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Crop load and water stress effects on daily stem growth in peach (*Prunus persica*)

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Summary We investigated crop load and water stress effects on diurnal stem extension growth of field-grown peach (*Prunus persica* (L.) Batsch) trees. Neither the presence of fruit nor reduced irrigation significantly altered the timing of diurnal fluctuations in stem growth rate. Stems with subtending fruit had significantly reduced growth compared to stems with no subtending fruit. Crop load had no significant effect on relative stem extension rates and the majority of the reduction in absolute growth was the result of a smaller zone of elongation in fruit-bearing stems than in stems with no subtending fruit. Fruit removal did not increase growth rates within 24 h. When irrigation was reduced, the length of the stem elongation zone and total daily stem growth were significantly decreased relative to well-irrigated controls and the decreases were highly correlated with stem water potential. Compared with well-irrigated controls, relative stem extension rates of water-stressed trees were reduced at several times during the 24-h period, but the degree of reduction was not proportional to the difference in stem water potentials between the treatments.

Keywords: diurnal growth patterns, growth zone, stem elongation, water potential.

Introduction

Vegetative growth of fruit trees is strongly affected by competition with reproductive sinks (Forshey and Elfving 1989, Wardlaw 1990). In peach trees (*Prunus persica* (L.) Batsch), the seasonal growth of stems, leaves and trunk wood is reduced as crop load increases (Miller and Walsh 1988, Blanco et al. 1995, Grossman and DeJong 1995). Water stress also significantly reduces trunk growth (Mitchell and Chalmers 1982), tree biomass accumulation (Steinberg et al. 1990), and stem extension growth (Li et al. 1989) of peach trees. The inhibitory effects of crop load and water stress on vegetative growth in fruit trees have been previously studied over time scales of weeks to months. Because these seasonal patterns are the integrated result of many daily growth events, an understanding of daily growth patterns could be key to elucidating long-term carbon partitioning trends in fruit trees.

Reduced vegetative growth in cropping trees is thought to result from competition by the developing fruit for carbohydrates (Wardlaw 1990). Although it has been shown on a seasonal basis that fruit reduce the amount of carbohydrate available for stem growth in peach (Grossman and DeJong 1995), there have been no reports describing the nature of this competition on an hourly basis and so it is unclear whether a reduction in carbohydrate supply directly limits growth rates or if the degree of reduction is constant throughout the day. Several studies suggest that short-term growth rates can be very sensitive to carbohydrate supply. For example, Rawson and Munns (1984) showed that the daily growth of sunflower leaves was strongly related to the daily irradiance integral, and Kerr et al. (1985) found that extending the normal period of darkness by several hours led to reduced carbohydrate concentrations and leaf growth rates in soybean plants. Huber (1983) studied soybean plants with low root:shoot ratios and found that carbon was partitioned to roots and shoots equally during the daytime; however, at night the growth of stems continued whereas roots decreased in dry weight. Huber (1983) hypothesized that high turgor at night shifted the relative sink strength of growing shoots and roots in favor of the shoots.

The long-term (weeks to months) influence of tree water status on vegetative growth is well documented in fruit trees (Mitchell and Chalmers 1982, Li et al. 1989, Steinburg et al. 1990). Although there have been no studies of the effects of reduced irrigation regimes on hourly growth rates of fruit trees, studies in other species have demonstrated that total daily leaf growth is highly sensitive to plant water status (Boyer 1968, Watts 1974, Schultz and Matthews 1988, Stoneman et al. 1994). Acevedo et al. (1979) observed that leaves of well-irrigated maize plants had two growth peaks, one in the morning and one in the evening. Leaf growth rates in unirrigated plants were significantly reduced during the morning, but were greater than those of irrigated plants at night, demonstrating that water stress can significantly shift the diurnal timing of growth. Recently, we obtained evidence (Berman and DeJong 1997) for a diurnal peak in stem growth in lightly cropping, well-irrigated peach trees in the late afternoon that is associated with the recovery of xylem water potential (Ψ_W).

The purpose of the present study was to determine how daily patterns of stem growth of peach trees are affected by crop load and water stress. Specifically, we tested the hypotheses that (1) crop load and water stress shift the daily timing of stem growth fluctuations and (2) the extent of stem growth inhibition associated with these factors exhibits a diurnal pattern.

Materials and methods

Stem growth measurements

Experiments were conducted at the Department of Pomology Experimental Orchard of the University of California in Davis, CA and at the Wolfskill Experimental Orchard in Winters, CA. Linear extension growth of exposed peach tree (*Prunus persica*) stems was measured in the 4–8 internodes basal to the shoot apex. To determine the extent of the elongation zone on each shoot, ink dots were made at 1-mm intervals along the stem 24 h before the commencement of experiments. Where an ink dot was made on an elongating internode region, the ink dot was visibly distorted by growth. The basal end of the elongation zone was located by observing the position of the last distorted dot (basal border) after 24 h. The first internode of length greater than 2 mm was considered to delineate the apical end of the elongation zone (apical border) and was marked with a fine permanent marker line. The distance between the apical and basal borders was measured at 2–5-h intervals with digital calipers (Mitutoyo Corp., Tokyo, Japan). Absolute extension growth rate (AER) was calculated by dividing the change in distance between the marks by the amount of time between measurements. Relative extension growth rate (RER) was calculated as:

$$\mathrm{RER} = \frac{\Delta(\ln L)}{\Delta t}, \quad (1)$$

where L = elongation zone length (mm) and t = time between measurements (h). Because AER is the product of RER and growth zone size, the AER measurements allowed comparison of the total capacity for growth by stems in each treatment, whereas the RER measurements allowed comparison of the growth efficiency of stems of different sizes (Evans 1972) by expressing growth rates relative to growth zone size.

Fruit effects on stem growth

Growth of stems with and without subtending fruit was measured on 4-year-old peach trees (cv. O'Henry), bearing a commercial crop load (~250 fruit tree^{-1}), at the Wolfskill Experimental Orchard. Five west-facing 1-year-old stems bearing 3–5 fruits with well-exposed terminal shoots were selected to represent fruiting stems. Five vigorous shoots with no subtending fruits, from the same trees, served as the non-fruiting control stems. Growth was monitored over 24 h on May 10, 1993, and again on different trees on June 1, 1993.

Defruiting experiment

On May 22, 1993, twenty fruiting stems were selected on cropping 3-year-old peach trees (cv. Springcrest) at the Department of Pomology Experimental Orchard in Davis, CA. Springcrest is an early maturing cultivar and fruit was growing rapidly at the time of sampling. Stems were carefully selected for uniformity in size, orientation, and fruit load. Ten of the stems were on a group of three trees (3–4 stems tree^{-1}) and the remaining ten stems were on a group of four trees (2–4 stems tree^{-1}). The elongation zone was marked as described above and growth of this zone was measured over 24 h (from 0930 h on May 22 to 0930 h on May 23). The defruited treatment consisted of trees that were completely defruited (60–80 fruit removed) at the end of the 24-h period. The control treatment was made up of stems on the undisturbed trees. After a second 24-h period, the growth of the elongation zone was remeasured. For each stem, the growth rate on May 23 was normalized by dividing the rate of growth (mm day^{-1}) on this date by its rate on the previous day. Temperature differences on the two days led to greater growth on May 22 than on May 23 (maximum temperature May 22 = 37 °C and maximum temperature May 23 = 32 °C), thus normalized growth rates were less than unity.

Water stress experiment

In June 1995, a row of vigorously growing 4-year-old peach trees (cv. Dr. Davis) was selected at the Wolfskill Experimental Orchard. Trees were spaced 5.5×2 m apart and were irrigated by microjet sprinklers. The row was divided into thirds and each third received one of three irrigation treatments for 2 weeks. Reference evapotranspiration (ET_0) data were used to define the irrigation treatments. The ET_0 data were obtained from the California Irrigation Management Information System (CIMIS), which calculates ET_0 by a modified Penman equation. The irrigation treatments were: control treatment (CT) = ~120% ET_0 replacement, moderate stress treatment (MS) = ~72% ET_0 replacement, and water stress treatment (WS) = no irrigation. Cumulative ET_0 was 94 mm during the two weeks before measurement and mean daily maximum temperature was 34.5 °C.

On July 11, four trees were selected from each irrigation treatment. The growth rate of one well-exposed stem near the top of each tree was measured for 24 h, as described above. Stem water potential (Ψ_{ST}) was measured simultaneously with a pressure chamber by measuring the water potential (Ψ_W) of bagged leaves located 0.5 m below the elongation zone. Leaves were enclosed in a foil-coated plastic sheath for 1 h before measurement and it was assumed that the Ψ_W of the leaf had equilibrated with the xylem of the stem to which it was attached (McCutchan and Shackel 1992).

Results

Fruit effects on stem growth

Diurnal patterns of AER were similar in shape for fruiting stems and non-fruiting stems, but differed in magnitude (Figures 1A and 1C). No significant differences in RER of fruiting stems and non-fruiting stems were observed at any time on either date (Figures 1B and 1D). The length of the elongation zone was significantly smaller on fruiting stems than on non-fruiting stems (Figures 2A and 2C). Total daily stem growth was significantly reduced (> 50%) on fruiting stems compared to non-fruiting stems (Figures 2B and 2D). Defruiting had no significant effect on total stem growth during the 24 h following fruit removal (Table 1).

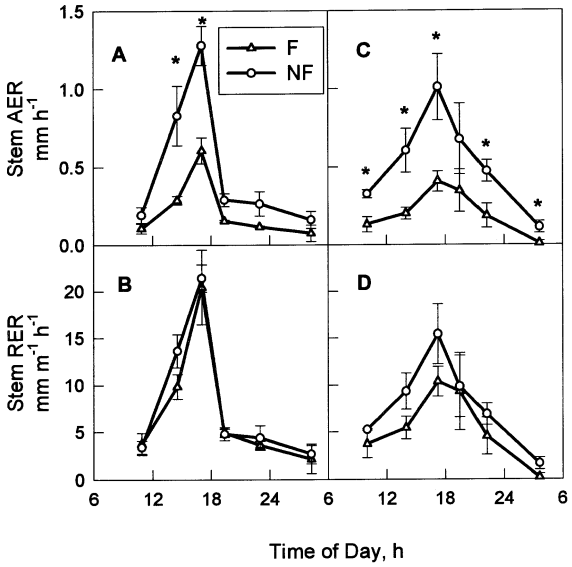

Figure 1. Diurnal growth rates of stems with 3–5 subtending fruit (F) and stems with no subtending fruit (NF). Absolute stem extension growth rate (AER) (A, C) and relative stem extension growth rate (RER) (B, D) on May 10, 1993 (A, B) and June 1, 1993 (C, D). Each point represents the mean growth rate of five stems. Error bars represent the standard error of the mean. Asterisks indicate significant differences between the stem types (Tukey's means separation test, $P < 0.05$).

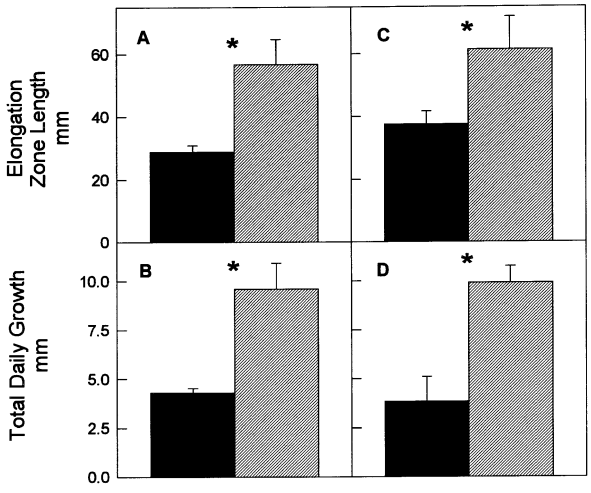

Figure 2. Daily growth parameters for stems with (F) (solid) and without (NF) (shaded) subtending fruit. Elongation zone length at the commencement of measurements on May 10, 1993 (A) and June 1, 1993 (C). Total extension growth over the 24-h measurement period on May 10, 1993 (B) and June 1, 1993 (D). Each value represents the mean of five stems. Error bars represent the standard error of the mean. Asterisks indicate significant differences between the stem types (Tukey's means separation test, $P < 0.05$).

Water stress experiment

For much of the day, Ψ_{ST} was significantly reduced in trees in the reduced irrigation treatments relative to that in trees in the control treatment (Figure 3). Diurnal fluctuations in stem AER and RER were similar in trees in the three irrigation treatments, with minimum rates in the morning and maximum rates in the evening (Figure 4). In trees in the MS treatment, stem RER was significantly reduced at ~1400 h and during the late night measurement interval (Figure 4B). The WS treatment significantly reduced stem RER below that of trees in the CT treatment for much of the 24-h sampling period (Figure 4D); however, the degree of reduction was not proportional to the difference in Ψ_{ST} between the CT and WS treatments. The largest difference in stem extension rates between trees in the WS and CT treatments occurred at ~1000 h when the WS treatment inhibited stem elongation growth (Figure 4C). During this period, Ψ_{ST} was rapidly declining in trees in all treatments and the difference in Ψ_{ST} between trees in the WS and CT treatments was 0.45 MPa. Later, at 1200 and 1600 h, the difference in Ψ_{ST} between the WS and CT treatments was just as large, but stem growth resumed in the water-stressed trees and RER of trees in the WS treatment was not significantly different from that of trees in the CT treatment. The size of the elongation zone was reduced by 17 and 30% by the MS and WS treatments, respectively, and the degree of reduction was highly correlated ($r^2 = 0.98$) with predawn Ψ_{ST} (Figure 5A).

Table 1. Normalized growth rate (mean ± SE) of defruited and control stems on May 23. The ANOVA did not detect a significant difference between treatments (Tukey's minimum significant difference (0.0827) was not achieved).

Treatment	Mean normalized rate
Control	0.884 ± 0.032
Defruited	0.865 ± 0.023

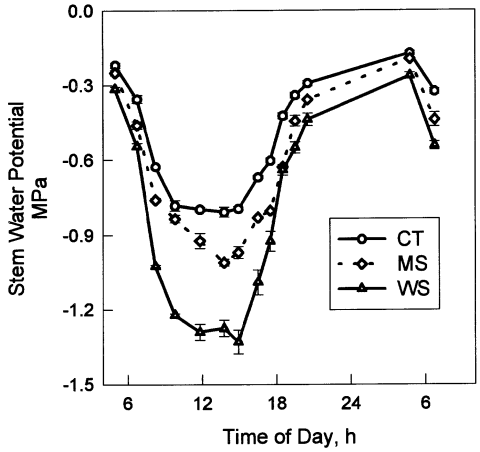

Figure 3. Daily pattern of stem water potential of trees from three irrigation treatments on July 11, 1995. Abbreviations: CT = control treatment, received 120% ET_0 replacement for two weeks before measurements; MS = moderate stress treatment, received 72% ET_0 replacement; and WS = water stress treatment, received no irrigation. Each point represents the mean of four pressure chamber measurements of bagged leaves on growing stems. Error bars represent the standard error of the mean.

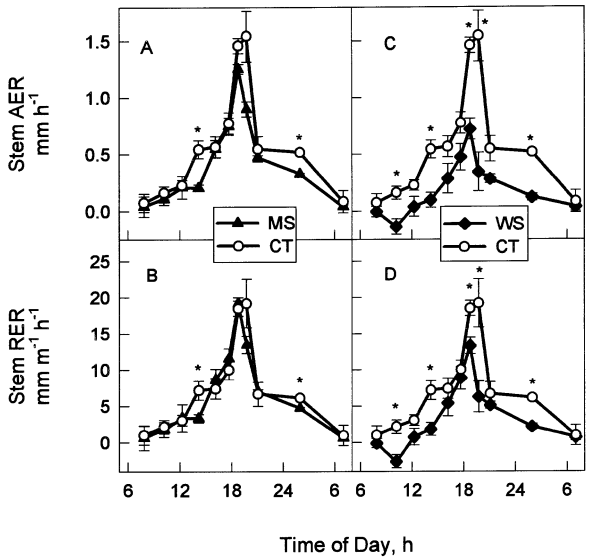

Figure 4. Diurnal stem growth patterns of trees in three irrigation treatments on July 11, 1995. The two-week irrigation treatments were: CT = control treatment, which received 120% ET_0 replacement; MS = moderate stress treatment, which received 72% ET_0 replacement; and WS = water stress treatment, which received no irrigation. Absolute stem extension growth rate (AER) (A, C) and relative stem extension growth rate (RER) (B, D) of MS (A, B) and WS (C, D) trees compared to the CT trees. Each point represents the mean of four tree measurements (one stem per tree). Error bars represent the standard error of the mean. Asterisks indicate significant differences between the MS or WS treatments and the CT treatment (Tukey's means separation test, $P < 0.05$).

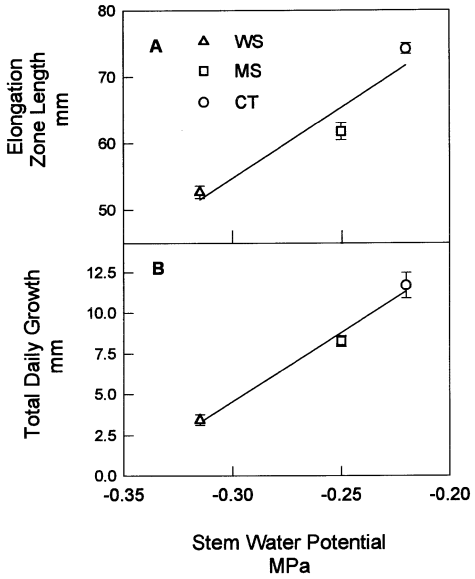

Figure 5. Daily growth parameters of stems on trees from three irrigation treatments on July 11, 1995. The two-week irrigation treatments were: CT = control treatment, which received 120% ET_0 replacement; MS = moderate stress treatment, which received 72% ET_0 replacement; and WS = water stress treatment, which received no irrigation. (A) Stem elongation zone length versus predawn stem Ψ_{ST} ($r^2 = 0.98$); and (B) total daily extension growth versus predawn stem Ψ_{ST} ($r^2 = 0.91$). Each value is the mean of four tree measurements (one stem per tree). Error bars represent the standard error of the mean. All values are significantly different (Tukey's means separation test, $P < 0.05$).

Total daily growth was reduced by 29 and 71% by the MS and WS treatments, respectively, and it was highly correlated ($r^2 = 0.91$) with predawn Ψ_{ST} (Figure 5B).

Discussion

Although both water stress and the presence of fruit reduced stem growth, neither treatment significantly altered the timing of the diurnal fluctuations in growth rate. In contrast, Acevedo et al. (1979) observed that unirrigated maize leaves had substantially lower growth rates than watered leaves during the day, but growth rates of the water-stressed leaves were greater than those of the control leaves during the evening.

Although RER of fruiting stems was not significantly different from that of non-fruiting stems (Figures 1B and 1D), the elongation zone was significantly smaller (Figures 2A and 2C), indicating that the observed reduction in total growth of fruiting stems was mostly the result of reduced growth zone size. Defruiting did not increase the total daily growth of fruiting stems within the first 24 h of fruit removal. Defruiting removed a major sink from the tree, and should have made large amounts of carbohydrate available to growing stems. For example, in apple, leaf starch content measured two days after defruiting had doubled in response to fruit removal (Wibbe and Blanke 1995). The lack of an increase in stem growth within 24 h after defruiting suggests that the short-term ability of the elongation zone to utilize carbohydrates was limited, either by the small size of the growth zone or by the short duration of the defruiting experiment.

Significant reductions in size of the growth zone were also observed in the water-stressed trees (Figure 5A). Similar drought-induced reductions in growth zone size have been observed in several species. In *Vitis*, the stem growth zone becomes more restricted over a period of days in response to water deficits (Schultz and Matthews 1988). Water stress reduces the length of the elongation zone in maize hypocotyls and roots (Saab et al. 1992). Lecoeur et al. (1995) observed that *Pisum sativum* L. leaves subjected to water stress during the period of maximal cell division have significantly reduced expansion rates later in development, even when fully watered, indicating that stress effects during the early stages of organ development persist in later growth.

Unlike the total growth response to fruit load, reductions in RER also contributed to the decreased total growth of stems in the MS and WS treatments (Figures 4B and 4D). Several factors may have contributed to decreased growth rates in the reduced irrigation treatments. Because photosynthetic rates of peach trees are inhibited by water stress (Steinberg et al. 1990, Berman and DeJong 1996), limiting carbohydrate supply may have reduced growth rates. Also, laboratory experiments have demonstrated that organ growth in water-stressed plants can be inhibited by reduced turgor (Hsiao et al. 1985, Dale 1988),

decreased cell wall extensibility (Cosgrove 1993) and ABA accumulation (Van Volkenburgh and Davies 1983, Saab et al. 1992). The finding that stems in the WS treatment decreased in length in the morning yet resumed positive growth in the afternoon, even when Ψ_{ST} was lower than in the morning, suggests that dynamic processes occur in growing stems throughout the day. Water-stressed plants can rapidly adjust cell wall properties (Serpe and Matthews 1992, Frensch and Hsiao 1994, Serpe and Matthews 1994) to regulate growth when turgor changes. Water-stressed growing tissues can also accumulate solutes to increase turgor or restore Ψ_W gradients to favor water flow into the growth zone (Meyer and Boyer 1981, Nonami and Boyer 1990, Frensch and Hsiao 1994). From our data, it is not possible to determine which of these processes was active during the day. Sensitive laboratory techniques have not yet been applied to plants growing under natural conditions and the factors that regulate diurnal growth at the cellular level in the field are not well understood.

The correlation between total daily growth of stems and peach tree water status (Figure 5B) is similar to the relationships observed for leaves of *Eucalyptus* (Stoneman et al. 1994), maize (Watts 1974), sunflower (Boyer 1968), and *Vitis* (Schultz and Matthews 1988). If the effects of reduced irrigation on daily stem growth of peach trees were scaled up to the whole tree over a period of weeks, we would expect a significant decrease in the amount of carbon partitioned to vegetative growth. We conclude that the sink strength of peach fruit is more resistant to water stress than stem elongation growth (cf. Berman and DeJong 1996). This differential response helps explain the success of deficit irrigation strategies, which are reported to reduce fruit tree vegetative growth without affecting fruit yield (Chalmers et al. 1981, Mitchell et al. 1989, Caspari et al. 1994).

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