Water stress and crop load effects on vegetative and fruit growth of 'Elegant Lady' peach [*Prunus persica* (L.) Batch] trees

Ahmed Mahhoua, Theodore M. DeJongb, Tiesen Caob, Ken S. Shackelb

^a Department of Horticulture IAV Hassan II, BP 6202, Rabat, Morocco a.mahhou@iav.ac.ma amahhou1@yahoo.fr

^b Department of Pomology, University of California Davis, Davis, CA 95616, USA

a.mahhou@menara.ma

Water stress and crop load effects on vegetative and fruit growth of 'Elegant Lady' peach [*Prunus persica* (L.) Batch] trees.

Abstract — Introduction. Vegetative and fruit growth in fruit trees are differentially sensitive to water deficit during the season depending on the stage of fruit growth. Attempts have been made to evaluate the possibilities of using regulated deficit irrigation to control vegetative growth and save water in the fruit industry. Materials and methods. Effects of water stress (WS) and crop load (CL) on fruit growth and carbon assimilation rates were evaluated in a 7-year-old 'Elegant Lady' peach orchard. A completely randomized block design with 2 × 3 factors [irrigation with two levels (control and WS) and CL with three levels (light, commercial and heavy)] was used. Results and discussion. Both WS and CL affected fruit growth during the last stages but not early on. CL did not affect trunk water potential which was, however, significantly reduced by WS throughout the day and the season. Trunk water potential of water-stressed significantly reduced by WS industrious the day and the season. Think water potential of water-stessed trees was lower than that of control trees throughout the day and the season regardless of CL. The magnitude of WS increased as the season progressed. Stomatal conductance, transpiration rate and CO₂ assimilation rate were not affected by CL but were reduced by WS. The trees responded (acclimated) to stress by progressively reducing their transpiration rate as the severity of stress increased. For each irrigation régime, assimilation rates were similar for all three crop levels. This indicated the existence of alternate sinks for assimilates when CL was low, which compensate for the reduction of fruit sink activity resulting from fruit thinning. Conclusion. Water deficit reduced trunk water potential, stomatal conductance, transpiration and photosynthesis in 'Elegant Lady' peach trees. However, CL had a limited effect on these functions. There were good correlations between trunk water potential and either stomatal conductance or assimilation rate in water-stressed trees but not in control trees. This indicates a poor coordination between leaf functions in peach trees under optimal conditions. However, these relationships were stronger under WS conditions. Thus, water use efficiency appeared to increase under water deficit conditions.

Prunus persica / drought stress / trees / fruits / pruning / growth / fruiting / water potential / stomata / transpiration

Effets du stress hydrique et de la charge fruitière sur la croissance végétative et le développement du fruit chez la variété de pêcher 'Elegant Lady' [Prunus persica (L.) Batch].

Résumé — Introduction. Chez les arbres fruitiers, la croissance végétative et le développement du fruit sont différemment sensibles au déficit hydrique au cours de la saison et selon le stade de formation du fruit. Des essais ont été menés pour évaluer les possibilités d'utilisation de l'irrigation en déficit régulé pour maîtriser la croissance végétative et économiser l'eau lors du développement du fruit. **Matériel et méthodes**. Les effets du stress hydrique (SH) et de la charge fruitière (CF) sur le développement du fruit et les taux d'assimilation du carbone ont été évalués dans un verger de pêchers 'Elegant Lady' de 7 ans. Le dispositif expérimental a comporté des blocs complètement randomisés de 2 × 3 facteurs : irrigation avec deux niveaux (témoin et SH) et CF avec trois niveaux (légère, commerciale et forte). Résultats et discussion. Le SH et la CF ont tous deux affecté la croissance de fruit pendant les dernières étapes de son développement mais pas dès son début. La CF n'a pas affecté le potentiel hydrique du tronc qui, cependant, a été sensiblement réduit par le SH tout au long du jour et de la saison. Le potentiel hydrique du tronc des arbres soumis à une contrainte en eau a été inférieur à celui des arbres témoins tout au long du jour et de la saison indépendamment de la CF. L'importance du SH a augmenté en même temps que la saison progressait. La conductance stomatique, le taux de transpiration et le taux d'assimilation de CO₂ n'ont pas été affectés par la CF, mais ils ont été réduits par le SH. Les arbres ont répondu (se sont acclimatés) au SH en réduisant progressivement leur taux de transpiration à mesure que la sévérité de la contrainte augmentait. Pour chaque régime d'irrigation, les taux d'assimilation ont été semblables quelle que soit la CF. Cela indiquerait que, quand la CF est basse, il existerait des puits alternatifs pour assimilats, qui compenseraient la réduction d'activité de puits du fruit résultant de l'éclaircissage des fruits. **Conclusion**. Le déficit en eau a réduit le potentiel hydrique du tronc, la conductance stomatique, la transpiration et la photosynthèse chez les pêchers Elegant Lady. Cependant, la CF a eu un effet limité sur ces fonctions. Il y a eu de bonnes corrélations entre le potentiel hydrique du tronc et soit la conductance stomatique soit le taux d'assimilation dans les arbres soumis au SH, mais pas dans des arbres témoins. Cela indiquerait une faible coordination entre les fonctions de la feuille chez ce pêcher en conditions optimales. Cependant, ces relations ont été plus fortes dans des conditions de SH. Ainsi, l'efficacité de l'eau apportée a semblé augmenter dans des conditions de déficit hydrique.

Prunus persica / stress dû à la sécheresse / arbre / fruits / taille / croissance / fructification / potentiel hydrique / stomate / transpiration

Received 8 March 2004 Accepted 28 September 2004

Fruits, 2005, vol. 60, p. 55–68 © 2005 Cirad/EDP Sciences All rights reserved DOI: 10.1051/fruits:2005013

RESUMEN ESPAÑOL, p. 68

^{*} Correspondence and reprints

1. Introduction

Vegetative and fruit growth in fruit trees are sensitive to water stress. However, the two parameters are differentially sensitive to water deficit during the season depending on the stage of fruit growth. The need for water use efficiency and the different vulnerabilities of reproductive and vegetative growth have led researchers to evaluate the possibilities of using regulated deficit irrigation to control vegetative growth and save water. Withholding irrigation for two weeks before and after the beginning of pit hardening has been reported to limit shoot growth and stimulate subsequent fruit growth in 'Golden Queen' peach [1]. During the period of rapid vegetative growth of Golden Queen peach trees, apparently both vegetative and fruit growth declined as irrigation quantity decreased [2].

Soil moisture stress decreases stomatal conductance and photosynthetic activity in fruit trees [3]. A close positive relationship between stomatal conductance and photosynthesis has been reported for apple over a wide range of environmental conditions. In fact, trees grown under stress, either due to soil moisture or high vapor pressure deficit, do not lose as much water as well-watered plants and can maintain some minimum level of photosynthesis [3].

Incipient water stress has been reported to significantly reduce the leaf stomatal conductance and transpiration rate without affecting the CO₂ assimilation rate in peach [4]. Similarly, daily mean leaf water potential (LWP) was reported to be lower in dry than in irrigated peach trees [5]. For all dates, the diurnal trends showed a decrease in LWP values of both dry and well irrigated plants from early morning until 14:30 and a recovery to higher values in the afternoon at 16:30. In this study, water deficit induced reductions in CO₂ assimilation rates which corresponded to reductions in transpiration rate [5].

Significant differences in seasonal patterns of stomatal conductance were observed among postharvest irrigation treatments in proportion to irrigation level in early harvested peaches [6]. Predawn water potential of the wet treatment remained constant at

-0.3 Mpa, whereas that of the dry treatment became more negative as the season progressed [6]. The seasonal increase in trunk radius of the dry-treatment trees was reduced by 33% relative to wet or medium treatments [6]. Dormant pruning weights were 13% less in dry treatments than in wet treatments [6]. Return bloom and fruit set were greater in dry treatments by (30 and 70)%, respectively. There were no significant differences among irrigation treatments for fruit yield or fruit size following commercial thinning in the following year. However, fruit maturity was slightly delayed in the dry treatment [6].

Total dry matter production of young potted peach trees was reduced with each incremental decrease in applied water [7]. Inhibition or reduction of lateral branching and new leaf production was observed soon after water stress was imposed. These two factors were the major contributors to differences in tree biomass production. Root production was maintained at similar levels in all but the driest treatment. The root fraction of total biomass increased from 0.4 to 0.6 as the level of water stress increased from (75 to 50)% of full irrigation. Growing leaves and internodes of the driest treatments reached maturity at a smaller size.

Regulated deficit irrigation induced clear differences in soil and predawn leaf water potential on 'Cal Red' peach trees. It also reduced stomatal conductance, net CO₂ assimilation and trunk growth. Leaves on trees subjected to regulated deficit irrigation were photosynthetically the most water-use efficient during the last part of the stress period [8]. Shoot length, fresh and dry weight, and the relative increment in trunk girth decreased as the level of crop load increased in 'Catherine' peach trees [9].

Water deficit imposed during the first phase of rapid fruit growth has been reported to significantly increase fruit size at harvest in peach [10]. However, small fruits were produced from trees receiving an imposed water deficit during the final accelerated fruit growth, or throughout the fruit development period. Water stress applied in the first stage of fruit growth induced a slight increase in fruit size if normal water supply was insured during the last two stages of

fruit growth in peach [11]. The last stage of very active fruit growth prior to harvest is very critical and remains sensitive to water shortage, which leads to a reduction in fruit size and yield.

Peach trees carrying heavy crop load (unthinned) had lower fruit water potential and higher fruit osmotic potential, and, consequently, lower fruit turgor compared with trees carrying a light crop load [12]. Peach fruit growth during the day was less and fruit shrinkage was greater in the heavy crop than in the light crop, and this appeared to be correlated with the lowest fruit water potential and turgor potential in the heavy crop [12]. Leaf water potential was also lower in the heavy crop compared with the light crop. The authors concluded that increased crop load increased fruit water deficit, which reduced fruit growth. Hence, the reduction in fruit size commonly associated with increased crop load may be due, at least in part, to the effect of crop load on fruit water relations.

Water stress significantly reduces trunk growth [2], stem extension growth [10] and tree biomass accumulation in peach trees [7]. Crop load also has an inhibitory effect on the growth of stems, leaves and trunk wood in peach [9, 13]. Reduced vegetative growth in cropping trees is usually attributed to the competition imposed by the developing fruit for carbohydrates. Fruit reduced the amount of carbohydrates available for stem growth in peach [13]. Neither the presence of fruit nor reduced irrigation significantly altered the timing of diurnal fluctuations in the stem growth rate in peach [14]. However, stems with subtending fruit had significantly reduced growth. Crop load had no significant effect on relative stem extension rates and most of the reduction in absolute growth was the result of a smaller elongation zone. Water shortage induced a significant reduction in the stem elongation zone and total daily stem growth: in particular, the stem elongation and growth rates appeared negatively correlated to the water potential.

The water status of well-watered 'Elegant Lady' peach trees was not affected by crop load [15]. However, in trees receiving reduced irrigation, the degree of water stress increased

with increasing crop load. Water stress negatively affected fruit fresh weight in all crop loads in peach [15]. On the contrary, the fruit dry weight was reduced only on trees with heavy crop loads (unthinned) but not on those with light to moderate crop loads. The reduction of fruit dry weight in heavily cropping trees was likely due to carbohydrate source limitations resulting from large crop demands and water stress limitations on photosynthesis [15].

Studies of fruit effects on leaf photosynthesis of fruit crops have given controversial results [16]. The "fruit effect" would manifest itself only under conditions where the leaf assimilation rate was at its full potential. Significant differences in leaf photosynthetic rate between the heavily cropping and nonfruiting trees have been reported to be most evident in July and August at the time of maximum accumulation of dry matter in the apple fruit [17]. Similarly, CO2 uptake and stomatal conductance increased in peach leaves during June and July when fruit dry weight accumulation was high [18]. However, there were no significant differences in leaf gas exchange characteristics between fruiting and defruited 'O'Henry' peach trees during early stages of fruit growth. During the early part of the last stage of fruit growth, CO₂ assimilation rates were slightly higher in fruiting than defruited trees. These increased assimilation rates were associated with an increase in leaf conductance. Thus, the fruit effect on photosynthesis appeared to be primarily related to stomatal behavior [18]. Thus, the presence of fruit can positively affect the rate of CO2 assimilation in peach but the magnitude of this effect is likely to depend on environmental conditions. If this "fruit effect" is related to carbohydrate demand, the relatively moderate crop load effects on CO2 assimilation [18] may be associated with the favorable environmental conditions under which the experiments were conducted. The latter would stimulate photosynthate demands by development of alternate sinks such as vigorous shoot and root growth.

The objectives of this study were to explore the influence of cropping (fruit sink demand) on leaf function (leaf assimilation rate, stomatal conductance and leaf transpiration rate) under fully irrigated and water

Table I.Applied irrigation during the growing season used to study the water stress effects on vegetative and fruit growth of 'Elegant Lady' peach trees. Two treatments are considered: control trees and water-stressed trees (Winters, California, USA, 1998).

Date	Irrigation for control trees (mm)	Irrigation for water-stressed trees (mm)	Potential evapotranspiration (mm per day)
15 June	33	-	36
20 June	-	-	55
27 June	47	-	43
6 July	47	-	46
13 July	47	-	47
20 July	47	12	50
24 July	-	12	47
27 July	47	12	44
3 August	47	16	47
10 August	47	12	-

deficit conditions and to use fruit growth potential measurement techniques to assess the influence of water stress on the ability of the tree to meet fruit growth demands.

2. Materials and methods

2.1. Plant material

This experiment was carried out in 1998 at the UC Davis Wolfskill Experimental Orchard, Winters, California. One hundred and twenty trees, in eight rows, of 7-year-old 'Elegant Lady' peach [*Prunus persica* (L.) Batschl orchard grafted on 'Lovell' rootstock, were selected for uniformity. The orchard was planted in a high density formation [(5.5 × 2) m spacing] and trained to a perpendicular-V [19]. Trees received standard commercial dormant pruning and care in terms of fertilization and pest management. Fruit harvest was performed in the first week of August.

2.2. Irrigation treatments

The experiment was set up in a completely randomized block design with four blocks. Eight pairs of adjacent half-rows were selected as blocks. Four half-rows corresponded to

the control irrigation treatment and the other four represented the water stress treatment. In order to prevent surface water movement between treatments, the water stress treatments were isolated by a border half-row on each side.

Reference evaporation (ET₀) data for the experimental location were obtained from the California Irrigation Management System (CIMIS). Irrigation was withheld until mid-June during the first stages of fruit growth, because of the very cool and wet spring. During May alone, the rainfall was 87 mm, of which 56 mm fell during the last four days of the month. Local reference evaporation data and irrigation schedule data were noted (*table I*).

2.3. Crop load treatments

Within each irrigation level, the control and water stress treatment rows were divided into five sub-plots, consisting of pairs of adjacent trees. Sub-plots were randomly assigned to one of three thinning treatments: light crop load (minimum 10 cm between fruit), commercial crop load (minimum 5 cm between fruit), and heavy crop load (no fruit thinned). Light and commercial crop load treatments were imposed by fruit thinning at the third week of May, five weeks before fruit harvest.

The experimental design consisted of a completely randomized design with (2 × 3) factors: factor A being irrigation with two levels (control and water stress) and factor B being thinning treatments with three levels (light, commercial and high crop load).

2.4. Fruit growth measurements

As soon as crop loads were imposed by fruit thinning, six fruits (three for each side of the perpendicular V) were randomly selected and tagged on each of four trees per treatment. Fruit growth was assessed from the beginning of June until the end of July by weekly measurements of maximum fruit diameter, using a digital caliper. At each measuring date, a sample of 30 fruits was harvested and used to estimate the relationship between fruit diameter and fresh and dry weights. Dry weight of fruits was taken after drying the fruits in a forced air draft oven at 65 °C until constant weight. The established relationship between fruit diameter and fruit weights was used to convert fruit diameter measurements on the experimental trees to corresponding fruit fresh and dry weights. The fruit measurements were used to express fruit growth as:

- fruit diameter growth (mm), fruit fresh weight growth (g) and fruit dry weight growth (g);
- relative fruit diameter growth (mm·day⁻¹),
 relative fruit fresh weight growth (mg·day⁻¹)
 and relative fruit dry weight growth (mg·day⁻¹);
- relative fruit diameter growth rate (mm·mm⁻¹·day⁻¹), relative fruit fresh weight growth rate (mg·g⁻¹·day⁻¹) and relative fruit dry weight growth rate (mg·g⁻¹·day⁻¹).

2.5. Trunk water potential measurements

Trunk water potential measurements were made at weekly intervals during the last five weeks before fruit harvest using a Scholander Pressure Chamber (Soil Moisture Equipment Co., Santa Barbara, CA). Measurements were performed in the morning (08:30 to 09:30), around midday (11:30 to 12:30) and in the afternoon (14:30 to 15:30)

under clear sky conditions, operating on shaded leaves, close to the main trunk. The chosen leaves were bagged, with plastic sheaths covered with aluminum foil, for at least half an hour before monitoring [20].

2.6. Leaf gas exchange measurements

Leaf gas exchange measurements were made at weekly intervals, in concomitance with trunk water potential monitoring, using a CIRAS-1 portable equipment PP System. Healthy mature leaves of approximately the same age and located in the outer portions of the canopy were used for measurements: in particular, eight leaves on four trees per each irrigation-crop load treatment were sampled. Gas exchange data were acquired with leaves kept orthogonal to sunlight direction. Gas exchange data allowed the determination of leaf conductance (mmol·m⁻²·s⁻¹), photosynthetic (µmol CO₂·m⁻²·s⁻¹), and transpiration (mmol H₂O·m⁻²·s⁻¹) activities.

2.7. Data analysis

The data was analyzed by a two-way analysis of variance as a (2×3) factor factorial in a randomized complete block design for general variance. The mean separation was performed using Duncan's Multiple Range test at a significant level of P < 0.05.

3. Results and discussion

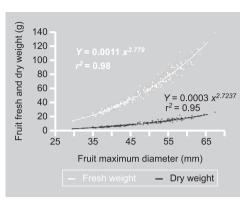
3.1. Fruit growth

The relationship of fruit fresh and dry weight to fruit diameter fit the logarithmic transformation equation $y = a x^b$ (*figure 1*). Palmer [21] reported that the relationship of fruit volume and both fresh and dry weight to diameter for two pear cultivars ('Barlett' and 'Packam Triumph') was also predicted by the logarithmic transformation.

3.1.1. Fruit diameter

In general, for fruit diameter, there was no interaction between the two irrigation and

Figure 1.
Relationship of fruit fresh and dry weight to the fruit maximum diameter in 'Elegant Lady' peach trees.



crop load factors for all the measuring dates. In particular, there was no main effect of irrigation. Fruit diameter on water-stressed trees was smaller than that of the control treatment starting from July 8 (*figure 2a*).

There was no effect of crop load for the first three measuring dates. There was a main effect of crop load starting the first of July with fruit diameter of the commercial crop load and light crop load being similar, but significantly higher than that of the heavy crop load. At the last measurement date the difference between light crop load and commercial crop load treatments was significant (figure 2a).

The fruit growth on stressed trees, even though of similar shape to the fruit on control trees, was lagging behind, indicating that stressed trees could not respond to the demand of the fruit. The negative effect of water deficit on fruit growth could be due to limited cell elongation and/or reduced photosynthesis.

Regarding the crop load effect, the trees had enough nutrients and photosynthates to insure appropriate fruit growth until the end of June. As the season progressed, the diameter fruit growth on heavy crop load trees became negatively affected; on the contrary, light crop load and commercial crop load had higher and similar diameter increases until the last measurement date. The heavy crop load trees became source-limiting during the growing season because of high fruit competition and could not respond to fruit demand, which resulted in a reduced fruit size.

3.1.2. Fruit diameter growth rate and relative growth rate

For the fruit diameter growth rate, no interaction between irrigation and crop load for all measuring dates was found. During the week of 24 June to 1 July and the third week of July, the fruits on heavy crop load trees were growing at a slower rate than those of light crop load and commercial crop load. During the first two weeks of July, both fruit growth and relative growth rates were higher for light crop load trees than for commercial crop load trees, which were themselves higher than those of heavy crop load trees.

No main effect of irrigation resulted during the first week of measurement. This could be explained by the heavy rain of the end of May. Starting from the second week of measurement, both growth and relative growth rates of the fruit diameter were higher for the control trees than for the waterstressed trees. The difference in growth rates persisted until the last measurement date and its magnitude increased as the season progressed.

For the crop load (CL) main effect the difference appeared, earlier than the water stress effect, during the first week of measurement. Thus, heavy crop load trees showed a slower fruit growth rate than that of the light crop load and commercial crop load trees, indicating that, even under non-limiting conditions, the trees could not respond to the demand of heavy crop load. The fruits on such trees were thus source-limiting and, as the season progressed (high climatic and fruit demands), the fruit growth rates became different between light crop load and commercial crop load trees.

3.1.3. Fruit fresh weight

For fruit fresh weight, no interaction between irrigation and crop load factors resulted for all measurement dates. A main effect of irrigation was shown starting July 8: the average fruit fresh weight on the control trees was higher than that of water-stressed trees. The difference between the control and water-stressed trees increased as the season progressed. No crop load effect was detected during the first three measurement dates.

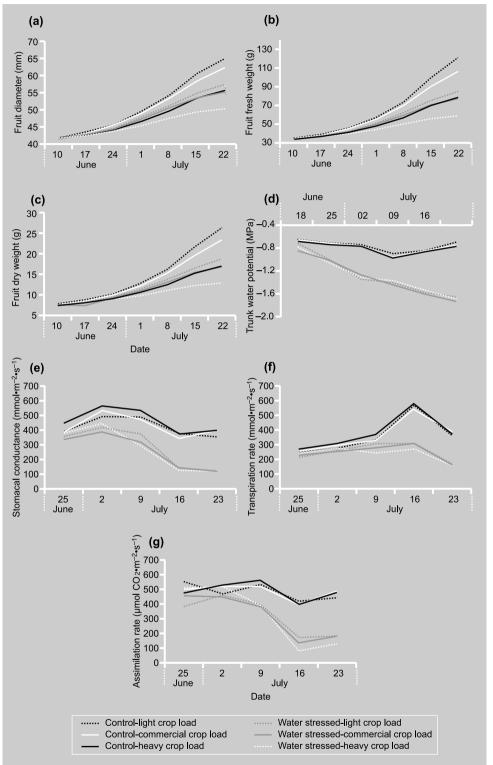
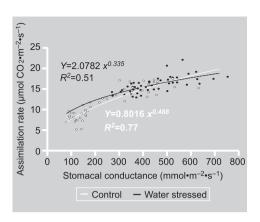


Figure 2.
Effects of crop load and irrigation on fruit growth and leaf function of 'Elegant Lady' peach trees: fruit diameter (a), fruit fresh weight (b), fruit dry weight (c), seasonal pattern of midday trunk water potential (d), stomatal conductance (e), transpiration rate (f) and CO₂ assimilation rate (g).

Figure 3.
The relationship between CO₂ assimilation rate and stomatal conductance at noon for control and water-stressed trees of 'Elegant Lady' peach trees.



The crop main effect appeared earlier than that of irrigation. The fruit fresh weight was smaller on heavy crop load trees than on trees with light crop load and commercial crop load. At the last measurement date, the difference between light crop load and commercial crop load was also evident (*figure 2b*).

3.1.4. Fresh weight growth rate and relative growth rate

For the fresh weight growth rate, no interaction between irrigation and crop load was found for all dates of measurements. There was a water stress main effect starting from 17th of June, while that of crop load was one week earlier. On heavy crop load trees, fruits had slower growth and relative growth rates than those on light crop load and commercial crop load plants. During the last weeks of measurement, the fruit growth rate and relative growth rate were different even for light crop load and commercial crop load trees. Even under optimal conditions and above a certain threshold of crop load, the competition among fruits becomes so intense as to impose limitation of the supply necessary for fruit growth.

3.1.5. Fruit dry weight

For fruit dry weight, there was no interaction between the water stress factor and the crop load factor, and no water stress main effect was detected during the first weeks of measurement. However, starting on 8th of July, the fruit dry weight appeared smaller on water-stressed trees than on the control trees and the magnitude of the difference increased with time. No crop load effect dur-

ing the first three weeks of measurement was shown. Starting 1st of July the fruit dry weight appeared smaller on heavy crop load trees than on light crop load and commercial crop load trees. Fruit dry weight of light crop load and commercial crop load trees was different in the last week of measurement. The crop load effect appeared prior to the irrigation effect indicating that, even at their maximum potential and under optimal conditions, peach trees could not respond to the high demand of heavy crop load and the fruit could be source-limiting, ending up being of a smaller size (*figure 2c*).

3.1.6. Fruit dry weight growth rate and relative growth rate

For the fruit dry weight growth rate, no interaction between irrigation and crop load was shown for all dates of measurement. The water stress main effect was evident starting from the 2nd date of measurement. The fruits on control trees grew at faster rates than those of water-stressed trees and the magnitude of the difference increased as the season progressed. No main effect of crop load was detected during the first 2 measurement dates; a significant crop load effect was found during the following two measurement days when fruit dry weight growth and relative growth rates were similar for the light crop load and commercial crop load trees and higher than for the corresponding heavy crop load trees. For the last two measurement dates, fruit dry weight growth and relative growth rates were higher for light crop load trees than for commercial crop load trees and higher than for heavy crop load trees. Heavy crop load reduced fruit growth just as water stress did, and the magnitude of this reduction increased with time as the climatic demand of fruit growth became significant.

3.2. Trunk water potential

Fot trunk water potential, no interaction between water stress and crop load and no crop load main effect were detected for the entire season regardless of time of measurement. However, there was a water stress main effect: trunk water potential of waterstressed trees was significantly lower than that of control trees, beginning in the morning (figure 2d). Thus, water stress reduced trunk water potential throughout the day and throughout the season and the magnitude of the difference between waterstressed and control trees increased as the season progressed. With time, the stress became severe as a result of high climatic demand and intense fruit growth and water depletion from the soil. In contrast, there was no crop load main effect, as for both water-stressed and control trees trunk water potential was similar for the three crop load levels. The seasonal pattern of midday trunk water potential showed a clear distinction in the trend between water-stressed and control trees independent of crop load. On the other hand, it is noticeable that during the first week of July even control trees were under-irrigated.

3.3. Stomatal conductance

No interaction between crop load and water stress regarding midday stomatal conductance was detected. No crop load main effect throughout the day and the season was shown. Early in the season, the moisture level in the soil was sufficient to maintain stomatal conductance in water-stressed trees at a level comparable with that of control trees. The water stress main effect appeared starting 2nd of July for noon and afternoon measurements and on 16th of July for morning measurements. As the season progressed and the severity of water stress increased, the trees responded by reducing their stomatal conductance (*figure 2e*).

3.4. Transpiration rate

Midday stomatal conductance showed a similar trend to the transpiration rate: there was no interaction between the crop load and water stress factors and no main crop load effect. The water stress main effect on the transpiration rate appeared on 9th July: on this day and thereafter, transpiration rates of water-stressed trees were significantly lower than those of control trees. Early in the season the moisture level in the soil was high enough to maintain a transpiration rate in the water stress treatment at a level similar to that of the control treatment. However, as

the season progressed and the severity of water stress increased, the trees reduced their transpiration rate. Water stress induced a lower transpiration rate regardless of crop load. On 9th of July, the difference among the transpiration rates between water-stressed and control trees was significant at noon and in the afternoon, but not in the morning. This suggests that, despite the advanced stage of water stress, the trees were still able to recover during the night, which allowed them to maintain a transpiration rate similar to that of the control trees. However, on 16th of July, the water stress was so severe that the trees could no longer recover during the night and thus maintained a lower transpiration rate beginning in the morning (figure 2f).

3.5. Photosynthetic rate

Regarding the seasonal pattern of midday assimilation rates there was no interaction between crop load and water stress and no crop load main effect appeared throughout the season. Starting 9th of July, a water stress main effect appeared and persisted until the last measurement date (figure 2g). Thus, starting on this date, the assimilation rate in water-stressed trees was significantly lower than that in control trees; the magnitude of this difference increased as the season progressed. The assimilation rate of waterstressed trees went from 80% of the control on the 9th of July to 56% on the 16th and 23rd of July. Crop load did not affect the assimilation rate in either water-stressed or control trees, suggesting that trees had alternate sinks with varying strengths, all competing for the same source. In fact, similar assimilation rates in trees for light crop load and heavy crop load indicates that trees with light crop load had alternate sinks which continued to drive photosynthesis at its maximum rate.

3.6. Diurnal pattern of assimilation rate

On the 9th July, there was no crop load or water stress main effect in the morning, or interaction between crop load and water stress throughout the day. However, there was a water stress main effect appeared at midday and in the afternoon. Thus, water-stressed trees were able to recover during

the night and maintained a similar assimilation rate to the control trees despite a significantly lower trunk water potential: its level did not reach the threshold that would have negatively affected the assimilation rate.

On the 16th of July again there was no interaction and no crop load main effect. There was a water stress main effect that appeared in the morning and persisted throughout the day. The assimilation rate decreased throughout the day for both control and water stress treatments and was significantly lower for water-stressed than for control trees. The assimilation rate in waterstressed trees was (68, 56 and 56)% of that of control in the morning, noon and afternoon, respectively. Thus, water stress reduced assimilation rates by 32% in the morning and 44% at noon and in the afternoon. There was no crop load main effect on assimilation rate throughout the day, suggesting that there were alternate sinks which continued to drive the assimilation rate even on trees with light crop load.

On the 23rd of July, there was no interaction between the crop load and water stress treatments and no crop load main effect. However, there was a water stress main effect in the morning, noon and afternoon and the assimilation rate in waterstressed trees was significantly lower than that of control trees throughout the day. The assimilation rate of water-stressed trees was (81, 56 and 50)% of the control trees in the morning, noon and afternoon, respectively. The assimilation rate decreased throughout the day in both control and water-stressed trees: it was reduced by (11 and 14.5)% in control trees; and by (39 and 48)% in waterstressed trees at midday and in the afternoon, respectively. Thus, water stress reduced the assimilation rate starting in the morning and induced a more pronounced decrease throughout the day.

3.7. Relationship between trunk water potential, stomatal conductance and photosynthetic rate

In control trees, there were poor correlations between trunk water potential and both stomatal conductance and the photosynthetic rate. In contrast, closer relationships were found for trees submitted to a water stress treatment. In control trees, a negative relationship between trunk water potential and stomatal conductance occurred. Under optimal water conditions, trunk water potential and stomatal conductance were high, and, as stomatal conductance increased, trunk water potential tended to decrease as a consequence of the high transpiration rate. This trend continued until a certain threshold where the tree could no longer respond to climatic demand and started to adjust to water stress by reducing stomatal conductance and the transpiration rate to limit water loss. Water-stressed trees had already reached such a threshold, so, with severe water stress, trunk water potential became even lower, as did stomatal conductance and the transpiration rate, which resulted from the previous high stomatal conductance and transpiration rate which led to a further decrease in trunk water potential.

Regarding the trunk water potential and photosynthetic rate relationship, as for trunk water potential and stomatal conductance, it was of the opposite trend in control and water-stressed trees. Thus, in control trees, trunk water potential was high and enclosed in a narrow range and so was the assimilation rate. In contrast, in water-stressed trees, both trunk water potential and the photosynthetic rate were low and as trunk water potential continued to decrease so did the photosynthetic rate. At the beginning, when trunk water potential in the water stress treatment was high and approaching that of control trees, the photosynthetic rate was also at a similar level to control trees. However, as trunk water potential decreased in response to stress, the photosynthetic rate was consequently reduced.

There is a close relation between stomatal conductance and the photosynthetic rate in both control and water-stressed trees. However, the correlation is better for the latter, indicating a poor coordination between stomatal conductance and the photosynthetic rate under optimal conditions. This relation tends to be improved as the tree experiences some water deficit.

For both water stress and control treatments, the relationship between the photosynthetic rate and stomatal conductance

was best predicted by the logarithmic transformation $y = a x^b$; the equations are $y = 2.0782 \ x^{0.335} \ (r^2 = 0.51)$ and $y = 0.8016 \ x^{0.488} \ (r^2 = 0.77)$ for control and waterstressed trees, respectively (*figure 3*). A better correlation existing between the photosynthetic rate and stomatal conductance in water-stressed trees is an indication of a better coordination under limiting conditions, allowing a more efficient use of limited resources.

4. Conclusion

During the early stages of the fruit growth in the season, the fruit growth curve showed similar trends for both control and waterstressed trees. However, as the season progressed (intensive fruit growth, increase in severity of water stress, and high climatic water demand), the fruit on water-stressed trees showed a slower growth rate. Both water stress and crop load reduced fruit growth rate, indicating that, at this stage, the trees were source-limiting and could no longer respond to fruit demand. The effect of water stress on fruit growth could be explained by insufficient water for cell elongation through which the fruit insures its growth during the last stages and/or through photosynthesis leading to a shortage in photosynthates preventing the fruit from satisfying its demand. The crop load effect on growth could be attributed to high competition existing among fruits toward a limited source (photosynthates) which resulted from water stress. Fruit growth declined as irrigation quantity decreased [2] and the smallest fruits were produced on trees receiving an imposed water deficit during the final accelerated fruit growth, or throughout the fruit development period [10]. The last stage of very active fruit growth prior to harvest is very critical and remains sensitive to water deficit, which leads to a reduction in fruit size and yield [11]. Water stress induced fruit fresh weight reduction at all crop loads in peach [15].

Water stress, but not crop load, significantly reduced trunk water potential which was significantly lower than that of control trees beginning in the morning, and remained so throughout the day and the season. The magnitude of the difference in trunk water potential between water-stressed and control trees increased during the season as the water deficit became severe. This resulted from a high climatic water demand, intense fruit growth and depletion of water from the soil. The seasonal pattern of midday trunk water potential showed a clear distinction in the trend followed by water status in control and water-stressed trees, independent of crop load. Leaf water potential of waterstressed plants was lower than that of the control from noon on [4]. Daily mean trunk water potential was lower in water-stressed than in control peach trees [5]. Predawn water potential of the control remained constant at -0.3 Mpa, whereas that of the water stress treatment became more negative as the season progressed [6]. Regulated deficit irrigation induced clear differences in soil and predawn leaf water potential on 'Cal Red' peach trees [8]. Leaf water potential was lower in heavy crop load peach trees compared with the light crop load [12]. Heavy crop load increased fruit water deficit, leading to limited fruit growth. The reduction of fruit size commonly associated with increased crop load may be due, at least in part, to the effect of crop load on fruit water relations

Water stress also significantly reduced stomatal conductance and the transpiration rate during the last stage of fruit growth, while crop load did not. During the early stages of the experiment, the level of soil moisture was sufficient to allow the water stress treatment to maintain levels of stomatal conductance and a transpiration rate similar to those of the control. However, as the severity of water stress increased, the trees responded by reducing their stomatal conductance and transpiration rate. The difference in transpiration rate between waterstressed and control trees appeared first at noon and in the afternoon indicating that, at this point, the trees were still able to recover overnight and maintain a sufficient transpiration rate the following morning. But, at later stages of the season, the transpiration rate of water-stressed trees was lower than that of control trees throughout the day starting in the morning. At this point,

water stress had reached a level where the trees could no longer recover overnight and thus maintained continuously a low transpiration rate. Soil moisture stress decreases stomatal conductance and photosynthetic rate in fruit trees [3]. The transpiration rate is generally higher for control than for waterstressed trees, reflecting the importance of the transpiration rate in controlling water loss. Trees grown under water stress do not lose as much water as control plants, and they have a low response to increasing the vapor pressure deficit which helps to maintain a sufficient level of photosynthetic activity [3]. Water stress significantly reduced stomatal conductance [4] and transpiration rate [4, 5] in peach trees [4]. Significant differences were observed in seasonal patterns of stomatal conductance among postharvest irrigation treatments in proportion to irrigation level in early harvested peaches [6].

Regarding the photosynthetic rate there was no crop load effect throughout the season. However, water stress reduced the photosynthetic rate as the season progressed and the fruit demand became higher. Thus, the negative effect of water stress observed on fruit growth could be explained in part by its effect on the photosynthetic process. Similar photosynthetic rates in trees with varying crop load indicated the existence of alternate sinks all competing for the same source. Such alternate sinks continued to drive photosynthesis at its maximum rate even on light crop load trees and would divert carbohydrates once the demand of the fruit was satisfied. Water stress also negatively affected the diurnal pattern of the photosynthetic rate and appeared first in noon and afternoon measurements. The trees were still able to recover during the night and maintained a similar photosynthetic rate to control trees despite low trunk water potential, which was not yet low enough to affect the photosynthetic rate. However, during the late stage of fruit growth, the negative effect of water stress on the photosynthetic rate appeared, starting in the morning and persisting throughout the day. At this stage the water stress had reached a point where the trees could no longer recover overnight in order to maintain a sufficient photosynthetic rate level, even in the morning. Studies of fruit effects

on the photosynthetic rate of fruit crops have given inconsistent results [16]. The fruit effect would manifest itself only under conditions where leaf assimilation was at its full potential. Water stress did not affect the photosynthetic rate in peach [4] but did in other fruit trees [3]. Reductions in CO₂ assimilation rates were caused by water deficit [5]. Regulated deficit irrigation induced net CO2 assimilation and trunk growth in 'Cal Red' peach trees [8]. Leaves on trees subjected to regulated deficit irrigation were photosynthetically more water-use efficient during the latter part of the stress period. Significant differences in leaf photosynthetic rate between the heavily cropping and non-fruiting trees are most evident in July and August at the time of maximum accumulation of dry matter in the apple fruit [17]. Similarly, CO₂ uptake and transpiration rate increased in peach leaves during June and July when fruit dry weight accumulation was high [18]. However, there were no significant differences in leaf gas exchange characteristics between fruiting and defruited 'O'Henry' peach trees during early stages of fruit growth. During the early part of the last stage of fruit growth, CO₂ assimilation rates were slightly higher in fruiting than defruited trees. These increased assimilation rates were associated with an increase in stomatal conductance. The fruit effect on the photosynthetic rate appeared to be primarily related to stomatal behavior [18]: the presence of fruit can apparently affect the rate of CO2 assimilation in peach but the magnitude of this effect is likely to depend on environmental conditions. If this 'fruit effect' is related to carbohydrate demand, the relatively moderate crop load effects on CO₂ assimilation reported [18] may be associated with the favorable environmental conditions under which the experiments were conducted. The latter would stimulate photosynthate demands by development of alternate sinks such as vigorous shoot and root growth [18]. There is a close positive relationship between stomatal conductance and photosynthetic rate in both control and water-stressed trees. A close relationship between stomatal conductance and photosynthetic rate has been reported for apple over a wide range of environmental conditions [3]. This would allow more favorable water use efficiency, since stomatal responses correspond to changes in photosynthetic activity.

References

- [1] Chalmers D.J., Mitchell P.D., Heek L. van, Control of peach tree growth and productivity by regulated water supply, tree density, and summer pruning, J. Am. Soc. Hortic. Sci. 106 (1981) 307–312.
- [2] Mitchell P.D., Chalmers D.J., The effect of reduced water supply on peach tree growth and yields, J. Am. Soc. Hortic. Sci. 107 (1982) 853–856.
- [3] Flore J.A., Lakso A.N., Moon J.W., The effect of water stress and vapor pressure gradient on stomatal conductance, water use efficiency, and photosynthesis of fruit crops, Acta Hortic. 171 (1985) 207–217.
- [4] Cheng L., Cheng S., Shu H.X.L., Effects of mild water stress on CO₂ assimilation and water use efficiency of field-grown peach trees, Acta Hortic. 374 (1996) 121–125.
- [5] Natali S., Bignami C., Cammilli C., Effects of different levels of water supply on gas exchanges of early ripening peaches, Acta Hortic. 374 (1996) 113–120.
- [6] Larson K.D., DeJong T.M., Johnson R.S., Physiological and growth responses of mature peach trees to postharvest water stress, J. Am. Soc. Hortic. Sci. 113 (1988) 296–300.
- [7] Steinberg S.L., Miller J.C., McFarland M.J., Dry Matter partitioning and vegetative growth of young peach trees under water stress, Aust. J. Plant Physiol. 17 (1990) 23–36.
- [8] Girona J., Mata M., Goldhamer D.A., Johnson R.S., DeJong T.M., Patterns of soil and tree water status and leaf functioning during regulated deficit irrigation scheduling in peach, J. Am. Soc. Hortic. Sci. 118 (1993) 580–586.
- [9] Blanco A., Pequerul A., Val J., Monge E., Gomez Aparisi J., Crop load effects on vegetative growth, mineral nutrient concentration and leaf water potential in 'Catherine' peach, J. Hortic. Sci. 70 (1995) 623–629.

- [10] Li S.H., Huguet J.G., Schoch P.G., Orlando P., Response of peach tree growth and cropping to soil water deficit at various phenological stages of fruit development, J. Hort. Sci. 64 (1989) 541–552.
- [11] Huguet J.G., Li S.H., Defrance H., Influence de la disponibilité en eau du sol sur la qualité des fruits chez le pêcher *Prunus persica* L., 9^e Colloque sur les recherches fruitières, Inra, Avignon, France, 1990, pp. 135–144.
- [12] Mc Fadyen L.M., Hutton R.J., Barlow E.W.R., Effects of crop load on fruit water relations and fruit growth in peach, J. Hortic. Sci. 71 (1996) 469–480.
- [13] Grossman Y.L., DeJong T.M., Maximum vegetative growth potential and seasonal patterns of resource dynamics during peach tree growth, Ann. Bot. 104 (1995) 247–254.
- [14] Berman M.E., DeJong T.M., Crop load and water stress effects on daily stem growth in peach (*Prunus persica*), Tree Physiol. 17 (1997) 467–472.
- [15] Berman M.E., DeJong T.M., Water stress and crop load effects on fruit fresh and dry weights in peach (*Prunus persica*), Tree Physiol. 16 (1996) 859–864.
- [16] Flore A.J., Lakso A.N., Environmental and physiological regulation of photosynthesis in fruit crops, Hortic. Rev. 11 (1989) 111–157.
- [17] Jones H.G., Carbon dioxide exchange of developing apple (*Malus pumila Mill.*) fruits, J. Exp. Bot. 32 (1981) 1203–1210.
- [18] DeJong T.M., Fruit effects on photosynthesis in *Prunus persica*, Physiol. Plantarum 66 (1986) 149–153.
- [19] DeJong T.M., Day K.R., Doyle J.F., Johnson R.S., The Kearney Agricultural Center perpendicular "V" (KAC-V) orchard system for peaches and nectarines, Hortic. Tech. 4 (1995) 362–367.
- [20] McCutchan H., Shakel K.A., Stem-water potential as a sensitive indicator of water stress in prune trees (*Prunus domestica* L. cv. French), J. Am. Soc. Hortic. Sci. 117 (1992) 607–611.
- [21] Palmer P.D., Pear fruit growth and the use of diameter to estimate fruit volume and weight, HortScience 21 (1986) 1003–1005.

Efectos del estrés hídrico y de la carga frutal en el crecimiento vegetativo y el desarrollo del fruto en la variedad de melocotonero 'Elegant Lady' [*Prunus persica* (L.) Batch].

Resumen — Introducción. En los árboles frutales, el crecimiento vegetativo y el desarrollo de la fruta muestran una sensibilidad desigual al déficit hídrico durante la temporada y según el estadio de formación del fruto. Se efectuaron algunos ensayos para evaluar las posibilidades de utilización del riego con déficit regulado con el fin de controlar el crecimiento vegetativo y ahorrar agua durante el desarrollo del fruto. Material y métodos. En una plantación de melocotoneros 'Elegant Lady' de 7 años, se evaluaron los efectos del estrés hídrico (SH) y de la carga frutal (CF) en el desarrollo del fruto, así como las tasas de asimilación del carbono. El diseño experimental estaba compuesto por bloques totalmente aleatorios de 2 × 3 factores: irrigación con dos niveles (testigo y SH) y CF con tres niveles (liviana, comercial, y alta). Resultados y discusión. Tanto el SH como la CF afectaron al crecimiento del fruto durante las últimas fases de su desarrollo, pero no desde su inicio. La CF no afectó el potencial hídrico del tronco que, sin embargo, fue sensiblemente disminuido por el SH a lo largo del día y de la temporada. El potencial hídrico del tronco de los árboles sometidos a limitaciones hídricas fue inferior al de los árboles testigo a lo largo del día y de la temporada con independencia de la CF. La importancia del SH aumentó al mismo tiempo que la temporada avanzaba. La conductancia estomática, la tasa de transpiración y la tasa de asimilación de CO2 no fueron afectadas por la CF, pero fueron disminuidas por el SH. Los árboles respondieron (se aclimataron) al SH reduciendo progresivamente su tasa de transpiración a medida que el rigor de la limitación se incrementaba. Para cada régimen de riego, las tasas de asimilación fueron similares fuera cual fuese la CF. Esto indicaría que, cuando la CF es baja, existirían pozos alternativos para asimilados que compensarían la reducción de actividad de los pozos de fruta causada por el aclareo de frutos. **Conclusión**. El déficit de agua redujo el potencial hídrico del tronco, la conductancia estomática, la transpiración y la fotosíntesis en los melocotoneros Elegant Lady. Sin embargo, la CF sólo tuvo un efecto limitado en dichas funciones. En los árboles sometidos a SH, y no en los testigos, se produjeron buenas correlaciones del potencial hídrico del tronco con la conductancia estomática o con la tasa de asimilación. Esto indicaría una baja coordinación entre las funciones de la hoja en este melocotonero en condiciones óptimas. No obstante, estas relaciones fueron más intensas en condiciones de SH. Así pues, la eficacia del agua aportada pareció incrementarse en condiciones de déficit hídrico.

Prunus persica / estrés de sequia / árboles / frutas / poda / crecimiento / fructificación / tensión de absorción / estoma / transpiración

To access this journal online: www.edpsciences.org