lakso, 1986; Ranney et al.,

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1991). There have been suggestions, for composite plants, that the restriction of water transport from roots to shoots (a decline in hydraulic conductance) may induce important differences that determine the degree to which a rootstock controls shoot growth (Landsberg and Jones, 1981; Olien and Lakso, 1986; Preston et al., 1981). Landsberg and Jones (1981) also suggested that the drought tolerance of a rootstock was conferred to a grafted scion. It is also

unclear if rootstocks show inherent differences in their capacity to control shoot growth that are independent of a simple linear relationship between the amount of root growth produced and the amount of shoot growth made. It remains particularly difficult to accurately determine root growth and distribution in field-grown plants.

Changes in dry matter partitioning may also take place with an increase in the amount of root growth relative to the growth of the shoot, i.e., a change in the root:shoot ratio. An increase in the root:shoot ratio, which may be attributable to an increased rate of root growth, reductions in root death, reductions in rate of leaf development or leaf abscission, will reduce the transpirational demand per unit root length. Increased root growth will also increase the volume of soil exploited and possible water uptake. The amount of root and its distribution in the soil affects the ability of the roots to absorb water.

The work described here shows how root growth and water use differ for a range of size-controlling apple rootstocks. Unworked rootstocks were used to avoid the added effects of the grafted scions influencing rootstock behavior. The aim of the work was to determine the drought tolerance of a wide range of commercial apple and some new selections from the rootstock-breeding program at HRI-East Malling.

EXPERIMENTAL APPROACH

In spring, potted commercial apple rootstocks of M.9, M.26, M.27 and MM.111, and some new selections from the rootstock breeding program at HRI-East Malling (AR 69-7, AR 295-6, AR 360-19, AR 486-1 and AR 628-2) were transferred to a glasshouse and arranged in a randomized block design with three levels of irrigation (Table 1). Immediately after bud burst, the number of developing buds on each rootstock stem was reduced to

four. At the beginning of June the amount of water received by some rootstocks was gradually reduced, exposing them to an increasingly dry soil to mimic a summer drought. This also allowed the growing rootstock to adjust to the conditions of drying soil, as would occur naturally during a dry period. Three different irrigation regimes were established, one at an optimal level to act as a control (A, 670 cm³ per day) and two at sub-optimal levels to induce drought stress (B, 322 cm³ per day, and C, 65 cm³). The timing and amount of irrigation applied were controlled precisely by electronic solenoid valves and a trickle irrigation system with pressure compensating nozzles. The rootstocks were growing in the glasshouse for 6 months prior to final growth analysis.

Growth Measurements

At the end of the experiment the rootstocks were harvested and divided into their component parts (fine and coarse roots, leaves, stem wood and branch wood) before drying at 80°C and determining the weight of dry matter. Roots were washed to remove all the compost and then separated into fine root (<2 mm in diameter) and coarse root (>2 mm in diameter). The total length of fine root was determined using a root length scanner. A calibration curve was used to convert measured scan lengths into actual root lengths. Coarse root length was measured with a rule.

Measurements of Gas Exchange and Drought Stress

The level to which a plant becomes drought stressed can be determined from measurements of leaf water potential. These measurements were made using a conventional leaf pressure chamber to determine xylem leaf water potentials in MPa. The more negative these measurements are, the greater the drought stress imposed on the plant. Measurements of stomatal conductance (how open stomata

are) were made using a diffusion porometer. The more open the stomatal pores are, the more water is lost by the leaf and potentially more carbon dioxide that can be fixed via photosynthesis.

Rootstock Stomatal Conductance and Leaf Water Potential

Measurements of stomatal conductance for the three irrigation treatments were made with concurrent measurements of leaf water potential. Typically, irrespective of rootstock, as the compost began to dry, leaf water potentials became more negative (an increase in drought stress) and stomatal conductance began to decline. This decline had the effect of reducing the amount of water lost by the rootstock. As the soil drying progressed throughout the experiment, marked differences between the measurements of stomatal conductance and leaf water potential were apparent with respect to treatment. Treatment C with the lowest amount of irrigation showed the greatest amount of drought stress, i.e., the most negative water potentials and the lowest values of stomatal conductance. The treatment differences, comparing the highest level of irrigation (treatment A) with the lowest (treatment C), were greatest with respect to stomatal conductance and water potential measurements for the more vigorous rootstocks.

At the end of the experiment (beginning of September), there were large differences in stomatal conductance and leaf water potential between plants receiving treatments A and C, particularly for the rootstocks M.26 and MM.111. Values of stomatal conductance were not related directly to previously published measurements of rootstock vigor but the most dwarfing rootstocks (M.27, AR 69-7 and AR 360-19) generally had the lowest stomatal conductance, whereas the most vigorous rootstocks (M.26 and MM.111) had the highest.

TABLE 1

Rootstocks investigated for their drought tolerance/susceptibility, arranged in order of their known ability to control scion vigor. The parental makeup of most of the selections from the East Malling rootstock breeding programs is also shown in parentheses.

Extremely dwarfing	Dwarfing	Semi-dwarfing	Vigorous
M.27 (M.13 x M.9)	M.9-EMLA[+]	M.26 (M.16 x M.9)	MM.111 (Northern Spy x Merton 793)
AR69-7 (AR10-2-6 OP*)	AR295-6 (Robusta 5(j) x Ottawa 3)		
AR360-19 (M.9 x M.27)	AR486-1 (Ottawa 3 x M.7)		
AR628-2 (Ottawa 3 x MM.106)			

*OP=open pollinated
[+]the parentage of M.9 is not known.

For plants in the well-watered treatment, rootstock differences in leaf water potential were less obvious. As with stomatal conductance, there were differences in leaf water potential between rootstocks of different dwarfing capacity. In general, leaf water potential was greater (less negative) for well-watered dwarfing rootstocks, whereas leaf water potential decreased (−2.0 MPa) for vigorous rootstocks. Differences between rootstocks were more marked when irrigation water was withheld.

Relationship Between Stomatal Conductance and Leaf Water Potential

The rate at which stomatal conductance decreased in response to a more negative leaf water potential differed between rootstocks (Fig. 1). Statistical analysis of stomatal conductance values, using leaf water potential as a covariate, showed that, for the dwarfing rootstocks M.27, M.9 and AR 360-19, stomatal conductance was not affected by leaf water potential whereas, with some of the vigorous rootstocks (e.g., AR 486-1 and AR 628-2), drought treatment differences could be explained by differences in leaf water potential. There was some evidence with the vigorous rootstocks AR 295-6, AR 486-1 and MM.111 that, when a threshold value of leaf water potential (between -1.5 to -2.0 MPa) was reached, a rapid decrease in stomatal conductance could be induced. Also, for each drought treatment, regression analysis was carried out to compare the slopes of the relationship between stomatal conductance and leaf water potential. Treatments A and B showed no significant differences between rootstocks. However, for treatment C the slope was significantly steeper for the rootstock AR 295-6 while the rootstocks AR 628-2 and AR 486-1 gave intermediate results.
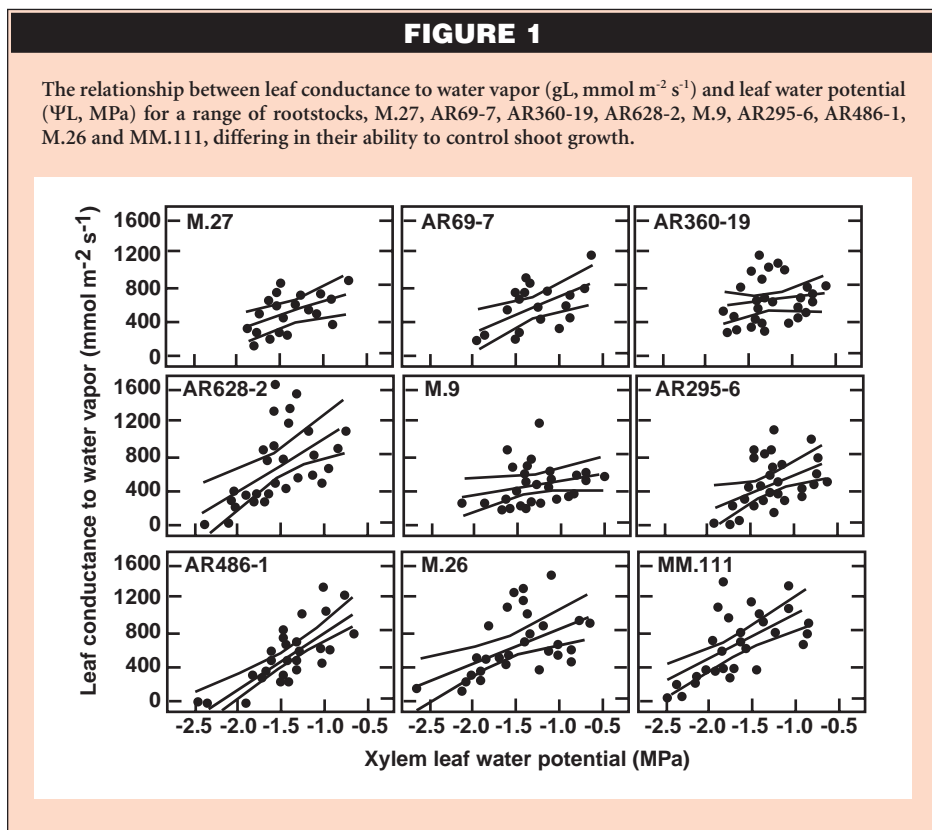
FIGURE 1

The relationship between leaf conductance to water vapor (gL, mmol m^{-2} s^{-1}) and leaf water potential (ΨL, MPa) for a range of rootstocks, M.27, AR69-7, AR360-19, M.9, AR295-6, AR486-1, M.26 and MM.111, differing in their ability to control shoot growth.

TABLE 2

Leaf number, leaf area (cm^2) and leaf dry wt (g) per plant, at harvest, after 6 months' growth for 3 irrigation treatments (A, B and C) and 9 rootstocks.

		M.27	AR69-7	AR360-19	AR628-2	M.9	AR295-6	AR486-1	M.26	MM.111	Treatment mean
Leaf number	A	230	118	161	95	121	119	104	258	163	152
	B	166	113	146	77	114	108	78	227	99	125
	C	125	92	88	59	71	85	62	199	82	96
Rootstock mean		174	107	132	77	102	104	81	228	115	
d.f. = 180; Rootstock P<0.001, SED 13.5; Irrigation treatment P<0.001, SED 7.8; Rootstock x irrigation treatment P=0.625, SED 23.3											
C as % of A = 100*C/A		54.3	78.0	54.7	62.1	58.7	60.0	59.6	77.1	50.3	
Leaf area	A	5538	3724	3774	6584	4080	5799	6866	5949	5253	5288
(cm^2 per plant)	B	4751	3986	3225	5431	4166	5515	4955	5308	4066	4600
	C	3075	3199	2180	3962	2789	4523	3963	4641	3030	3485
Rootstock mean		4455	3644	3060	5325	3678	5279	5261	5300	4117	
d.f. = 180; Rootstock P<0.001, SED 357.9; Irrigation treatment P<0.001, SED 206.7; Rootstock x irrigation treatment P=0.443, SED 620.0											
C as % of A=100*C/A		55.5	85.9	57.8	60.1	68.3	87.4	57.7	78.0	57.7	
Leaf dry weight	A	42.7	33.3	32.8	60.7	34.0	52.4	62.3	44.3	45.4	45.3
(g per plant)	B	30.5	34.4	27.2	49.4	37.3	48.1	45.3	39.5	39.2	39.0
	C	25.5	28.5	19.3	36.6	24.6	38.5	35.9	36.9	29.2	30.6
Rootstock mean		32.9	32.1	26.4	48.9	32.0	46.3	47.8	40.2	38.0	
d.f. = 180; Rootstock P<0.001, SED 3.13; Irrigation treatment P<0.001, SED 1.81; Rootstock x irrigation treatment P=0.286, SED 5.4											
C as % of A=100*C/A		59.7	85.5	58.8	60.3	72.3	73.5	57.6	83.3	64.3	

Changes in Rootstock Shoot Growth

The amount of leaf growth changed with respect to both rootstock and drought. In all rootstocks leaf dry weight declined with increasing soil drying for the majority of rootstocks observed, i.e., M.27, AR 360-19, AR 628-2, MM. 111 and AR 486-1, by around 40% (when comparing treatment A, the control with C, the lowest amount of irrigation) (Table 2). At the other end of the treatment response leaf area only declined by around 15% for AR 69-7 and M.26 rootstocks.

Determinations of leaf number and leaf area per plant showed that differences in treatment response between rootstocks were due mainly to changes in leaf number. There was, however, no evidence to indicate that rootstocks behaved any differently in response to drought stress. An assessment was also made of the number of leaves abscised over the 6-month growth period. This shows that much of the difference in total rootstock leaf area was due to differences in leaf number.

Changes in stem cross-sectional area (girth) were also determined over the 6-month growth period. Girth incremental growth is an important factor in assessing rootstock vigor as well as leaf area development and reproductive potential. Here changes in girth increment could not be related simply to rootstock vigor. The rootstock M.9 grew the least, while the largest increase in increment was evident with the rootstock AR 295-6. In all cases with the exception of M.9 the girth incremental growth was depressed by drought stress.

Changes in Rootstock Root Growth and Root Length

The total root dry weight (coarse and fine root combined) differed considerably between the extremely dwarfing and the dwarfing rootstocks (Table 3). Coarse roots were believed, on the basis of their diameter and appearance (heavily thickened), to be mainly structural (supportive) and transportive in function (carry water and mineral nutrients). The finer roots, however, are assumed to be those most likely to be involved in the direct uptake of water and minerals.

More roots were produced generally by the less dwarfing rootstocks, irrespective of root class size, although the small amount of root produced by MM.111 contradicts this trend. Significant differences in root dry weight between drought treatments were confined to the coarser root class, but in many cases, clear trends were apparent in the responses to drought stress. The rootstocks AR 360-19, AR 628-2, AR 295-6 and AR 486-1 showed large relative reductions in root growth when grown under droughts (treatment C) compared to the well-watered controls (treatment A), whereas M.27, M.9 and MM.111 all showed an increase in dry matter of either the coarse or the fine root fraction. Only AR 69-7 and M.26 showed positive increases in both the root size fractions measured, with the relative increase being greatest for M.26.

The differences in fine root length between rootstocks and treatments were similar to those recorded for root dry weight. Specific root length (calculated by dividing total root length by root dry weight) was determined to assess whether the relationship between root weight and root length changed in response to drought. The relationship did not change with drought stress or rootstock type, i.e., 1 g of dry root was around 42 m long.

ROOTSTOCK RESPONSES TO DROUGHT STRESS
Shoot Responses to Drought Stress

The results reported here show that, for the range of rootstocks examined, stomatal conductance was generally greater for the more growth invigorating rootstocks than for the restricting (Atkinson et al., 2000). This agrees with observations that stomatal densities (number of stomata per unit leaf area) are greater on the leaves of vigorous rootstocks (Beakbane and Majumder, 1975). The implications of this are important, not

TABLE 3

Total root dry matter (g) of coarse (>2 mm diameter) and fine roots (<2 mm diameter) at harvest, after 6 months' growth for 3 irrigation treatments.

Irrigation treatment	Group 1							Group 2			
	M.27	AR69-7	AR360-19	M.9	M.26	MM.111	Mean[1]	AR628-2	AR295-6	AR486-1	Mean[2]
Coarse root (>2 mm in diameter)											
A Control	1.53	1.01	1.58	2.72	2.96	0.94	1.79	5.68	10.58	6.78	7.68
B Reduced irrigation	1.80	1.62	1.18	3.06	3.24	0.92	1.97	3.87	11.76	5.63	7.09
C Droughted	1.64	1.14	0.96	1.79	3.56	0.69	1.63	4.06	4.58	4.83	4.49
Rootstock mean	1.66	1.26	1.24	2.52	3.25	0.85		4.54	8.97	5.75	
For rootstocks in group 1. d.f. = 56; Rootstock P<0.001, SED 0.39; Irrigation treatment P=0.475, SED 0.28; Rootstock x irrigation treatment P=0.871, SED 0.68											
For rootstocks in group 2. d.f. = 28; Rootstock P<0.001, SED 1.01; Irrigation treatment P=0.009, SED 1.01; Rootstock x irrigation treatment P=0.054, SED 1.75											
C as % of A = 100 C/A	*107*	*113*	*60.7*	*65.8*	*120*	*73.4*		*71.5*	*43.3*	*70.3*	
Fine root (<2 mm in diameter)											
A Control	7.62	4.06	5.71	8.04	5.43	5.08	5.99	11.44	17.87	12.69	14.00
B Reduced irrigation	6.26	5.94	5.77	9.33	4.97	5.94	6.37	8.76	15.92	12.95	12.54
C Droughted	6.95	4.59	4.26	9.69	6.99	5.95	6.41	9.04	11.87	8.96	9.96
Rootstock mean	6.94	4.86	5.25	9.02	5.80	5.66		9.75	15.22	11.53	
For rootstocks in group 1. d.f. = 56; Rootstock P<0.001, SED 0.90; Irrigation treatment P=0.771, SED 0.64; Rootstock x irrigation treatment P=0.765, SED 1.56											
For rootstocks in group 2. d.f. = 28; Rootstock P<0.001, SED 1.01; Irrigation treatment P=0.004, SED 1.01; Rootstock x irrigation treatment P=0.385, SED 1.91											
*C as % of A = 100 *C/A*	*91.2*	*113*	*74.6*	*120*	*129*	*117*		*79.0*	*66.4*	*70.6*	

only because of the greater stomatal conductance and its potential to enhance photosynthesis (Beakbane, 1967; Lakso, 1979), but also because of the concomitant increase in the transpiration rate. For some of the rootstocks examined here, e.g., AR 628-2, maximum observed values of stomatal conductance were greater than expected from published observations of the rootstocks' capacity to control scion shoot growth (about 14-17% more growth than M.27) (Webster et al., 1997).

Having higher maximum values of stomatal conductance for some of these AR-rootstocks does correlate with the rootstocks' ability to produce more root dry weight in relation to their capacity to control scion growth, e.g., AR 295-6 and AR 486-1 (Atkinson et al., 1999). Leaves of trees on vigorous rootstocks may be expected therefore to be more stressed, i.e., have more negative leaf water potentials than those of dwarfing rootstocks, if their transpiration rates were greater because of the higher values of stomatal conductance and the rates of water supply were similar. However, similar stress levels (same leaf water potentials) between vigorous and dwarfing rootstocks suggest that the ability to move water within the rootstock, across the graft union or through the stem must increase with its vigor (Atkinson et al., submitted; Olien and Lakso, 1984).

Measurements of stem and root anatomy show that the numbers and size of the xylem vessel elements increase with rootstock vigor and should theoretically yield an increase in measurable sap flow or transpiration rate (Beakbane, 1941, 1953).

The reason leaves on dwarfing rootstocks, such as M.27, AR 69-7 and AR 360-19, did not show the same degree of drought stress (leaf water potential values did not fall below -2.0 MPa) as leaves on vigorous rootstocks (AR 295-6 and AR 486-1) can be explained by a reduction in the total amount of water used. The dwarfing rootstocks had smaller total leaf areas compared with the vigorous rootstocks (Atkinson et al., 1999). The mean numbers of leaves abscised per plant, compared to the control treatment A, during the drought treatments were also greater for the dwarfing rootstocks.

Differences in the amount of root dry matter have been shown to correlate with the rootstocks' ability to control the vegetative shoot growth (Atkinson, 1980; Rogers, 1939). The greater amount of root mass produced by the dwarfing rootstock AR 295-6, for example, may explain why the value of leaf water potential for this rootstock did not fall below -2.0 MPa as

occurred with the semi-dwarfing M.26; both rootstocks had similar leaf areas per plant. Of all the rootstocks examined, AR 295-6 also had the largest amount of leaf area when droughted (Atkinson et al., 1999), but stomatal closure restricted the amount of drought stress (i.e., decline in leaf water potential lower -2.0 MPa).

Stomatal closure is an important indicator of a plant's ability to respond to water deficit and its relationship with leaf water potential can therefore be used to determine the plant's response to water deficits (Lakso, 1979). In this study, the statistical correlation between stomatal conductance and leaf water potential was frequently positive, with some rootstocks (AR 295-6, AR 628-2 and AR 486-1) having threshold stress values around -2.0 MPa, below which stomatal conductance decreased rapidly. This threshold value was very similar to that quoted by Lakso (1979) for apple, but it appears these values can change with leaf age as well as leaf preconditioning to drought stress. It appears that the stomatal response to drought stress may have acclimated to changes in soil or leaf water levels.

This was particularly evident for the more vigorous rootstocks AR 486-1, M.26 and MM.111 and was not simply related to the amount of root. For the more dwarfing rootstocks (M.27, AR 69-7 and AR 360-19), there was less evidence to support a positive relationship between rootstock water status and the rate of water loss. In part, this was due to the absence of values of stomatal conductance for the dwarfing rootstocks at leaf water potentials below -2.0 MPa. However, the stomatal responsiveness to changes in leaf water potential varied with the rootstock.

Stomatal insensitivity to decreasing leaf water potential, which was apparent with M.26 and to some degree M.9, provides a means by which growth is maximized until soil water supplies are depleted, i.e., there was better control of leaf drought stress than with some of the other rootstocks. Statistical analysis did show that the slope of the regression between stomatal conductance and leaf water potential for AR 295-6, and to a lesser extent for AR 628-2 and AR486-1, was significantly steeper compared to the other rootstocks. For the rootstock AR 295-6, this rapid response was accompanied by the largest production of root biomass of all the rootstocks examined. Complete stomatal closure was evident for all the rootstocks with leaf drought stress reduced leaf water potential to value more negative than -2.5 MPa.

The rootstocks AR 295-6, AR 628-2

and AR486-1 all had Ottawa 3 as a parent (Saunders, 1911). Some of these AR rootstocks appear to offer an opportunity to control scion vigor in the absence of limitations in root size and the tree's potential to capture soil water. This feature appears to be associated with those rootstocks that have Ottawa 3 as a parent. A parent of Ottawa 3 was the ornamental crabapple Robin, which was bred for the harsh climate of the Canadian prairies and is known to show good root anchorage. Robin was obtained from a cross with a wild crabapple (*Malus baccata*) which has similar attributes (Saunders, 1911). The possible parental influence of crabapple and its nature warrants further investigation.

Lakso (1979) showed that substantial reductions in photosynthesis may not occur until leaf drought stress reached water potential values below -3.0 MPa. Both the rootstocks M.26 and AR 295-6 produced large leaf areas and had high Huber values relative to the other rootstocks examined. The Huber value is a measure of efficiency with which a stem is able to supply its leaves with water.

Root Responses to Drought Stress

The rootstocks compared in this experiment differed greatly in their ability to control scion size (Webster et al., 1997). When grown as unworked with scions, they also produced very different quantities of both coarse and fine roots over a 6-month growing period. The production of different amounts of root length may be associated with how a rootstock controls scion vegetative vigor. Evidence from experiments where root growth has been restricted showed that the observed reduction in root length, in the absence of water deficits, can produce a scion dwarfing (Atkinson et al., 1997).

Significant differences in root length were measured between some of the rootstocks in these experiments. The very dwarfing rootstock clones M.27, AR 69-7 and AR 360-19 all had similar total lengths of coarse root and fine root. There was, however, no simple relationship between the quantities of roots produced (coarse, fine or total) and the ability of the rootstocks to control scion vigor as a group. The rootstock AR 295-6, for example, despite being ranked around the vigor potential of M.9 as a rootstock (Webster et al., 1997), produced considerably more root (coarse and fine) than either M.26 or MM.111, rootstocks of significantly greater vigor potential. This inability to match root growth of rootstocks with their

scion dwarfing capacity has been noted with other apple rootstocks grown in orchard trials with Cox's Orange Pippin as the scion (Atkinson et al., 1990). However, the field trials comparing rootstock effects on scion vigor were not irrigated and it is possible that the full vigor potential of some of the rootstocks was not expressed in these trials (Webster et al., 1997).

This lack of relationship between root dry matter production and shoot vigor is most clearly evident with the rootstock MM.111 which produced less root dry matter, particularly coarse root, than some of the more dwarfing rootstocks such as M.27 and M.9. Short-term dry root dry matter production may indeed not reflect rootstock vigor but rather initial root establishment rate, which is slow for MM.111 (Howard pers. comm.). Nevertheless, despite this limited production of root MM.111 showed the largest amount of shoot growth over the 6-month experiment. This is what would be expected from observations of differences in rootstock vigor, MM.111 being the most invigorating dwarfing rootstock examined here (Ferree and Carlson, 1987).

Soil water deficits affected the growth of coarse and fine roots differently and this response varied with rootstock. For the rootstocks AR 295-6, AR 360-19 and AR 628-2, root growth declined in response to drying soil, whereas with the rootstocks AR 69-7 and M.26 root growth increased slightly. M.26 is known to show good drought tolerance (Ferree and Carlson, 1987) and production of new roots in response to drought may be associated with this tolerance. If this hypothesis is correct the rootstocks AR 295-6, AR 360-19 and AR 628-2 may prove to have poor drought tolerance. Further experiments are needed to test this. In the work described here, many of the rootstocks showed an ability to maintain and in some cases increase in their root:shoot ratio in response to soil drying.

The way in which dry matter is used to produce the roots' architectural structure (e.g., root diameter, number of secondary roots and root density [amount of root per unit soil volume]) may also have important implications in the uptake efficiency of water and nutrients by roots (Taylor, 1983). Measurements of specific root length for fine roots clearly showed that the length of root produced per unit dry weight remained constant, irrespective of rootstock or treatment. The ratio of coarse to fine dry root weight was similarly consistent.

In general the ratio of coarse to fine root with most rootstocks remained constant despite soil drying. This ratio was in the majority of cases maintained at a near constant value despite changes in root growth. This indicates that the initiation of secondary roots (fine roots in this case) in relation to primary roots (coarse roots) was, with most rootstocks, unaffected by soil drying.

The exceptions to this were with M.9 and AR 295-6 where the ratio declined in response to drought stress. Where the ratios of coarse to fine roots did change, the rootstock M.9 was particularly interesting, not only because the ratio of coarse to fine root decreased with the increase in soil drying, but also because of how this was achieved. For M.9, coarse root dry matter declined while fine root production increased. Such a change in root structure may possibly enhance the capacity of a root system to extract water. Other studies also have shown M.9 to be more drought tolerant (Fernandez et al., 1997).

In contrast, for rootstocks like M.26, the coarse to fine root ratio increased in response to reduced irrigation. The consistency of the root length to root weight ratio and the ratio of lengths of coarse and fine roots for the majority of apple rootstocks tested suggest that dry matter partitioning shows little ability to change in a way which might contribute to enhancing water uptake during soil drought stress.

When used as rootstocks these plants would have no natural foliage of their own, but that is not to say that the rootstock does not have influence on scion leaf development. This influence may be an important component in understanding the rootstock/scion water use. Clearly, when allowed to produce their own shoots considerable differences exist in the amount of dry matter partitioned to leaves. As would be expected leaf number, area and weight all declined with drought along with the amount of leaf area supplied relative to stem cross-sectional area.

The reduction in leaf area supplied per unit stem cross-sectional area, with drought, suggests that most rootstock stems become less efficient at transporting water to their leaves as the soil dries. The rootstock AR 295-6 is the exception. The ratio of its leaf area to stem cross-sectional area remained constant in response to drought stress. The explanation for how this happens is unclear but this may be part of the explanation for the growth of this rootstock, both in terms of root dry matter and length of root.

There may also be changes in the distribution, number and size of the water conducting xylem elements (vessels) in response to droughting. Changes in xylem size and morphology will have important implications in determining drought tolerance. It already has been shown that there is a correlation between rootstocks with both a low proportion of living tissue (parenchyma and ray cells) and a high proportion of vessels in the root xylem and an increase in rootstock vigor (Beakbane and Thompson, 1939, 1947).

Several studies have attempted to characterize the tolerance of rootstocks to soil water content. Both M.26 and MM.111 have been classified as intolerant to flooding, and M.111 is also frequently described as highly drought tolerant (Carlson, 1967; Rom and Brown, 1979). From this it might be concluded that the drought response of M.26 should be similar to that of MM.111. There is, however, no physiological justification to connect drought and flooding tolerance. One suggestion is that drought tolerance, at least in part, is determined by root dry matter production (Olien and Lakso, 1984), with invigorating rootstocks such as MM.111 being the most tolerant. Conversely, it has been argued that a limited ability of a root system to supply the shoot with water dwarfs the shoot (Tubbs, 1973).

This was not, however, the case when shoot growth was compared with vigor. The shoot extension growth of unworked rootstocks increased with the rootstocks' known vigor potential and occurred despite the fact that shoot development was restricted to four shoots per rootstock. More vigorous rootstocks may intrinsically have a greater capacity to produce a larger number of shoots than the more dwarfing rootstocks.

The existence of a relationship between shoot dry matter and rootstock vigor is important because it indicates that the vigor of shoots on unworked rootstocks is relative to that expected from scion shoots growing on the same rootstocks. It is also encouraging from this examination that unworked rootstocks still exhibit shoot vigor which reflects their expected scion vigor controlling capacity and aids the validity of using unworked rootstocks to determine drought tolerance. These experiments, and this vigor relationship in particular, also infer that the capacity of a rootstock to control scion vigor, or at least a significant part of the control, resides in the rootstock itself rather than an interaction between scion and rootstocks and perhaps the union.

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