



## Drought tolerance of apple rootstocks: Production and partitioning of dry matter

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Received 11 May 1998. Accepted in revised form 3 November 1998

**Key words:** apple, drought stress, irrigation, *Malus domestica* Borkh., rootstock, water deficits

### Abstract

The drought tolerance of the commercial apple (*Malus domestica* Borkh.) rootstocks M9, M26, M27 and MM111, and some new selections from the rootstock breeding programme at HRI-East Malling (AR69-7, AR295-6, AR360-19, AR486-1 and AR628-2), was assessed using potted, glasshouse-grown, unworked rootstocks. After an initial period of growth under well-watered conditions the amount of irrigation was gradually reduced, for some treatments, to simulate natural drying in the soil. At the end of a six-month growth period, the rootstocks were harvested and the production of dry matter and its partitioning to various plant parts determined. The rootstocks exhibited large differences in shoot and root dry matter, and root length but not all the rootstocks showed declines in root mass or length in response to the droughting treatment. The dwarfing rootstocks tended to have smaller amounts of both coarse (>2 mm diameter) and fine roots (<2 mm diameter), than the more vigorous rootstocks. Irrespective of rootstock or irrigation treatment there was a close linear relationship between coarse and fine root. There was also no change in the length/weight relationship for fine roots irrespective of rootstock or irrigation treatment, i.e. 42 m of fine root weighed 1 g dry weight. In some cases the amount of root produced could be directly correlated with the rootstock known potential to control scion vigour, but this was not true for all the rootstocks examined. The absence of this relationship was particularly evident in some of the new selections of rootstock. The possible causes for these differences, compared with commercially used rootstocks, is discussed in relation to the origin and parentage of the rootstock selections. Despite this lack of a root length/vigour relationship, the amount of dry matter partitioned to shoot growth reflected the rootstocks' known vigour. The different responses of these rootstocks to drought are discussed along with their implications for understanding the mechanisms by which rootstocks are thought to dwarf scion shoots.

### Introduction

The effective use of irrigation has become a key component in the reliable production of high quality fruit crops. The benefits of applying water to fruit tree crops are now generally well known (Higgs and Jones, 1990, 1991; Lötter et al., 1985). The top fruit growing regions of the UK, which are predominantly in southern England, are frequently subject to dry summer pe-

riods; under these circumstances irrigation has been shown to increase fruit size (Atkinson et al., 1998; Higgs and Jones, 1991; Hipps et al., 1990). However, there are many situations where growers do not have access to irrigation water or, alternatively, cannot afford to apply it.

Plants are able to adapt to changes in the availability of soil water in a number of ways. Frequently, the rate of leaf area production declines as the soil dries (Higgs and Jones, 1990). Under more severe conditions of soil drying leaf area may decline as a result

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of leaves being shed. Acclimation changes in dry matter partitioning may take place with an increase in the amount of root produced relative to the growth of the shoot, i.e. a change in the root:shoot ratio (Landsberg and Jones, 1981). An increase in the root:shoot ratio, which may be attributable to an increase in the amount of root, reductions in root death, reductions in rate of leaf development or increases in leaf abscission, will reduce the transpirational demand per unit root length, and, if increased root growth is the cause, will also increase the volume of soil exploited and the potential for water uptake (Passioura, 1972; Taylor, 1983). The amount of root and its distribution in the soil affects the ability of the roots to absorb water (Faust, 1989). Differences in the amount of apple root are a probable major cause for the variable contribution (between 40 to 68%) roots have in determining the total plant conductance to water flow (Baxter and West, 1977; Davies and Lakso, 1979; Landsberg and Jones, 1981). Stem measurements of conductance have been shown to be higher, along with greater amounts of functional xylem, compared with values for the supporting root system (Davies and Lakso, 1979).

The work presented here describes how dry matter production and its partitioning differ for a range of apple (*Malus domestica* Borkh.) rootstocks with different scion size-controlling capacity, and how the partitioning changes as the growing medium dries. Unworked rootstocks were used to avoid the possible confounding effects that some scions may have when grafted on rootstock (Atkinson, 1980). The intent was to test a potential method of measuring the drought tolerance of glasshouse-grown rootstocks, at an early stage in rootstock selection programmes, without the need for expensive and long-term field trials. The growth responses of these rootstocks are also examined to determine if differences in dry matter production and partitioning, in response to water deficits, might supplement our understanding of the mechanism by which rootstocks dwarf scions.

## Materials and methods

### *Plant material and culture*

Nine different rootstocks were compared, four traditional clones (M27, M9, M26 and MM111) and five advanced selections from HRI-East Malling's apple rootstock breeding programme (AR69-7, AR360-19, AR628-2, AR295-6 and AR486-1). The rootstocks

used were non-grafted, one-year-old, rooted stool bed shoots. Size of each clone of rootstock used in this experimentation varied, but only material within one size class (measured by stem cross-sectional area) was used. There were also differences in root mass at planting between and within a rootstock clone, but these were minimised by root pruning. These rootstocks were planted in pots (capacity 14 dm<sup>3</sup>) in a loam-free potting compost (Richmoor) incorporating 4 kg m<sup>-3</sup> of Osmocote, (18% N, 6% P<sub>2</sub>O<sub>5</sub> and 12% K<sub>2</sub>O, w/w/w), with a release time of 2–3 months. The rootstock parentage and their relative capacities to control scion vigour are shown in Table 1. The field performance of these rootstocks in screening trials has already been described (Webster et al., 1997).

### *Irrigation regimes*

Directly after planting in the containers in March, the rootstocks were placed outside and given adequate irrigation for one month before bud break; this was to ensure good establishment and promote new root growth. In April, the pots were transferred to a glasshouse and, shortly after bud burst, the number of developing shoots on each rootstock stem was reduced to four. From the beginning of June, the plants were watered automatically, using a trickle irrigation system with pressure compensating nozzles. This system enabled the duration and timing of the irrigation events to be controlled accurately. The precise details of the timings and the amounts of irrigation given are shown in Table 2. In order to mimic summer soil drying and allow the plants to acclimate to this, at the end of June the amount of water applied to some of the rootstocks was gradually reduced, so exposing them to an increasing soil water deficit (Wang and Stutte, 1992). Three different watering regimes were established, one at an abundant level to act as a control (A = approximately 2100 cm<sup>3</sup> per day) and two at sub-optimal levels to induce soil drying and plant water deficit (B, reduced irrigation approximately 325 cm<sup>3</sup> per day and C, droughted approximately 65 cm<sup>3</sup> per day). The amount of water received by each plant was assessed by measuring the volume of irrigation water collected (see Table 2).

### *Experimental design and analysis*

The potted rootstocks were arranged in a fully randomised block design to compare the nine rootstocks at three levels of irrigation (A, B and C). There were 10 blocks that each consisted of three rows of

Table 1. Rootstocks investigated for their drought tolerance/susceptibility, arranged in order of their known ability to control scion vigour. The parental make-up of most of the selections from the East Malling rootstock breeding programmes are also shown in parentheses

| Extremely dwarfing         | Dwarfing                          | Semi-dwarfing  | Vigorous                          |
|----------------------------|-----------------------------------|----------------|-----------------------------------|
| M27 (M13 × M9)             | M9-EMLA <sup>+</sup>              | M26 (M16 × M9) | MM111 (Northern Spy × Merton 793) |
| AR69-7 (AR10-2-6 OP*)      | AR295-6 (Robusta 5(j) × Ottawa 3) |                |                                   |
| AR360-19 (M9 × M27)        | AR486-1 (Ottawa 3 × M7)           |                |                                   |
| AR628-2 (Ottawa 3 × MM106) |                                   |                |                                   |

\*OP – open pollinated.

<sup>+</sup> – the parentage of M9 is not known.

Table 2. The changes in the irrigation treatment schedule used to achieve a slow increase in soil and plant water deficits (drought stress) for rootstocks in pots, and the actual measured quantities (cm<sup>3</sup> per day) of water received by the plants

| Day of year          | 164 <sup>1</sup>                          | 178       | 199       | 213          | 182   | 200        | 217        | 242        |
|----------------------|---|-----------|-----------|--------------|---|------------|------------|------------|
| Dates and duration   | 13/6-26/6                                 | 27/6-17/7 | 18/7-31/9 | 1/10-harvest | 1 July  | 19 July    | 5 Aug.     | 30 Aug.    |
| Irrigation treatment | Irrigation (minutes per day) <sup>2</sup> |           |           |              | Quantity of water applied (cm <sup>3</sup> per day) |            |            |            |
| A Control            | 45  | 45        | 60        | 60           | 1500  | 2100       | 2100       | 2100       |
| B Reduced irrigation | 45  | 20        | 10        | 10           | 671 ± 32.4  | 336 ± 10.7 | 323 ± 18.3 | 327 ± 17.5 |
| C Droughted          | 45  | 10        | 5         | 2            | 346 ± 19.3  | 174 ± 6.0  | 64 ± 7.8   | 66 ± 6.0   |

<sup>1</sup>The day of the year on which the treatments commenced or sample measurements taken (January 1, being day 1).

<sup>2</sup>The cumulative time per day when the plants received irrigation.

nine trees. All 27 rootstock × irrigation treatment combinations were represented within each block (3 plants/rootstock, nine plants per irrigation treatment). Blocks 2 – 9 were used for experimental data, while blocks 1 and 10 guarded the outside blocks along their length. Each block had 3 guard trees at each end. All the guard trees were of potted rootstocks, similar to those used in the main experiment. Statistical analysis used analysis of variance (ANOVA). The standard error of the difference between means (SED) and significance probabilities were calculated for rootstock, treatment and rootstock × treatment interactions. The degrees of freedom (d.f.) that are shown will vary between analyses due to time constraints, some variates were recorded for only five blocks and total branch dry weight was recorded for only six blocks. Also, many of the variates had missing values. Due to considerable variability between the sizes of the roots of the different rootstocks, at the end of the experiment, the statistical analysis of root growth, was carried out after partitioning the rootstocks into two size groups. These groupings were determined by the amount of root mass produced and not by the scion growth control capacity of the rootstock. The ‘small root mass rootstock’ group 1 consisted of M27, AR69-7, AR360-19,

M9, M26, and MM111, while the ‘large root mass rootstocks’ group 2 contained AR628-2, AR295-6 and AR486-1.

#### *Dry matter partitioning and root growth*

After six months of growth the plants were harvested and divided into their constitutive parts (roots, leaves, stem and branches) and, with the exception of the roots, dried at 80 °C to constant weight. Roots were washed gently to remove all the compost and then separated by hand into ‘fine roots’ (<2 mm in diameter) and ‘coarse roots’ (>2 mm in diameter). The total amount of fine root was quantified using a root length scanner (Comair, Commonwealth Aircraft Corp. Ltd., Melbourne, Australia), while coarse root length was measured with a ruler. After the length measurements had been made, roots were dried at 80 °C to constant weight and the amount of dry matter in both size classes was determined. The partitioning of roots into two different size classes may be not be solely justified on a physiological/functional basis as Atkinson (1983) has suggested that both coarse and fine root can be shown to be important in water uptake.

In all cases the amount of dry matter produced was largely a reflection of the total dry matter gained throughout the post planting period, although in some cases the dry matter present when the rootstock was planted made a significant contribution. Observations from a subsequent experiment, carried out in the same way (data not shown here) indicated that the root dry matter present at the start of the experiment did not differ between rootstocks ( $P$  0.161), but after the period of adequate watering there were differences ( $P$  0.026) between rootstocks. These differences in the production of root dry matter were not, however, a reflection of rootstock vigour, but of the rootstock's root establishment rate.

## Results

### *Rootstock and treatment effects on root growth*

#### *Dry weights of roots*

After six months growth in pots, there were large differences between several of the rootstocks in the dry weight of coarse root formed, irrespective of treatment (Table 3). Least coarse root was formed by the most invigorating rootstock MM111 and there were only small amounts of coarse root formed by the very dwarfing rootstock clones M27, AR69-7 and AR360-19. Slightly more coarse root was formed by the dwarfing M9 and the semi-dwarfing M26 but considerably more by the very dwarfing AR628-2 and the dwarfing AR486-1. Another dwarfing clone, AR295-6, formed the most coarse root, more than three times the amount formed on M9, a rootstock which preliminary trials show to be of similar scion vigour controlling potential.

Similar differences between rootstocks were measured in the amounts (dry mass) of fine roots formed (Table 3). The very dwarfing M27, AR69-7, AR360-19, the semi-dwarfing M26 and the invigorating MM111 all had similar amounts of fine root at the end of the six-month period. More fine root was recovered from the very dwarfing AR628-2 and the dwarfing M9 and AR486-1 while the most fine root was recovered from the dwarfing clone AR295-6.

The droughting treatment (C) had no significant effect upon the amounts of fine or coarse root developed on the rootstocks in group 1, while significant treatment effects were evident for fine and coarse root dry mass on the rootstocks analysed in group 2. No significant rootstocks  $\times$  irrigation treatment interactions were recorded.

The ratios of coarse to fine root dry weight differed between rootstocks, but appeared unrelated to rootstock vigour (data not shown). The rootstocks M27 and MM111 had the largest rates with 4–5 times more coarse than fine root, respectively. With the exception of AR628-2, all the extremely dwarfing rootstocks had ratios of approximately 4 times as much coarse root relative to fine. For the dwarfing rootstocks, AR486-1 and AR295-6, the ratio was around 2; whereas for M9 the ratio ranged from 3–5 depending on irrigation treatment. For the other rootstocks the ratio was largely independent of treatment with the exception of M9 and AR295-6, where the relative amount of coarse root decreased with the imposition of the droughting treatments.

#### *Length of roots*

There were significant differences between rootstocks in the total lengths of coarse and fine roots recovered from the pots after growth for six months (Figure 1). With the exception of rootstock AR628-2, the extremely dwarfing rootstocks produced around 20 cm of coarse root. The dwarfing rootstock M9 produced 35 cm while the semi-dwarfing M26 produced 50 cm and both the rootstocks AR295-6 and AR486-1 produced around 100 and 80 cm, respectively. A similar pattern was evident with the fine roots. Again, AR295-6 produced significantly more root than any other rootstock within its group, i.e. with a rootstock mean of 590 m. With the exception of AR628-2, the extremely dwarfing rootstocks produced between 200 to 230 m fine roots as did the vigorous MM111 and the semi-dwarfing M26. The extremely dwarfing AR628-2, M9 and AR486-1 produced between 350 and 425 m per plant.

There were no statistically significant main treatment effects of droughting treatment (C) on the total lengths of either coarse or fine root recovered from the rootstocks analysed in group one, after six months growth (Figure 1). There was however, a significant effect of irrigation treatment on the lengths of fine roots measured for the rootstocks within group two. The fine root lengths on AR295-6, AR628-2 and AR486-1 were all reduced by the droughting treatment C. The fine and coarse root lengths of M9 and M26 did not change when these rootstocks were fully droughted.

When fine root dry matter was compared directly with fine root length a clear linear relationship was evident ( $r = 0.93$ ), independent of either rootstock or treatment (Figure 2). Calculations of specific root

Table 3. Total root dry matter (g) of coarse (&gt;2 mm diameter) and fine roots (&lt;2mm diameter) at harvest, after six months growth

| Irrigation treatment   | Group 1 |        |          |      |      |       |                   | Group 2 |         |         |                   |
|--|---------|--------|----------|------|------|-------|-------------------|---------|---------|---------|-------------------|
|  | M27     | AR69-7 | AR360-19 | M9   | M26  | MM111 | Mean <sup>1</sup> | AR628-2 | AR295-6 | AR486-1 | Mean <sup>2</sup> |
| 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 $\times$ 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 $\times$ irrigation treatment $P = 0.054$ , SED 1.75. |         |        |          |      |      |       |                   |         |         |         |                   |
| <i>C as % of A = 100 C/A</i>   | 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 $\times$ 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 $\times$ irrigation treatment $P = 0.385$ , SED 1.91. |         |        |          |      |      |       |                   |         |         |         |                   |
| <i>C as % of A = 100 *C/A</i>  | 91.2    | 113    | 74.6     | 120  | 129  | 117   |                   | 79.0    | 66.4    | 70.6    |                   |

length, in metres, per gram dry weight for the fine roots, revealed no statistically significant rootstock or irrigation treatment differences (data not shown). A gram dry mass of root for all rootstocks was approximately 42 m in length. Pooling the data from different rootstocks and treatments gave a correlation of 0.90 between the dry masses of fine and coarse roots (Figure 3).

#### Rootstock and treatment effects on leaf development

Counts of leaves present on the plants at the termination of the experiment, after 6 months growth showed M26 had the most leaves per plant (Table 4). M27, which had fewer leaves than M26, also produced significantly more leaves than most of the other rootstocks. Total leaf area per plant was least on AR360-19, although AR69-7 and M9 also produced lower than the average total leaf area. The rootstocks that produced the largest leaf areas per plant were AR628-2, M26, AR486-1 and AR295-6. Total leaf dry mass per plant were also higher than average for these same four rootstocks.

When the irrigation supply was reduced (treatment B), the numbers of leaves per plant on most rootstocks

were decreased. Although treatment B also reduced total leaf area per plant and the total leaf dry mass per plant, the effects were less consistent, with some rootstocks, such as AR69-7, M9 and AR295-6, unaffected by the treatment (Table 4). The most severe droughting treatment (treatment C) caused a greater reduction in the same three variables and in this case the reductions were apparent on all rootstocks. No statistically significant interaction between rootstocks  $\times$  irrigation treatment effects were measured for any of these three leaf variables.

The rootstocks differed in the numbers of leaves that abscised during the course of the experiment. MM111 shed most leaves and AR360-19 and AR486-1 also both dropped more leaves than the other rootstocks (data not shown). A reduction in the water supplied (treatments B and C) in most cases, but especially with treatment C, increased the number of abscised leaves. When leaf abscission for the treatments B and C was expressed relative to the control treatment (A) there were marked differences between the rootstocks (data not shown). Leaf loss expressed in this, way relative to the control treatment, was much greater for the more dwarfing rootstocks such as M27

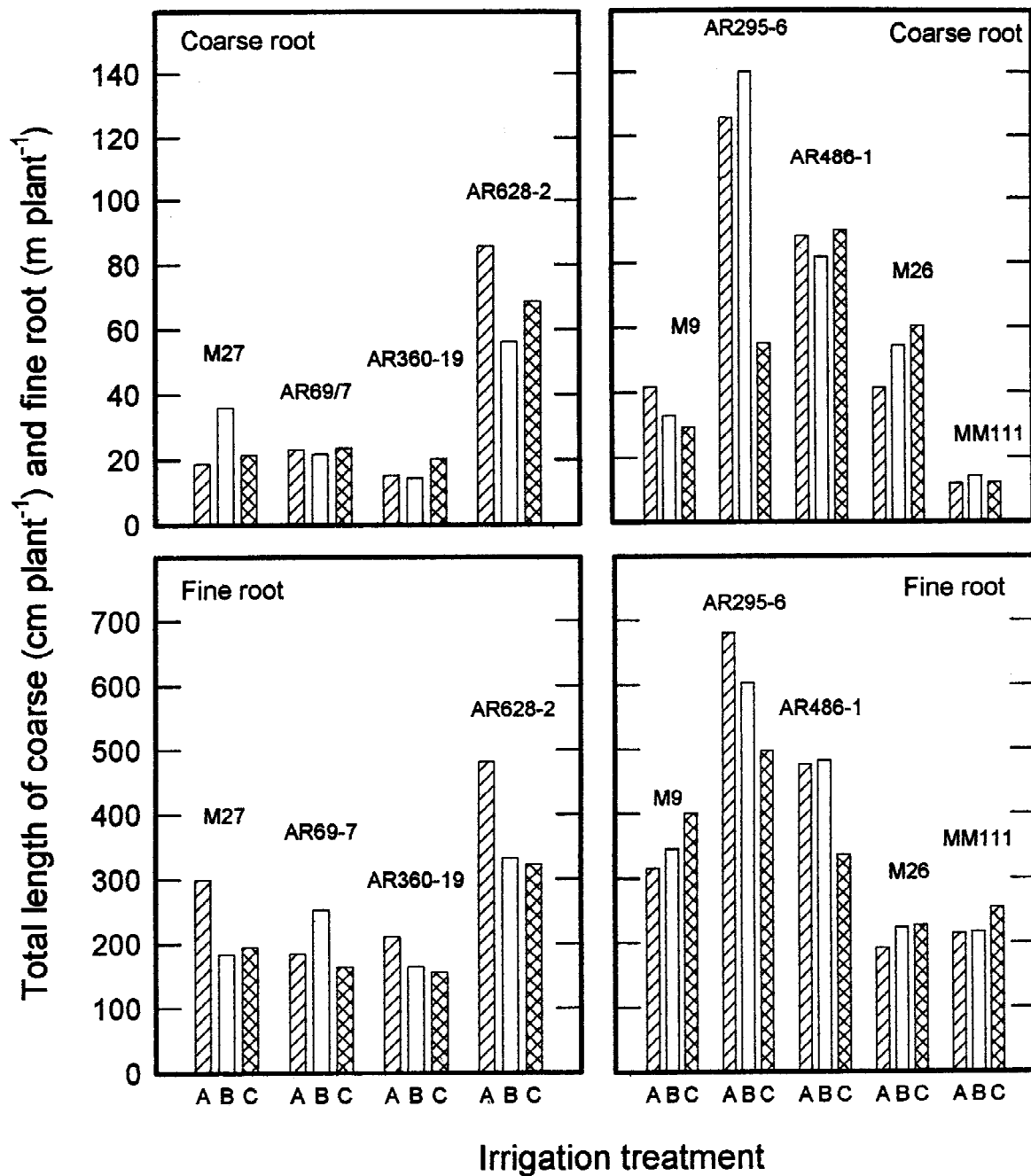


Figure 1. Total root length, partitioned to coarse (cm/plant) (>2 mm in diameter) and fine (m/plant) (<2 mm in diameter) roots, at harvest, after six months growth. Irrigation treatments are shown as A, abundant irrigation; B, reduced irrigation and C, droughted. Footnote: Statistical analysis was performed on two separate groups of rootstock depending on their ungrafted root size, group one consisted of M27, AR69-7, AR360-19, M9, M26, MM111 and group two, AR628-2, AR295-6, AR486-1. Coarse roots for rootstocks in group 1. d.f. = 53; Rootstock  $P < 0.001$ , SED 0.29; Irrigation treatment  $P = 0.823$ , SED 0.21; Rootstock  $\times$  irrigation treatment  $P = 0.972$ , SED 0.51. Coarse roots for rootstocks in group 2. d.f. = 28; Rootstock  $P = 0.198$ , SED 0.21; Irrigation treatment  $P = 0.316$ , SED 0.21; Rootstock  $\times$  irrigation treatment  $P = 0.236$ , SED 0.35. Fine roots for rootstocks in group 1. d.f. = 56; Rootstock  $P < 0.001$ , SED 0.14; Irrigation treatment  $P = 0.899$ , SED 0.09; Rootstock  $\times$  irrigation treatment  $P = 0.311$ , SED 0.24. Fine roots for rootstocks in group 2. d.f. = 28; Rootstock  $P < 0.001$ , SED 0.09; Irrigation treatment  $P = 0.05$ , SED 0.09; Rootstock  $\times$  irrigation treatment  $P = 0.560$ , SED 0.17.

Table 4. Leaf number, leaf area (cm<sup>2</sup>) and leaf dry wt (g) per plant, at harvest, after six months growth

|   | M27  | AR69-7 | AR360-19 | AR628-2 | M9   | AR295-6 | AR486-1 | M26  | MM111 | 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 $\times$ 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 (cm <sup>2</sup> per plant)   | A    | 5538   | 3724     | 3774    | 6584 | 4080    | 5799    | 6866 | 5949  | 5253           | 5288 |
|   | 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 $\times$ 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 (g per plant)   | A    | 42.7   | 33.3     | 32.8    | 60.7 | 34.0    | 52.4    | 62.3 | 44.3  | 45.4           | 45.3 |
|   | 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 $\times$ 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  |                |      |

Table 5. The analysis of fine root length (log) and analysis of fine root length (log) adjusted using leaf area (log) as a covariate

| Irrigation treatment  | Group 1 |        |          |       |       |       |                   | Group 2 |         |         |                   |
|---|---------|--------|----------|-------|-------|-------|-------------------|---------|---------|---------|-------------------|
|   | M27     | AR69-7 | AR360-19 | M9    | M26   | MM111 | Mean <sup>1</sup> | AR628-2 | AR295-6 | AR486-1 | Mean <sup>2</sup> |
| Anova   |         |        |          |       |       |       |                   |         |         |         |                   |
| A Control   | 5.944   | 5.418  | 5.412    | 5.804 | 5.688 | 5.563 | 5.638             | 6.419   | 6.786   | 6.239   | 6.481             |
| B Reduced irrigation  | 5.392   | 5.910  | 5.244    | 6.035 | 5.578 | 5.562 | 5.620             | 6.086   | 6.541   | 6.379   | 6.335             |
| C Droughted   | 5.348   | 5.365  | 5.095    | 6.220 | 5.635 | 5.688 | 5.558             | 6.116   | 6.415   | 5.859   | 6.130             |
| For rootstocks in group 1. d.f. = 70; Rootstock $P < 0.001$ , SED 0.154; Irrigation treatment $P = 0.745$ , SED 0.108; Rootstock $\times$ irrigation treatment $P = 0.171$ , SED 0.266.                           |         |        |          |       |       |       |                   |         |         |         |                   |
| For rootstocks in group 2. d.f. = 31; Rootstock $P < 0.001$ , SED 0.082; Irrigation treatment $P = 0.001$ , SED 0.081; Rootstock $\times$ irrigation treatment $P = 0.082$ , SED 0.141.                           |         |        |          |       |       |       |                   |         |         |         |                   |
| Covariate anova   |         |        |          |       |       |       |                   |         |         |         |                   |
| A Control   | 5.802   | 5.400  | 5.488    | 5.728 | 5.351 | 5.349 | 5.520             | 6.184   | 6.707   | 6.124   | 6.339             |
| B Reduced irrigation  | 5.414   | 5.765  | 5.404    | 6.038 | 5.400 | 5.594 | 5.603             | 6.059   | 6.629   | 6.342   | 6.343             |
| C Droughted   | 5.526   | 5.513  | 5.446    | 6.435 | 5.470 | 5.777 | 5.694             | 6.287   | 6.514   | 5.994   | 6.265             |
| For rootstocks in group 1. d.f. = 61; Rootstock $P < 0.001$ , SED 0.144; Irrigation treatment $P = 0.398$ , SED 0.107; Rootstock $\times$ irrigation treatment $P = 0.171$ , SED 0.242; covariate $P = < 0.001$ . |         |        |          |       |       |       |                   |         |         |         |                   |
| For rootstocks in group 2. d.f. = 30; Rootstock $P < 0.001$ , SED 0.066; Irrigation treatment $P = 0.082$ , SED 0.085; Rootstock $\times$ irrigation treatment $P = 0.023$ , SED 0.124; covariate $P = 0.002$ .   |         |        |          |       |       |       |                   |         |         |         |                   |

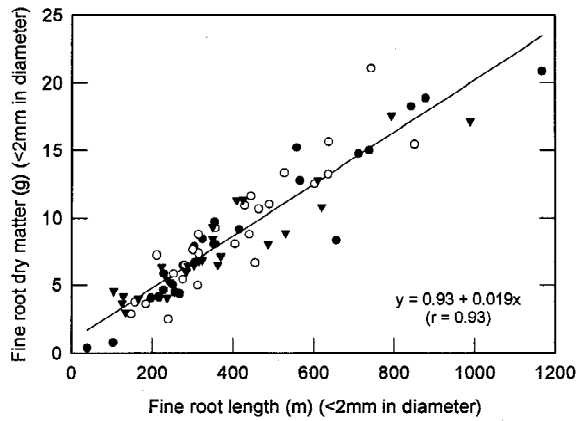


Figure 2. The relationship between coarse root dry weight and fine root dry weight for a range of apple rootstocks subject to different irrigation regimes. Data are presented without differentiating between different rootstocks. Irrigation treatments were as follows: A (filled circle), B (open circle) and C (triangle). Footnote: The apple rootstocks used are shown in Table 1 and the irrigation regimes are described in Table 2. Each point refers to the mean for each rootstock irrigation treatment combination.

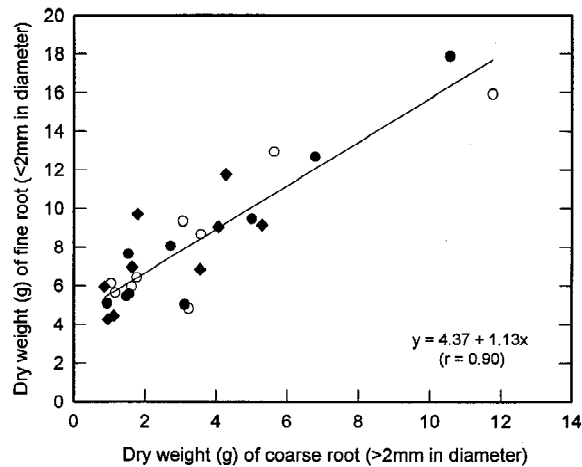


Figure 3. The relationship between fine root length (m) (<2 mm in diameter) and root dry weight (g). Data are presented from the complete analysis of four experimental blocks, without differentiating between different rootstocks. Irrigation treatments were as follows: A (filled circle), B (open circle) and C (diamond). Each point refers to the mean for one plant.

and AR69-7. In both these cases over 60% more leaves were lost on rootstocks in treatment C compared to treatment A. While, for the rootstock MM111, there was little treatment difference in the relative number of leaves lost.

#### Rootstock root length and leaf area

The relationship between leaf area and root length was also analysed using the log of fine root length ad-

justed by the log of leaf area as a covariate (Table 5). The amount of root length was analysed in the two-rootstock groups as used in the analysis of variance of root dry matter. Analysis of fine root length alone showed that for the group 1 rootstocks there were no significant treatment effects. The log of leaf area was a highly significant covariate, indicating that the amount of leaf area was strongly influenced by fine root length (Table 5). Within the group 1 rootstocks the means calculated with or without leaf area as a covariate were generally similar. The most obvious exception was the rootstock M26, where more roots were evident than expected from its leaf area. For the group 2 rootstocks there were highly significant treatment and rootstock effects with and without leaf area covariate analysis. The covariate analysis was also highly significant, indicating that the observed differences in fine root length were accounted for by differences in leaf area.

#### Rootstock and treatment effects on shoot growth

The rootstocks differed considerably in the amount of shoot growth, and hence mass of aerial dry matter, made in the six-month duration of the experiment. Figure 4 shows the mean shoot dry matter accumulated for treatments B+C. This combination of treatments was thought to be the most appropriate to compare the performance of these potted rootstocks with those planted in previous experiment conducted in the field, which received no irrigation (Webster et al., 1997). The general comparative pattern was, however, similar whatever irrigation treatment was used. Least shoot extension was made by the rootstocks M27, AR69-7, AR360-19 and M9. The invigorating MM111 and the semi-dwarfing M26 rootstocks made most shoot growth. Both irrigation treatments (B and C) reduced shoot growth made by the rootstocks, but there was no significant difference between these two treatments (data not shown). Reduced irrigation produced a large reduction in growth of two rootstocks M27 and MM111, whilst it produced no significant reduction in growth of AR69-7.

Although shoot development was restricted to 4 branches per rootstock, the amount of shoot growth made by the different rootstocks, was related to rootstock vigour as predicted in Table 1 whether expressed as total shoot length or mass of dry matter. Although dry mass of M9 was less than anticipated (Figure 4).

The increments in stem cross-sectional area during the course of the six-month experiment are shown in Table 6. Lower than average increment stem in cross-



Table 6. The change in cross-sectional stem area (mm<sup>2</sup>) measured between planting and harvest, after six months of growth

| Treatment  | M27  | AR69-7 | AR360-19 | AR628-8 | M9    | AR295-6 | AR486-1 | M26   | MM111 | Treatment mean |
|--|------|--------|----------|---------|-------|---------|---------|-------|-------|----------------|
| A Control  | 82.1 | 100.4  | 97.7     | 119.2   | 64.5  | 136.4   | 168.0   | 106.9 | 123.5 | 111.0          |
| B Reduced irrigation   | 67.9 | 92.9   | 91.0     | 118.7   | 107.3 | 127.5   | 119.7   | 86.4  | 132.6 | 104.9          |
| C Droughted  | 53.5 | 91.1   | 86.7     | 92.0    | 67.7  | 105.8   | 100.3   | 79.6  | 92.6  | 85.8           |
| Rootstock mean   | 67.8 | 94.8   | 91.8     | 109.9   | 79.8  | 123.2   | 129.3   | 91.0  | 116   |                |
| d.f. = 180; Rootstock $P < 0.001$ , SED 8.43; Irrigation treatment $P < 0.001$ , SED 4.87; Rootstock $\times$ irrigation treatment $P = 0.028$ , SED 14.6. |      |        |          |         |       |         |         |       |       |                |
| $C$ as% of $A = 100 * C/A$   | 65.2 | 90.7   | 88.7     | 77.2    | 105.0 | 77.6    | 59.7    | 74.5  | 75.0  |                |

Table 7. Amount of leaf area (cm<sup>2</sup>) per mm of trunk girth (Huber value), at harvest, after six months growth

| Treatment  | M27 | AR69-7 | AR360-19 | AR628-2 | M9  | AR295-6 | AR486-1 | M26 | MM111 | Treatment mean |
|--|-----|--------|----------|---------|-----|---------|---------|-----|-------|----------------|
| A Control  | 121 | 81     | 83       | 133     | 100 | 107     | 127     | 124 | 109   | 109            |
| B Reduced irrigation   | 113 | 85     | 72       | 114     | 88  | 117     | 102     | 116 | 82    | 99             |
| C Droughted  | 78  | 70     | 50       | 90      | 68  | 102     | 88      | 103 | 69    | 80             |
| Rootstock mean   | 104 | 79     | 68       | 112     | 86  | 108     | 106     | 114 | 87    |                |
| 180; Rootstock $P < 0.001$ , SED 7.26; Irrigation treatment $P < 0.001$ , SED 4.19; Rootstock $\times$ irrigation treatment $P = 0.622$ , SED 12.57. |     |        |          |         |     |         |         |     |       |                |
| $C$ as% of $A = 100 * C/A$   | 64  | 86     | 60       | 68      | 67  | 95      | 69      | 84  | 69    |                |

sectional (SCA) area was recorded on M27 and M9. The greatest increment in stem SCA was recorded on AR486-1 and AR295-6, whilst MM111 also made more incremental growth than most of the other rootstocks. The reduced irrigation treatment (B) had no main effect on stem increment but the droughting treatment (C) reduced it significantly. A significant rootstock  $\times$  irrigation treatment interaction occurred with stem incremental area. With some of the rootstocks (M27, AR486-1 and M26) treatment B reduced stem increment greatly whilst with others (MM111 and M9) this treatment appeared to increase stem increment slightly. Similarly, the droughting treatment had no effect on the stem increment of M9. The relationship between unit basal stem girth and the total leaf area (the Huber value) was also analysed at end of the experiment (Table 7) and this showed significant rootstock differences. AR360-19, AR69-7 had the lowest leaf area per stem girth and M26 and AR628-2 the highest. Severe droughting (treatment C) also reduced significantly the total leaf area per unit stem girth.

## Discussion

### Rootstock response to soil water deficit

There have been several studies that have attempted to characterise the tolerance of apple rootstocks to soil water content. Both M26 and MM111 have been described frequently as highly drought tolerant (Carlson, 1967, Ferree and Carlson, 1987; Rom and Brown, 1979). 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 MM111, being the most tolerant on account of their greater dry matter production.

Here, soil water deficits affected the production of coarse and fine roots differently and this response varied with rootstock. For the rootstocks AR295-6, AR360-19 and AR628-2, production of fine and coarse roots declined in response to increasing soil water deficit, whereas with the rootstocks AR69-7 and M26, root production increased slightly.

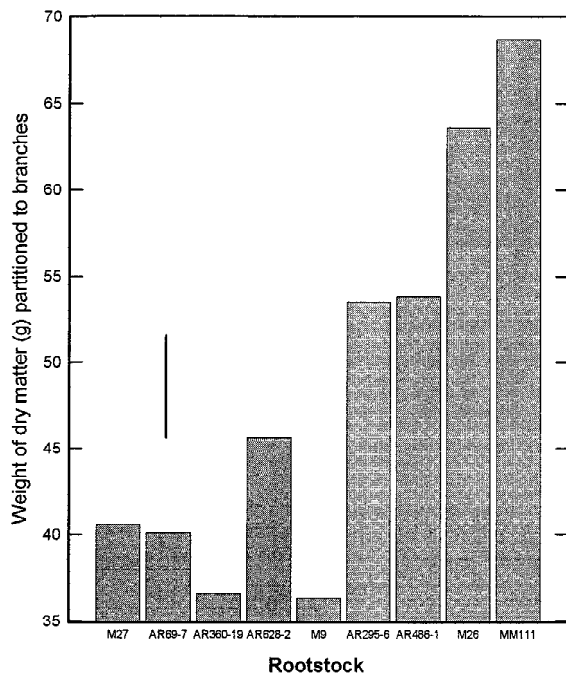


Figure 4. The mean total amount of dry matter (g) partitioned to shoot growth, for treatments B and C, at harvest, after six months growth. Footnote: Branch number was restricted to four developing shoots throughout the experiment. Statistical analysis is shown from treatments B and C and the results from 6 blocks; d.f. = 85; Rootstock  $P < 0.001$ , SED 5.80; Irrigation treatment  $P < 0.001$ , SED 2.74; Rootstock  $\times$  irrigation treatment  $P = 0.963$ , SED 8.21. The vertical line shows the rootstock SED.

Specific root length for fine roots clearly showed that the length of root produced per unit dry weight remained constant, irrespective of rootstock or irrigation treatment. The ratio of coarse to fine dry root weight was similarly consistent; despite changes in total root dry matter production. This indicates that the initiation of second order roots (fine roots in this case) in relation to first order root (coarse roots) was, with most rootstocks, unaffected by soil drying. The exceptions to this were with M9 and AR295-6 where the coarse: fine ratios declined in response to droughting. For M9, coarse root dry matter declined while fine root production increased. Such a change in root structure may enhance the capacity of a root system to extract water. Citrus rootstocks with the larger amounts of fibrous roots tended to have greater hydraulic conductivities and enhanced rates of soil water depletion (Syvertsen and Graham, 1985). It is also evident, that the conductance of a root system increases in the presence of new root growth or white root (Baxter and West, 1977). This increase in conductance may, however, be

due to an enhancement in root surface area rather than any difference in water absorption capacity between woody (old roots) and white roots (Atkinson, 1980). As water transport across the cortex occurs through the apoplast, which creates a high hydraulic resistance, the loss of the cortex during secondary thickening may increase water uptake in older roots relative to younger roots (see Landsberg and Jones, 1981). In contrast to the decline in coarse: fine root ratios with M9, with rootstocks like M26, the coarse to fine root ratio increased in response to reduced irrigation; a similar response has been shown for trees such as oak, chestnut and sycamore (Higgs, Higgs and Collard, 1996, 1997).

The rootstock MM111 produced relatively less root growth than other rootstocks in this experiment. However, MM111 is known to establish slowly following transplanting and may have responded differently if the experiment had been extended over more than one growing seasons (Ferree and Carlson, 1987). In contrast the rootstock M26 did not appear to suffer from a slow rate of root initiation. The ability of M26 to increase dry matter partitioning to both fine and coarse root when grown with the least amount of water, suggests an ability to tolerate greater soil water deficits, as suggested by Ferree and Carlson (1987).

When used with a scion these rootstocks would not have their own leaves, but rootstocks are able to influence scion leaf development. This influence is an important component in the understanding of rootstock/scion water use (Higgs and Jones, 1990). There were considerable differences between these rootstocks in the production and partitioning of dry matter to leaves. For example M27, a fully dwarfing rootstock, produced a relatively high number of leaves compared to other stocks of similar or greater vigour potential. This was due to the greater production of syleptic shoots on M27 rootstock (data not shown). With all the rootstocks examined, leaf number, area and weight all declined with drought along with the amount of leaf area relative to stem cross-sectional area (Huber value). Some of the differences in leaf area at the end of the experiment can be attributed to the treatments. Treatments B and C induced an increase in leaf abscission, which was particularly apparent with the dwarfing rootstocks M27 and AR69-7. While the rootstock MM111 irrespective of treatment lost more leaves than any other rootstock, but there were no treatment differences. These results show a predicted means of conserving water use, through leaf loss (see Introduction), as well as, obvious root-

stock differences in the pattern on leaf abscission and renewal.

A higher Huber value is thought to relate to a reduction in the impact of xylem embolism on stem water transport (Tyree and Dixon, 1986), presumably due to water transport capacity in excess of the current flux of water to meet the transpirational demand. Under drought conditions, the reduction in leaf area supplied per unit stem cross-sectional area shows that most rootstock stems and roots become less efficient at transporting water as the soil dries. This was not the case with the rootstock AR295-6, for which the Huber value remained constant when droughted. As yet, it is unclear if this is associated with anatomical feature(s) of its xylem, but this rootstock was shown to produce a large amount of root dry matter relative to its scion vigour potential. Anatomical changes in xylem (vessel number and size) have already been shown to correlate well with rootstocks of different scion dwarfing potential (Beakbane and Thompson, 1939, 1947). Dwarfing rootstocks tending to have smaller diameter xylem vessels and fewer vessels per unit stem cross-sectional area compared to vigorous rootstocks.

Examination of the relationship between fine root length and leaf area, using covariate analysis, showed that the amount of leaf area produced was highly correlated with the length of fine root. In most cases withholding of water produced no significant change in the relationship between leaf area and fine root length. The conserving of this relationship suggests that it is likely to be important in determining the amount of leaf area produced and the rootstocks growth potential. A rootstock such as M26, produced and or retained more root than expected, in the covariate analysis using leaf area, may have an advantage during periods of low soil water availability.

Despite there being an incomplete correlation between root dry matter and rootstock vigour for all the rootstocks examined as shown previously (Atkinson, 1980; Rogers, 1939); this was not the case when comparing shoot growth and rootstock vigour. The total shoot extension growth reflected the rootstocks' known vigour potential, despite the fact that shoot development was restricted to four shoots per rootstock. The existence of a relationship between shoot dry matter production on non-grafted rootstocks and rootstock effects on scion vigour is important because it indicates that the vigour of the rootstocks own shoots was similar to that expected from a scion shoot grafted onto the same rootstocks. The results, particularly those from MM111, also show that rootstock effects

on scion vigour cannot be attributed to root volume at least in the growth period immediately following establishment, even though this may have an indirect influence and interaction in drought conditions. This ability to control the aerial growth of the unworked rootstock is encouraging because it supports the usefulness of this experimental approach in determining drought tolerance of unworked rootstock.

#### *The mechanisms by which rootstocks influence scion growth*

The amount of root system a rootstock produces and its ability to supply the shoot with water has also been implicated in the development of a mechanistic understanding of how the shoot is dwarfed (Tubbs, 1973). Differences in root length have been suggested to be associated in some way with how a rootstock controls a scion's vegetative vigour (Atkinson, 1980; Atkinson et al., 1990; Rogers, 1939). It is unclear, however, if this is an influence of root length or perhaps an increase in the number of active root tips that determine scion vigour; the latter being more apparent with vigorous rootstocks (Atkinson, 1980; Fernandez et al., 1995; Rogers, 1939). The growth of apple shoots can be reduced by restricting the rooting volume and this occurs in the absence of any measurable leaf water deficit, but total root length per tree declines (Atkinson et al., 1997; Webster, unpublished).

Significant differences in root length were measured between some of the rootstocks in these experiments. The very dwarfing rootstock clones, M27, AR69-7 and AR360-19 all had similar total lengths of coarse root and fine root. However, not all the rootstocks showed a linear relationship between the quantities of roots produced (coarse, fine or total root) and their potential to control scion vigour (Atkinson, 1980). The rootstock AR295-6, for example, had approximately the scion vigour potential of M9 as a rootstock (Webster et al., 1997), but produced considerably more root (coarse and fine) than either M26 or MM111, which are two rootstocks of significantly greater vigour potential. Lack of correlation between the root growth of some rootstocks and their ability to dwarf a grafted scion has been noted in much longer-term field trials (Atkinson et al., 1990). Under some conditions, such as in unirrigated field trials, the full scion vigour potential of some rootstocks may not be expressed as a result of transient water deficits as is possible in the orchard trials described by Webster et al. (1997).

An absence of a simple positive relationship between root dry matter production and vigour is clearly evident, in these experiments, particularly with the very invigorating rootstock MM111. Root dry matter production in this experiment may reflect the initial root production rate after planting rather than the longer-term potential. Initial root production rate in MM111 is known to be slow (Howard, pers. comm.). The roots and shoots of vigorous rootstocks, however, have a longer growing season (Kamboj et al., 1997; Rogers, 1939). Nevertheless, despite this limited production of root, MM111 showed the largest amount of shoot growth over the six-month period. The measurements of shoot growth support the observations from rootstocks of different vigour; MM111 being the most invigorating dwarfing rootstock examined here (Ferree and Carlson, 1987; Higgs and Jones, 1990).

Tolerance to drought can often be overcome or avoided if a plant or rootstock has a large root system (see Higgs and Jones, 1990). This is likely to equate with an increase in the hydraulic conductance of the root system and the associated changes in water transport, mineral uptake and physiological potential as rootstock vigour increases. Tolerance to drought with apple can be achieved by using more vigorous rootstocks; however, during periods of favourable soil water status, control of scion growth would be lost using this strategy. Here, two of the extremely dwarfing and one of dwarfing rootstocks, i.e. AR628-3, AR295-6 and AR486-1, produced considerably more root mass than evident with more vigorous rootstocks, particularly M26. Some of these AR rootstocks appear to offer an opportunity to control scion vigour 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. One of the parents of Ottawa 3 was the ornamental crab apple 'Robin', which was bred for the harsh climate of the Canadian prairies and is known to show good root anchorage itself being obtained from a cross with a wild crab-apple (*Malus baccata*) which has similar attributes (Saunders, 1911). The possible parental influence of crab apple and its nature warrants further investigation.

### Acknowledgements

The Ministry of Agriculture, Fisheries and Food funded this research. We thank L Taylor for technical assistance, G Kingswell for the statistical advice and

analysis and Drs D I Dunstan and N A Hipps for their comments on an earlier version of this manuscript.

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*Section editor: H Lambers*