

## A comparison of the combined effect of water stress and crop load on fruit growth during different phenological stages in young peach trees.

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### SUMMARY

The combined effect of fruit load and water stress on fruit water content and dry-matter accumulation was analysed for three phenological stages of fruit growth. Irrigation treatments were no irrigation during Stage I (NI-SI), Stage II (NI-SII), or Stage III (NI-SIII) compared with a fully irrigated control. Three thinning treatments were imposed within each irrigation treatment resulting in fruit loads ranging from low to high. Fruit harvests at the end of Stage I, II and III were used to determine total tree fruit fresh and dry matter after each stage of fruit development. Fruit water accumulation was highly sensitive to the effect of water stress at high fruit loads in all fruit developmental phases, but reductions in fruit water content were more apparent during Stages II and III than during Stage I. On the other hand, fruit dry-matter accumulation was relatively insensitive to water stress at any fruit load level and developmental stage. However, reductions in dry-matter accumulation were obtained during Stage III from those trees that were not irrigated during Stage I (NISI). Since these reductions occurred only for mid-to-high fruit load conditions, the decreases in fruit growth during Stage III appeared to be related to a carbon source limitation. The possible reasons for this source limitation are discussed.

**W**ater stress, among other factors, has a major role in limiting peach fruit growth in Mediterranean climates. However, the expression of water stress effects on fruit growth can be modulated by fruit load (Berman and DeJong, 1996; Naor *et al.*, 1999; Naor *et al.*, 2001). In general, high fruit loads tend to increase the sensitivity of fruit growth to deficit irrigation (Berman and DeJong, 1996; Girona *et al.*, 2003). For instance, Berman and DeJong (1996) showed that during Stage III of fruit growth, fruit dry-matter accumulation was more greatly affected by water stress in heavily cropped trees than in lightly cropped trees. To the best of our knowledge, the combined effects of the water stress and fruit load on fruit growth have not been explored during Stage I or Stage II of fruit development.

The mechanism which fruit growth can be limited by fruit load is through total carbon availability or carbon transport to fruits (DeJong and Grossman, 1995). Water stress related reductions to fruit growth can be more complex, limiting growth through turgor related reductions in cell wall extension or reducing cell division, as well as decreasing carbon through reductions in photosynthesis (Bradford and Hsiao, 1982). The combination of water stress and fruit competition through over-cropping should provoke greater reductions in fruit growth than each one individually.

When quantifying fruit growth in terms of dry-weight accumulation, two different types of limitations can be defined: i) source-limitation if the amount of carbon available is not enough to support potential fruit growth, and ii) sink-limitation if there is enough carbon to supply the potential fruit growth but total crop growth is limit-

ed because of insufficient sink capacity. Carbon transport to fruit and/or competition for carbon from other organs can be reasons for below-potential growth in sink-limited fruits (Pavel and DeJong, 1993; DeJong and Grossman, 1995). Pavel and DeJong (1993) demonstrated how fruit growth limitations changed in response to different fruit loads, from source-limited during Stage I and III, to sink-limited during Stage II. This research demonstrates the need for considering the phenological stages of fruit development in a complete seasonal evaluation of the interaction between fruit load and water stress on fruit growth. In addition the sensitivity of fruit growth to water stress processes may change with the developmental phases (i.e. cell division and cell expansion during Stage I and III, respectively, are regarded as sensitive to water stress, while the pit hardening period during Stage II is considered to be less sensitive to water stress (Chalmers *et al.*, 1981; Chalmers *et al.*, 1983).

Furthermore, when considering the implications of water stress and fruit load on final fruit size, it is possible that water deficits occurring at different fruit loads during early stages of fruit development may affect growth during subsequent phases of fruit development. For instance, it has been reported that fruits having experienced water stress during Stage II can experience compensatory growth rates later (Li *et al.*, 1989; Chalmers *et al.*, 1981). However this event has not been found in other studies (Girona *et al.*, 1993; Girona *et al.*, 2003; Boland *et al.*, 1993; Goldhamer *et al.*, 2001), and perhaps differences in fruit load could explain some of the disparity among these studies.

Therefore, the goal of this project was to study the combined effect of crop load and water stress during Stage I, II, or III on fruit growth. In addition, carry-over

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the recommendations of Turner and Long (1980). These measurements were taken two or three times per fruit growth stage. Midday stem water potential ( $\Psi_{\text{stem}}$ ) (McCutchan and Shackel, 1992) was also measured on the same days and at the same time of the day as  $\Psi_1$  by selecting leaves close to the trunk within the canopy. At least 2 h before the measurements, intact leaves were placed within a bag of covered by aluminium foil. Two measurements per experimental plot on the two central trees of the medium thinning treatment were made for the control and the plots receiving the cut off treatment at any given sampling time.

Net leaf  $\text{CO}_2$  assimilation rate (A) was determined using a portable IRGA system (Model ADC LCA-2, The Analytical Development Co. Ltd., Hoddesdon, Herts, UK). Calculations of gas exchange were made according to the equations of von Caemmerer and Farquhar (1981). Measurements were taken on mature, well-exposed sunlit leaves at solar noon according to the same sampling pattern as for  $\Psi_1$ .

*Vegetative growth measurements*

Trunk circumference (cm) (TC) was measured at 20 cm above ground level at bloom and at the end of each fruit developmental stage. The average relative growth rate ( $\text{cm cm}^{-1} \text{day}^{-1}$ ) (RGR) for TC during each developmental stage was calculated as:

$$RGR = \frac{\log_e TC_2 - \log_e TC_1}{T_2 - T_1} \quad (1)$$

where:  $TC_1$  (cm) and  $TC_2$  (cm) are the measurements at the beginning and end of each developmental stage (DeJong and Grossman, 1995).  $T_2 - T_1$  is the number of days in each developmental stage.

The effect of the irrigation treatments on shoot elongation growth was monitored by tagging four shoots on each experimental tree (a total of  $4 \times 288$  shoots). Shoot length was measured with a metric tape before irrigation was applied and at the end of each phenological fruit growth stage.

#### *Fruit measurements*

One-third of the trees from each plot were harvested at the end of the three fruit development stages. For each harvested tree, the fruits per tree were counted and the total fresh weight per tree measured. A fruit sample of 24 fruits from each tree was taken to the laboratory to determine fruit dry weight; fruits were dried at  $72^\circ\text{C}$  to constant weight. These data were used to determine a fresh/dry weight conversion factor for each treatment and harvest period.

#### *Statistical analysis and quantification of treatment limitations for fruit growth*

The effect of irrigation treatments on the sensitivity of fruit dry weight to fruit load was tested by an analysis of covariance (ANCOVA). This was done at two fruit load levels: low fruit load ( $< 65$  fruits per tree) and high fruit load ( $> 125$  fruits per tree). Using these boundaries allowed us to include more than nine trees for each fruit load level. The ANCOVA at two fruit load levels was used to distinguish the effect of irrigation treatment at

interactions between water stress and crop load during early periods on subsequent fruit growth stages were also considered with respect to final fruit size. The underlying hypothesis of this research is that the interaction between fruit load and water stress as observed during Stage III (Berman and DeJong, 1996) should also be observed during Stage I of fruit development due to similarities in susceptibility of the growth processes to carbon limitations, but not during Stage II of fruit development (Pavel and DeJong, 1993; Grossman and DeJong, 1995). To accomplish these objectives a number of trees were well irrigated whereas other trees were not irrigated during the different phenological stages of fruit growth. Fruit thinning was applied to achieve a range of crop loads one month after fall bloom. At the end of each fruit developmental stage, a subsample of trees was harvested for each combination of irrigation, fruit growth stage, and thinning treatment.

#### MATERIALS AND METHODS

The experiment was conducted in 1996 at the Estació Experimental de Lleida at the Corbins experimental site (RTA) in a four year old peach (*Prunus persica* L. Batsch) orchard ('Groc de l'Escola'). Peach trees were spaced at  $4 \times 2$  m, and trained to a central leader. Irrigation was applied by means of a drip system with two  $8 \text{ l h}^{-1}$  drippers per tree. The plot was managed using commercial practices with a mowed cover crop strip between rows.

The experiment was laid out as a split-plot design with four complete blocks and 12 irrigation and crop load treatments. The main plots (irrigation) were buffered. Irrigation treatments were based on cutting off the irrigation during different fruit growth stages (NISI: no irrigation during fruit growth stage I, NI-SII: no irrigation during stage II, and NI-SIII: no irrigation during stage III). These treatments were compared to a control treatment (C) in which irrigation was supplied to provide fall water requirements according to the water budget method (Goldammer and Snyder, 1989). Differential fruit thinning was imposed within irrigation treatments to obtain a range of fruit loads. This was done by hand thinning a total of 288 trees (48 elemental plots with six peach trees per experimental plot) in which three different thinning intensities were applied: high (about 200 fruits per tree), medium (about 110 fruits per tree) and low (fewer than 50 fruits per tree). Although the thinning procedures were theoretically applied as discrete treatments to the individual trees the end result was a nearly continuous range of fruit loads per tree ranging from heavily cropped to lightly cropped trees. Fruit thinning was carried out four weeks after fall bloom. Irrigation treatments were initiated immediately after fruit thinning.

#### *Tree status measurements*

To evaluate the plant water status, midday leaf water potential ( $\Psi_1$ ) was measured on fully expanded sunlit leaves sampled from the outside part of the tree at solar noon. Measurements were taken with a plant water status console (Model 3005, Soil Moisture Equipment Corp., Santa Barbara, CA, USA) using the pressure chamber technique (Scholander *et al.*, 1965) following

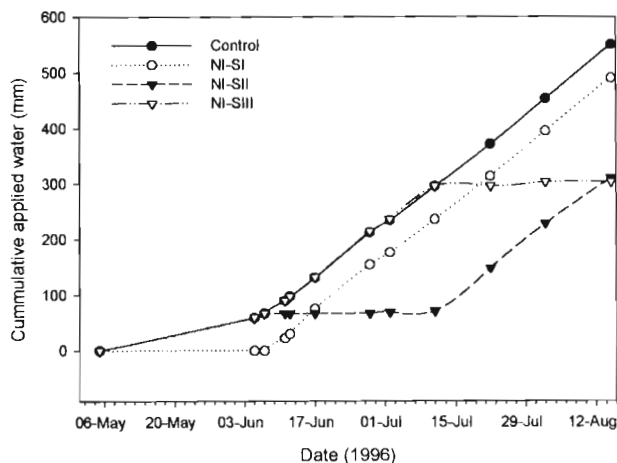


FIG. 1  
Seasonal patterns of the cumulative applied water for the different irrigation treatments.

low fruit load competition from those when competition was potentially higher. ANCOVA tests were performed from data considering trees as sample units, and by using the PROC GLM from reference reports SAS (1988). The heterogeneity of slopes (TRT\*Fruit load) was tested before assigning statistical significance to the effects of the irrigation treatments.

The procedure described by DeJong and Grossman (1995) was used to quantify fruit growth limitations to water deficit during each fruit growth phase. This method enables an estimation of the degree of sink and source limitation on fruit growth. The calculation requires a continuous function of fruit growth rate in dry weight that is dependent on fruit load. A brief summary of the calculations is outlined as follows:

The potential relative growth rate (potRGR) was calculated for each phenological stage as:

$$\text{potRGR} = \frac{\log_e W_{2(<30)} - \log_e W_{1(<30)}}{T_2 - T_1}, \quad (2)$$

where  $W_{2(<30)}$  and  $W_{1(<30)}$  are the mean individual fruit dry weights (g) at harvest dates  $T_2$  and  $T_1$ , corresponding to trees having fewer than 30 fruits per tree.  $W_{1(30)}$  during Stage I was estimated from a sample of 24 fruits at fruit thinning before any treatment was applied.

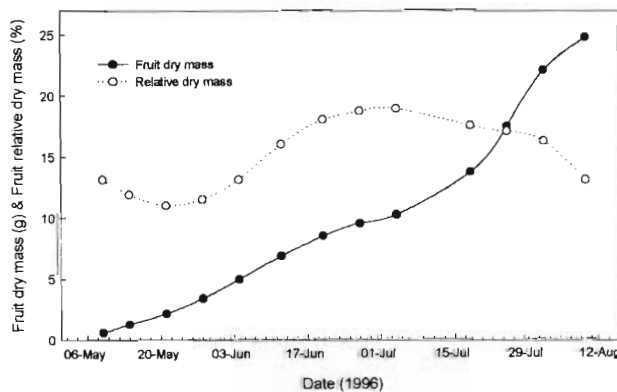


FIG. 2  
Seasonal patterns of fruit dry mass and relative fruit dry mass for control treatment conditions and commercial crop load.

The total potential fruit sink demand rate of control trees (PSINK) ( $\text{g tree}^{-1} \text{day}^{-1}$ ) was modelled as:

$$\text{PSINK} = \frac{(W^*_{1}(e^{\text{potRGR}(T_2-T_1)} - W^*_{1}))n}{T_2 - T_1}, \quad (3)$$

where  $n$  is the fruit number, and  $W^*_{1}$  is the mean fruit dry weight (g) at the onset of each developmental stage.

The potential source supply rate (PSOURCE) ( $\text{g tree}^{-1} \text{day}^{-1}$ ) was estimated from dry weight growth rate under source-limited conditions, when fruit load exceeded 220 fruits/tree in control trees.

$$\text{PSOURCE} = \frac{(W_{2(>220)} - W_{1(>220)})n}{T_2 - T_1}, \quad (4)$$

where  $W_{2(>220)}$  and  $W_{1(>220)}$  are the mean individual fruit dry weight (g) at the specified fruit load range at harvest dates  $T_2$  and  $T_1$ , respectively.

The rate of actual total fruit dry weight growth rate (ACTUAL) ( $\text{g tree}^{-1} \text{day}^{-1}$ ) during each developmental stage for an irrigation treatment was calculated as:

$$\text{ACTUAL} = \frac{(W_2(f_n) - W_1(f_n))}{T_2 - T_1}, \quad (5)$$

where  $W_2(f_n)$  and  $W_1(f_n)$  are the quadratic response function ( $f_n; W = an^2 + bn + c$ ) of total fruit dry weight ( $W$ ) to fruit count per tree ( $n$ ) at harvest dates  $T_2$  and  $T_1$ , respectively. For the Stage I period and for all irrigation treatments, the initial response function was determined from the average fruit dry weight of a sample of 24 fruits

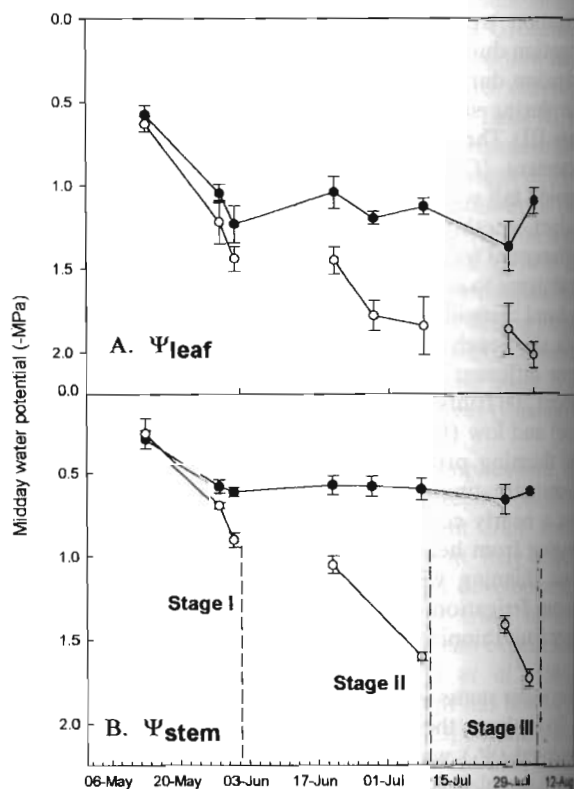


FIG. 3  
Seasonal patterns of midday leaf water potential (A) and midday stem water potential (B) corresponding to the different irrigation treatments. Each symbol represents the mean of 8 measurements. Error bars indicate  $\pm$  standard error as obtained from ANOVA using SAS.

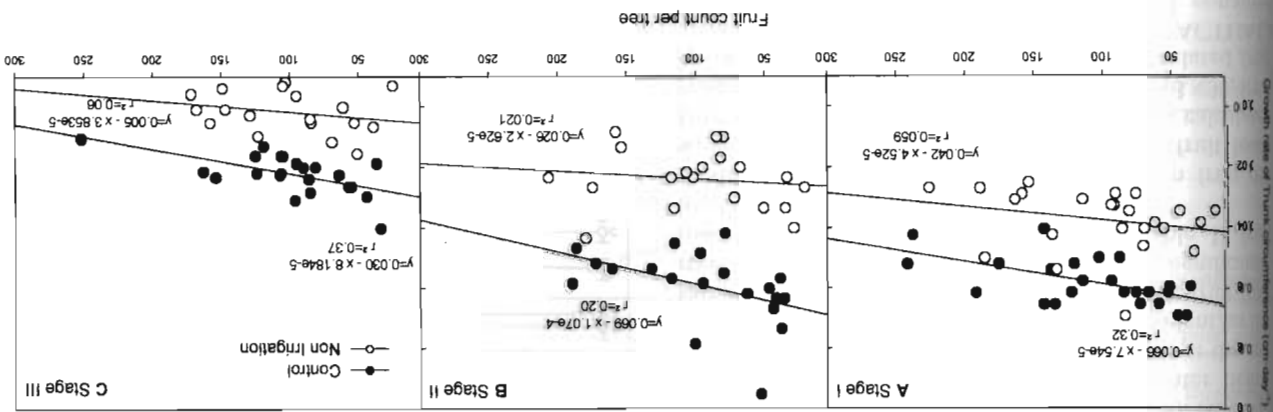


FIG. 4. Effect of fruit load on relative growth rate of trunk circumference during Stage I (A), Stage II (B) and Stage III (C) for the different irrigation treatments. Each symbol represents a single tree observation.

were relatively small ( $\Psi_{STEM}$  values of -0.6 MPa for Control compared with -0.9 MPa for NI-SI), whereas during Stage II and Stage III differences were larger and the most negative values of  $\Psi_{STEM}$  reached approximately -1.7 MPa for both NI-SII and NI-SIII (Figure 3B). Leaf net assimilation rate (A) was reduced by the last day of Stage I for NI-SI compared to the control trees. At the end of both Stage II and Stage III, reductions in A were very pronounced with rates of only 3 to 4  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  being measured in the NI-SII and NI-SIII treatments (Table 1).

Water deficit during Stage I for NI-SI was enough to substantially reduce trunk circumference growth (Figure 4). Increased fruit loads also reduced trunk growth

during this stage in both treatments (control and NI-SI). However, during Stage II, fruit load only significantly reduced trunk growth in control trees. All non-irrigated trees had very low growth rates during this period (NI-SII). Trunk growth rates during Stage III were lower than in any other stage. Trunk growth in the control trees was noticeable and dependent on fruit load, whereas in NI-SIII trees, trunk growth was close to zero and effects of fruit load were not observable. Shoot extension growth was affected to a lesser extent in the NI-SII and shoots of NI-SIII treatment trees were not significantly shorter than those of control trees. Cutting off irrigation during the non-irrigated periods noticeably reduced fruit water content. Although reductions occurred throughout the range of fruit loads considered in this study, differences were more apparent at the highest fruit loads. Among the different phenolog-

RESULTS

The cumulative irrigation applied in the control treatment until the end of Stage III was 550 mm. NI-SI saved only 10% of the water applied with respect to control trees, whereas NI-SII and NI-SIII yielded much greater irrigation savings, around four times higher than NI-SI. Water savings were almost identical in NI-SII and NI-SIII (Figure 1).

The studied cultivar manifested a typical seasonal pattern of fruit growth with the highest accumulation of dry matter occurring during Stage III, i.e. 17%, 30% and 50% of the total dry matter accumulated in Stage I, Stage II and Stage III, respectively (Figure 2). Fruit growth during Stage III, however, appeared slightly less pronounced than in other cultivars (Pavel and DeJong, 1993; DeJong and Grossman, 1995). Both  $\Psi_1$  and  $\Psi_{STEM}$  in the Control trees tended to decline throughout May and thereafter maintained values of about -1.2 and -0.6 MPa for  $\Psi_1$  and  $\Psi_{STEM}$ , respectively (Figure 3).

Differences in water status between control trees and deficit-irrigated trees varied substantially depending on the developmental stage. During Stage I the differences

TABLE 1. Probabilities for the sources of variation in net assimilation rate during the last day of every phenological period studied. Effects tested in ANOVA

Effects tested in ANOVA	Stage I	Stage II	Stage III
Irrigation Treatment (TRT)	0.0476 <sup>(*)</sup>	0.0009	0.0003
Block (Blq)	n.s.	0.0052	0.0453
TRT*Blq	n.s.	n.s.	n.s.
Fruit Load (FL)	n.s.	n.s.	n.s.
TRT*FL	n.s.	n.s.	n.s.
Means for the Treatment effect (TRT)			
Average	12.6 a	10.1 a	11.3 a
Control	12.6 a	10.1 a	11.3 a
NI-SI	9.8 b	11.4 a	11.7 a
NI-SII	13.0 a	3.4 b	10.8 a
NI-SIII	12.8 a	10.5 a	4.5 b

\*Probability according to ANOVA analysis (SAS, 1988)

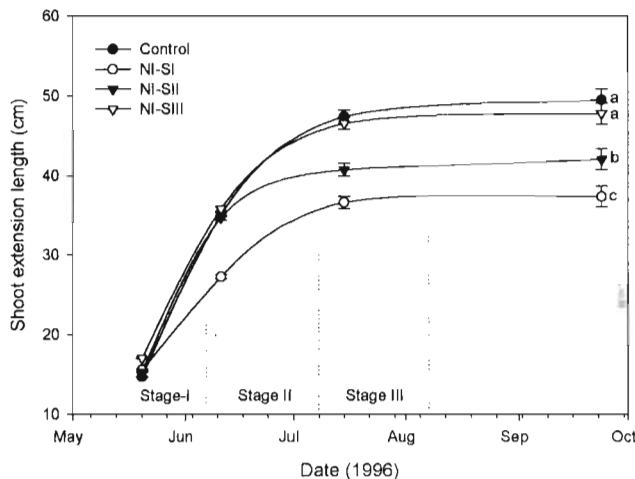


FIG. 5  
Seasonal patterns of shoot extension length for the different irrigation treatments. Each symbol represents the mean of 72 trees. Error bars indicate  $\pm$  SE as obtained from ANOVA using SAS. Different letters indicate statistical difference in cumulative shoot growth according to a Tukey's test at  $P < 0.05$ .

ical periods. Stage III produced the clearest fruit water content differences between irrigation treatments with values in NI-SIII substantially lower than in any other treatment (Figure 6). After the first two non-irrigated periods, fruit water content in the trees with fruit recovered completely, and NI-SI and NI-SII treatment trees had similar values to those of the control during Stages II and III, respectively (Figure 6).

Fruit dry matter, in contrast to fruit water content, was not affected by water stress during the non-irrigat-

ed treatment periods (Table II and Figure 6). However a carry-over effect from the previous water deficit period was apparent in the NI-SI treatment at the end of Stage II and this effect was even more evident for the same treatment after Stage III. In the high fruit load trees, NI-SI fruit dry weight values were significantly lower than in any other treatment (Table II fruit load > 125, and Figure 6).

Since irrigation treatment differences in fruit dry weight were not significant at very low fruit loads (< 65), potential sink demand (PSINK) was calculated from the average of all trees with fruit load < 30, irrespective of irrigation treatments. The calculated fruit growth rates for each developmental stage (ACTUAL) indicated that NI-SI fruits during Stage I remained relatively unaffected and that NI-SII fruits, during Stage II, were also not reduced compared with the control (Figure 7). During Stage III, NI-SIII fruits also did not reflect noticeable differences in growth from those of control, however, there was an apparent reduction in total fruit growth in NI-SI treatment trees at that time. PSINK and PSOURCE tended to increase with developmental stage. However the increase in potential supply from Stage II to Stage III was probably hampered in the case of NI-SI since calculated values of fruit growth for the maximum crop load trees remained substantially less and fruit dry weight at the end of Stage III was significantly less than for any other treatment with high fruit load conditions (Table II, > 125).

PSOURCE was higher than PSINK at about 160 fruits per tree during Stage I and III, whereas during Stage II, this event occurred at a lower fruit load (125 fruits per tree).

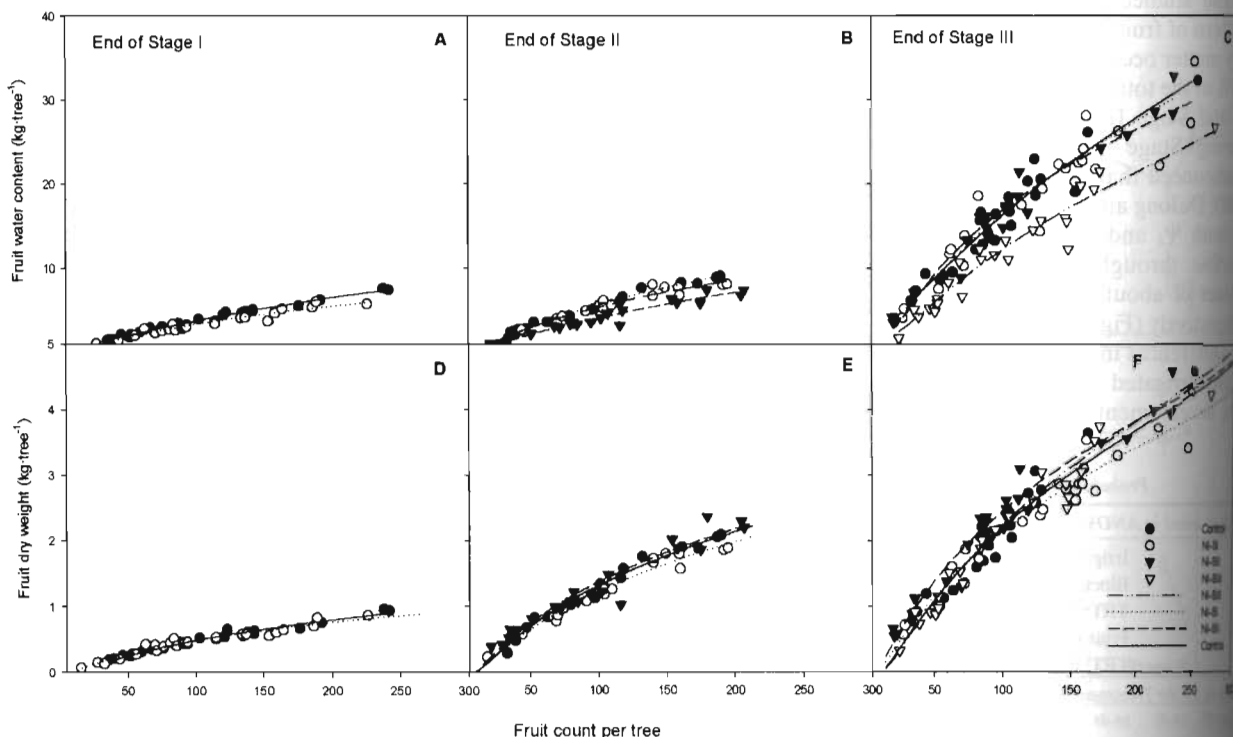


FIG. 6  
Effects of fruit load on fruit water content at the end of Stage I (A), Stage II (B) and Stage III (C), and on the fruit dry weight at the end of Stage I (D), Stage II (E) and Stage III (F). Each symbol represents a single tree observation. Data per irrigation treatment is fitted according to a logarithmic function.

TABLE II  
Probabilities for the test of heterogeneity of slopes in the ANCOVA analysis of fruit dry weight per tree as a function of number of fruits for low and high fruit load levels. Each tree represents a statistical unit

Effect Tested in ANCOVA	Low fruit load (<65)		High fruit load (>125)	
	Treatment (TRT)	Covariable (n° fruits)	Treatment (TRT)	Covariable (n° fruits)
Comparison for Stage I	n.s.	n.s.	n.s.	n.s.
	Heterogeneity of slopes (TRT x n° fruits)	0.0001	0.695	0.678
Comparison for Stage II	n.s.	0.0072	0.0039	1.94ab
	Heterogeneity of slopes (TRT x n° fruits)	n.s.	0.0001	0.527
Comparison for Stage III	n.s.	0.0581	0.0001	0.958
	Heterogeneity of slopes (TRT x n° fruits)	n.s.	0.0001	0.967
Least square means (kg tree <sup>-1</sup> )	Control	0.534	1.94ab	3.57 a
	NI-SI	0.527	1.79b	3.01 b
Least square means (kg tree <sup>-1</sup> )	Control	0.223	0.695	3.52 a
	NI-SI	0.232	0.678	3.59 a

n.s., non statistical significance at P<0.05 using ANCOVA test (SAS 1988).  
Different letters mean statistical significance at P<0.05 using Student's t-test (Fdiff option of reports SAS, 1988).  
n° Probability according to ANCOVA test (SAS 1988).

DISCUSSION

During Stage I, the combined effect of fruit load and water stress on fruit dry-matter accumulation was negligible. (Figure 6 and Table II). The same pattern of response for fruit growth in dry matter between treatments was observed during Stage II and III, with no clear evidence of increased carbon limitation due to water stress. These observed results, at least during Stage III, appear to be in conflict with those of Berman and DeJong (1996), who reported greater dry-matter reductions in fruits that experienced water stress at high fruit loads than in those at low fruit loads. A possible reason why an interaction between fruit load and water stress, was not evident during Stage III in our experiment could be that the highest fruit load levels achieved were not strong enough to limit carbon availability at the same rate as in Berman and DeJong (1996). In this study with four year old peach trees planted at high density, maximum fruit counts were 250 fruits on trees that were allotted 8 m<sup>2</sup> per tree. On the other hand Berman and DeJong (1996) reported mean fruit loads of 561 fruits per tree on trees that were allotted 11 m<sup>2</sup>. Fruit load expressed in fruit numbers per allotted surface area, resulted in maximum loads for heavy cropped trees in our study of 31 fruits m<sup>-2</sup> whereas in the study of Berman and DeJong (1996) unthinned trees reached an average

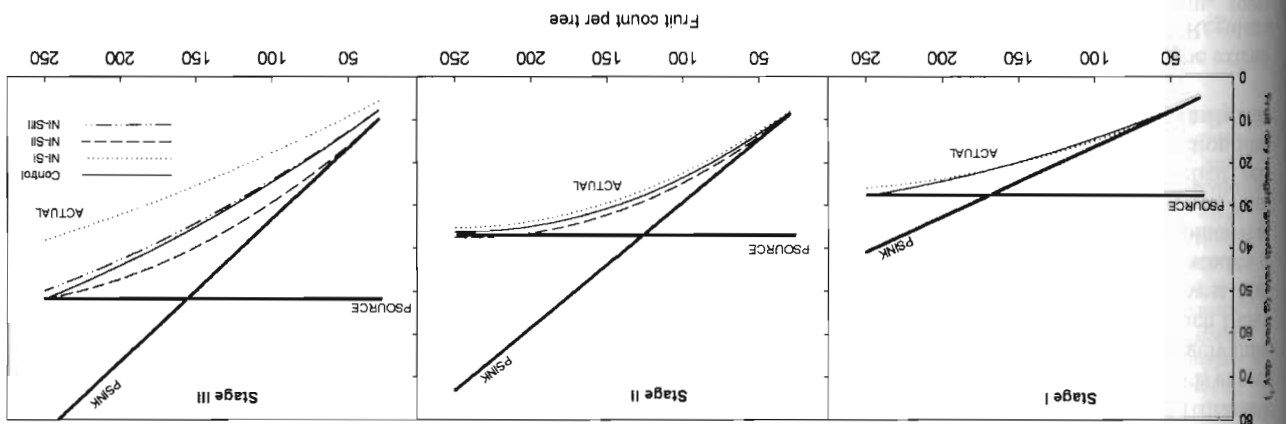


FIG. 7  
Relationship between fruit load and rates of potential sink demand (PSINK), potential source supply (PSOURCE), actual total fruit dry weight growth (ACTUAL) for the different irrigation treatments and each fruit growth development stage: Stage I (A), Stage II (B) and Stage III (C).

of 51 fruits  $m^{-2}$ . This difference in the heaviest crop load treatments between the two studies is the result of the fact that heavier crop loads are more difficult to achieve in young peach trees of some varieties. Another factor that should be taken into account is that early-maturing cultivars have shorter phenological growth phases and since they have less time available for growth they also produce smaller fruits than late-maturing cultivars (Berman *et al.*, 1998). Early-maturing cultivars, however, have been traditionally bred with the target of increasing fruit size and thus the pressure for increased carbon demand over shorter fruit growth periods is higher than in late maturing cultivars (DeJong *et al.*, 1987; Berman *et al.*, 1998). The cultivar used in Berman and DeJong (1996) ('Elegant Lady') matures about two weeks earlier than the cultivar used in this study. This could have also contributed to a lower sensitivity to fruit load. Whatever the reason for less limiting carbon conditions for fruit growth, interactions between fruit load and water stress were not consistently found in this study even during the most sensitive period to water stress (Stage III).

Fruit water content was always reduced by water stress along the range of different fruit loads independently of the phenological stage considered. This fact corroborates the research of Berman and DeJong (1996) who asserted that dry-weight growth was relatively insensitive to water stress compared to fresh weight growth. However, reductions in fruit water content for water stressed trees were less evident during Stage I and most exacerbated during Stage III (Figure 6). These differences could be related to the fact that water deficit levels were not, *a priori*, identical among phenological stages. According to treatment differences in  $\Psi_{STEM}$  (minimum values around -1.7 MPa, Figure 3B), water deficits during Stage II and Stage III were clearly evident whereas the levels of water deficit reached during Stage I were only mild (-0.9 MPa, Figure 3B). However, the concept of what mild water stress represents during Stage I may depend on the process being evaluated. From a canopy growth standpoint, the implications of this very mild water stress level on shoot elongation growth were more severe during Stage I than during Stage II (Figure 5). In addition, the only component of seasonal fruit dry matter affected by water stress in any of the tested irrigation treatments was Stage III fruit-growth for fruits in treatments receiving water stress during Stage I. Clearly water deficit (the level of tissue dehydration) and water stress (the effect of dehydration on function) did not convey the same meaning when comparing different phenological stages or processes (Bradford and Hsiao, 1982).

According to the conceptual framework of the Source-Sink demand model used in this study, there could be two explanations for the carry-over effect of the NI-SI treatment on the fruit growth during Stage III. PSINK may have been affected by water stress during Stage I, perhaps by means of a reduction in cell division or cell enlargement, thus reducing the fruit growth potential during subsequent periods of fruit growth. Alternatively, PSOURCE was reduced because the NI-SI treatment experienced a significant reduction in leaf net assimilation rate and/or leaf photosynthetic surface area that affected subsequent availability of assimilates to fruits. The hypothesis of an altered sink potential

for NI-SI treatment fruit during Stage III seems unlikely since fruit dry weight at low fruit loads was not affected by the irrigation treatments (Table II). Recalculation of PSINK considering only NI-SI data, provided a very similar response to that of the control (data not included). The second hypothesis, that PSOURCE could have been reduced in NI-SI treatment trees, seems to have little support from the slight decreases in leaf net assimilation rate that occurred during Stage I followed by assimilation rates equivalent to the Control during Stage II or Stage III (Table I). Furthermore decreases in A were dramatic during stages II and III non-irrigation treatments but dry-weight growth rates at high fruit load were similar among irrigation treatments (Table II; Figure 7). However, the implication of the significant reduction in shoot extension growth for NI-SI treatment should not be neglected. The decrease in shoot length had been effective for more than two months by the time Stage III started. Moreover, early shoot growth is considered important for fruit growth since it occurs close to fruits compared with late shoot growth which occurs mainly in watersprouts (DeJong *et al.* 1987). These factors could result in less photosynthetic leaf area directly supporting fruit growth and thus a possible reduction in the carbon reservoir available for fruit growth as compared with control trees with the same amount of fruit. In other words, fruit count may not be a good indicator of tree fruit load when comparing NI-SI and control treatments during Stage III due to the differences in canopy size and capacity for obtaining readily available carbon for fruit growth. The NI-SI treatment probably had a higher effective fruit load than control trees for the same fruit count.

The results of this experiment showing little effect on dry-matter fruit growth by the moderate-to-severe water stress applied during stage III seems rather surprising, since for fresh market oriented production, this is considered the most sensitive period for irrigation. However, this belief is mostly derived from the decrease in fruit size that commonly occurs when irrigation is reduced during Stage III. Indeed, Girona *et al.* (1993) found significant reductions in fruit size as a result of water stress during Stage III but no effect on fruit dry weight. Furthermore, Naor *et al.* (1999 and 2001) in nectarines studied the combined effect of water stress and fruit load on final fruit size and found dramatic effects for most of the range of fruit loads. This is expected when considering that final fruit size is largely influenced by changes in water content since a peach fruit is made up of approximately 85 % water at harvest. Fruit dry weight, however was not reported in the studies of Naor *et al.* (1999 and 2001), but in prunes, Lampinen *et al.* (1995), found no reduction in fruit dry weight as a result of water stress during Stage III. Water deficit near harvest is a common practice in prune production since deficit irrigated prunes can be dried more easily than when full irrigation is applied near harvest.

The practical implications of this study can be extended to the use of an irrigation technique called Regulated Deficit Irrigation (RDI) (Behboudian and Mills, 1997). The objective of this technique is to conserve water and reduce excessive vegetative growth in high density planted trees, which theoretically can produce a benefit in final fruit size (Chalmers *et al.*, 1981) but the latter event

growth was evident during Stage III in fruits from trees not irrigated during Stage I (NI-SI). According to the Source-Sink demand model, a possible explanation for these growth reductions may be related to a reduction in the potential source supply. Since substantial reductions in assimilation rates per unit of leaf area did not impair the capacity to allocate dry matter to the fruits during the period in which water stress occurred (Stage II and Stage III, in NI-SII and NI-SIII, respectively), we hypothesize that the reduction in shoot growth during early shoot development (Stage I) could have impacted the development of leaves close to fruits and thus reduced the carbon supply to fruits during the later period of high demand (Stage III).

In summary, for the growing conditions of this experiment (mid-to-late season cultivar and young trees), the influence of fruit load on water stress sensitivity to fruit growth in dry matter seemed negligible in all stages of fruit development. However, an impairment in fruit

- BEHROUZIAN, M. H. and MILLS, T. M. (1997). Deficit irrigation in deciduous orchards. *Horticultural Reviews*, **21**, 105-31.
- BERMAN, M. E. and DEJONG, T. M. (1996). Water stress and crop load effects on fruit fresh and dry weights in peach (*Prunus persica*). *Tree Physiology*, **16**, 859-64.
- BERMAN, M. E., ROSATI, A., PAGE, L., GROSSMAN, Y. L. and DEJONG, T. M. (1998). Using simulation modelling to estimate the relationship between date of fruit maturity and yield potential in peach. *Fruit Varieties Journal*, **52**, 229-35.
- BOLAND, A. M., MITCHELL, P. D., JERRIE, P. H. and GOODWIN, I. (1993). The effect of regulated deficit irrigation on tree water use and growth of peach. *Journal of Horticultural Science*, **68**, 261-74.
- BRADFORD, K. J. and HSIAO, T. C. (1982). Physiological responses to moderate water stress. *Encyclopedia of Plant Physiology*, **NS**, *Physiological Plant Ecology II*, vol. 12 B, 550-87.
- CHALMERS, D. J., MITCHELL, P. D. and VAN HEER, L. (1981). Control of peach tree growth and productivity by regulated water supply: tree density, and summer pruning. *Journal of the American Society for Horticultural Science*, **106**, 307-12.
- CHALMERS, D. J., OLSSON, K. A. and JONES, T. R. (1983). Water relations of peach and orchards. In: *Water deficits and plant growth*, Vol. VII. Academic Press, Inc., London and New York, 197-232.
- DEJONG, T. M., DOYLE, F. F. and DAY, R. K. (1987). Seasonal patterns of reproductive and vegetative sink activity in early and late maturing peach (*Prunus persica*) cultivars. *Physiologia Plantarum*, **71**, 83-8.
- DEJONG, T. M. and GROSSMAN, Y. L. (1995). Quantifying sink and source limitations on dry matter partitioning to fruit growth in peach trees. *Physiologia Plantarum*, **95**, 437-43.
- GIRONA, J., MATA, M., GOLDHAMER, D. A., JOHNSON, R. S. and DEJONG, T. M. (1993). Patterns of soil and tree water status and leaf functioning during regulated deficit irrigation scheduling in peach. *Journal of the American Society for Horticultural Science*, **118**, 580-6.
- GIRONA, J. (2003). Peach tree response to single and combined regulated deficit irrigation regimes under shallow soils. *Journal of the American Society for Horticultural Science*, **128**, 432-40.
- GOLDHAMER, D. and SNYDER, R. L. (1989). *Irrigation scheduling: A guide for efficient on-farm water management*. University of California Division of Agriculture and National Resources. Publ. 21454.
- VON CAEMMERER, S. and FAROUHAR, G. D. (1981). Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves. *Plants*, **153**, 376-87.
- GOLDHAMER, D. A., SALINAS, M., SOLER, M. and MORIANA, A. (2001). Peach trees perform similarly despite different irrigation scheduling methods. *California Agriculture*, **55**, 25-9.
- GROSSMAN, Y. L. and DEJONG, T. M. (1995). Maximum fruit growth potential following resource limitation during peach growth. *Annals of Botany*, **75**, 561-67.
- LAMPINEN, B. D., SHACKEL, K. A., SOUTHWICK, S. M., OLSSON, B. and YEAGER, J. T. (1995). Sensitivity of yield and fruit quality of French prune to water deprivation at different fruit growth stages. *Journal of the American Society for Horticultural Science*, **120**, 139-47.
- LI, S. H., HUGUERTU, J. G., SCHOCH, P. G. and ORLANDO, P. (1989). Response of peach tree growth and cropping to soil water deficit at various phenological stages of fruit development. *Journal of Horticultural Science*, **64**, 541-52.
- MCCUTCHEAN, H. and SHACKEL, K. A. (1992). Stem-water potential as a sensitive indicator of water stress in prune trees (*Prunus domestica* L. cv. French). *Journal of the American Society for Horticultural Science*, **117**, 607-611.
- NAOR, A., KLEIN, I., HUPERT, H., GRINBLAT, Y., PERES, M. and KAUFMAN, A. (1999). Water stress and crop level interactions in relation to nectarine yield, fruit size distribution, and water potentials. *Journal of the American Society for Horticultural Science*, **124**, 189-193.
- NAOR, A., HUPERT, H., GRINBLAT, Y., PERES, M., KAUFMAN, A. and KLEIN, I. (2001). The response of nectarine fruit size and mid-day stem water potential to irrigation level in stage III and crop load. *Journal of the American Society for Horticultural Science*, **126**, 140-3.
- PAVEL, E. W. and DEJONG, T. M. (1993). Source- and sink-limited growth periods of developing peach fruits indicated by relative growth rate analysis. *Journal of the American Society for Horticultural Science*, **118**, 820-4.
- SAS. (1988). *SAS/STAT User's Guide*, release 6.03 edn. SAS Institute Inc., Cary, NJ, USA.
- SCHOLANDER, P., HAMMEL, H., BRADSTREET, E. and HEMINGSEN, E. (1965). Sap pressure in vascular plants. *Science*, **148**, 339-45.
- TURNER, N. C. and LONG, M. I. (1980). Errors arising from rapid water loss in the measurement of leaf water potential by the pressure chamber technique. *Australian Journal of Plant Physiology*, **7**, 527-37.
- VON CAEMMERER, S. and FAROUHAR, G. D. (1981). Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves. *Plants*, **153**, 376-87.