Weaver, R.J. and S.B. McCune. 1960. Effects of overcropping Ali-
Weaver, R.J. and R.M. Pool. 1986. Effect of various levels of crop-
ning on Vitis vinifera grapevines. Amer. J. Enol. Viticult. 19:185-
193.
Winkler, A.J. 1931. Pruning and thinning experiments with grapes.

---

WATER DEFICITS AND ROOTING VOLUME MODIFY PEACH TREE GROWTH AND WATER RELATIONS

E.L. Proebsting
Washington State University Irrigated Agriculture Research and Extension Center, Prosser, WA 99350

P.H. Jerie and J. Irvine
Institute for Irrigation and Salinity Research, Tatura, Victoria 3616, Australia

Additional index words. Prunus persica, leaf conductance, leaf water potential, flowering

Abstract. To compare the effects of water deficits and restricted root volume, 1- and 2-year-old peach trees (Prunus persica L.) with roots divided among four 2.5-liter pots were irrigated daily with 30% (deficit irrigation) or 100% (non-deficit) replacement of water used the day before. The water was applied to one, two, or all four pots during the period of rapid terminal growth. After 7 weeks, all trees received 100% replacement of water used the previous day. After terminal growth ended, the root : shoot ratio of the 2-year-old trees was adjusted by 1) tripling available soil volume, 2) removing two-thirds of lateral branches, 3) both 1 and 2, 4) treatment 3 defoliated, or 5) left unchanged. Deficit irrigation reduced midday leaf water potential, leaf conductance, and terminal growth equally, regardless of root volume, whereas in non-deficit irrigated trees these factors were proportional to the irrigated soil volume. After deficit irrigation ended, terminal growth resumed at rates above those of the trees with non-deficit irrigation and applied to all four pots and proportional to the severity of growth reduction during deficit irrigation. Pruning and defoliation increased leaf conductance within 3 days. Increased soil volume increased leaf conductance after 4 weeks. Deficit irrigation nearly eliminated flowering for the following year. Tripling the soil volume overcame the effect of deficit irrigation on flowering, but pruning did not. Defoliation inhibited flowering. The effect of restricted irrigated soil volume was similar to that of deficit irrigation. Increasing root : shoot ratios by adjusting the soil volume or by pruning the shoot always increased leaf conductance.

Successful fruit growing requires maximum partitioning of photosynthates to fruit yield, size, and quality, while maintaining sufficient vegetative and root growth to support the plant. Ideal partitioning would minimize photosynthates allocated to wood and fruit that is removed by pruning and thinning. Fruit trees are managed toward these goals by cultivar and rootstock selection, planting density, irrigation, soil management, mineral nutrition, pruning, and thinning. The widespread adoption of irrigation systems capable of applying precise amounts of daily water to small or large portions of the soil surface makes it possible to add manipulating plant water status to the list of management techniques for controlling partitioning of photosynthates (Peretz et al., 1986).

Regulated deficit irrigation (inducing plant water deficits by applying less water than the plant uses) can reduce excessive vegetative growth of peaches and pears without reducing fruit growth and yield (Chalmers et al., 1981 and 1986; Mitchell and Chalmers, 1982; Mitchell et al., 1984). Water applied from a single point (Chalmers et al., 1983; Mitchell and Chalmers, 1983; Turner, 1986). Stomata closed on wheat and sunflower leaves that were kept fully turgid by pressure applied to the roots as the soil dried (Gollen et al., 1986). Seedlings of Zea mays L. grown with roots divided between two containers, one of which was allowed to dry, closed their stomata even though $L$ turgo, and ABA content were unaffected (Blackman and Davies, 1985). Cytokinin reversed this closure. Thus, roots send signals to shoots via growth regulators and water fluxes that control carbon allocation to growth.

If roots in dry soil become inactive physiologically then effective root volume can be controlled by deficit irrigation at a single point (Chalmers et al., 1983; Mitchell and Chalmers, 1982). Vegetative growth was directly proportional to soil volume (Tan and Buttery, 1982), while fruiting was inversely proportional (Richards, 1986). It has been proposed that cytokinins from the root sustain the equilibrium by promoting shoot growth proportional to the number of active root tips (Richards and Rowe, 1977a).

Stomatal opening, which exerts significant control over photosynthesis as well as water use, may be regulated by leaf water potentials ($\Psi_L$) (Chalmers et al., 1983; Olsson and Milthorpe, 1983; Turner, 1986). Stomata closed on wheat and sunflower leaves that were kept fully turgid by pressure applied to the roots as the soil dried (Gollen et al., 1986). Seedlings of Zea mays L. grown with roots divided between two containers, one of which was allowed to dry, closed their stomata even though $L$ turgo, and ABA content were unaffected (Blackman and Davies, 1985). Cytokinin reversed this closure. Thus, roots send signals to shoots via growth regulators and water fluxes that control carbon allocation to growth.

Received for publication 11 Apr. 1988. H/LA Paper no. 88-8. Project no. 0918. College of Agriculture and Home Economics Research Center, Washington State Univ., Pullman, WA 99164. Work was supported by a grant from the Reserve Bank of Australia, Rural Credits Development Fund. The cost of publishing this paper was defrayed in part by the payment of page charges. Under postal regulations, this paper therefore must be hereby marked advertisement solely to indicate this fact.
were six replicates. Such a practice, deficit irrigation from trickle emitters, offers the potential to exercise the physiological effects of both plant water deficits and restricted root volume at appropriate developmental stages. This experiment was designed to study separately and interactively the effects of altered root volume and regulated water deficits on plant water relations, terminal growth, and flowering of peach trees.

Materials and Methods

Peach trees were grown in a structure with a glass roof and wire mesh walls with their roots divided among four 2.5-liter pots. The soil was an equal mix of sand and peatmoss with water-holding capacity of 32% by weight, ~800 ml/pot. The trees were fertilized each week with a commercial soluble fertilizer mix at a rate that provided 750 mg N/week per tree. Pesticide sprays were applied as required.

The trees were irrigated with microtube emitters, four per tree, each delivering 25 ml/min. The emitters were calibrated periodically and checked frequently.

Because the root volume was small, relative to daily water volume used, soil moisture changed so rapidly that it had little significance in this experiment. Soil moisture values depended entirely on when they were measured.

Two-year-old trees. Nursery trees of an early ripening JIISR cling peach selection (B7 x OS) had been grown for 1 year in their four pots. These trees bore flowers that set some fruit, most of which dropped near the time of pit hardening. At the start of the 1986-87 growing season, these trees were 1.5 to 2 m tall with numerous side branches 20 to 40 cm long.

Thirty trees were assigned to six treatments with five replications. The replications were blocked by tree size. The experimental design was split plot. The main plots compared non-deficit irrigation (N) with deficit irrigation (D) during the 8 weeks from 23 Oct. to 12 Dec. The sub-plots compared effective root volume, achieved by putting all four emitters in one pot (N1 or D1), or dividing them, two each in two pots (N2 or D2), or one each in four pots (N4 or D4). After 13 Dec., all trees received non-deficit irrigation in four pots (N4) until 10 Feb., when terminal growth had essentially stopped.

Non-deficit trees were irrigated to replace water as it was used by the tree, as determined by weighing pots. Irrigation was in 4-min increments applied one to five times per day, depending on evaporative demand.

The D treatment was applied cautiously, beginning at 50% of the N treatment water use. Some daytime wilting was observed during the first 2 weeks of the D treatment. As daily pan evaporation rates increased, the D irrigation rate remained constant at 400 ml/day, which averaged 30% of N4 applications, maintaining the average soil moisture content slightly above permanent wilting.

One-year-old trees. The newly planted trees were allowed to establish root systems and ~30 cm of shoot growth on two shoots per tree before D treatments were started. The treatments were identical to those used for the second-year trees. There were six replicates.

Non-deficit irrigation was scheduled to prevent wilting and to minimize leaching. Deficit irrigation was applied in 100-ml increments at 1030, 1130, 1230, and 1330 hr. The sequence was not started until the shoots first wilted. For example, if the trees did not wilt until noon, two of the four irrigations were eliminated. The D trees received 40% of the water provided N

trees between 19 Nov. and 2 Dec., and 15% between 3 Dec. and 9 Jan.

At the end of the D irrigation period (9 Jan., treatments D1, D2, and D4 were irrigated on a N schedule, becoming the same as N1, N2, and N4.

Adjusted root : shoot ratios. The experiment using the 2-year-old trees was terminated on 10 Feb. The trees were used in a new experiment with five treatments and six replicates in a randomized block experiment. The previous treatments were used as blocks. Each of the five new treatments appeared among the trees that had received each of the original treatments.

The root : shoot ratio was allowed to readjust by 1) tripling the soil volume by removing the bottoms from the original four pots and placing them on 20 liters of the sand–peat mix, 2) reducing the foliage canopy to one-third by systematically removing two out of three lateral from the central leader, 3) treatment 1 plus treatment 2, 4) treatment 3 defoliated except for two to four leaves at the tip of the more vigorous shoots, and 5) maintaining non-pruned trees in the original 10 liters of soil divided among four pots.

Measurements. Terminal growth of two tagged shoots on each tree was measured each week. Evapotranspiration was measured each week on the 2-year-old trees by weighing before and after a 5-hr test period. Leaf conductance (gs) was measured every other day during the morning with an automatic porometer (Delta-T Devices MKII, Burwell, Cambridge, U.K.). Midday leaf water potential (ΨL) was measured each week with a Scholander pressure bomb. Osmotic potential (Ψs) was measured at the end of the deficit period by the psychrometric method on turgid leaves.

The amount of bloom per tree was rated in Sept. 1987 on a scale of 1 = very sparse to 5 = very abundant.

Each data set was analyzed by analysis of variance. Means were separated by LSD (0.05).

Results

During deficit irrigation. Deficit irrigation reduced leaf water potential (ΨL) (Table 1). Daily irrigation prevented extremely low ΨL from developing in the tree. In the 1-year-old trees, where wilting was allowed to start before the trees were irrigated, low ΨL (below −2.0 MPa) was relieved within 2 hr (−1.8 MPa after 1 hr, −1.4 MPa after 2 hr compared with −1.2 to −1.3 MPa for N trees). The leaves were turgid after 2 hr.

Reduced soil volume reduced ΨL in the N1 2-year-old trees, not in the 1-year-old trees. There was no effect of root volume on ΨL in the D trees.

Deficit irrigation lowered osmotic potential (Ψs) in the 1-year-old trees but not in the 2-year-old trees (Table 1). Irrigated soil volume did not affect Ψs.

Water deficit and reduced root volumes reduced gs in both 1- and 2-year-old trees (Table 1). Root volume affected gs only in the N treatments. In treatments N1, D1, D2 and D4 of the 2-year-old trees, gs approached zero.

Water use was reduced in proportion to gs (Table 1). The stomata of D 2-year-old trees closed enough to hold water use to values that conserved the 400 ml of water the trees were allowed each day. Reduced irrigated root volume also reduced water use.

Shoot growth was reduced by water deficit and by reduced root volume in both 1- and 2-year-old trees (Table 2). Reduced root volume reduced shoot growth in N trees but did not affect D trees during the deficit period.

When N was restored to all four pots of the 2-year-old trees,
Table 1. Water relations of 1- and 2-year-old peach trees during deficit irrigation from 19 Nov. to 9 Jan. and 23 Oct. to 12 Dec., respectively, and their interaction with soil volume.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Non-deficit (N)</th>
<th>Deficit (D)</th>
<th>LSD (0.05)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Irrigated soil volume (liters)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>One-year-old trees</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Midday leaf water potential (Ψ_L; MPa)</td>
<td>-0.9</td>
<td>-1.2</td>
<td>-1.4</td>
</tr>
<tr>
<td>Leaf osmotic potential, end of deficit period (Ψ_o; MPa)</td>
<td>-2.5</td>
<td>-3.4</td>
<td>-3.6</td>
</tr>
<tr>
<td>Leaf conductance (mmol·s⁻¹·m⁻²)</td>
<td>76</td>
<td>52</td>
<td>44</td>
</tr>
<tr>
<td>Two-year-old trees</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Midday leaf water potential (Ψ_L; MPa)</td>
<td>-1.0</td>
<td>-1.2</td>
<td>-1.3</td>
</tr>
<tr>
<td>Leaf osmotic potential, end of deficit period (Ψ_o; MPa)</td>
<td>-1.8</td>
<td>-2.6</td>
<td>-2.0</td>
</tr>
<tr>
<td>Leaf conductance (mmol·s⁻¹·m⁻²)</td>
<td>20</td>
<td>16</td>
<td>20</td>
</tr>
<tr>
<td>Water use, deficit period (ml·hr⁻¹)</td>
<td>43</td>
<td>12</td>
<td>12</td>
</tr>
<tr>
<td>Water use, post-deficit (ml·hr⁻¹)</td>
<td>144</td>
<td>152</td>
<td>154</td>
</tr>
</tbody>
</table>

*Data are means of five (2-year-old) or six (1-year-old) replications times the number of observations (six to eight, except one for osmotic potential).
*Within-row comparisons only.

Table 2. Shoot growth of 1- and 2-year-old trees during and after deficit irrigation from 19 Nov. to 9 Jan. and 23 Oct. to 12 Dec., respectively, and its interaction with soil volume.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Non-deficit (N)</th>
<th>Deficit (D)</th>
<th>LSD (0.05)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Irrigated soil volume (liters)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Time of measurement</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>One-year-old trees</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>During deficit</td>
<td>5.0</td>
<td>10.0</td>
<td>10.0</td>
</tr>
<tr>
<td>After deficit*</td>
<td>4.3</td>
<td>12.4</td>
<td>9.0</td>
</tr>
<tr>
<td>Total</td>
<td>12.4</td>
<td>21.5</td>
<td>10.4</td>
</tr>
<tr>
<td>Two-year-old trees</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>During deficit</td>
<td>4.3</td>
<td>7.0</td>
<td>11.8</td>
</tr>
<tr>
<td>After deficit*</td>
<td>2.5</td>
<td>10.0</td>
<td>8.3</td>
</tr>
</tbody>
</table>

*Data are means of five (2-year-old) or six (1-year-old) replications.
*Non-deficit, water applied to soil volumes as during deficit.
*Non-deficit, water applied to full 10 liters of soil, all trees.

Growth resumed at rates equal to or greater than that of trees that had received N to all four pots for the whole season. This surge of growth lasted only 4 to 5 weeks as all the trees ended their terminal growth.

In the 1-year-old trees, N was restored to the same soil volume that had been irrigated during the deficit period. The N trees grew very little in the post-deficit period, but the D trees grew vigorously in proportion to the soil volume so that total growth equaled that of the N trees.

After natural drop, only 26 peaches remained on the trees until harvest on 12 Jan.; 16 on N trees, 10 on D trees. Fruit size was not affected by treatment.

Post-deficit water relations. Water relations mostly stabilized within 2 weeks after the N was resumed. Two-year-old trees that had received either D or N to a restricted soil volume showed gs significantly higher than unrestricted trees after N was restored to the full soil volume. During the D period the terminal growth rate was closely linked to gs. In the post-deficit period, growth rates increased without proportional increases in gs. The rate of water use by 2-year-old trees previously exposed to water deficit or reduced soil volume resumed at high rates, but less than that of the N4 trees (Table 1).

Adjusted root : shoot ratio. All treatments increased gs relative to the control (Table 3). Pruning and defoliation increased gs within a week. Increased soil volume affected gs more slowly, with gs becoming significantly higher than the control 4 weeks after the treatments were started.

Pruned plus defoliated trees developed much lower Ψ_L 1 week following treatment (Table 3). Pruned trees with increased soil volume also had lower Ψ_L than the control 1 week after the start of the treatment. Increased soil volume gradually developed lower Ψ_L by late in the period. The soil volume effect developed slowly, the reduced leaf area effect developed in just a few days, and the two effects were additive.

Reducing the leaf area by pruning and by defoliation reduced water use immediately (Table 3). Increasing soil volume did not have an immediate effect, but, by the 5th week, water use had increased relative to the control in all three treatments that included increased soil volume.

Pruning and defoliation both increased terminal growth (Table 3). By February, the trees were clearly into endodormancy. Nevertheless, a few centimeters of growth were stimulated by treatments that reduced the shoot length but not by increasing root growth.

Flowering. Flower density was decreased by water deficit from 23 Oct. to 12 Dec., but not affected by root volume differences at that time (Table 4). Tripling the soil volume on 10 Feb. of trees subjected to deficit irrigation increased flowering from very sparse to very abundant. Pruning on 10 Feb. reduced flowering slightly. Defoliation inhibited flowering drastically.

Discussion

Peach trees in this experiment responded to deficit irrigation or to reduced soil volume similarly. Growth rates were correspondingly reduced if deficit irrigation was imposed or if water
Table 3. Effect of tripling available soil volume, pruning two-thirds of the foliage, and defoliation on stomatal conductance, leaf water potential, and water use during the first and fifth weeks following treatment and terminal growth of 2-year-old peach trees in mid to late summer.2

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Tripped soil volume</th>
<th>Pruned</th>
<th>Tripped soil volume, pruned</th>
<th>Tripled soil volume, pruned, defoliated</th>
<th>Control</th>
<th>LSD *&lt;i&gt;(0.05)&lt;/i&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaf conductance (g&lt;sub&gt;s&lt;/sub&gt;; mmol·s&lt;sup&gt;-1&lt;/sup&gt;·m&lt;sup&gt;-2&lt;/sup&gt;)</td>
<td>64</td>
<td>80</td>
<td>89</td>
<td>117</td>
<td>48</td>
<td>8</td>
</tr>
<tr>
<td>Leaf water potential (Ψ&lt;sub&gt;L&lt;/sub&gt;; Mpa)</td>
<td>-1.03</td>
<td>-1.06</td>
<td>-1.22</td>
<td>-1.35</td>
<td>-0.90</td>
<td>.15</td>
</tr>
<tr>
<td>Water use, first week (ml·hr&lt;sup&gt;-1&lt;/sup&gt;)</td>
<td>213</td>
<td>172</td>
<td>158</td>
<td>89</td>
<td>209</td>
<td>12</td>
</tr>
<tr>
<td>Water use, fifth week (ml·hr&lt;sup&gt;-1&lt;/sup&gt;)</td>
<td>196</td>
<td>140</td>
<td>170</td>
<td>126</td>
<td>140</td>
<td>20</td>
</tr>
<tr>
<td>Terminal growth (cm)</td>
<td>3.0</td>
<td>7.5</td>
<td>7.5</td>
<td>11.8</td>
<td>3.2</td>
<td>4.4</td>
</tr>
</tbody>
</table>

*Data are means of six replicates times four observations for g<sub>s</sub> and Ψ<sub>L</sub>, one observation for water use and terminal growth.

Table 4. Effect of early summer deficit irrigation and late summer pruning, root volume expansion, and defoliation on bloom density.2

<table>
<thead>
<tr>
<th>Treatments applied 10 Feb.</th>
<th>Non-deficit (N)</th>
<th>Deficit (D)</th>
<th>Bloom density (rating)&lt;sup&gt;D&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>4.3 ab</td>
<td>1.0 c</td>
<td></td>
</tr>
<tr>
<td>Pruned (2/3 foliage removed)</td>
<td>3.3 b</td>
<td>1.3 c</td>
<td></td>
</tr>
<tr>
<td>Repotted (soil volume tripled)</td>
<td>4.7 a</td>
<td>5.0 a</td>
<td></td>
</tr>
<tr>
<td>Pruned and repotted</td>
<td>3.3 b</td>
<td>4.0 ab</td>
<td></td>
</tr>
<tr>
<td>Pruned, repotted, defoliated</td>
<td>1.3 c</td>
<td>1.7 c</td>
<td></td>
</tr>
</tbody>
</table>

*Data are means of three replicates.

*<i>1 = very sparse, 2 = sparse, 3 = moderate, 4 = abundant, 5 = very abundant.</i>

*Mean separation by Duncan's multiple range test, <i>P = 0.05</i>.

The average Ψ<sub>L</sub> figures do not support a hypothesis that growth was reduced by relatively short-term water stress.

Furthermore, average midday Ψ<sub>L</sub> was well above Ψ<sub>s</sub>, confirming the visual observation that the leaves were turgid most of the time. Two weeks after D started, the 1-year-old D trees wilted at -2.0 to -2.4 MPa. Five weeks later, Ψ<sub>s</sub> was -3.4 MPa, suggesting considerable osmotic adjustment by the D trees. There was no significant osmotic adjustment in the 2-year-old trees. Photosynthesis may have been insufficient to permit an increase in solutes, in part because g<sub>s</sub> was very low in the 2-year-old trees.

Increasing the root : shoot ratio by increasing the available volume of soil, by pruning, and by defoliation supports the view that the growth rate of these trees did not respond to D primarily because of water stress. The small amount of growth that was stimulated in spite of developing endodormancy was inversely proportional to Ψ<sub>L</sub>, but positively related to g<sub>s</sub> (Table 3). The greater the drought stress, the more growth. Stomates ordinarily were close at low Ψ<sub>L</sub> (Chalmers et al., 1983; Hand et al., 1982; Olsson and Milthorpe, 1983). In this experiment, another factor overrode that response, producing a strong negative relationship of g<sub>s</sub> against Ψ<sub>L</sub>. As a result, water was lost at a faster rate per leaf and Ψ<sub>L</sub> decreased wherever the root : shoot ratio was increased.

An initial argument could be made that growth control through either D or soil volume restriction was exerted through water relations. Both treatments reduced g<sub>s</sub>. This had the effect of holding Ψ<sub>L</sub> within a normal range of daytime values unless water applications were reduced severely enough to induce wilting. When this was done, water potentials decreased to -2.0 to -2.4 MPa, where wilting occurred. Leaf conductance did not respond to irrigation under these conditions.

Plant water deficits and restricted soil volume produced similar responses in g<sub>s</sub> and in shoot growth. Control of g<sub>s</sub> and shoot growth by restricted root volume is believed to be mediated by hormones produced in active root tips (Blackman and Davies, 1985; Richards, 1986; Richards and Rowe, 1977a; Turner, 1986).

Pruning and defoliation reduced flowering but increasing soil volume, presumably activating root tips, greatly increased flowering (Table 4). These effects were independent of equally significant effects on leaf water potential. Flower bud formation was influenced by water deficit in November and by repotting or defoliation in February-March.

Reducing the active root system by withholding water from part of the root system affected peach trees in a manner similar
to, but distinct from, the effect of water deficits. Reduced volumes reduced leaf conductance, water use, and shoot growth, as did water deficit, but with a lesser effect on leaf water potential and no effect on osmotic potential. Water deficit reduced flowering; increasing soil volume overcame that effect.

**Literature Cited**


