# Comparison of growth potentials of epicormic shoots of nectarine trees grown on size-controlling and vigorous rootstocks

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SUMMARY

The vegetative performance of four nectarine tree scion/rootstock combinations, with varying growth capacities, were analysed in the Spring after the canopy:root ratio was dramatically reduced by severe pruning in the dormant season. We anticipated that severe pruning and reduction of the shoot:root ratio would mitigate known root water supply limitations related to the various rootstocks and determine if other factors associated with the rootstocks would control the rates of epicormic shoot growth. The trees used in this field experiment were 3 years-old, with 'May Fire' nectarine grafted onto four different rootstocks: 'Nemaguard' (a vigorous seed-propagated control, *P. persica* × *P. davidiana* hybrid) and three size-controlling rootstocks, 'K146-43', 'P30-135' (*P. salicina* × *P. persica* hybrids) and 'K-119-50' (*P. salicina* × *P. dulcis* hybrid). At the beginning of the trial, there were clear differences in plant dimensions, confirming the higher vigour induced by 'Nemaguard' compared to the other rootstocks. Reducing the canopy:root ratio was able to annul potential differences in weekly shoot-extension growth rates and cumulative extension growth of individual shoots during the Spring flush of re-growth after pruning. This supported the idea that there were no rootstock-specific signals (hormonal or physical) that caused large differences in extension growth rates of individual epicormic shoots on trees. However, there were clear differences in total epicormic shoot re-growth per tree that were associated with initial tree size at the time of severe pruning, indicating the importance of trunk and root storage in influencing the amount of growth stimulation after dormant pruning.

Differences in peach scion growth have been documented for a series of hybrid rootstocks compared to growth on the vigorous standard rootstock, 'Nemaguard'. Furthermore, it has been shown that the major growth differences between trees on different rootstocks occur during the Spring flush of shoots (Weibel *et al.*, 2003), and that differences in shoot growth can be particularly pronounced among epicormic shoots following normal dormant pruning (Basile *et al.*, 2003). It has been suggested that the size-controlling mechanism in dwarfing apple rootstocks is related to differences in hormone production by the roots (Lockard *et al.*, 1982; Soumelidou *et al.*, 1994; Kamboj *et al.*, 1999), or to differences in plant water relations potentially related to root hydraulic conductance (Olien an Lakso, 1986; Cohen and Naor, 2002). Previous data from our laboratory suggested that water relations and hydraulic conductance could be factors involved in size-control in recently developed peach rootstocks, but hormonal factors have not been ruled out (Basile *et al.*, 2003).

The hydraulic conductance concept depends on a dynamic balance between water demand by the shoot and the ability of roots to supply water at a rate sufficient to maintain a high enough water potential to drive shoot growth (Berman and DeJong, 1997). Basile *et al.* (2003) documented that there were differences in the diurnal patterns of stem water potential between vigorous and size-controlling rootstocks and that these differences correlated with shoot growth rates of the scion. Trees on

the more size-controlling rootstocks experienced more negative minimum water potentials and a greater daily period of water stress, relative to trees on the more vigorous rootstock, when all trees received the same amount of irrigation.

Although previous research has linked plant water relations to the physiology of size-controlling rootstocks, it does not rule out the involvement of other mechanisms. Thus we wanted to study the Spring shoot growth of trees on a range of size-controlling rootstocks under conditions in which it was unlikely that potential differences in the dynamics of tree water potential and root hydraulic conductance would play much of a role. We hypothesised that if the equilibrium between the shoot and the root was substantially perturbed by drastically increasing the root:shoot ratio, then shoot growth would not be limited by water relations. If major differences in individual shoot growth rates occurred between trees on the various rootstocks under these circumstances, then other rootstock-based mechanisms (such as hormonal signals) would be implicated in mediating the differences in growth associated with the various rootstocks. On the other hand, if there were no major differences in individual shoot growth between trees on the different rootstocks in response to dramatic increases in the root:shoot ratio, qualitative differences in hormone production by the various rootstocks could at least be ruled out.

To increase the root:shoot ratio substantially, all major scaffold branches were pruned to 1 – 1.5 m above the ground just prior to bud break in the Spring. Since roots

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are known to store carbohydrates that support growth of the scion during the Spring (Oliveira and Priestley, 1988), it was anticipated that such a drastic reduction in the scion relative to the root would stimulate epicormic shoot growth in proportion to the imbalance created between the root and shoot, and that epicormic shoot length growth was likely to be related to the number of growing shoots per tree. Thus two experimental treatments were imposed. One in which the number of shoots growing per tree was not controlled, and another in which the number of growing shoots was thinned to less than 50% of the number that initially sprouted. The specific objectives of the experiment were to determine if the growth rates of the new epicormic shoots, produced on severely pruned trees, would differ between rootstocks and, secondly, to determine how the number of shoots growing per tree would influence shoot growth among the different rootstocks.

## MATERIALS AND METHODS

The experiment was conducted at the University of California, Department of Pomology Experimental Orchard in Davis, in 2003. The work was done with nectarine trees [*Prunus persica* (L.) Batsch], cultivar 'May Fire', grafted on four different rootstocks (12 trees per rootstock): 'Nemaguard' (a vigorous seed-propagated control, *P. persica* × *P. davidiana* hybrid) and three size-controlling rootstocks, 'K146-43', 'P30-135' (*P. salicina* × *P. persica* hybrids) and 'K-119-50' a (*P. salicina* × *P. dulci*s hybrid). Previous research had shown that 'P30-135' and 'K119-50' produced trees that were generally 10–20% smaller than trees on 'Nemaguard', whereas trees on 'K146-43' were about 40-50% smaller than standard trees (Weibel *et al*., 2003).

Trees had been planted in 2000 in an orchard with twelve, four-tree sub-plots (each containing one each of the four rootstocks) in two rows with border trees on the ends of the rows and in adjacent rows. The trees were at the start of their fourth year in the orchard when the experiment was initiated, and had not been pruned since being transplanted from the nursery after the first year. The orchard was irrigated with micro-sprinklers (12 h continuously) 1 d before weekly measurements during May, June and July.

At the end of February, all the minor branches on each tree were removed and all major scaffolds were cut to a height of 1 – 1.5 m above ground level.

At the beginning of March, the trunk circumference of each tree was measured 10 cm from the graft union, and the trunk cross-sectional area (TCSA) was calculated. On 8 April, shoots of six trees per rootstock were thinned. The tree with the smallest TCSA was thinned to a total of six remaining shoots. All other shoot-thinned trees were thinned to the number of shoots proportional to the effective ratio of shoots:TCSA of the first tree.

*Shoot extension growth measurements*

On 12 April, four shoots per plant were chosen for weekly extension-growth measurement and, subsequently, 13 growth measurements were made (on days of the year: 102, 111, 118, 125, 132, 139, 148, 155, 162, 168, 177, 182 and 190). The total length and number of nodes on each shoot were measured on each date.

Diurnal patterns of relative extension growth rate (RER) were determined on two shoots per tree on nine dates (on days of the year: 125, 132, 139, 148, 155, 162, 168, 177 and 182). In the evening before each measurement day, two fine ink marks were made on each shoot: the first on the first visible node and the second on the fifth node. The distance between the two marks was measured using a digital camera (Nikon Model E 995; Nikon Inc., Melville, NY, USA). Two pictures per shoot, of the marked zone only, were taken at a 24 h interval. The distance between the camera objective and each shoot was constant by holding the shoot against a brace attached to the camera.

Stem growth was evaluated as relative extension growth rate (RER) computed as follows:

$$RER = (Lh - Lk)/t \times Lk$$

where $Lh$ is the distance (in mm) between the ink marks measured at time of day $h$, $Lk$ is the distance (mm) between the same ink marks at the previous measurement time of day ($k$), and $t$ is the time between the two measurements.

Four shoots per rootstock were collected each week throughout the growing season. Shoot dry mass (fresh shoots were weighed and oven-dried at 65°C to constant mass) and shoot length were determined to obtain the seasonal pattern of shoot weight increase per shoot-length for each rootstock.

*Plant water status and temperature measurements*

Stem water potential measurements were made according to McCutchan and Shackel (1992) on the same nine dates and at the same time of day as the stem extension growth measurements above. One day before each measurement, two shaded mature leaves per tree were covered with plastic bags coated with aluminium foil, in order to allow the leaf water potential to equilibrate with the stem water potential. On each date, two stem water potential measurements were taken: one just before dawn (pre-dawn stem water potential) and a second around solar noon (midday stem water potential). Stem water potential was measured with a pressure chamber (Soil Moisture Equipment, Santa Barbara, CA, USA).

Air temperatures were obtained from a CIMIS (California Irrigation Management Information System) weather station located within 0.8 km of the experimental site.

*Quantification of vegetative growth*

At the end of the Spring growth season (18 July), two representative shoots were collected from each tree. The total length and number of nodes were determined, and each shoot was then sub-divided into primary and secondary shoots and leaves. Each shoot component was oven-dried at 65°C to constant mass and weighed to determine the percentage dry weight (DW) of each component.

On 23 July, all the remaining shoots on the trees in the experiment were harvested. The total number of shoots per tree and the total shoot fresh mass per plant were determined (by counting and weighing directly in the field). The total DW of shoots was calculated by

determining the fresh weight (FW) of sub-samples (approx. 30% of total FW) oven-dried at 65°C to constant mass, and weighed again in order to determine the DW:FW ratio.

Statistical analyses of the data used SAS statistical software (SAS Institute Inc., Cary, NC, USA). Analysis of variance (ANOVA) was used to test rootstock- and shoot-thinning effects on shoot growth and stem water potential data. Means separation between rootstocks was carried out at the $P = 0.05$ level of significance by the Tukey pair-wise comparison test.

RESULTS

There were no significant differences in cumulative seasonal shoot extension, weekly shoot extension growth rates, or daily RER between tress grafted on any of the four rootstocks (except on the last measurement day, when trees grafted on 'P30-135' had higher RER than trees on 'K119-50' and 'K146- 43'; Figure 1). During the growing season, weekly shoot extension growth rates and daily RER peaked around day-148 and day-177. These peaks were associated with seasonal patterns in air temperature (Figure 1D).

On days 132, 139, 148, 155, 162 and 182 pre-dawn stem water potentials measured on trees grafted on 'K146-43' were significantly lower (Figure 2A) than those of trees grafted on the other rootstocks.

During all stem water potential measurement days, the midday stem water potentials (Figure 2B) of trees on
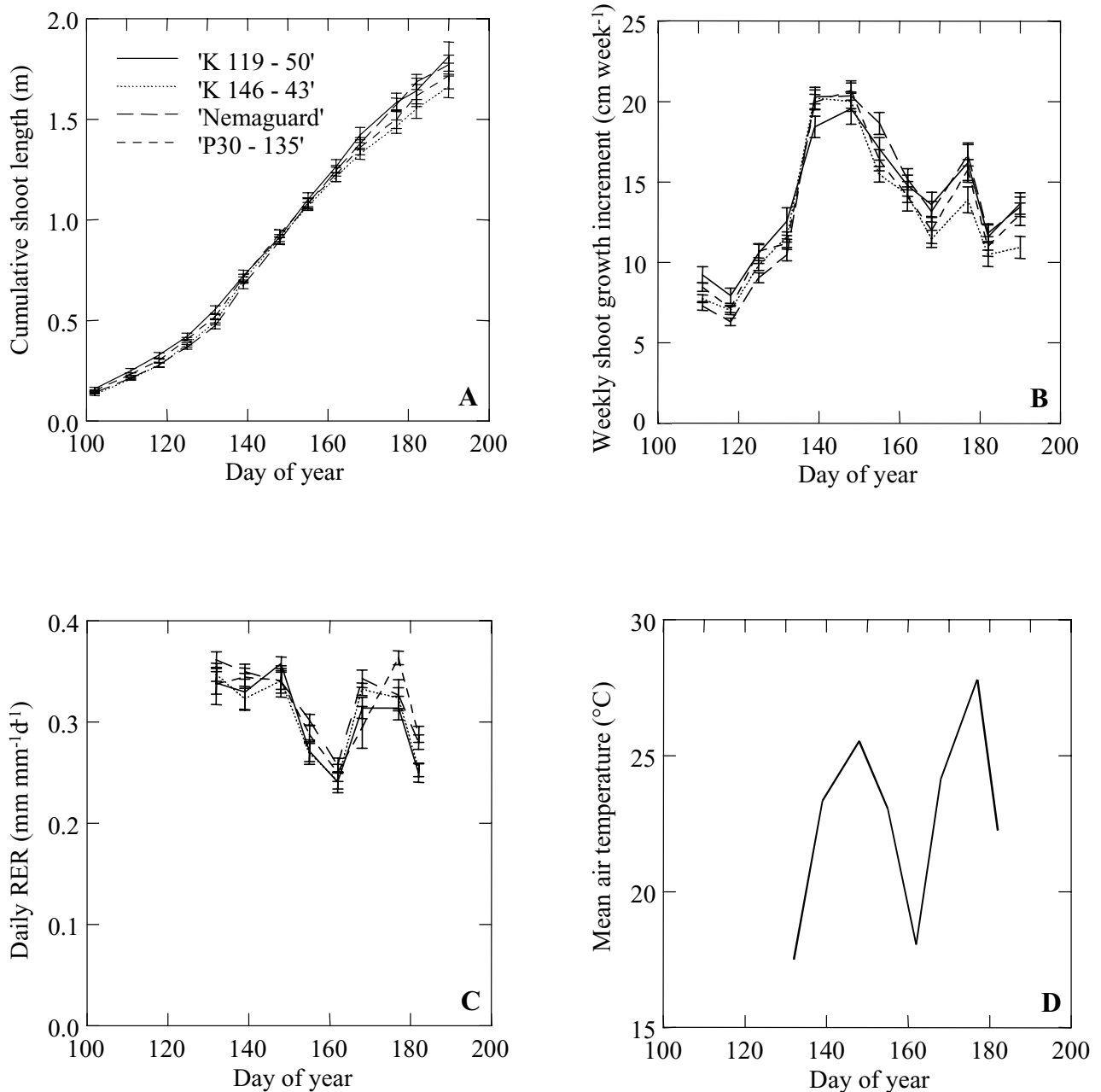


Fig. 1
Seasonal patterns of: Panel A, cumulative shoot extension growth; Panel B, weekly shoot extension increment; Panel C, daily relative extension growth rates for stems of nectarine trees on 'K119-50', 'K146- 43', 'Nemaguard' or 'P30-135' rootstocks. Bars indicate standard error of the mean. Panel D indicates the seasonal pattern of mean air temperature over the period of study.
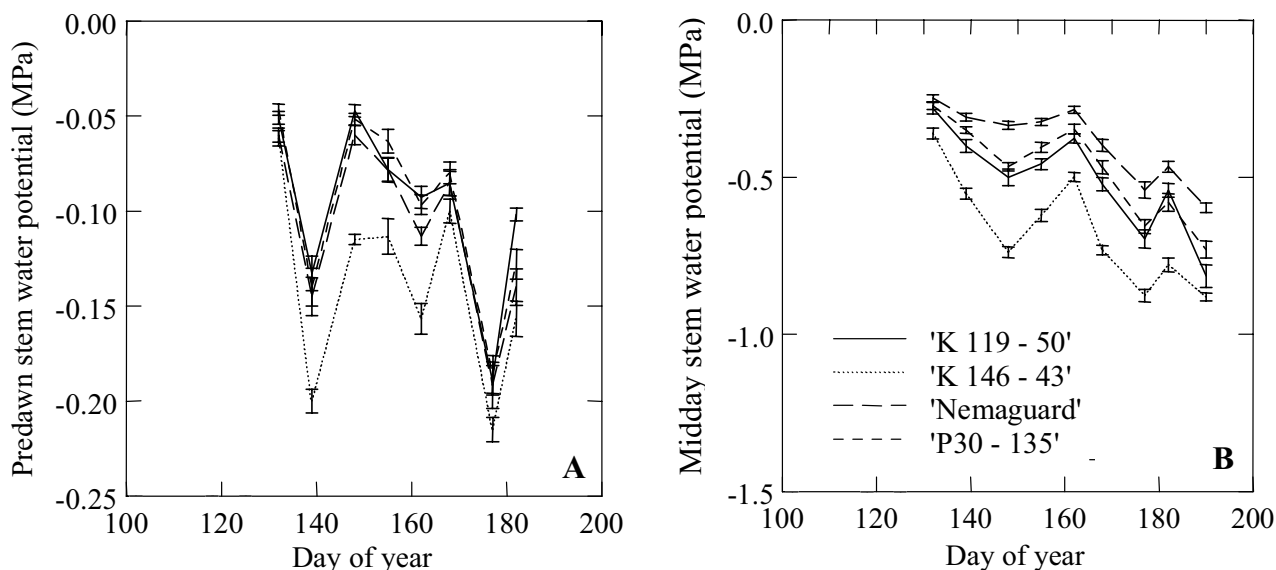
'K146-43', were significantly lower than those on 'Nemaguard', 'P119-50' and 'P30-135'. On days 148, 155, 162, 168, 177 and 190, the midday stem water potentials (Figure 2B) of trees on 'K119-50' and 'P30-135' were significantly lower than those on 'Nemaguard'. Moreover on day-139, the midday stem water potential of trees on 'K119-50' and, on day-182, of trees on 'P30-135' (Figure 2B) were significantly lower than those on 'Nemaguard'.

There were no significant differences in pre-dawn and midday stem water potentials between shoot-thinned and non-thinned trees, or significant interactions (ANOVA) between rootstock and shoot thinning treatment.

There were no significant differences in shoot length, number of nodes, internode length, total shoot DW, or the percentage of primary shoots or leaves to total shoot DW (Table I) based on two shoots collected per plant on 18 July between trees on different rootstocks. However, the percentage of shoot DW invested in secondary shoots was greater on 'Nemaguard' than on two of the other rootstocks for thinned trees (Table I).

There were clear differences in plant size at the time of initial treatment, as indicated by TCSA. The TCSAs of trees on 'Nemaguard' were significantly larger than on all other rootstocks (Table II).

Destructive measurements in July indicated significant differences in the numbers of shoots between trees on 'Nemaguard' and on the other rootstocks (Table II). Total canopy DWs were also significantly greater for trees on 'Nemaguard' than for the other trees. Rootstock did not significantly influence average shoot DWs (except between thinned trees on 'Nemaguard' and thinned trees on 'K146-43'), but there was a trend toward shoots on shoot-thinned 'Nemaguard' trees being smaller than those on the size-controlling rootstocks, presumably because of the higher number of shoots per tree.

Regression analyses indicated clear relationships

between TCSA and the number of shoots per tree across all rootstocks, within each shoot-thinning treatment (Figure 3). However, there was no clear shoot-thinning effect on the relationship between total shoot DW and TCSA, as data from all four rootstocks appeared to fit the same curve (Figure 4).

The mean number of nodes was greater (i.e., the effect of thinning on the number of nodes was significant; Table
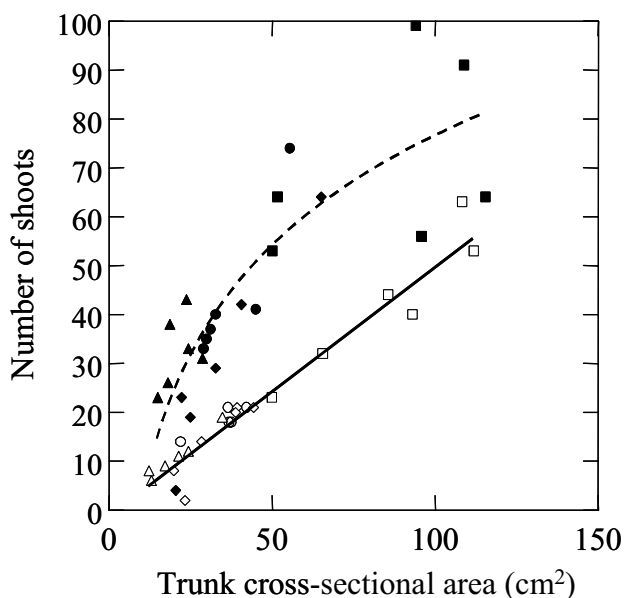
TABLE I

*Mean shoot length, number of nodes, internode length, average shoot dry weight (DW), percentage of primary shoot DW to total shoot DW, percentage of secondary shoot DW to total shoot DW, and percentage of leaf DW to total shoot DW for trees on 'Nemaguard', 'K 119-50', 'P30-135' or 'K 146-43' rootstocks as a function of thinning treatment*

| Rootstock | Length (m) | | Number of nodes | | Internode length (cm) | | Total shoot dry weight (kg) | | Percentage of primary shoots to total shoot DW | | Percentage of seconday shoots to total shoot DW | | Percentage of leaves to total shoot DW | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Non-thinned | Thinned | Non-thinned | Thinned | Non-thinned | Thinned | Non-thinned | Thinned | Non-thinned | Thinned | Non-thinned | Thinned | Non-thinned | Thinned |
| 'Nemaguard' | 2.07 | 2.00 | 72.9 | 75.2 | 2.90 | 2.70 | 0.29 | 0.37 | 37.6 | 30.8 | 18.8 a | 24.7 a | 43.6 | 44.5 |
| 'K119-50' | 2.08 | 1.99 | 71.0 | 74.8 | 2.90 | 2.70 | 0.26 | 0.31 | 38.4 | 34.2 | 18.4 a | 19.8 b | 44.6 | 46.0 |
| 'P30-135' | 1.98 | 2.04 | 72.0 | 75.0 | 2.80 | 2.70 | 0.31 | 0.30 | 34.5 | 36.0 | 20.0 a | 19.1 b | 45.4 | 44.9 |
| 'K146-43' | 1.91 | 1.93 | 70.6 | 74.5 | 2.70 | 2.60 | 0.24 | 0.31 | 36.8 | 31.4 | 17.1 a | 20.9 ab | 46.1 | 47.7 |
| Rootstock | ns | | ns | | ns | | ns | | ns | | (*) | | ns | |
| Thinning | ns | | (*) | | (**) | | ns | | (**) | | (**) | | ns. | |
| Rootstock × Thinning | ns. | | ns | | ns | | ns | | ns | | (*) | | ns | |

Data were obtained from two of the longest shoots per plant.
The last three lines of each panel indicate the statistical significance of the effects of rootstock, thinning and rootstock × thinning.
Means followed by a different letter within a column indicate significant differences (Tukey's HSD, $P = 0.05$).
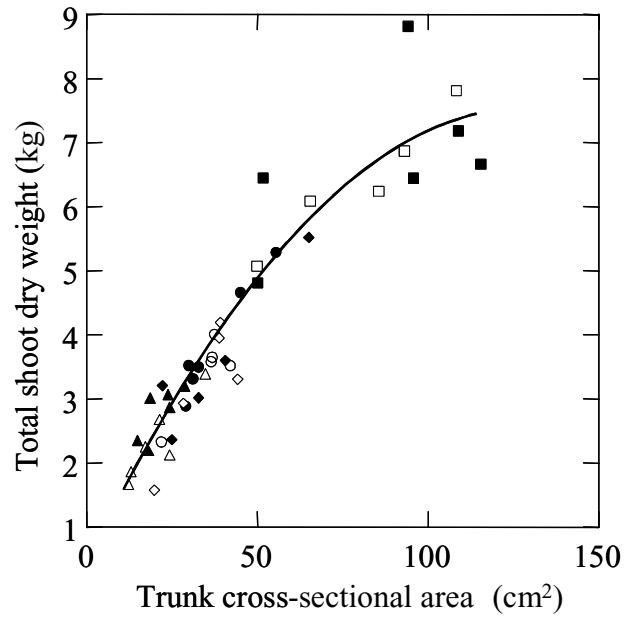ns, *, **: not significant or significant at $P = 0.05$ or 0.01, respectively.



FIG. 4
Relationship between total shoot dry weight (DW) and TCSA for trees on 'K119-50', 'K146-43', 'Nemaguard' or 'P30-135' rootstocks as a function of shoot-thinning treatment. ○ thinned plants grafted on 'K119-50'; ● non-thinned plants grafted on 'K119-50'; △ thinned plants grafted on 'K146-43'; ▲ non-thinned plants grafted on 'K146-43'; □ thinned plants grafted on 'Nemaguard'; ■ non-thinned plants grafted on 'Nemaguard'; ◇ thinned plants grafted on 'P30-135'; ◆ non-thinned plants grafted on 'P30-135'. The regression curve equation is $y = -0.0004\,x^2 + 0.11\,x + 0.38$, $r^2 = 0.92$.

I), but the internode length of shoots from shoot-thinned trees was less (i.e., the effect of thinning on internode length was significant; Table I) than from non-shoot-thinned trees, resulting in equivalent shoot lengths at the end of the growth period. This result is probably related to differences in shoot density and intra-canopy light exposure. The main axis (primary shoot) of shoots sampled from non-shoot-thinned trees had a higher percentage shoot DW than in thinned trees, whereas the opposite was true for the secondary shoots (Table I). Thus, secondary shoot growth appeared to respond to the less dense canopy in shoot-thinned trees.

At the end of the experiment, all shoots were harvested. The number of shoots in the non-shoot-thinned plants was approx. twice that in shoot-thinned trees for a given rootstock (Table II). Mean shoot DW per tree, obtained by weighing all shoots in the canopy, indicated that individual shoot weights from shoot-thinned trees were approx. double those of individual shoot weights from non-thinned plants (Table II). Thus, there was a strong "compensation" between number of shoots per plant and average shoot DW per shoot (Figure 4). This resulted in similar values for total shoot DW per TCSA between shoot-thinned and non-shoot-thinned trees on each rootstock.

There were clear relationships between seasonal mean midday stem water potential and TCSA (Figure 5), and canopy shoot DW (Figure 6) that appeared to be related to the characteristics of each rootstock. Trees that maintained the least negative stem water potentials tended to be the largest, and sustained most shoot growth.
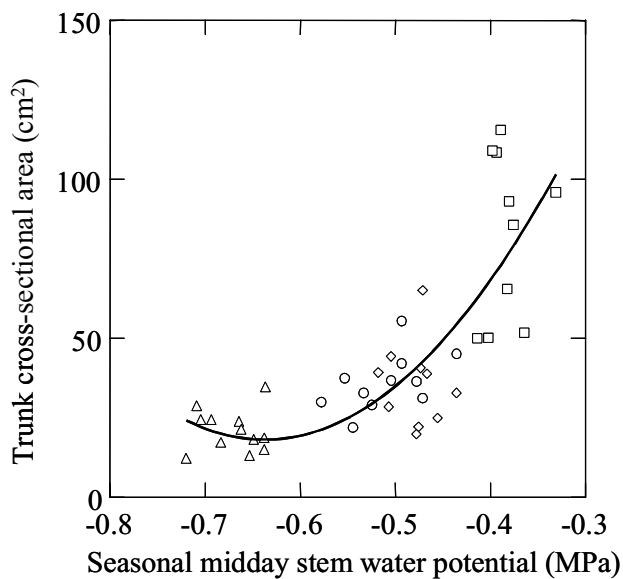
FIG. 5
Relationship between TCSA and seasonal mean midday stem water potential for nectarine trees on 'K119-50', 'K146-43', 'Nemaguard' or 'P30-135' rootstocks. ○ plants grafted on 'K119-50'; △ plants grafted on 'K 146-43'; □ plants grafted on Nemaguard; ◇ plants grafted on 'P30-135'. The regression curve equation is $y = 890.37\,x^2 + 1134.9\,x + 380.83$; $r^2 = 0.66$.
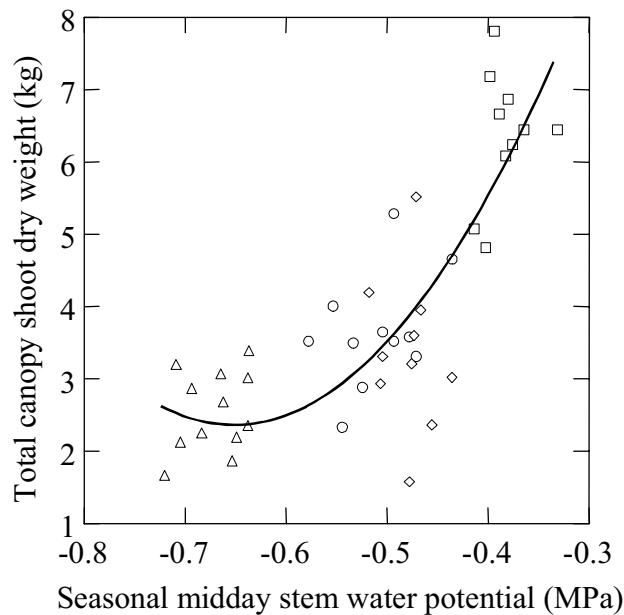


FIG. 6
Relationship between total canopy shoot dry weight and seasonal mean midday stem water potential for trees on 'K 119-50', 'K 146-43', 'Nemaguard' or 'P 30-135' rootstocks. ○ plants grafted on 'K119-50'; △ plants grafted on 'K146-43'; □ plants grafted on 'Nemaguard'; ◇ plants grafted on 'P30-135'. The regression curve equation is $y = 50.18x^2 + 64.99\,x + 23.51$; $r^2 = 0.68$.

## DISCUSSION

At the beginning of this experiment, there were clear differences in plant dimensions. Trees grafted on 'Nemaguard' rootstock were larger (Table II) than on the other rootstocks. The purpose of the severe pruning and shoot-thinning treatments was to increase the root:shoot ratio substantially, in order to reduce or eliminate limitations in root water supply related to the rootstocks. This assumed that differences in stem water potentials reported in previous studies were related to the ability of the roots to supply the transpirational demands of the shoots (Basile *et al.*, 2003). At the end of the experiment (9 July), the rootstocks had not caused significant differences in cumulative extension growth, weekly shoot extension growth or daily RER of individually tagged shoots. Furthermore, rootstock effects on the relationship between number of shoots (Figure 3) and shoot canopy DW (Figure 4) per unit TCSA appeared consistent among rootstocks, indicating that the total amount of re-growth was primarily a function of initial tree-size across all rootstocks. Thus,

these data appear to contradict the hypothesis that rootstock-specific signals control extension growth rates of individual epicormic shoots on trees growing on size-controlling nectarine rootstocks, as has often been proposed to explain the dwarfing phenomenon (Simons, 1987).

However, contrary to expectations, even under circumstances in which the size of the scion was severely reduced compared to the root, significant differences in pre-dawn and midday stem water potentials were observed between trees on the various rootstocks. The magnitude of the differences in midday stem water potential between trees on 'Nemaguard' and 'K146-43' were similar to the differences reported for the same rootstocks by Basile *et al.* (2003). However, these differences do not appear to have had the same influence on the extension growth rate of the rapidly growing shoots selected, or on the mean length of all shoots on a rootstock, as reported by Basile *et al.* (2003). Differences in the results from this study,

TABLE II
*Mean trunk cross-sectional area (TCSA), number of shoots, canopy dry weight (DW) and average shoot DW per shoot for trees on 'Nemaguard', 'K 119-50', 'P 30-135' or 'K 146-43' rootstock as a function of thinning treatment*

| Rootstock | TCSA (cm$^2$) | | Number of shoots | | Total shoot weight (kg) | | Average DW per shoot (kg) | |
|---|---|---|---|---|---|---|---|---|
| | Non-thinned | Thinned | Non-thinned | Thinned | Non-thinned | Thinned | Non-thinned | Thinned |
| 'Nemaguard' | 86.0 a | 85.7 a | 71.2 a | 42.5 a | 6.73 a | 6.41 a | 0.10 a | 0.17 a |
| 'K119-50' | 37.2 b | 34.9 b | 43.3 b | 18.4 b | 3.86 b | 3.42 b | 0.09 a | 0.19 ab |
| 'P30-135' | 34.3 b | 32.3 b | 30.2 b | 14.3 b | 3.54 b | 3.19 b | 0.11 a | 0.19 ab |
| 'K146-43' | 21.4 b | 20.5 b | 32.3 b | 10.8 b | 2.78 b | 2.33 b | 0.09 a | 0.23 b |
| Rootstock | (**) | | (**) | | (**) | | ns | |
| Thinning | ns | | (**) | | ns | | (**) | |
| Rootstock × Thinning | ns | | ns | | ns | | (*) | |

Data were obtained from the whole canopy harvest.
The last three lines indicate the significance of the effects of rootstock, thinning and rootstock × thinning.
Means followed by a different letter within a column are significantly different (Tukey's HSD, $P = 0.05$).
ns., *, **: not significant or significant at $P = 0.05$ or $0.01$, respectively.

compared to Basile *et al*. (2003) are hard to reconcile, but it should be noted that the relative severity of dormant pruning differed dramatically between the two studies. The severity of pruning between trees on different rootstocks in the previous study also varied more than in our study. The average biomass routinely pruned-off the trees on 'Nemaguard' rootstock in the dormant season was approx. four-to-five times more than from trees on the smallest 'K146-43' rootstock (DeJong *et al*., 2004). Mean midday stem water potentials in the present study were clearly related to TCSA and total canopy shoot DW growth of trees on the various rootstocks (Figures 5 and 6) in a manner similar to the previous study. Since differences in stem water potential were correlated with the initial size of the trees, and total canopy shoot growth also correlated with the size of the tree (Figure 4), it is not possible to separate the effects of rootstock-related differences in initial tree size and stem water potential on total canopy shoot-growth responses. However, as no apparent differences in shoot extension growth rates were caused by differences in stem water potential in this study, it seems likely that initial tree-size was the most important factor that influenced canopy growth in these experiments. Thus it appears that the potential availability of storage reserves to support the growth of new epicormic shoots may have been the primary factor that determined both the number of new shoots initiated and the growth rate of those shoots. Somehow, the initial imbalance in root:shoot ratio, caused by severe pruning, appears to have over-ridden any influence of stem water potential on shoot extension growth as was found in other studies (Basile *et al*., 2003; Solari *et al*., 2006).

It is interesting that the pre-dawn stem water potential values of the trees on 'K146-43' rootstock were generally lower than for trees on the other rootstocks (Figure 2); but were generally higher than for trees on 'Nemaguard' in the previous study (Basile *et al*., 2003). It is difficult to explain why the pre-dawn water potential should be different between rootstocks, especially if the response varies with site. The soils differed significantly between the sites of these experiments. The previous experiment was conducted in a fine sandy loam soil, while the current work was in a heavier clay loam soil. Perhaps the root hydraulic characteristics of specific rootstocks vary with soil properties, which could explain some of the variation in rootstock performance reported in comparative studies (Reighard *et al*., 2004)

In this study, the total growth in shoot biomass of trees correlated quite strongly with TCSA across all rootstocks, regardless of shoot-thinning treatment (Figure 4). This result is surprising as shoot-thinned trees had fewer than 50% as many shoots per TCSA as non-shoot-thinned trees, and clearly demonstrates the high degree of plasticity of shoot growth responses in nectarine trees. It also indicates the importance of initial tree-size when studying vegetative growth responses related to size-controlling rootstocks or pruning treatments. Once differences in tree-size are established it is apparent that subsequent vegetative growth responses will be highly dependent on the size of the tree at the beginning of the growing season, and probably on the relative amount of biomass that was removed since the last season (dormant pruning). In the present experiment, virtually all the existing shoot biomass was removed before the new season, so what grew back was proportional to the TCSA of the remaining stump. Presumably, if only half the shoot biomass had been removed, less than half of the new shoot biomass would have been produced, and the new growth would have been a function of the initial size of the tree, the amount of canopy removed, and the proportion of the original canopy that remained. This highlights the importance of size-controlling rootstocks for decreasing overall tree-size in an orchard (Simons, 1987) and why this objective cannot be achieved solely by pruning. The larger the initial tree-size, the greater the amount of biomass that must be removed to achieve a given, limited tree-size and the greater the strength of the re-growth (Mika, 1986). Thus, if trees are substantially more vigorous and larger than desired for optimal management conditions, tree-size reduction by dormant pruning will lead to an inefficient cycle of heavy pruning and strong re-growth.

Clearly, much needs to be learned about the growth controlling mechanism involved in the size-controlling rootstocks studied in this report. However, it seems clear that the differential growth responses of trees on the various rootstocks were not attributable to hormonal signals transported from the roots that control the potential growth rate of individual shoots of the scion. Other research has indicated that the growth rate of individual shoots growing on different rootstocks can be related to differences in tree water-relations associated with the specific rootstock; but growth responses to differences in tree water-relations can apparently be masked by imposing major alterations in the shoot:root ratio through severe dormant pruning. The results of this study emphasise the complexities in the scion:rootstock relationship of fruit trees and emphasise the importance of considering relative scion-rootstock equilibria when studying scion-rootstock interactions involving dwarfing rootstocks.

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