Mitigation of effects of extreme drought during stage III of peach fruit development by summer pruning and fruit thinning

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Summary A water deficit during stage III of fruit growth was established with the aim of determining if it is possible to achieve an improvement in tree water status by summer pruning and fruit thinning. The experiment was set up as a randomized block split-plot design across trials (irrigation) where pruning was assigned to the main plot and fruit thinning to the sub-plots. The irrigation treatments were (1) standard full irrigation (FI), and (2) suppression of irrigation during stage III of fruit growth until leaves visibly withered (LWI); the pruning treatments were (1) experimental summer pruning (EP), and (2) standard summer pruning (CP); and three fruit thinning intensities were applied to facilitate analysis of the effects of the treatments in relation to fruit load. Changes in amount of light intercepted and in tree stem water potential (Ψstem) were evaluated. The EP treatment reduced the amount of light intercepted by the tree. In the FI treatment, there was a significant reduction in fruit growth measured as both water accumulation and dry mass accumulation. Under FI conditions, reductions in fruit load as a result of EP were not accompanied by a significant improvement in Ψstem. In the LWI treatment, EP produced a significant improvement of 0.17 MPa in Ψstem, but there was no improvement in fruit growth compared with CP trees. A reduction in fruit load from 350 (commercial load) to 150 per tree significantly improved Ψstem by 0.3 MPa at the end of stage III of fruit growth. These results indicate that improvements in water status in response to pruning may be insufficient to promote fruit growth if the pruned trees are unable to provide an adequate supply of assimilates to the developing fruits.

Keywords: fruit growth, fruit load, light interception, root starch, stem water potential.

Introduction

In many irrigated zones in the Mediterranean area, the availability of water in extremely dry years may be insufficient to meet crop water requirements. In these cases the flow of water along the irrigation channels may be interrupted before the end of the normal irrigation period for numerous fruit crops. In mid-late maturing peach trees, these limitations can coincide with stages of high sensitivity to water stress, such as stage III of fruit development (Li et al. 1989, Berman and DeJong 1996, Naor et al. 1999, Besset et al. 2001, Girona et al. 2004).

Confronted with a period of prolonged water deficit, peach fruit expansion growth could be limited by two mechanisms: (1) limitation by carbohydrate availability owing to a decrease in photosynthetic rate (Hsiao 1973, Bradford and Hsiao 1982); and (2) direct limitation of fruit growth as a result of a reduction in cell turgor in response to water stress (Kramer and Boyer 1995). The limitation caused by carbohydrate availability could be compensated by fruit thinning, because reducing the number of fruits per tree increases the amount of carbohydrates available for the remaining fruits (Wardlaw 1990, Grossman and DeJong 1994, Naor et al. 1997, 1999). The direct limitation of fruit growth by water stress could be mitigated by reducing canopy transpiration by summer pruning. If a considerable reduction in water consumption were obtained, more water would remain in the soil, which could benefit fruit growth (Li et al. 2003a). However, summer pruning decreases canopy leaf area and may thus reduce canopy light interception (Palmer et al. 1992) and tree photosynthetic capacity (Marini and Barden 1987), which may lower the supply of carbohydrates available to support fruit growth.

Although several authors have demonstrated the key role played by the elimination of vegetation in the survival of trees under conditions of extreme drought (Proebsting and Middleton 1980), and others have speculated on a possible improvement in fruit growth in response to pruning (Li et al. 2003b), no study designed to determine the beneficial effect of summer pruning on fruit growth as a technique of water stress relief has yet been published.

The aim of using summer pruning as a technique of water stress relief is to obtain a substantial improvement in tree water status. The amount of pruning is critical because it must be extensive enough to provide stress relief, but it must have only a minimal effect on the supply of carbohydrates to the fruits. With this trade-off in mind, we developed an experimental summer pruning method that eliminated vegetative units that could compete with fruit growth, i.e., water sprouts, syleptic
shoots and about one third of large fruiting shoots (Audergon et al. 1993, Marsal et al. 2003). Our specific objectives were: (1) to ascertain if it is possible to achieve an improvement in tree water status by a partial reduction in vegetative area and to determine if this improvement benefits fruit growth during extreme drought; and (2) to compare summer pruning and fruit thinning as techniques for water stress relief during periods of extreme drought.

Materials and methods

Experimental plot
The experiment was carried out during the year 2003 in an area of 0.45 ha in a commercial orchard located in the province of Huesca (41.6° N, 0.26° E), Spain. The soil is loam textured and more than 2 m deep. During the experiment there was no precipitation, mean maximum daily temperature was 34 °C and mean minimum relative humidity was 54%. We monitored 108 peach trees of a mid-late maturing cultivar (Prunus persica (L.) Batsch. cv. ‘O’Henry’). Trees were 5 years old and were grafted onto “GF 677” hybrid rootstock. Row spacing was 5 × 3 m and trees were trained to a vase system. The plot had an automated drip irrigation system with four pressure-compensating emitters (2 l tree⁻¹ h⁻¹). The trees were irrigated daily. The amount of water applied was monitored with a multi-jet water meter (Model D85, Wehrle, Emmendingen, Germany). The plot was managed according to commercial practices, including a mechanized summer pruning.

Irrigation treatments
Two irrigation treatments were applied: full irrigation (FI) and suppression of irrigation during stage III of fruit development until leaves wilted visibly (LWI). Leaf wilting occurred when stem water potential (Ψstem) reached −1.80 MPa. On passing this threshold, irrigation was applied weekly. The water requirements of the trees were calculated by a water balance method. The Penman-Monteith method determined the reference evapotranspiration (ET₀), and the crop coefficients (Kc) were estimated as described by Doorenbos and Pruitt (1977). The two irrigation treatments were applied from stage III of fruit growth until harvest; otherwise, trees in both treatments were fully irrigated according to standard procedures.

Summer pruning treatments
At the onset of stage III of fruit development, two summer pruning treatments were applied: experimental summer pruning (EP) and commercial summer pruning (CP). The EP treatment consisted of the elimination of the water sprouts in the basal part of the tree, plus the removal of most of syleptic shoots growing in the crotches of the main scaffolds, plus the removal of one third of the fruiting shoots. The CP consisted of a mechanized topping in summer after EP was applied. The vegetation removed by pruning was weighed.

Fruit thinning
Fruit thinning, which is typically carried out midway through stage II of fruit growth, was delayed until the onset of stage III, to control the effect of fruit load exclusively during stage III, and thereby eliminate any interaction among phenological stages and applied treatments. Three thinning intensities were applied to obtain a range of fruit loads: a heavy load, in which the trees were not thinned; a medium load, which corresponded to a commercial thinning and in which the minimum spacing between fruits was 20 cm; and a light load, with a minimum spacing between fruits of 40 cm.

Experimental design
A randomized block split-plot (3 blocks-replicates) design across trials (irrigation) was used. The pruning treatments were randomly assigned as main plots and the fruit thinning treatments were randomly distributed as sub-plots. Each sub-plot consisted of five trees in a row, of which the three central trees were the experimental trees, and the exterior trees served as a buffer.

Measurements
Photosynthetic active radiation (PAR) intercepted by each tree was determined by measuring irradiance at ground level in the shaded area below the canopy with a linear ceptometer (probe length of 80 cm; Accupar Linear PAR, Decagon Devices, Pullman, WA, as described by Klein et al. (2001)). Measurements were taken during stage III of fruit development, at solar noon ± 30 min on completely clear days. For each tree, eight radial measurements were made below the canopy, separated by angles of 45°, centered at the base of the trunk and on which the end of the ceptometer was placed. On each occasion, a measurement was also made in an open area with no interference from the canopy. The percentage of PAR intercepted by the tree was calculated as (100(1 – mean value below the canopy/value outside the canopy)).

To evaluate tree water status, stem water potential (Ψstem) was determined weekly during stage III of fruit growth with a pressure chamber (Model 3005, Soil Moisture Equipment, Santa Barbara, CA) following procedures outlined by McCutchan and Shackel (1992). Measurements were taken at solar noon ± 30 min on a leaf situated in the basal part of the central tree of each sub-plot. The leaves were covered with a black plastic bag and aluminum foil for 1 h before the measurements were made.

Random samples of two fruits per tree were labeled and fruit size was determined by measuring the equatorial diameter with a digital caliper (Mitutoyo, Tokyo, Japan) weekly from the onset of stage III of fruit growth until the time of harvest.

At the onset of stage III of fruit growth a sample of 24 fruits per tree was taken. Mean fresh mass of the fruit at the start of stage III (FW₁) was determined by dividing the total fresh mass of a sample from a tree by the number of fruits in the sample. The dry mass of the samples was calculated after drying them to constant mass in a forced air draft oven at 70 °C. The mean dry mass of the fruit at the onset of stage III (DW₁) was calculated by dividing the total dry mass of the sample from a tree by the number of fruits in the sample.

Fruits were harvested in two consecutive pickings, according to fruit color. The first harvest was on August 22 and the
second was on August 27. The number of fruits per tree and their total fresh mass were determined at each harvest and for every experimental tree. Mean fresh mass of the fruit at harvest (FW) was estimated by dividing the total fresh mass of the harvested fruits per tree by the number of fruits. A sample of 24 fruits per tree was taken from the first harvest and mean dry mass of the fruit at harvest (DW) was determined as described previously.

Fruit growth analysis
Mean growth of the fruit resulting from water accumulation (W) was determined as:

\[ W = \frac{(FW_2 - FW_1) - (FW_1 - DW_1)}{t_2 - t_1} \]  

where \( t_1 \) and \( t_2 \) are the starting date of stage III and the harvesting date (mean date of the two pickings performed during the harvest), respectively. Mean growth of the fruit as a result of dry matter accumulation (D) was determined as:

\[ D = \frac{DW_2 - DW_1}{t_2 - t_1} \]  

Effects of the treatments on \( \Psi_{stem} \) were analyzed by repeated measures analysis of variance (ANOVA) over time. Effects of the treatments on fruit \( W \) and fruit \( D \) were evaluated by analysis of covariance (ANCOVA), which tested for heterogeneity in the slope of treatment responses to fruit load. Analyses were performed with the SAS software package (SAS Institute, Cary, NC). Statistical significance was established for \( P < 0.05 \). Tukey’s test was applied for the separation of the least square means for the treatments that differed significantly.

Results
The total annual amount of water applied in the FI irrigation treatment was 605.4 mm, whereas trees in the LWI irrigation treatment received 369.6 mm. These annual differences in water supply reflect the different amounts of water delivered during stage III of fruit growth: trees in the FI treatment received 297 mm and trees in the LWI treatment received only 56.7 mm, i.e., trees in the LWI treatment received 20% of the water supplied to trees in the FI treatment during stage III of fruit growth.

In the EP treatment, an average of 3.29 kg tree\(^{-1}\) (SD = 0.41) of vegetative fresh mass was removed, equivalent to about 18.5% of the mean total vegetation of a tree. In the CP treatment an average of 0.54 kg tree\(^{-1}\) (SD = 0.03) of vegetative fresh mass was removed, representing about 2.42% of the mean total vegetation of a tree.

Fruit loads of trees in the three fruit thinning treatments were somewhat variable: mean high loads were ~538 fruits tree\(^{-1}\) (SD = 139), mean medium loads were ~346 fruits tree\(^{-1}\) (SD = 73) and those with low loads averaged 238 fruits tree\(^{-1}\) (SD = 92).

The treatments caused significant changes in the percentage of PAR intercepted (Figure 1). The EP treatment caused an immediate reduction of between 9 and 12% in the amount of PAR (Figure 1). The greater the amount of vegetation removed during pruning, the greater the reduction in percentage of PAR intercepted by the tree (Figure 2). The CP treatment caused no detectable change in the amount of PAR intercepted (Figure 1). After application of the summer pruning treatments, and as the productive cycle progressed, the irrigation treatments had differential effects on the time course of changes in the percent of PAR intercepted. Trees in the FI treatment showed an increase in PAR interception of 3% in the period between summer pruning and harvest, whereas the PAR intercepted by trees in the LWI treatment tended to remain constant during the same period (Figure 1).

Before application of the treatments, the experimental trees had \( \Psi_{stem} \) values of between −0.62 and −0.74 MPa (Figure 3). Trees in the FI treatment maintained \( \Psi_{stem} \) values around −0.87 MPa with slight oscillations throughout the study (Figure 3). Trees in the LWI treatment showed a considerable de-
crease in $\Psi_{stem}$, within 1 week after suppression of irrigation, and the reduction increased with time (Figure 2). When $\Psi_{stem}$ of trees in the LWI treatment reached $-1.80$ MPa, leaf wilting was observed. On passing this threshold, a weekly irrigation was applied, causing transient recuperation of $\Psi_{stem}$ (Figure 3).

By the end of the reproductive cycle, $\Psi_{stem}$ of trees in the LWI treatment reached values between $-2.00$ and $-2.30$ MPa. Trees in the EP + LWI treatment combination tended to maintain a better water status than trees in the CP + LWI treatment combination and their enhanced water status became more evident as the water stress increased (Figure 3). Repeated measures ANOVA over time revealed that the average improvement in $\Psi_{stem}$ of 0.17 MPa during the study period was significant (Table 1). On the other hand, neither of the pruning treatments had a significant effect on $\Psi_{stem}$ in trees receiving FI (Table 1).

Fruit thinning of trees in the LWI treatment produced a noticeable improvement in $\Psi_{stem}$ 34 days after the onset of stage III of fruit growth (Figure 4). In the final stage of the experiment, $\Psi_{stem}$ of trees with low fruit loads (mean of 206 fruits tree$^{-1}$) improved by 0.52 MPa compared with trees with high fruit loads (mean of 494 fruits tree$^{-1}$) (Figure 4).

The effects of fruit load on $W_{car}$ and $D_{car}$ were significant for trees in all of the treatments (Table 2). Both fruit growth parameters decreased with increasing fruit load independently of the irrigation and summer pruning treatments (Figure 5). Nevertheless, the fruit load effect was more significant in trees in the FI treatment than in the LWI treatment (Table 2), and furthermore the effect of fruit load on fruit size was observed earlier in trees in the FI treatment than in trees in the LWI.
treatment (28 days versus 42 days after the start of the treatments) (Figure 6).

Independently of fruit loads, the fruit growth parameter values were lower in trees in the LWI treatment than in trees in the FI treatment, with decreases in the least square means of 43 and 41% for $\text{W}_{\text{GR}}$ and the $\text{D}_{\text{GR}}$, respectively (Table 2). Comparing the summer pruning treatments within the FI irrigation treatment, EP trees had significantly lower $\text{W}_{\text{GR}}$ and $\text{D}_{\text{GR}}$ values than CP trees throughout stage III of fruit growth (Table 2). In contrast, within the LWI irrigation treatment, there were no significant differences in the fruit growth parameters between EP trees and CP trees (Table 2).

The PSS for trees growing under LWI conditions, which was calculated from the whole population of trees in both pruning treatments because no significant difference between pruning treatments was found, was estimated at 57 g tree$^{-1}$ day$^{-1}$ of dry mass during stage III of fruit growth (Figure 7). This value was lower than the PSS of trees in the FI treatment, which was calculated at 100 and 120 g tree$^{-1}$ day$^{-1}$ of dry matter during stage III of fruit growth for EP and CP trees, respectively (Figure 7).

The irrigation and summer pruning treatment combinations differentially affected RSC (Figure 8). The RSC values were lower for trees in the LWI irrigation treatment than for trees in the FI treatment (Table 3). Within the FI treatment, EP had a greater effect on fruit load than CP (Figure 8; and see significance of heterogeneity test from the covariance analysis in Table 3): for fruit loads of more than 300 fruits per tree, EP trees started to

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Table 1. Effects of summer pruning, sampling time and the summer pruning × sampling time interaction on stem water potential ($\Psi_{\text{stem}}$), analyzed by repeated measures ANOVA over time and in relation to the irrigation treatment applied. Abbreviations: FI = irrigation fully meeting the water requirements of the trees; LWI = suppression of irrigation during stage III of fruit development until leaf withering; LSM = least square means; CP = commercial summer pruning; and EP = experimental summer pruning.

<table>
<thead>
<tr>
<th>Effects on $\Psi_{\text{stem}}$</th>
<th>Irrigation treatment</th>
<th>FI</th>
<th>LWI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Summer pruning</td>
<td>0.2944 $^1$</td>
<td>0.0058</td>
<td></td>
</tr>
<tr>
<td>Time</td>
<td>0.0001</td>
<td>0.0001</td>
<td></td>
</tr>
<tr>
<td>Summer pruning × time</td>
<td>0.6072</td>
<td>0.9938</td>
<td></td>
</tr>
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</table>

$^1$ Probability according to the repeated measures ANOVA over time.

Table 2. Probabilities for the test of heterogeneity of slopes in ANCOVA on fruit $W_{\text{GR}}$ and $D_{\text{GR}}$. Within a column, means followed by different letters are significantly different at 5% according to Tukey’s test. Abbreviations: FI = irrigation fully meeting the water requirements of the trees; LWI = suppression of irrigation during stage III of fruit development until leaf withering; LSM = least square means; CP = commercial summer pruning; and EP = experimental summer pruning.

<table>
<thead>
<tr>
<th>Effects subject to covariance analysis</th>
<th>$W_{\text{GR}}$</th>
<th>$D_{\text{GR}}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Between irrigation treatments (FI versus LWI)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Treatment (irrigation)</td>
<td>0.0001 $^1$</td>
<td>0.0001</td>
</tr>
<tr>
<td>Covariable (no. fruits)</td>
<td>0.0001</td>
<td>0.0001</td>
</tr>
<tr>
<td>Heterogeneity of slopes (irrigation × no. fruits)</td>
<td>0.7035</td>
<td>0.3919</td>
</tr>
<tr>
<td>LSM; irrigation treatments (g day$^{-1}$)</td>
<td>FI</td>
<td>2.22 a</td>
</tr>
<tr>
<td></td>
<td>LWI</td>
<td>1.27 b</td>
</tr>
</tbody>
</table>

| Between summer pruning treatments within FI |
| Treatment (summer pruning) | 0.0029 | 0.0414 |
| Covariable (no. fruits)    | 0.0001 | 0.0001 |
| Heterogeneity of slopes (pruning × no. fruits) | 0.7225 | 0.7640 |
| LSM; summer pruning treatments (g day$^{-1}$) | CP | 2.26 a | 0.30 a |
|                                         | EP | 2.02 b | 0.26 b |

| Between summer pruning treatments within LWI |
| Treatment (summer pruning) | 0.6767 | 0.3945 |
| Covariable (no. fruits) | 0.0014 | 0.0004 |
| Heterogeneity of slopes (pruning × no. fruits) | 0.4954 | 0.2079 |
| LSM; summer pruning treatments (g day$^{-1}$) | CP | 1.30 | 0.18 |
|                                         | EP | 1.24 | 0.16 |

$^1$ Probability according to covariance analysis.

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Figure 4. Relationship between the fruit load and stem water potential within the LWI irrigation treatment during stage III of fruit growth. Relationships between fruit load and stem water potential were adjusted to a simple linear equation for each day of evaluation. Asterisks (*) indicate a significant slope for $P < 0.001$. Abbreviation: LWI = suppression of irrigation during stage III of fruit development until leaf wilting.

Figure 7. The PSS for trees growing under LWI conditions, which was calculated from the whole population of trees in both pruning treatments because no significant difference between pruning treatments was found, was estimated at 57 g tree$^{-1}$ day$^{-1}$ of dry mass during stage III of fruit growth. This value was lower than the PSS of trees in the FI treatment, which was calculated at 100 and 120 g tree$^{-1}$ day$^{-1}$ of dry matter during stage III of fruit growth for EP and CP trees, respectively (Figure 7).
Under FL conditions, EP resulted in a 17% reduction in the maximum amount of dry mass that a tree is capable of providing to the fruits (PSS; Figure 7). This reduction could be attributed to the decrease in the amount of PAR intercepted as a result of the EP treatment (Figure 2). Several authors have found a significant reduction in canopy photosynthetic efficiency following summer pruning (Ferree et al. 1984, Lakso and Corelli-Grapadelli 1992, Li et al. 2003a). If our estimate of the reduction in available assimilates is accurate, it should be possible to find an inhibitory effect of EP on the accumulation of reserves in tree roots at the end of the annual cycle, because the accumulation of reserves in fruit trees is related to cropping practices established in the final stage of fruit growth (Loescher et al. 1990). We found that, at high fruit loads, EP trees had lower RSC than CP trees (Figure 8). However, at low fruit loads, RSC did not differ between EP and CP trees. Under the conditions of our trial, the appearance of new shoot growth after imposition of the treatments had no effect on RCS and was unaffected by the summer pruning and fruit thinning treatment, indicating that the lack of a difference in RSC between EP and CP trees with low fruit loads must be independent of changes in carbon acquisition during the study period. Beyond this, however, we have no explanation for the lack of response of RCS to pruning at low fruit loads, although it is clear that EP inhibited carbon accumulation.

Based on the results obtained under FL conditions, we speculate that, under LWI conditions, EP pruning reduced carbohydrate availability to the fruit, because it resulted in a significant reduction in the amount of PAR intercepted by the tree. However, under LWI conditions, water stress reduced leaf photosynthesis so much that differences in tree leaf area between pruning treatments likely had much less influence on total carbon acquisition per tree than comparable differences under FL conditions (Boyer 1976, Kaiser 1987). In our study, net assimilation rate decreased from 10 µmol CO$_2$ m$^{-2}$ s$^{-1}$ under well-watered conditions to 3 µmol CO$_2$ m$^{-2}$ s$^{-1}$ under conditions of maximum water stress (data not shown). Furthermore, under LWI conditions, the average improvement (0.17 MPa) in $\Psi_{stem}$ obtained in response to EP pruning and the associated improvement in photosynthesis at the leaf level (1.85 µmol CO$_2$ m$^{-2}$ s$^{-1}$) may imply EP trees in the LWI treatment experienced more favorable conditions for reserve accumulation than EP trees in the FI treatment. This explanation may also account for the absence of a significant effect of EP on RCS under LWI conditions (Table 3). Nevertheless, if EP had caused a negative impact on fruit growth capacity by reducing available reserves, it would be more difficult to detect under LWI conditions than under FL conditions. The use of PSS as a means of verification under conditions of water deficit may be unsuitable for analyzing the effect of EP on assimilate generation capacity under water-stress (T.M. DeJong, University of California, Davis, CA, personal communication), because expression of fruit growth is not only limited by assimilate availability, but also by the limitation of cell turgor on fruit expansion growth (Hsiao 1973, Bradford and Hsiao 1982). The lack of differences in fruit $D_{GR}$ could indicate that the presumed limitation of carbohydrates in response to the EP treatment was negated by the EP-induced improvement in tree water status.

Discussion

To isolate the effects of carbon availability from those related to water status on fruit growth, we studied the effects of EP under FL conditions and found that the changes in tree water status produced by EP were not significant (Table 1). On the other hand, under LWI conditions, EP gave rise to an average improvement of 0.17 MPa in $\Psi_{stem}$ (Table 1). These findings indicate that two processes should be considered when analyzing fruit growth responses to EP under conditions of water deficit: (1) improvement in tree water status and (2) changes in carbon availability for fruit growth.
It appears that exhaustive summer pruning under drought conditions does not necessarily enhance fruit carbon allocation. This explanation may be partly because reducing the amount of radiation intercepted by a tree can limit total carbon acquisition, but it may also be associated with the dependence of the structural units remaining on the tree for carbon from units that were removed by pruning. In a parallel study in which pruning was carried out by eliminating large branches (large branches are considered autonomous for carbon), there was a significant improvement in both tree water status and fruit growth (author’s unpublished observations).

A reduction in fruit load from 300 fruits (commercial load) to 150 fruits per tree under conditions of water stress, produced an improvement in $\Psi_{stem}$ of 0.30 MPa (Figure 4), indicating that low fruit loads coupled with conditions of water stress led to an improvement in tree water status (Berman and DeJong 1996, Naor et al. 2001, Naor 2004) and a reduction in fruit competition (Wardlaw 1990, Grossman and DeJong 1994). However, fruit thinning did not produce an improvement in tree water status until 34 days after its application (Figure 4), and fruit growth did not show a significant response to fruit load until 42 days after fruit thinning (Figure 6). This delay in fruit growth response could reflect a dependence on the pattern of water stress development, but other factors such as time elapsed since the application of thinning, timing of the onset of maximum fruit expansion growth, or degree of water stress achieved, cannot be discarded as modulators, because the exact mechanism by which thinning improves water status

Figure 6. Relationship between fruit load and mean fruit diameter (D), measured on trees in the FI treatment (A) and the LWI treatment (B) during stage III of fruit growth, and fitted to a linear equation for each evaluation day. Equations were adjusted to the mean D of the fruit (2 fruits tree$^{-1}$; $n = 27$). Significance: * = $P < 0.05$; ** = $P < 0.01$; and *** = $P < 0.001$. Abbreviations: FI = irrigation fully meeting the water requirements of the trees; LWI = suppression of irrigation during stage III of fruit development until leaf wilting; CP = commercial summer pruning; and EP = experimental summer pruning.

Figure 7. Relationship between fruit load and growth in dry matter for the total fruit per tree (tree’s $D_{GR}$) during stage III of fruit growth. The relationship between fruit load and the tree’s $D_{GR}$ was fitted to a hyperbolic equation. Each value represents one tree. Abbreviations: PSS = potential source supply; FI = irrigation fully meeting the water requirements of the trees; LWI = suppression of irrigation during stage III of fruit development until leaf wilting; CP = commercial summer pruning; and EP = experimental summer pruning.

Figure 8. Relationships between fruit load and root starch content (RSC) during winter dormancy. Relationships were fitted to a polynomial equation. Each value represents one tree. Abbreviations: FI = irrigation fully meeting the water requirements of the trees; LWI = suppression of irrigation during stage III of fruit development until leaf wilting; CP = commercial summer pruning; and EP = experimental summer pruning.
Table 3. Probabilities for the test of heterogeneity of slopes in ANCOVA on root starch content (RSC) during winter dormancy. Means followed by different letters in the same column are significantly different at 5% according to Tukey’s test. Abbreviations: LSM = least square means; FI = irrigation fully meeting the water requirements of the trees; LWI = suppression of irrigation during stage III of fruit development until leaf wilting; CP = commercial summer pruning; and EP = experimental summer pruning.

<table>
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<th>Effects subject to covariance analysis</th>
<th>RSC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Treatment (irrigation)</td>
<td>0.0026</td>
</tr>
<tr>
<td>Covariable (no. fruits)</td>
<td>0.0614</td>
</tr>
<tr>
<td>Heterogeneity of slopes (irrigation × no. fruits)</td>
<td>0.2663</td>
</tr>
<tr>
<td>LSM; irrigation treatments (g day⁻¹)</td>
<td></td>
</tr>
<tr>
<td>FI</td>
<td>12.33 a</td>
</tr>
<tr>
<td>LWI</td>
<td>8.34 b</td>
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<tr>
<td>Treatment (summer pruning)</td>
<td>0.4402*</td>
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<tr>
<td>Covariable (no. fruits)</td>
<td>0.0010</td>
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<tr>
<td>Heterogeneity of slopes (pruning × no. fruits)</td>
<td>0.0487²</td>
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<tr>
<td>LSM; summer pruning treatments (g day⁻¹)</td>
<td></td>
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<tr>
<td>CP</td>
<td>13.15</td>
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<tr>
<td>EP</td>
<td>10.67</td>
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<tr>
<td>Treatment (summer pruning)</td>
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<tr>
<td>Covariable (no. fruits)</td>
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<td>Heterogeneity of slopes (pruning × no. fruits)</td>
<td>0.3806</td>
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<tr>
<td>LSM; summer pruning treatments (g day⁻¹)</td>
<td></td>
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<tr>
<td>CP</td>
<td>9.61</td>
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<tr>
<td>EP</td>
<td>7.41</td>
</tr>
</tbody>
</table>

1 Probability according to covariance analysis.
2 When the heterogeneity of the slopes is significant, the assumptions for a covariance analysis are not valid and therefore the probability followed by an asterisk (*) is not relevant.

has not been elucidated.

Because stage III of peach fruit growth is extremely sensitive to water deficit, we assume that the main factor limiting peach fruit growth under water-stress conditions is tree water status. However, our finding that EP improved tree water status without improving fruit growth, seems to indicate that assimilate availability is as important as improved tree water status. We conclude that a suitable technique for mitigating the adverse effects of a water deficit on fruit growth should produce an improvement in tree water status and at least maintain assimilation capacity. However, it appears difficult to reach a compromise between these objectives by application of extensive summer pruning when the orchard is already being managed for optimal canopy light interception.

Acknowledgments

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