

Diurnal patterns of stem extension growth in peach (*Prunus persica*): Temperature and fluctuations in water status determine growth rate

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Field measurements of stem extension growth rate in peach (*Prunus persica* [L.] Batsch) exhibited a consistent diurnal pattern. Stem extension rate was lowest in the early morning and increased throughout the day. In the late afternoon, 2–3-fold increases in extension rate occurred and were sustained for 2 to 4 h. After this growth surge, rates precipitously declined and remained low during the night. The temperature response of stem growth rate at constant water potential was determined using potted trees in a dark growth chamber. Under such conditions, stem growth rate was strongly dependent on air temperature. In the field, the observed stem growth rate deviated from that predicted on the basis of temperature. These deviations were proportional to the rate of change in stem water potential. A model was constructed to predict diurnal patterns of stem extension rate using temperature and water potential data. The model was tested using data from undisturbed trees and from trees in which water potential was artificially manipulated. Growth patterns predicted by the model were in general agreement with observed rates.

Key words – Diurnal growth patterns, growth modelling, peach, *Prunus persica*, water relations.

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Introduction

In tree crops, the control of vegetative growth is of substantial interest, since vigorous vegetative growth increases management costs and negatively influences fruit yield and quality (Day et al. 1989, DeJong and Day 1991). Excessive carbon partitioning to vegetative organs reduces harvest index, and represents carbon that could potentially have been invested in the crop. Peach (*Prunus persica* [L.] Batsch) is a vegetatively vigorous fruit tree species. Young cropping trees have been observed to partition over 25% of seasonal aboveground biomass to stem growth (M. E. Berman. 1996. Thesis, Univ. of California, Davis, CA, USA). In commercial orchards, peach trees are summer pruned and dormant

pruned to remove excessive shoot growth. Neither commercially acceptable dwarfing rootstocks nor chemical control of vigor are available. Pruning is labor-intensive and represents a significant production cost. Understanding the factors governing vegetative growth in tree crops may allow more efficient management strategies.

Environmental factors clearly have a large influence on vegetative vigor. Plant growth is strongly influenced by temperature (Ong and Baker 1985) and fruit tree vegetative growth is enhanced by increased irrigation (Forshey and Elfving 1989, Li et al. 1989, Caspari et al. 1994). Seasonal effects of temperature and water relations on vegetative growth are the integrated results of many daily growth events. Studies of diurnal growth patterns provide insight into how environmental factors

control growth rates on an hourly basis. These short-term interactions, when scaled over weeks to months, are important determinants of seasonal carbon partitioning trends.

In some previous reports, a clear relationship between diurnal growth patterns and air temperature has been observed. In wheat (Kemp and Blacklow 1980), willow (Stadenberg et al. 1994) and maize (Watts 1974), leaf expansion rates tracked air temperature. In barley, Gallagher and Biscoe (1979) demonstrated that hourly leaf growth rates normalized for temperature were strongly correlated with leaf water potential. In other studies, the relationships between environmental factors and diurnal growth patterns are not clear. For example, field growth rates of maize, sorghum (Acevedo et al. 1979), willow (McDonald et al. 1992), bunchgrass (Busso and Richards 1993) and Scots pine (Kenninen 1985) do not appear to track air temperature. Water relations clearly affected growth rates in these cases; however strong correlations between growth rate and water status were not observed.

The fact that plant growth rates over short time scales often do not correlate well with single factors indicates that growth rates are determined by complex plant-environment interactions. Temperature and plant water status can affect growth simultaneously and may act antagonistically to each other. Additionally, dynamic plant metabolic processes may result in transient and nonlinear growth responses. To successfully understand how growth in the field is related to temperature and plant water status, the effects of these factors must be separated and quantified individually. The present work was undertaken to describe the daily pattern of peach stem growth in the field and to understand how growth rate relates to natural fluctuations in temperature and plant water status. A distinct and consistent diurnal pattern of stem growth was observed. From repeated field observations and experiments in controlled environments, a model was developed which predicts daily patterns of stem growth rate using temperature and water potential data.

Abbreviations – Ψ_p , turgor pressure (MPa); Ψ_{ST} , stem water potential (MPa); Ψ_w , water potential (MPa); FD, fast transition to darkness; LVDT, linear variable displacement transducer; Q_{10} , temperature coefficient; RCW, rate of change of stem water potential (MPa h^{-1}); SD, slow transition to darkness; SER, stem extension rate (mm h^{-1}); TPR, temperature-predicted growth rate (mm h^{-1}).

Materials and methods

Stem extension rate measurements

Measurements of stem extension rate (SER) were made on well-exposed stems of peach trees (*Prunus persica* [L.] Batsch). Trees were 3–5 years old, trained to a Kearney perpendicular-V (DeJong et al. 1995), located at the University of California, Dept of Pomology Experimental Orchard in Davis, CA. SER was measured by making

fine ink marks on the stem with permanent markers. The distance between the marks, was measured using digital calipers (Mitutoyo Corp., Tokyo, Japan) which measured within 0.1 mm with 95% accuracy. SER was calculated by dividing the change in distance between the marks by the amount of time between measurements. During the day, the measurement interval was 2–3 h. From 2000 h until 0500 h, measurements required flashlight illumination. Since stem growth can be sensitive to phytochrome interactions (Casal and Sanchez 1994), night measurements were made at longer intervals (3–6 h) to minimize illumination artifacts. On each date, 4–5 adjacent stems per tree were measured. SER was measured in the 4–6 internodes just basal to the shoot apex, a region typically spanning 5–7 cm.

For ease of measurement, growth of the most vigorous stems was observed. These stems were not representative of the majority of growing stems on the tree in terms of absolute growth rate and seasonal duration of growth. The majority of stems on a tree were observed to grow slowly, and often ceased elongating by June. The stems that were used for measurements grew rapidly and elongation continued as late as September. However, the diurnal patterns of extension growth rate were observed to be identical in shape for vigorous stems, slowly growing stems, and secondary lateral stems (data not shown). Therefore, the growth pattern of vigorous stems was considered to be representative of all stems on the tree in terms of relative growth response to air temperature and tree water status.

Growth of other *Prunus* species

On June 6, 1995, SER was measured in the afternoon and evening on 3-year-old trees of peach (cv. Springcrest) and five other *Prunus* species growing in adjacent rows at the UC Davis Pomology Dept Experimental Orchard. The species measured were *Prunus armeniaca* (cv. Patterson), *Prunus avium* (cv. Black Tartarian), *Prunus dulcis* (cv. Nonpareil), *Prunus salicina* (cv. Red Beaut) and *Prunus domestica* (cv. Improved French). SER was measured as described above for peach, using ink marks and digital calipers.

Temperature measurements

Air temperature was measured using a shaded thermistor temperature probe at canopy height (2.5 m). Mean hourly temperatures were calculated and recorded on a CR21 Datalogger (Campbell Instrument, Logan, UT, USA). Thermistor measurements were checked against weather station data from a California Irrigation Management Information System (CIMIS) weather station located 1 km from the field site. Weather station temperatures and those measured directly with thermistors were not significantly different, so thereafter weather station data were used to estimate temperature at the field site.

Stem water potential measurements

Stem water potential (Ψ_{ST}) was measured using the method described by McCutchan and Shackel (1992). Plastic sheaths similar in shape and size to peach leaves were constructed and covered with aluminum foil. These bags were placed over fully mature leaves basal to the stem elongation zone. After a period of at least 1 h, bagged leaf Ψ_w was assumed to have equilibrated with that of the xylem in the stem to which it was attached. The leaf was then cut and its Ψ_w measured in a pressure chamber. Leaves 0.5–1.0 m basal to the extension zone were used for measurement to minimize leaf removal effects on the carbohydrate and water relations of the extension zone. This type of measurement allowed Ψ_{ST} of the same stem to be measured repeatedly using different leaves.

Shading experiments

Vigorous stems on one of the two main scaffolds of each tree were selected and SER and Ψ_{ST} were measured as described above. To increase water potential in the selected stems, the opposite scaffold was sprayed with water and covered with tarps. This effectively reduced the transpirational load of the tree and led to Ψ_{ST} increases in the uncovered scaffold. The light and temperature environment of the exposed stems being measured were unaffected by shading the opposite side of the tree. Rapid removal of the tarps caused rapid decreases in Ψ_{ST} on the unshaded side. SER of shaded trees was compared to that occurring simultaneously in unshaded trees.

Growth chamber measurements

In March 1995, 1-year-old peach trees (cv. O'Henry on cv. Nemaguard) were planted in 20-l plastic pots in standard potting mix (Supersoil, Rod McLellan Co., So. San Francisco, CA, USA) and placed in a lath house. Four weeks after vegetative bud break, trees were moved to a controlled environment chamber where they received a 14-h photoperiod with lamps (M400/U metal halide, H38 HT-1000 mercury vapor, Sylvania, Danvers, MA, USA) providing $450 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$. Light was measured with a Li 185B quantum meter (Li-Cor, Lincoln, NE, USA). For 2 weeks the trees were grown with a sinusoidal temperature regime mimicking that of the field, with a daily maximum of 36°C and minimum of 12°C .

SER was measured using linear voltage displacement transducers (LVDT, Transtek Co., Hartford, CT, USA). The growing shoot tip was attached to a fine copper wire with a padded clamp. The wire ran over a low-friction pulley and the free end was connected to the weighted core of the LVDT, so that vertical growth by the shoot resulted in equal and opposite movement of the LVDT core. The wire was kept at a tension of 2 g to eliminate extraneous movements caused by air currents in the growth chamber. Output was plotted against time and

the data fitted with a moving kernel function (Chu and Marron 1991). This type of curve fitting smoothed signal noise and the first derivative of the fitted function was calculated to estimate growth rate.

Growth chamber temperature experiments

After 18 days of growth under the normal temperature regime, growth of stems at different temperatures was measured during the dark period. Air temperature was brought to 35°C after the lights were turned off. Within 60 min, water potential and SER reached steady state values. Air temperature in the chamber was then step changed in 5°C increments, from 35°C down to 15°C then back to 35°C . Temperature transitions took ~ 5 min and growth was recorded for 30 min at each temperature. Three stems with similar growth rates, each from a different tree, were selected for measurement. This experiment was repeated a second night with three different stems.

The elongation zone of stems grown in the growth chamber was much shorter than that of field-grown stems (~ 3 cm vs ~ 6 cm). This size difference resulted in different SER at similar temperatures, but it was assumed that the shape of the SER-temperature curve was the same for field-grown trees and potted trees in the growth chamber, given that both were grown under similar temperature regimes. To apply the relationship observed in the growth chamber to the larger field-grown stems, a temperature quotient (Q_{10}) was calculated. Q_{10} is the factor by which a rate changes with a 10°C change in temperature and is not sensitive to size. An exponential function was fit to the growth chamber data and using function-predicted rates at 10°C intervals, a Q_{10} was calculated after Larcher (1980). Because one exponential function fit all the growth chamber data points, it was assumed that Q_{10} was constant over the range of 15 – 35°C .

Water potential experiments

Seven hours after commencement of the photoperiod, the temperature in the chamber was stabilized at 25°C with lamps providing $450 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$. Stems were attached to the LVDTs and several leaves, 0.5 to 1.0 m basal to the extension zone, were bagged. After 1 h at constant conditions, one of two treatments, slow transition to darkness (SD) or fast transition to darkness (FD), was imposed. SD treatment consisted of the growth chamber lamps being incrementally dimmed every 5 min until complete darkness was achieved after 40 min. In the FD treatment, lights were turned off abruptly. For both treatments, SER was continuously measured and bagged leaf water potential was measured every 10 min. Air temperature was maintained at $25 \pm 2^\circ\text{C}$ for the duration of the experiments. FD and SD treatments were imposed on two dates, yielding data from 5 and 6 stems, respectively.

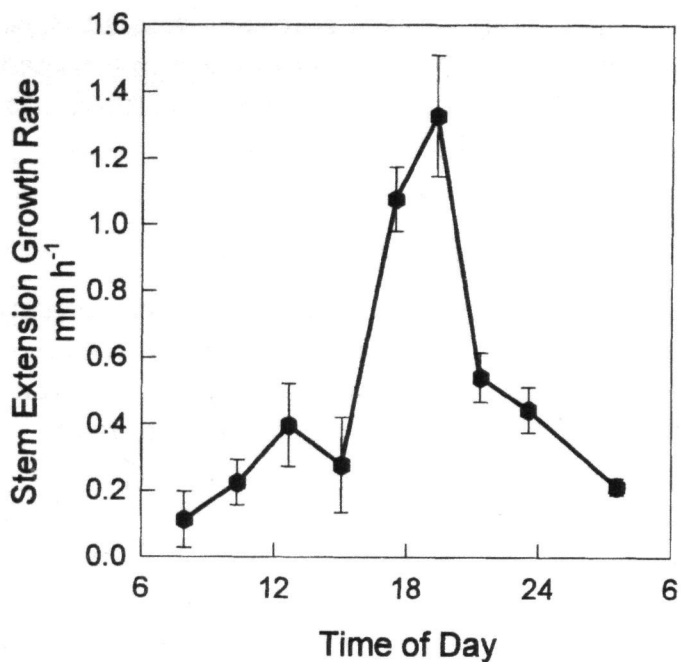


Fig. 1. A typical diurnal pattern of peach stem extension growth rate (SER), from a 4-year-old peach tree (cv. O'Henry) on 29 June, 1994. Each point represents the mean stem extension rate of 5 well-exposed stems growing at the top of the tree. Error bars represent the SE of the mean.

Results

Daily pattern

On cloudless days, SER was lowest in the early morning and was 700–800% greater in the late afternoon/early evening. The timing of maximal growth shifted from ~1700 h in April and early May to ~1900 h in July and August. A typical daily growth pattern is presented in Fig. 1. No substantial differences in daily SER pattern were observed among several cultivars, including O'Henry, Springcrest, Mayglo, Elberta and Dr Davis. On 6 June, 1995, stem growth was measured on peach and five other *Prunus* species including apricot, almond, cherry, prune and plum. Although there were differences among species in absolute growth rate, the late afternoon and evening growth patterns of the five other *Prunus* species were similar to that of peach. Maximum SER always occurred in the evening (Fig. 2).

Extension growth rate and environmental factors

SER values from four study dates, when Ψ_{ST} and air temperature data were collected simultaneously, were

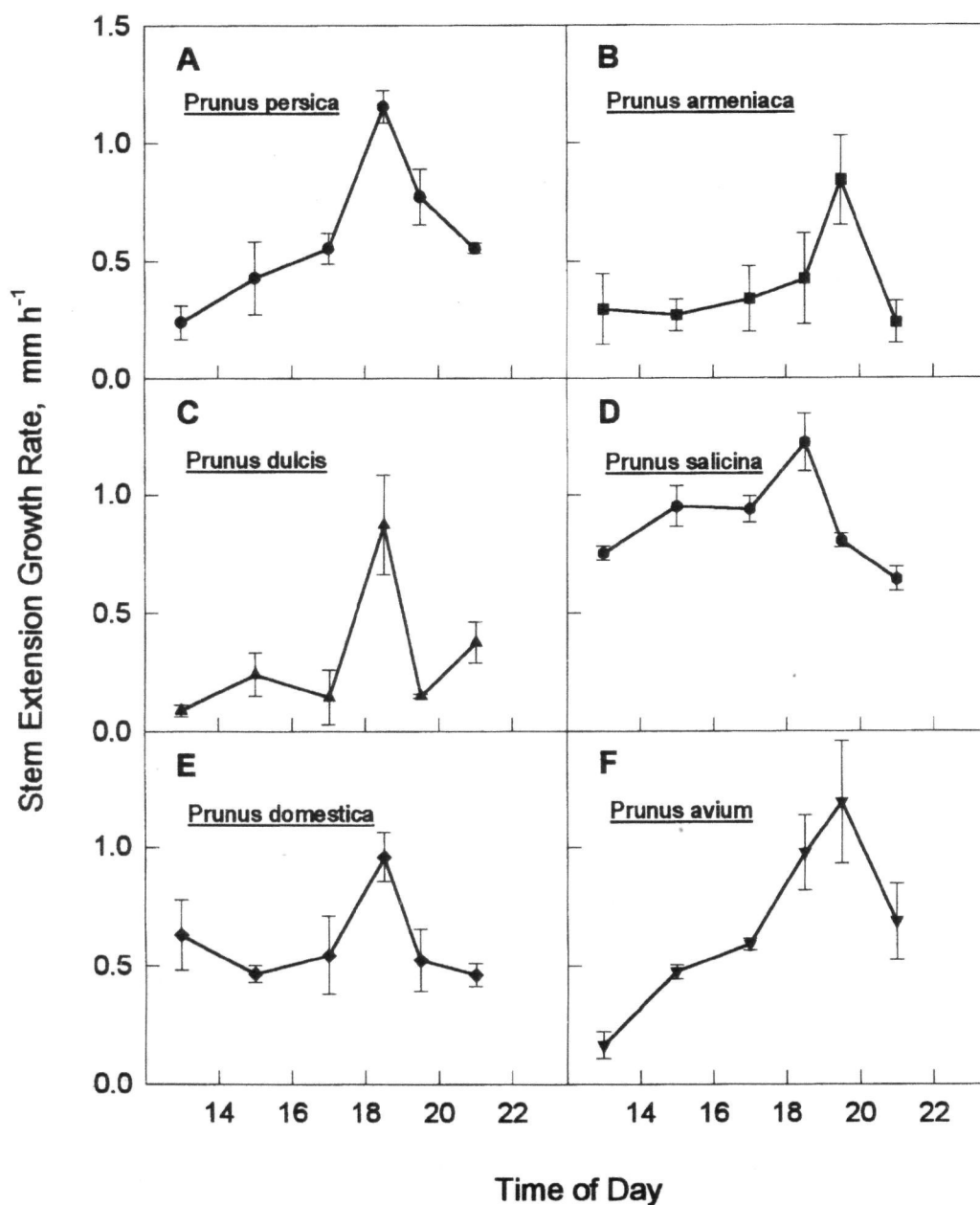


Fig. 2. Stem extension rate of several *Prunus* species on 4 June, 1995. Growth rate was measured on young trees growing in adjacent rows. A, peach (*Prunus persica*); B, apricot (*Prunus armeniaca*); C, almond (*Prunus dulcis*); D, Japanese plum (*Prunus salicina*); E, French prune (*Prunus domestica*); F, cherry (*Prunus avium*). Each point represents the mean rate of three stems. Error bars represent the SE of the mean.

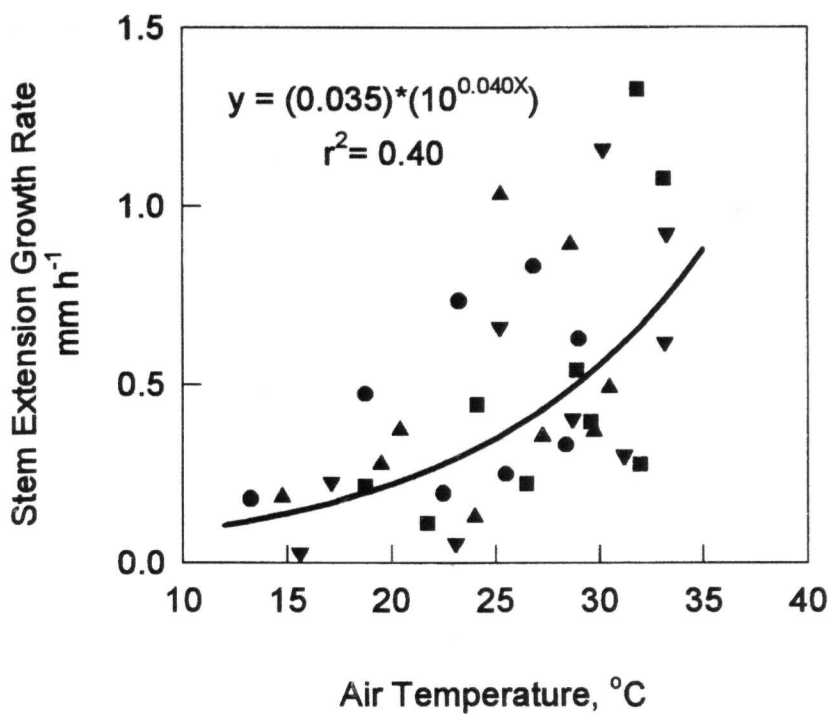


Fig. 3. Stem growth rate in the field vs air temperature. Data are from diurnal measurements made on four dates. Each symbol type represents data from one of four sampling dates. Each point represents the mean growth rate of 4–5 stems from a single tree.

significantly ($P < 0.05$) but weakly ($r^2 = 0.40$) correlated with air temperature (Fig. 3). When SER was measured in the dark with constant stem water potential (Ψ_{ST}), it was strongly correlated with temperature (Fig. 4). In an attempt to account for the difference between the growth-temperature relationship in the field (weak correlation) and in the growth chamber (strong correlation), a temperature-based model predicting growth rate was developed. The relationship observed in Fig. 4 was applied to the larger field-grown stems by use of the temperature quotient (Q_{10}). SER-temperature data (Fig. 4)

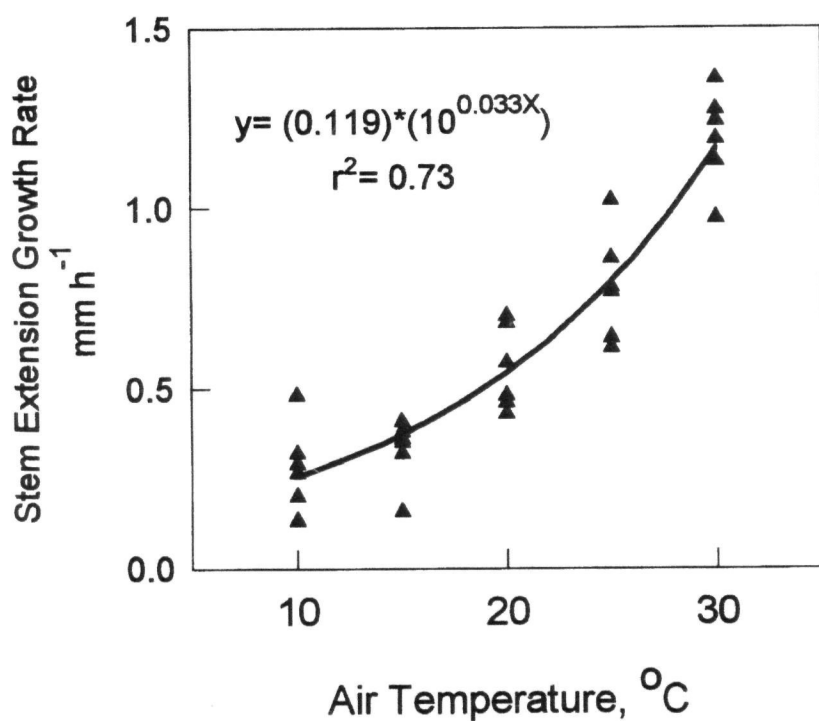


Fig. 4. Stem extension rate of trees in the dark at different temperatures. Each point represents the growth rate of one stem on a potted tree in a dark growth chamber.

were fit to an exponential function ($r^2 = 0.73$) and using this function, Q_{10} was calculated after Larcher (1980):

$$Q_{10} = \exp \left[\left(\ln \left(\frac{GR_{T_2}}{GR_{T_1}} \right) \right) \times \left(\frac{10^\circ\text{C}}{(T_2 - T_1)} \right) \right] \quad (1)$$

where GR_{T_1} and GR_{T_2} represent growth rates (in mm h^{-1}) at air temperatures T_1 and T_2 (in $^\circ\text{C}$).

An equation was then developed to predict what daily growth patterns would have been in the field if temperature were the only controlling factor. It was assumed that the Q_{10} calculated in the growth chamber was representative of stems in the field. It was also assumed that late-night SER values, measured from 2200 h to 0500 h when changes in plant water status were minimal, represented values determined mostly by temperature. The resulting model predicted growth rate at any temperature using the calculated Q_{10} , daily temperature data, average night temperature and average night SER:

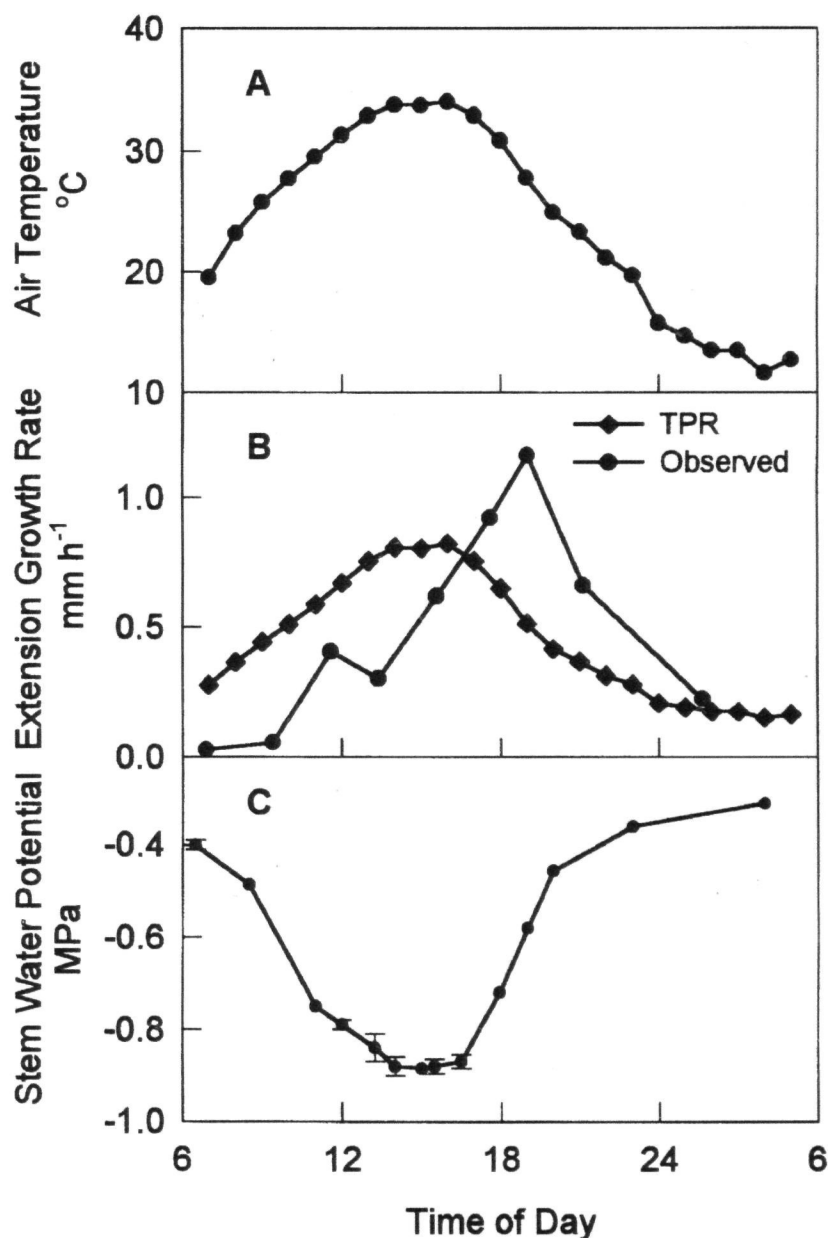


Fig. 5. Environmental parameters and growth rates for 25 July, 1994. A, average air temperature; B, hourly predictions of stem extension rate from the temperature-growth model (see text, Eq. 2) and the actual observed stem extension rate; C, the diurnal pattern of stem water potential (Ψ_{ST}). Each water potential point represents the mean of two measurements and error bars represent the SE of the mean.

$$\text{TPR}_X = \left[Q_{10}^{\left(\frac{T_X - T_N}{10^\circ\text{C}} \right)} \right] \times [\text{GR}_N] \quad (2)$$

where TPR_X is the average temperature-predicted rate (TPR) over time interval X (in mm h^{-1}), T_X is the average temperature over time interval X (in $^\circ\text{C}$), GR_N is the average night growth rate and T_N is the average night temperature.

Night growth rates, night temperatures and daily temperature data from the four measurement dates were used to calculate TPR values. Representative data from one date are presented in Fig. 5A,B. The daily SER pattern significantly deviated from the TPR pattern. The rates were consistently below the TPR in the morning, and greater than the TPR in the evening and these deviations seemed to correspond with the slope of the Ψ_{ST} curve, which was negative in the early part of the day and positive later in the day (Fig. 5C). To quantify this relationship, the average TPR was calculated for each SER measurement time interval. The deviation of each SER point from the TPR was then plotted against the rate of change of Ψ_{ST} (RCW) during that time interval. The SER deviations from TPR were highly correlated with RCW (Fig. 6).

The regression equation shown in Fig. 6 was combined with Eq. 2 to develop a model which predicts SER over any time interval:

$$\text{GR}_X = \left(\left[Q_{10}^{\left(\frac{T_X - T_N}{10^\circ\text{C}} \right)} \right] \times [\text{GR}_N] \right) + \left[\left(4.26 \frac{\text{mm}}{\text{MPa}} \right) (\text{RCW}_X) - \left(0.02 \frac{\text{mm}}{\text{h}} \right) \right] \quad (3)$$

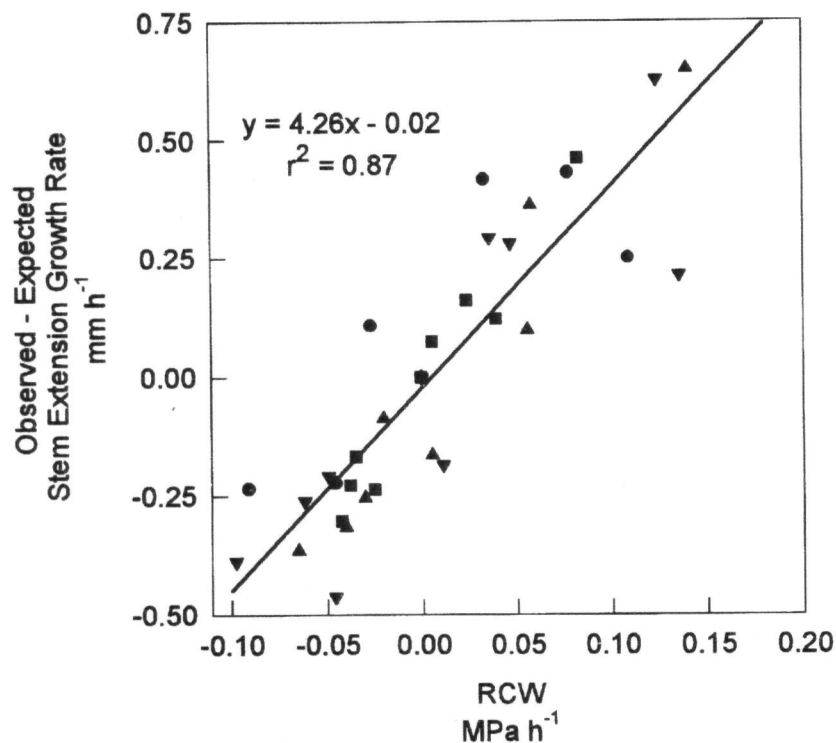


Fig. 6. The difference between the observed stem extension rate and the expected rate based on the temperature growth model (See text, Eq. 2) plotted against the observed rate of change in Ψ_{ST} (RCW). For each date, the night growth rate = TPR and thus the deviation from the expected rate = 0. It was assumed that the RCW corresponding to these times = 0. Each symbol type represents data from one of four sampling dates.

where GR_X is the predicted growth rate over time interval X (in mm h^{-1}), T_X is the average temperature over time interval X (in $^\circ\text{C}$) and RCW_X is the rate of Ψ_{ST} change over time interval X (in MPa h^{-1}).

Testing the model

Diurnal SER, temperature and Ψ_{ST} data not previously used in the generation of the model were available from three dates. These data were put into the model to generate three predicted daily SER curves. The curves predicted by the model and the actual observed SER curves were similar in shape (Fig. 7). To further test the predictive capacity of the model, Ψ_{ST} was artificially altered at different times of day. Partial shading at 1300 h resulted in increased Ψ_{ST} (Fig. 8A). SER on the partially shaded tree was significantly ($P < 0.05$) greater than on the control tree during the period of shading (Fig. 8C). Removal of the shade at 1445 h resulted in negative RCW and a sharp decline in SER. Partial shading at 1500 h caused a more rapid afternoon recovery of Ψ_{ST} relative to the control tree (Fig. 8B) and SER was significantly increased in the shaded tree relative to the control during the afternoon measurement interval (Fig. 8D). Temperature and

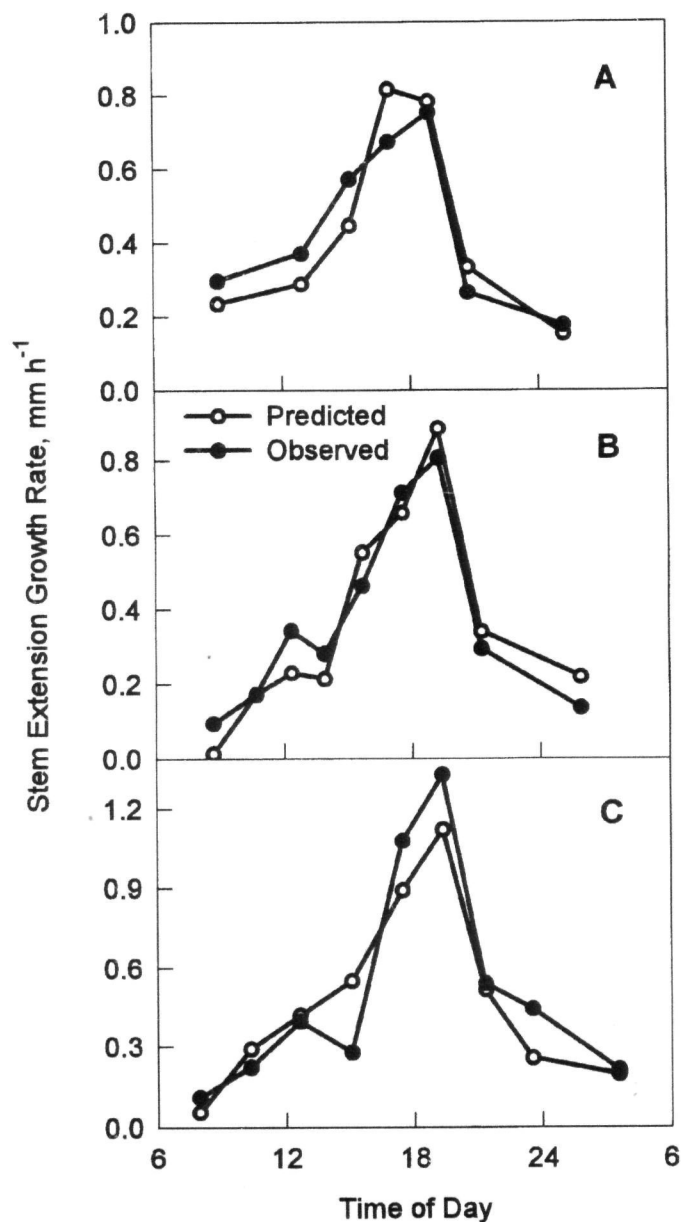
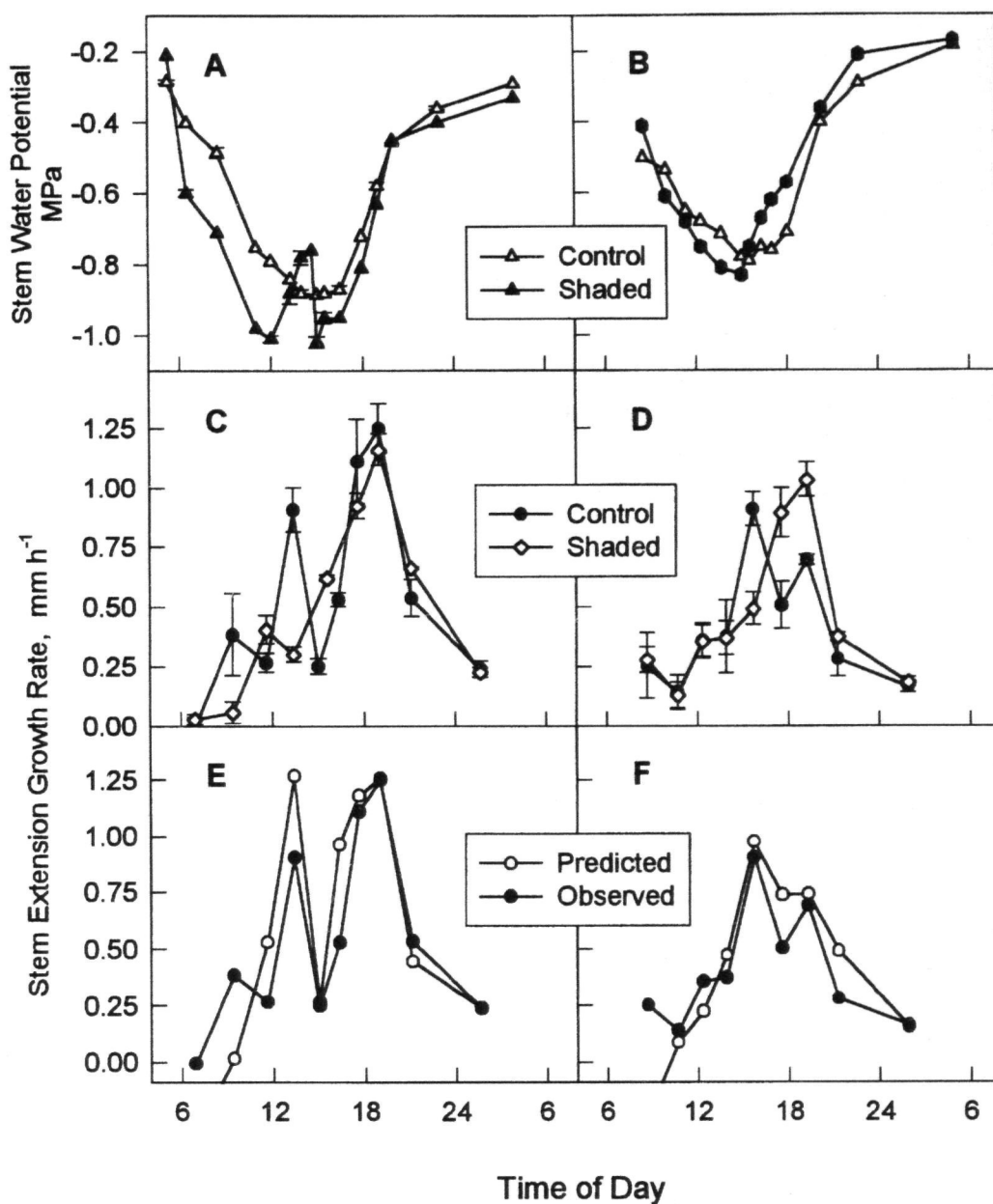


Fig. 7. Observed stem extension rate and the rate predicted using the growth model (See text, Eq. 3) for 3 dates. A, 3 June, 1994; B, 22 June, 1994; C, 29 June, 1994.

Fig. 8. Summary of data from shading experiments. Panels A, B and C show patterns of Ψ_{ST} ($n = 2$, error bars represent SE of the mean), stem extension rate and modeled predictions of stem extension rate, respectively, for control trees and trees that were half-shaded at 1300 h and then unshaded at 1445 h on 25 July, 1994. Panels D, E and F show patterns of Ψ_{ST} ($n = 1$), stem extension rate and modeled predictions of stem extension rate, respectively, for control trees and trees that were half-shaded at 1500 h on 22 June, 1994.



RCW data from the shaded trees were used as input for the model to generate predicted SER curves (Fig. 8E,F) which generally matched the shape of the actual growth curves.

The predicted values from the shading experiments (Fig. 8E,F) and from the undisturbed trees (Fig. 7) were plotted against corresponding observed values (Fig. 9). The resulting plot demonstrates the general ability of the model to predict SER behavior, with variable accuracy. The predicted growth curves were in phase with the actual growth curves, however at times there were substantial discrepancies between the predicted and observed rates (e.g. AM rates in Fig. 8E,F). Comparison of data points with a 1:1 line indicates that the model has a slight tendency to overestimate high growth rates and underestimate low growth rates.

Growth chamber experiments

To investigate RCW effects on SER without interfering temperature effects, measurements were made on trees growing in a controlled environment chamber. Although stem growth rates were highly variable, strong RCW effects were evident. Dimming the lights slowly in the SD treatment resulted in an average Ψ_{ST} increase of 0.16

MPa over 30 min (Fig. 10A) and increased rates of SER for over 70 min (Fig. 10B). Turning lights off abruptly in the FD treatment led to a rapid increase of 0.15 MPa in Ψ_{ST} (Fig. 10A) and a transient 300% increase in SER (Fig. 10B). Within 30 min SER returned to a rate 25% above the original value. In both the FD and SD treatments, there was a slight lag between the maximum RCW (occurring during the first 10 min) and the maximal SER response (observed at ~15 min).

Discussion

Previous studies of growth in the field have identified the qualitative importance of temperature and Ψ_w on growth rates, but have failed to quantify growth rates in relation to these factors. Separating the effects of temperature and water status is difficult in the field because these parameters change constantly and inversely (Fig. 5A,C). By combining field measurements and growth chamber observations, we derived a novel relationship between water relations and growth rate and constructed a model which predicts daily growth patterns with reasonable accuracy.

Temperature governs SER when Ψ_{ST} fluctuations are minimal (Fig. 4). Many growth and respiratory pro-

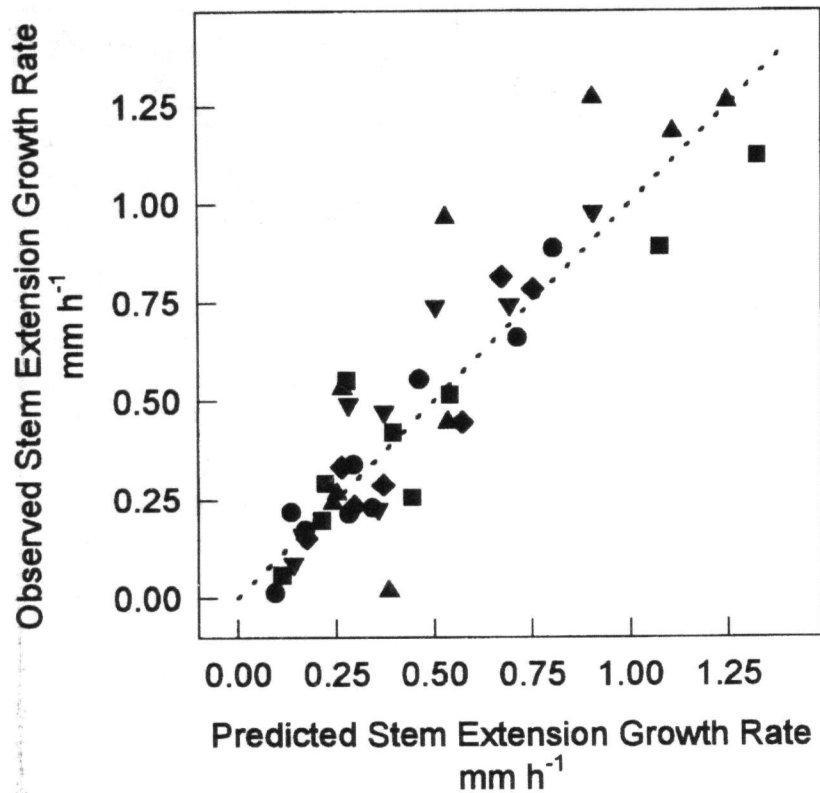


Fig. 9. Summary of growth model predictions (See text, Eq. 3) from undisturbed trees (Fig. 7) and shaded trees (Fig. 8C,F). Each point is stem extension rate predicted by the growth model plotted against the observed rate. A line of slope = 1 is included to visualize deviance of the predicted rates from observed. Each symbol type represents data from one of six trees.

cesses have a Q_{10} similar to the Q_{10} of 2.11 calculated for peach SER. For example, maize leaf extension rate has a reported Q_{10} of 2.0 (Watts 1972) and peach fruit respiration rate has a reported Q_{10} of 2.03 (Pavel and DeJong 1993). The weak correlation between SER and temperature in the field (Fig. 3) demonstrates the importance of Ψ_{ST} effects on growth rate. The growth model estimates SER values as the sum of temperature and water relations effects. While this empirical construction is certainly an oversimplification of the complex relationships among temperature, water relations and cell expansion, the correlation between RCW and SER deviations from TPR is fairly strong (Fig. 6), allowing rate prediction with a two-variable model.

The large effects of changing water status on plant organ growth rates have been previously observed in many studies (Acevedo et al. 1971, Christ 1978, Wenkert et al. 1978, Cosgrove 1993). Decreases in Ψ_w reduce or halt growth while raising Ψ_w increases growth rate. These previous experiments involved sudden step-changes in Ψ_w rather than the extended periods of Ψ_w fluctuation that occur daily under field conditions. However, qualitatively, previous results are similar to those observed for peach in the current study, where daily RCW fluctuations correlate with SER deviations from TPR (Fig. 6) and artificial manipulations in water status have strong effects on SER (Figs 8 and 10).

Previous experiments show that the growth response to changing Ψ_w is usually transient, with the original growth rate being partially or fully restored within minutes to hours (Shackel et al. 1987, Serpe and Matthews

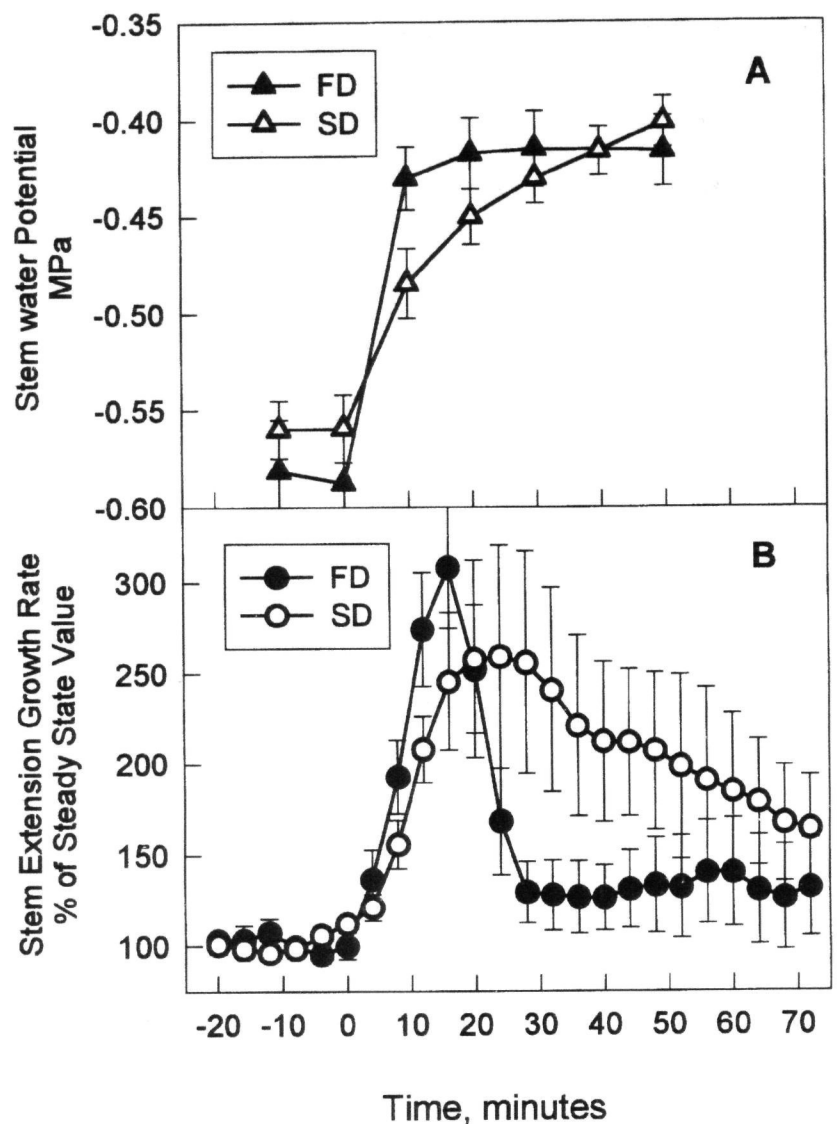


Fig. 10. Time course responses of stem extension rate and Ψ_{ST} to changes in growth chamber lamp intensity. Light intensity was $450 \mu\text{mol m}^{-2} \text{s}^{-1}$ prior to the onset of darkening treatments at time = 0. In the FD treatment, lights were abruptly shut off at time = 0. In the SD treatment, lights were gradually dimmed and total darkness was achieved after 40 min. Temperature was maintained at $25 \pm 2^\circ\text{C}$. A, mean Ψ_{ST} ; B, mean SER presented as a percentage of the steady state value observed prior to dark treatment. Error bars represent the SE of the mean (FD, $n = 5$; SD, $n = 6$).

1992, Cosgrove 1993). These results indicate that homeostatic mechanisms exist in growing cells to maintain target growth rates. These homeostatic processes include rapid adjustments in cell wall properties (Shackel et al. 1987, Serpe and Matthews 1992, Frensch and Hsiao 1994) and regulation of turgor pressure (Ψ_p) by solute accumulation (Meyer and Boyer 1981, Frensch and Hsiao 1994). The transient growth peak observed in Fig. 10 shows that homeostatic processes act in peach stems when water status is altered. However, in the field, these mechanisms apparently do not fully keep pace with the constantly changing Ψ_{ST} , so that SER deviates from TPR for much of the day.

Measurements of Ψ_{ST} describe the water potential of the stem xylem, not the Ψ_w of the expanding cells. Therefore the mechanisms which relate changing water status to cell expansion rate in peach stems are unknown. Our diurnal Ψ_{ST} patterns are very similar to those observed for peach stem water content by Simonn-

eau et al. (1993), with stem dehydration occurring during the early part of the day and rapid rehydration occurring in the evening as transpiration decreased. In young soybean stems, Nonami and Boyer (1993) observed a Ψ_w gradient favoring water flow from the xylem into expanding cells. They observed that this gradient, rather than Ψ_p , was the major factor controlling short-term changes in growth rate (Nonami and Boyer 1990). If peach SER is similarly controlled by the Ψ_w gradient between the xylem and the elongating cells, then RCW may correlate with SER by reflecting changes in the steepness of this gradient as the tree dehydrates and rehydrates.

Our results indicate that changes in water status occurring over periods of hours strongly influence SER in the field. For example, in Fig. 1, over 40% of the total daily growth took place in just 4 h, from 1600 to 2000 h, during the rapid recovery of Ψ_{st} . Laboratory studies have documented the importance of Ψ_p (Shackel et al. 1987, Serpe and Matthews 1992), solute accumulation (Meyer and Boyer 1981, Frensch and Hsiao 1994), cell wall property adjustment (Cosgrove 1993, Serpe and Matthews 1994) and water potential gradients (Nonami and Boyer 1990, 1993) in controlling growth rates. Due to technical challenges, none of these parameters has been precisely measured under field conditions. More research is needed to understand how these controlling factors influence growth during the extended transitions in water status which occur in the field.

To our knowledge, no one has previously quantified growth rates in relation to changes in plant water status or used this relationship to account for daily growth patterns in the field. However, previous reports show that the daily growth patterns of maize and sorghum leaves (Acevedo et al. 1979), wild grass leaves (Busso and Richards 1992, 1993), willow leaves (McDonald et al. 1992) and pine stems (Kenninen 1985) are very similar to that of peach stems, with maximum growth rates between 1600 h and 1900 h, during the period of rapid water potential recovery. The fact that a diverse range of plants, including grasses, conifers and *Prunus* species (Fig. 2), have similar diurnal growth patterns indicates that the temperature and water status interactions driving diurnal fluctuations in peach SER are common to many plants under field conditions and that the growth rate model developed in this study should be adaptable to other species.

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