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SUMMARY

The effects of full irrigation and two levels of water stress on tree physiology were investigated in a French prune orchard. The control treatment received approximately 100% of the estimated seasonal crop water requirements throughout the season. The moderate and severe water stress treatments were managed to decline from a fully watered status in late spring to a midday stem water potential of –1.5 and –2.0 MPa, respectively, by harvest. Water stress caused a clear reduction in stem water potential throughout the daylight period, as well as reductions in leaf conductance and photosynthesis, and all of these reductions were more severe with increasing water stress. In a moderate and severe stress treatment, the photosynthetic rate of fully exposed leaves was reduced to 90% and 81% respectively, of the control treatment. There was a linear decline in light saturated photosynthesis with a decline in stem water potential. However, the stress treatments also influenced leaf orientation and the resulting incident light distribution on leaves within the canopy, such that light was more uniformly distributed in canopies under water deprivation than it was under full irrigation. The overall effect of water stress was that the moderate and severe stress treatments had 101% and 93% respectively of calculated canopy photosynthesis compared with the control. This may account for the observed tolerance of prune production to deficit irrigation. A midday depression in assimilation was observed on most days in all treatments, but was not associated with feedback inhibition resulting from carbohydrate accumulation in leaves.

Hendrickson and Veihmeyer (1946) found that growing French prunes in California on deep valley soils without irrigation had no negative effects on yields compared with irrigated controls after five years. Irrigation cutoff at up to 37 d before harvest resulted in a substantial water saving with no negative impacts on dry fruit yield in French prune (Goldhamer *et al.*, 1994). Moderate stress treatments during stage II (lag phase) and III (second exponential phase) of fruit growth have shown possible beneficial effects on dry fruit yield in French prune (Lampinen *et al.*, 1995).

The physiological adjustments that allow French prune dry fruit production to continue unaffected with significantly less water applied than potential crop evapotranspiration have not been investigated. Regulated deficit irrigation (RDI) can significantly reduce water use without decreasing yields in other fruit tree crops including peach (Chalmers *et al.*, 1981), pear (Mitchell *et al.*, 1984) and apple (Irving and Drost, 1987). However, the detailed physiological responses of fruit trees to RDI have not been elucidated (Caspari *et al.*, 1994).

It is well established that water deficits lead to reductions in conductance and photosynthesis (Cornic and Massacci, 1996). For measurement of photosynthesis, the leaf is normally turned perpendicular to the sun's rays. DeJong (1990) has suggested that comparisons of assimilation rates at light saturation may not be the most relevant to crop performance, because

few leaves in a normal canopy are in this orientation. Single-leaf photosynthesis normally follows a hyperbolic light response and saturates at 25–50% of full sunlight in apple (Campbell *et al.*, 1992), whereas the canopy response is much more gradual and may not saturate even at full sunlight (Lakso, 1994). However, it is difficult to measure canopy photosynthesis on trees and the design of most portable photosynthesis systems does not allow the leaf to be turned at more than minor angles from perpendicular to the sun's rays without shading the leaf by the chamber.

Photosynthesis can be inhibited by stomatal and non-stomatal factors under water stress (Boyer, 1971; Lawlor, 1995). Chaves (1991) concluded that the effects of water deficit on carbon assimilation are mainly due to stomatal closure. Farquhar and Sharkey (1982) concluded the stomatal limitation to photosynthesis is usually slight whether or not the plants are stressed. Tan and Buttery (1982) found that stomatal conductance was only at 28% that of the fully-watered control plants, whereas photosynthesis was 78% of the control value one day after re-watering in peach, indicating that stomata were not the primary factor limiting photosynthesis. In kiwifruit, water stress reduced photosynthesis without reducing internal CO_2 suggesting that stress was acting by directly inhibiting biochemical processes (Chartzoulakis *et al.*, 1993). Lawlor (1995) concluded that under mild water stress stomatal closure appeared to be the main factor influencing photosynthesis, while under more severe stress metabolic inhibition plays a more important role.

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A midday depression in photosynthesis not associated with any apparent water stress has been observed in many species and has been attributed to various factors. Bunce (1982) attributed the midday depression in soybean to vapour pressure deficit (VPD) related effects. Correia *et al.* (1990) suggested that the midday decline in photosynthesis in grapevine resulted from a direct inhibitory effect of high light at the chloroplast level. Roy and Salager (1992) attributed a midday depression in *Qualea rosea* (a tropical rainforest tree species) to vapour pressure deficit or direct light effects on photosynthesis. The midday photosynthesis depression in wheat has also been attributed to feedback inhibition due to a buildup of soluble carbohydrates (Azcon-Bieto, 1983). Chen *et al.* (1993) found that starch concentrations were higher in stressed compared with fully-watered soybean leaves, consistent with a sink limitation. An increase in photosynthesis associated with increasing fruit load in grape (Downton *et al.*, 1987) and apple (Wünshe *et al.*, 2000) suggests that photosynthesis could be sink limited.

A variety of crop plants have been observed to alter leaf angle in response to water deficit including, cowpea (Shackel and Hall, 1979), wheat (Peinetti and Ledent, 1990), soybean (Wang *et al.*, 1994) and pepper (Alvino *et al.*, 1994). The altered leaf inclination angles can reduce photosynthetic photon flux density load on the leaf, leading to lower leaf temperature and less transpirational water loss (Ishida *et al.*, 1999). In soybean, light and temperature affected the rapid reversible leaf movements on a time scale of minutes while leaf water potential had an effect on a longer time scale of weeks (Kao and Forseth, 1992).

Less work has been done on effects of water stress on leaf angle in orchards. The continuously changing position of the sun through the day and the seasons, combined with tall, discontinuous canopies, add considerable complexity to the canopy light regime in an orchard compared with a uniform row crop. Deficit irrigated walnut trees had steeper leaf angles and more folding of the lamina about the midrib (Martens *et al.*, 1991). In olive, leaves move upwards during drought, exposing more of the silver reflective undersides of leaves to the sun resulting in increased radiation reflection (Schwabe and Lionakis, 1996). Torrecillas *et al.* (1999) suggested that altered leaf inclination angle in apricot allowed the plant to regulate water loss and minimize leaf heating.

The ability of French prune to maintain dry fruit yields under moderate water deprivation suggests that physiological mechanisms are compensating for the expected decreases in single leaf net carbon assimilation normally associated with water deprivation. The objective of this study was to quantify and model the combined effects of water stress on leaf photosynthetic characteristics and leaf and canopy light interception characteristics, to test whether changes in leaf angle could minimize the negative effects of water stress on canopy carbon assimilation (A_{can}) in French prune.

MATERIALS AND METHODS
Site description, cultural practices, and experimental design

These experiments were conducted during 1994–1996 in a commercial French prune (*Prunus domestica* L. 'French') orchard in Butte County, California that was 18 years old at the initiation of the study. The soil was classified as a Gridley clay loam (Carpenter *et al.*, 1926). Trees were planted at a 5.5 × 5.5 m spacing. A randomized block design was utilized with five replications of each of three treatments, with 16 trees in each replicate arranged in a 4 × 4 pattern for a total experimental area of 0.73 ha. Within each treatment, a subset of trees were chosen for detailed physiological measurements.

Irrigation regimes

The irrigation treatments used in this study have been described elsewhere (Lampinen *et al.*, 2001). Briefly, the three drip irrigation treatments used were a control (T1), moderate stress (T2) and severe stress treatment (T3). T1 irrigation volume (ET_c) was calculated weekly based on estimated crop coefficients (Goldhamer and Snyder, 1989) and modified Penman reference crop water use (ET_o) obtained from a nearby weather station (California Irrigation Management Information System Station #12, Durham, CA, USA). The water applications were recommended when the midday stem water potential (Ψ_{stem}) deviated from values which were considered fully-irrigated (–0.5 MPa in April to –0.9 MPa in August) based on the data of McCutchan and Shackel, (1992). T2 was based on a target level of water stress, aiming at a decline in midday Ψ_{stem} over the season of approximately 0.2 MPa per month reaching –1.5 MPa by harvest. T3 was designed to decline by about 0.3 MPa per month reaching approximately –2.0 MPa by harvest (Lampinen *et al.*, 2001).

Measurements

Ψ_{stem} (McCutchan and Shackel, 1992) was measured with a Scholander pressure chamber (Soil Moisture Equipment, Santa Barbara, CA, USA) on leaves from the trunk or main scaffold. For the purposes of irrigation management, Ψ_{stem} was measured on two trees per plot (total of ten trees per treatment) on an approximately weekly basis.

Net carbon assimilation (A_l) and leaf conductance (g_l) were measured on selected trees in each treatment throughout the day on 28 May, 31 May, 18 June, 26 June, 9 July, 13 July, 17 July, 23 July, 31 July, 7 Aug., 13 Aug., 20 Aug., 24 Aug., 11 Sept., and 1 Oct., 1994, using a portable field photosynthesis system (PP Systems, Haverhill, MA, USA). Trees selected for measurement had a midday Ψ_{stem} close to the target midday value for that treatment and time in the season. Selection was based on previous midday Ψ_{stem} trends as well as predawn water potential measurements made on the day of measurement. Recently fully-expanded leaves currently in full sunlight were positioned perpendicular to the sun for assimilation and conductance measurements, Ψ_{stem} measurements were made throughout the day on the same trees that were used for A_l and g_l. For the purpose of data presentation, A_l and g_l data were grouped into 1.5 h categories.

Light response of A_l was measured in both morning and afternoon on 8 June, 20 June, 29 June, 2 July, 9 July and 20 July, 1995. Irradiance was manipulated using varying layers of neutral density filters suspended on wooden frames above the leaf. Maximum assimilation
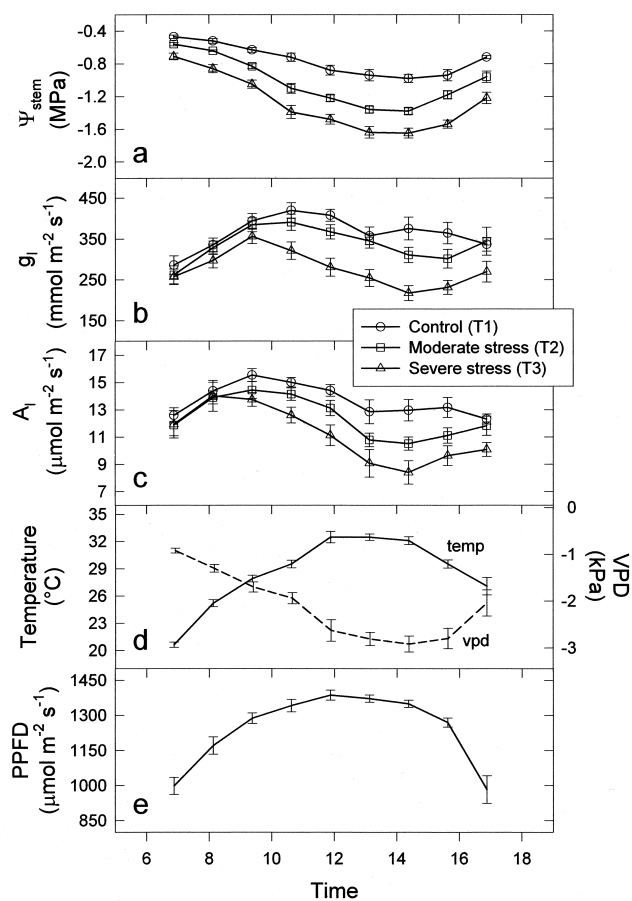
Diurnal patterns of seasonal mean (a) Ψ_{stem}, (b) g_l, (c) A_l, (d) temperature and VPD and (e) photosynthetic photon flux density (direct radiation) in the three treatments for 1994. Figures are summaries for diurnal measurements done on 15 d from 28 May to 2 October. Vertical bars indicate $\pm$ 2 SE.

rate (A_{max}) was determined by fitting an exponential rise to a maximum equation to the data using the curve fitting routines in Sigmaplot (SPSS Inc., Chicago, IL 60611, USA).

Canopy light interception was measured approximately every 1.5 h throughout the day on 21 April, 31 May, 26 June, 9 July, 17 July, 31 July, 13 Aug., 20 Aug., 7 Sept., 11 Sept., and 2 Oct., 1994. One hundred measurements were made in a grid pattern covering the area in the middle of each plot with an Accupar light bar (Decagon Devices, Pullman, WA, USA).

Leaf angle distribution with respect to direct sunlight was estimated by using the photosynthetically active radiation sensor on the PP Systems portable field photosynthesis system. One hundred measurements were made from the bottom to the top of each of the northeast, southeast, southwest, and northwest sides of the tree at approximately 0900, 1100, 1300 and 1500 hours, respectively. At these times, the sunlit side of the tree was measured. The light sensor was held parallel to each sampled leaf and a reading was taken. One or two trees from each treatment were measured on 18 June, 20 June, 22 June, 9 July, 11 July, 20 July, 13 Aug., and 15 Aug., 1995. The photosynthetic flux density (PPFD) data were grouped into 12 equal categories for analysis.

To test for carbohydrate accumulation as a source of negative feedback for photosynthesis, on 29 May, 1995, individual leaves or whole branches on control trees (T1) were shaded from the sun by 1) other branches, 2) enclosing in foil covered plastic bags, or 3) covering with plywood panels early in the morning. Then, at various times during the day, leaves were exposed to full sun and the A_l response was followed using the PP Systems portable photosynthesis system. Leaves chosen for these measurements were in positions on the tree where they would be expected to be in full sun for a substantial part of the day.

Canopy assimilation and leaf angle data were grouped into categories and treatment means were compared using the least-significant-difference test in the SAS statistical program GLM procedure (SAS Institute, 1988). Stepwise multiple regression analysis (SAS Institute, 1988) was used to assess the importance of the variables influencing assimilation rate.

RESULTS
Assimilation and conductance

Averaged over all dates of measurement in 1994, Ψ_{stem} in selected T1 trees decreased from just after sunrise until a minimum was reached around 1400–1600 hours when a gradual recovery began (Figure 1a). Selected trees in T2 and T3 showed a similar diurnal pattern, with lower values of Ψ_{stem} compared to the control at all times of day (Figure 1a).

Leaf conductance (g_l) in fully irrigated T1 trees began to increase shortly after the sun began striking the trees in the morning, reaching a maximum g_l around 1000 hours followed by a gradual decline throughout the day (Figure 1b). Leaves of T2 trees reached a peak in g_l slightly earlier than leaves of trees in T1 and then declined gradually throughout the day until the last measurement period when g_l recovered to the same value as in T1 (Figure 1b). The g_l in T3 trees peaked earlier and declined to significantly lower levels than in T1 and T2 after about 1000 hours (Figure 1b). As in T2, a slight recovery of g_l occurred in T3 in late afternoon although it did not reach the value of either the T1 or T2 trees (Figure 1b).

The A_l patterns were similar to the g_l patterns with significant differences between T1 and T2 after 1000 hours until a slight recovery occurred in T2 to a similar level as T1 in late afternoon (Figure 1c). The A_l in T3 peaked earlier and had a significantly lower A_l compared with both T1 and T2 after about 1000 hours and this difference continued throughout the rest of the day (Figure 1c). A slight afternoon recovery in A_l occurred in T3, although like g_l, it did not reach the value of either T1 or T2 (Figure 1c). In T1 there was an approximately 16% decline in A_l from 1000 hours to 1300 hours.

Averaged over all dates of measurement in 1994, temperature increased throughout the morning, reached a plateau in afternoon and then declined. The VPD was inversely related to temperature (Figure 1d). Because PPFD was measured at an angle perpendicular to the sun during single-leaf assimilation measurements, light flux densities were already near 1000 $\mu mol\ m^{-2}\ s^{-1}$ by the time the first measurements were taken at approximately 0700 hours (Figure 1e).
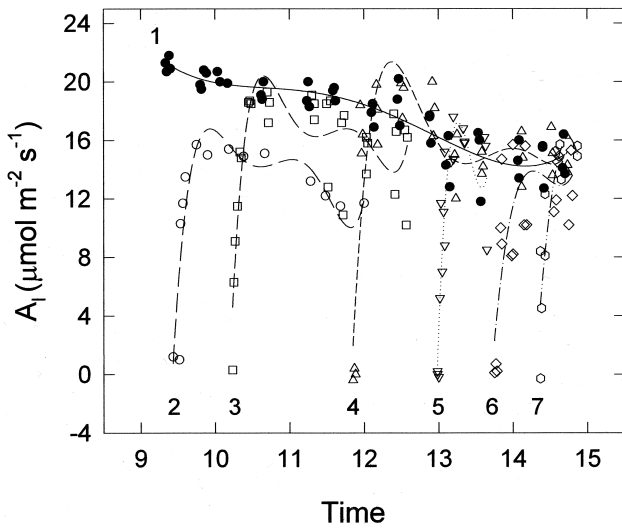
FIG. 2

Responses of branches of a control tree that had been shaded by a variety of means prior to being pulled into the sun on 5/25/95 (a). Group 1 (•) consists of data from two control branches that had been in the sun for at least 1.5 h before the start of measurements. Treatment branches were (2) pulled into sun just before the sun would have normally reached the branch, (3) uncovered from plywood which had been covering the branch since just after sunrise, (4) pulled into sun as in branch 2, (5) uncovered from cardboard cover, (6) pulled into sun as in branch 2, and (7) removed from plastic and foil bag that had been on since sunrise.

A stepwise multiple regression analysis was performed on all of the assimilation rate data collected in 1994 using Ψ_{stem}, VPD and temperature as covariates. The results showed that Ψ_{stem} was the most important of the factors influencing assimilation rate, accounting for about 47% of the variability in leaf assimilation rate (data not shown). The second most important factor influencing assimilation rate was VPD, although it only accounted for about an additional 2% of the remaining variability. If temperature was used in the regression in place of VPD, it accounted for less tha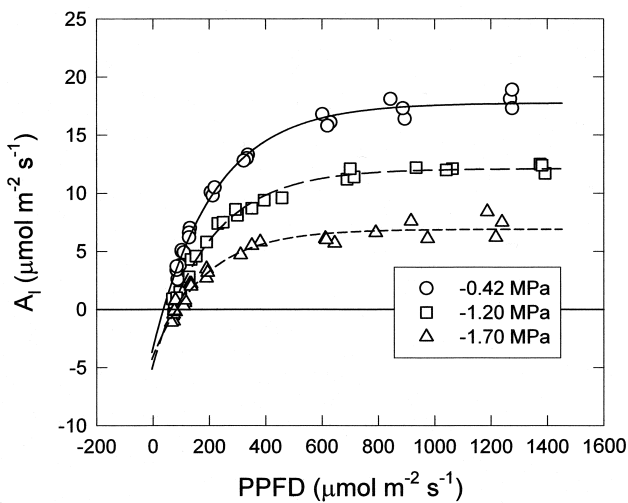n 1% of additional variability. If both VPD and temperature were used as covariates with Ψ_{stem}, VPD entered the regression first accounting for 2% additional variability and temperature accounted for an additional 2% (data not shown).

When the shaded leaves of a fully irrigated tree were pulled into the sun, the assimilation rate increased to values similar to those in the sun-exposed leaves within 15 min (Figure 2). The low assimilation rate of leaves on branch 2 was probably because this branch normally received only a brief period of sunlight each day. Rates of assimilation of branches uncovered later in the day never exceeded that of the continuously sun-exposed control leaves (Figure 2). Control leaves did, however, show a decline in assimilation of about 30% between 1000 hours and 1300 hours (Figure 2), with the tree exhibiting a typical diurnal decline in Ψ_{stem} from early morning to midday (data not shown). These data were collected on 25 May, 1995, relatively early in the growing season, on a tree with a midday Ψ_{stem} of about –0.8MPa.

Light response curves

A total of 46 light response curves were generated across a range of environmental conditions on trees from all three treatments. A representative sample of curves across a range of stem water potentials (Ψ_{stem}) is shown in Figure 3. The general shape of the curves was similar with light saturation occurring around 800 μmol m^{-2} s^{-1}. Because of the similarity of the curves, the data from all 46 light response curves were fit to an exponential rise equation using a common value for the intercept and initial slope and allowing A_{max} to be estimated. A_{max} decreased linearly as Ψ_{stem} decreased (Figure 4).

Leaf/sun angle distribution

The cosine response of the PP Systems PPFD sensor was very close to the theoretical cosine response suggesting that the measured PPFD should be well correlated with the leaf/sun angle (data not shown). This relationship was used to estimate leaf/sun angle from PPFD values.

The PPFD was measured at 0900, 1100, 1300, and 1500 hours on one or two trees per day for each treatment on each of eight days from mid-June to mid-
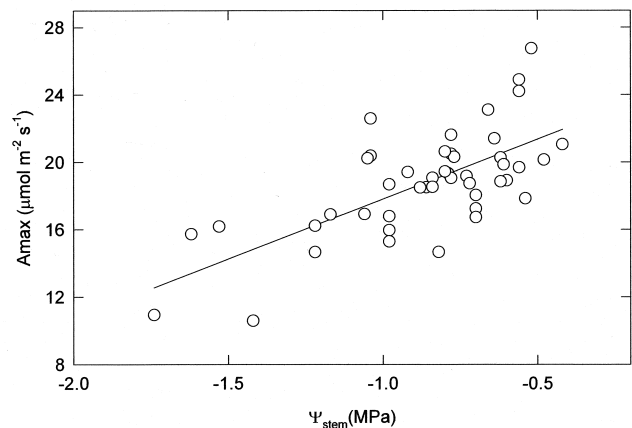

FIG. 3

Three representative light response curves at a range of Ψ_{stems} in 1995 for the three treatments. Curves were fit to an exponential rise to a maximum equation of the form: Assimilation = $A_{max} \times (1–exp(–0.0040 \times PPFD)) – 4.036$.

FIG. 4

A_{max} versus Ψ_{stem} for 46 light response curves measured in on selected days of June–July, 1995 for the three treatments. Regression equation is $A_{max} = 24.91 + 7.10 \times \Psi_{stem}$ ($r^2 = 0.47$).
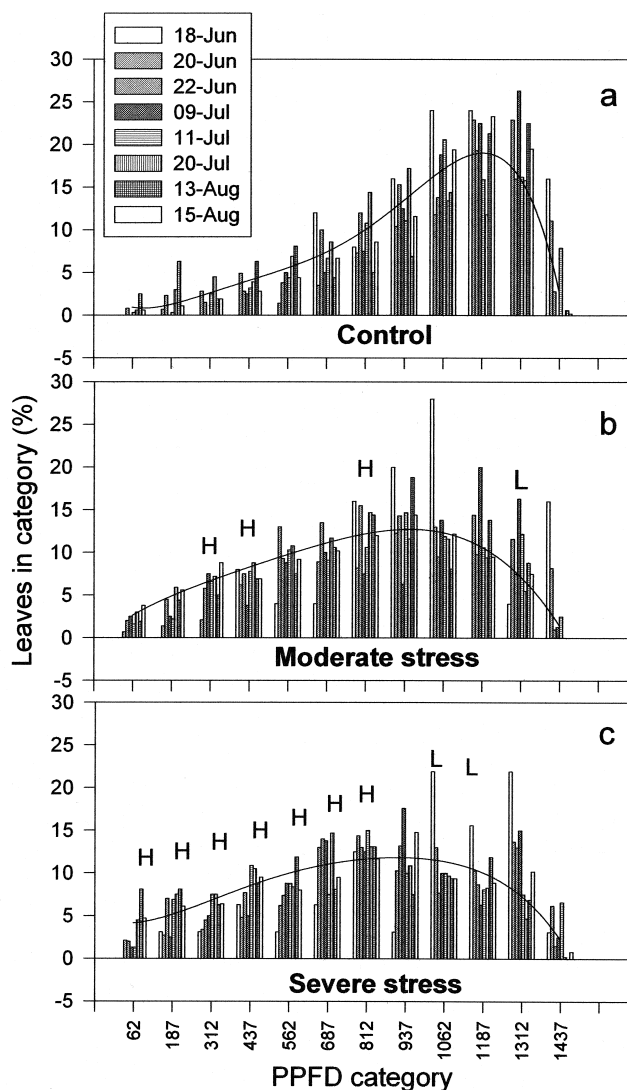
FIG. 5
Percentage of leaves versus PPFD category for the 1995 season for leaves from (a) control (b) moderate stress and (c) severe stress treatment trees as estimated using the cosine response as described in text. Letters indicate that category mean is significantly higher (H) or lower (L) than the corresponding category mean in the control trees (LSD, 5%).
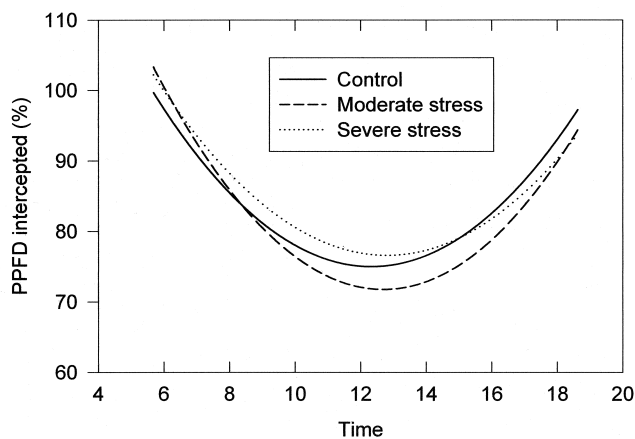

FIG. 6
Mean percent radiation interception over the course of the day for the 1994 season. Lines are second-order polynomials fit to data from eleven diurnal sets of measurements done from 21 April to 2 October, 1994. The r^2 values were 0.63, 0.64 and 0.52 for the control, moderate and severe stress treatments respectively.

August in 1995. There was no clear effect of time of day on the distribution of leaves in the different PPFD categories within a treatment (data not shown), and also no apparent differences in this distribution over the mid-June to mid-August measurement period (Figure 5). However, there were significant differences in the number of leaves in some PPFD categories in T2 and T3 compared with T1 (Figure 5). Mean PPFD for T1, T2, and T3 over the season and times of day was 981, 800 and 776 μmol m^{-2} s^{-1}, respectively, with mean PPFDs of the two stress treatments being significantly lower than that of the control. This mean PPFD corresponded to average leaf/sun angles of 32, 45 and 47 degrees, respectively. Because of the lack of a seasonal effect on sun/leaf angle distribution, the data for the eight sampling days were combined and analysed as the combined data set. T2 had significantly more leaves in the 312, 437 and 812 PPFD categories and significantly fewer leaves in the 1312 PPFD category compared with

T1 (Figure 5). T3 had significantly more leaves in the 62, 187, 312, 437, 562, 687, and 812 PPFD categories and significantly fewer leaves in the 1062 and 1187 PPFD categories compared with T1 (Figure 5).

All measurements of A_l were done on leaves that were turned perpendicular to the sun's rays. However, the vast majority of leaves on a tree are not oriented in this manner. To obtain a more realistic estimate of canopy assimilation (A_{can}), the relative assimilation rates of leaves for their actual leaf/sun angles were estimated by combining data from the light response curves with the leaf/sun angle distribution data. The first step in this process was estimating the light response curves for leaf assimilation measured in the field. Because the shape of the light response curves was similar for a particular A_{max}, the mean-treatment-assimilation values for each time category (0900, 1100, 1300, 1500 hours; Figure 1c) were used to generate light response curves with the equation described in Figure 3. These data were then combined with the estimate of mean leaf/sun angle distributions at the nearest time of day. Finally, the leaf/sun angle of each leaf class was used to estimate the relative amount of sunlight intercepted by each of the PPFD categories. This value was then expressed as the net carbon assimilation per unit leaf area for each of the treatments. The mean daily pattern of light interception over the 1994 season is shown in Figure 6. There were no significant treatment differences in light interception at any time of day. The percent light interception at each of the time categories was estimated from Figure 6 and used to modify the canopy assimilation estimates based on the actual amount of light intercepted.

Although the single-leaf assimilation rate was higher at all times of day for T1 compared with the stress treatments, the same was not true for the estimated canopy assimilation (Figure 7). Until about 1000 hours, the estimated canopy assimilation rate was higher in T2 and T3 than in T1 (Figure 7). In the afternoon, T1 trees had the highest estimated rate followed by T2 trees and T3 trees (Figure 7). Expressed as a percent of T1, the integrated daily value of A_{can} was 101% and 93% in T2 and T3 respectively (Figure 7).
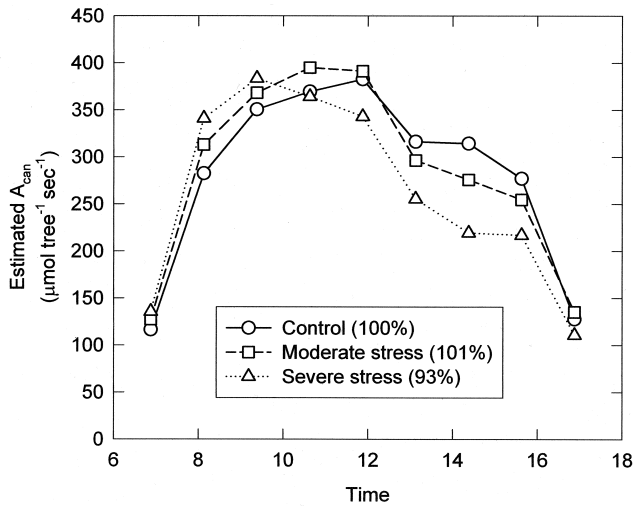
FIG. 7

Mean A_{can} estimated from single leaf CO_2 exchange plus leaf angle and light response curve data. Number following treatment in legend indicates daily A_{can} as percentage of control.

DISCUSSION

Our physiological data are consistent with earlier studies that, overall, prune yield is tolerant of moderate water stress (Goldhamer et al., 1994; Lampinen et al., 1995). Furthermore, in our study Ψ_{stem} proved to be a useful measure of plant water status that could be related to both conductance and carbon assimilation. Our results indicate that water stress effects on leaf angle distribution (Figure 5) can compensate for the clear reductions that occur in g_l and A_l (Figure 1) to give an overall similar level of daily estimated canopy photosynthesis (Figure 7). Although the moderate and severe stress treatments received an average of 58 and 39% of ET_c for the three years of the study compared with 109% ET_c for T1 (Lampinen et al., 2001), mean midday Ψ_{stem} for the moderate and severe stress treatments were only about –0.21 MPa and –0.34 MPa lower than the control (Lampinen et al., 2001). The average treatment differences in Ψ_{stem} were larger than this for the subset of trees used for our detailed study (Figure 1), suggesting that overall treatment effects may have been even less severe than estimated by the diurnal carbon assimilation data in Figure 7.

A slight midday depression in A_l was detected in all irrigation treatments, particularly T2 and T3 (Figure 1c). The fact that the peak in A_l in the control treatment trees (T1) occurred before the peak in conductance additionally suggests that there were some non-stomatal impacts on A_l. A midday depression observed in wheat (Azcon-Bieto, 1983) and grape (Downton et al., 1987) has been suggested to be due to feedback inhibition of assimilation due to carbohydrate buildup in the leaf. This did not appear to be the case in our study because leaves kept in the shade for different periods during the day and then subsequently moved into the sun, quickly reached the depressed rate measured in leaves continuously exposed to the sun (Figure 2). The depression also did not appear to be due to high light inhibition of assimilation such as that observed by Correia et al. (1990) since the light response curves showed no decrease in A_l at high light flux densities (Figure 3). A decreasing Ψ_{stem} was associated with the gradual decline in A_l from mid-morning to mid-afternoon that occurred in the control trees (Figure 2) as well as the more severe afternoon depressions in A_l in moderate and severe stress trees (Figure 1a and c). There was also a decrease in the mid-morning peak associated with decreasing Ψ_{stem} (Figure 1). The midday depression resulting from water deprivation was most probably due to direct stomatal effects. This agrees with the conclusions of Chaves (1991) that carbon assimilation is depressed under moderate water stress mostly as a result of stomatal closure.

The recovery in A_l and g_l late in the day in both of the stress treatment trees that occurred at the same time as A_l and g_l were continuing to decrease in the control trees indicates that different factors were limiting in the control trees versus the stress treatment trees. In the stress treatment trees, the recovery was most probably a result of the improving Ψ_{stem} whereas in the control trees the leaves were probably responding to the decreasing light flux densities late in the day.

Stressed trees had a shift in leaf angle such that leaves were, on average, more paraheliotropic agreeing with the results of Torrecillas et al. (1999) in apricot. Theoretically, the change in leaf angle allowed more leaves to be closer to the light saturation point (rather than above it) potentially increasing A_{can}. When the effect of changes in leaf angles was taken into account, the estimated A_{can} for moderate and severe stress treatments respectively, were 101% and 93% of the control (Figure 7). This compares with mean single-leaf assimilation rates of 90% and 81% of the control for the same two treatments, calculated by integrating under the assimilation curves of Figure 1c. Similar results were obtained by DeJong (1990) who suggested that measuring A_l on leaves turned perpendicular to the sun's rays may not give an accurate indication of canopy assimilation because very few leaves in a canopy are oriented in this manner. Because the stress treatment trees had significantly different leaf/sun inclination angles compared with the control trees, relative treatment effects on photosynthesis would be biased by estimating A_{can} based on leaves oriented perpendicular to the sun's rays.

The change toward more optimal leaf/sun inclination angles combined with the decreased carbon allocation to vegetative growth and the decreased fruit drop observed in both stress treatments (Lampinen et al., 2001) suggests that trees in the moderate stress treatment could potentially be as productive as trees in the fully-watered control. The moderate stress treatment produced similar, but not greater, dry fruit yields and monetary returns compared with the control (Lampinen et al., 2001).

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