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EFFECT OF WATER STRESS AND RECOVERY ON THE
GROWTH AND DIURNAL RESPONSES OF 'REDHAVEN'
PEACH TREES (PRUNUS PERSICA, L.)

presented by

Mary Ellen Houle

has been accepted towards fulfillment
of the requirements for

M.S. degree in Horticulture


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EFFECT OF WATER STRESS AND RECOVERY ON THE
GROWTH AND DIURNAL RESPONSES OF 'REDHAVEN'
PEACH TREES (PRUNUS PERSICA, L.)

By

Mary Ellen Houle

A THESIS

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ABSTRACT

EFFECT OF WATER STRESS AND RECOVERY ON THE GROWTH AND DIURNAL RESPONSES OF 'REDHAVEN' PEACH TREES (PRUNUS PERSICA, L.)

By

Mary Ellen Houle

Growth, growth rates, leaf water potential (ψ_1) and stomatal conductance were observed for greenhouse peach trees (Prunus persica, L.) under a rapid water stress (RWS) and a slow water stress (SWS). Leaf emergence and leaf growth were more sensitive to drought than trunk or shoot growth. Leaf growth rates (RWS) recovered fastest. Growth was reduced 20-35% for the RWS, 18-24% for the 50%, and 25-64% for the 25% treatment. ψ_2 of RWS leaves declined 0.18 MPa after one week. Significant differences in stomatal conductance (SWS) followed the significant reduction in growth.

Diurnal responses of greenhouse peach trees were observed during water stress and recovery. Stomatal conductance and transpiration were significantly reduced after one week. Leaf water potential declined 0.62 MPa under severe stress. Osmotic potential differed under mild stress. Turgor potential varied 0.12 MPa throughout the stress. Trunk diameters increased 5.5 and 6.5% for the stressed and control trees. No treatment differences after rewatering indicated recovery.

To My Mother



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INTRODUCTION

In the last 20 years, the advent of trickle irrigation has made irrigation feasible in peach orchards where, previously, overhead sprinkler irrigation has yielded marginal economic benefit. As the technology in trickle irrigation progresses, the demand for efficient, effective, and economical schedules for peach orchard irrigation increases. Scheduling irrigation according to Class A pan evaporation (E_{pan}) or soil water status are relatively easy methods (Elfving 1982); however, because only a portion of the root system is wetted around a trickle irrigation emitter, when and where to monitor soil water status become difficult questions. In addition, soil water or evaporation monitoring methods do not account for growth physiological status or water needs of the tree. Incorporating parameters of growth and water status could improve the efficacy of an irrigation schedule.

In the process of identifying parameters for developing an irrigation schedule, several questions surface:

1. What are the growth characteristics of the nonbearing and bearing peach tree?
2. What are the diurnal and seasonal responses of stomatal conductance and plant water potential?

3. How do the growth and water status parameters respond under water stress?
4. What is the relative sensitivity of the growth and water status parameters to water stress?

Several recent papers on the growth characteristics of peach trees indicated that the growth of vegetative and reproductive structures of peaches followed predictable daily and seasonal patterns. Trunk and shoot diameters fluctuated diurnally with maxima before sunrise and minima during midafternoon (Kozlowski 1968, Powell 1976). Annual trunk circumference growth increased faster in nonbearing trees than in bearing trees. As trunk circumference increased, the average length of shoots decreased while the average number of shoots increased. Trunk size was also highly correlated with other measurements of tree growth and size, e.g., dry weight increments, leaf area, number of leaves, tree volume (Chalmers and van den Ende 1975). A curvilinear relationship between trunk cross-sectional area (TCA) and shoot length with correlations of 0.88 to 0.99 has been documented for peaches (Khatamian and Hilton 1977); and it was suggested that TCA was an adequate indicator of tree vigor (Khatamian and Hilton 1977, Westwood and Roberts 1970). Equations for predicting leaf emergence and leaf growth have been developed for peaches and cherry. Light, temperature, degree-day accumulations, precipitation, soil moisture and days from full bloom data were among the variables included (Eisensmith et al. 1981, Haun and Coston 1983).

Peach fruit growth and development were characterized by a three-stage growth curve which exhibited rapid, slow, and rapid increases

in fruit dry weight (DW) increments (Chalmers and van den Ende 1975). The growth flushes of fruit DW and shoot diameter were juxtaposed during the fruiting season. During DW Stage II, the increment in shoot diameter increased as the increment in fruit dry weight decreased (Chalmers and Wilson 1978). Chalmers et al. (1981) scheduled irrigation according to the dry weight stages of fruit growth. By reducing irrigation to 12.5% of the irrigation requirement during DW Stage II, vegetative growth was reduced without affecting yield.

The diurnal variations in water status and stomatal function are well documented for peach, as well as other fruit trees (Chalmers and Wilson 1975, Davies and Lakso 1979, Goode and Higgs 1973, Hendrickson 1926, Kozlowski 1968, Klepper 1968, Xiloyannis et al. 1980, Young et al. 1981). The diurnal responses have been correlated with the environmental factors--light, temperature, and humidity (Davies and Lakso 1979, Goode and Higgs 1973, Klepper 1968, Stanley et al. 1983). Stomatal conductance reached a maximum before noon and a minimum by midafternoon (Hendrickson 1926, Young et al. 1981); whereas the peak in transpiration generally occurred after midday, when temperatures and vapor pressure deficits were greatest (Kramer 1967, Landsberg and Jones 1981). Plant water potential became most negative between 1000 and 1600h, and least negative overnight (Chalmers and Wilson 1978, Goode and Higgs 1973, Klepper 1968, Xiloyannis et al. 1980, Young et al. 1981). Water flux in and out of the plant was the primary regulator of these diurnal curves; however, environmental factors and



position in the canopy affected the extent and duration of the change (Chalmers and Wilson 1978, Klepper 1968).

As the season progressed, stomatal conductance and water potential values changed to reflect maturation, adaptation to the environment, and accommodation of the carbohydrate and water demands of fruiting (Chalmers and van den Ende 1975, Chalmers and Wilson 1978, Davies and Lakso 1978). During DW Stage III stomata remained open longer during the day (Chalmers et al. 1983). Xylem water potential of well-watered trees remained constant between -0.5 and -0.8 MPa (Xiloyannis et al. 1980); however, leaf water potential for trees watered intermittently became as much as 0.8 MPa more negative late in the season (Chalmers and Wilson 1978), Proebsting and Middleton 1980). In addition, trees with a heavy fruit load wilted sooner after irrigation than trees with few or no fruit (Chalmers and Wilson 1978).

Diurnal and seasonal osmotic adjustment of cellular solute concentration has been reported for some plant species under water stress, including apple trees (Davies and Lakso 1978, Goode and Higgs 1973, Hsiao et al. 1976, Lakso et al. 1981). A capacity for osmotic adjustment to maintain turgor in peaches has been suggested in recent literature; however, the results were not consistent or conclusive (Young et al. 1981, 1982). Young et al. (1982) concluded that approximately 30% of a drought induced reduction in leaf water potential could be explained, statistically, by a concomittant decrease in osmotic potential. No studies of osmotic regulation of cell turgor for field grown peach trees has yet been published.

The methodology for determination of stomatal conductance, leaf water potential, and osmotic potential has been defined and critiqued (Brown and Tanner 1983, Scholander et al. 1965, Slavik 1974). Porometry has become the accepted field method for determination of stomatal opening and stomatal resistance to water vapor and gas exchange. The principle for determining stomatal resistance with a steady state or null balance porometer, the state of the art in porometry, is simple: "Day air is blown into the ventilated chamber at a rate (measured) just sufficient to keep the pre-determined air humidity constant. A balance is maintained between the flux of transpired water and the air flow" (Slavik 1974). Resistance is then determined from the equation

$$r = \left(\frac{100}{r.h} - 1 \right) \frac{A}{f}$$

where: r = resistance ($s\ cm^{-1}$)

$r.h$ = relative humidity

A = leaf area within the chamber (cm^2)

f = flux of dry air ($cm^3 s^{-1}$)

Expressing stomatal resistance as its reciprocal, stomatal conductance, has become accepted because stomatal conductance was linearly related to stomatal operature (Raschke 1976).

Pressure chamber methods reliably estimate leaf and xylem water potential. The leaf is hermetically sealed in the steel chamber with the cut end of the petiole exposed to the atmosphere. Gradually the pressure within the chamber is increased using compressed nitrogen



until small bubbles of xylem sap are visible at the cut petiole surface. The pressure at which this occurs is equal to the pressure required to force water from the cells surrounding the xylem into the xylem stream (Wilkins 1969, Slavik, 1974). Because the osmotic potential of the xylem sap is near zero, its component of the water potential is negligible (Slavik 1974). Humidification of the compressed gas, wrapping the leaf in a plastic bag, or placing dampened filter paper in the chamber will help reduce water loss from the leaf and reduce the chances for erroneously low water potential (Davies and Lakso 1979a, b, Slavik 1974).

The most reliable results of estimating osmotic potential are obtained from a pressure volume curve and with dewpoint thermocouple hygrometry. For the pressure-volume method, a pressure bomb is used to express sap from live tissue at various pressure intervals until no more sap is exuded and the turgor pressure is relieved. The mass of the accumulated sap is plotted against the reciprocal of the pressure. The linear portion of the curve, when extrapolated to the y-axis, intercepts the y-axis where $\psi_w = \psi_s$. For the dewpoint thermocouple hygrometry method, a segment of previously frozen leaf tissue is sealed within a chamber containing thermocouples which allow simultaneous cooling of the thermocouple junction and measurement of the declining temperature. As the thermocouple is electrically cooled, water vapor condenses on the thermocouple junction. The electrical energy used to condense the water vapor is "proportional to the dewpoint and may be calibrated in terms of water potential" (Slavik 1974).

Plant parameters used to develop an irrigation schedule should reliably represent tree growth and water status, and the data should be readily obtained in the field. Trunk growth and leaf water potential are possible candidates. Trunk growth has been highly correlated with shoot growth and other parameters of growth and size (Chalmers and Wilson 1978, Khatamian and Hilton 1977). Diurnal contraction and swelling of the trunk reflected the sensitivity of diameter changes in response to daily water fluxes in the tree (Kozlowski 1968, Powell 1976). Trunk diameters are easily measured with vernier calipers or millimeter micrometers. Constant recording of trunk diameter changes can be monitored with dendrometers or linear transducers (Kozlowski 1968, powell 1976).

Black et al. (1977) experimented with supplying irrigation water in liters of water per cm TCA per cm E_{pan} . Adjusting TCA measurements for degree of canopy cover in the orchard may be necessary for estimating water needs from E_{pan} . TCA was believed to underestimate tree size and may have resulted in overwatering smaller trees.

Plant water potential has been proposed as an indicator of stress to be incorporated into irrigation scheduling (Anon. 1983 Proebsting et al. 1981). As an indicator of stress, xylem water potential was most reliable before dawn (Xiloyannis et al. 1980); whereas, midafternoon xylem and leaf water potentials tended to reflect the hot, dry environment more than the stressed status of the tree (Proebsting and Middleton 1980, Xiloyannis et al. 1980). Leaf position, leaf age, time of day and season, and environmental factors influence water potential (Anon. 1983, Klepper 1968, Proebsting and

Middleton 1980, Stanley et al. 1983); and therefore, these factors must be considered to insure uniform sampling with minimal error.

Production of soil water conditions in a pot similar to field conditions has been questioned. Wilting and soil water depletion occurred in seven to ten days after watering was terminated in several experiments with potted plants (Davies and Lakso 1979, Tan and Buttery 1982, Young et al. 1981). Soil water depletion can require four weeks in an orchard (Cullinan and Weinberger 1931, Hendrickson 1926, Xiloyannis et al. 1980). Some preconditioning may occur in trees which experience slowly developing or intermittent water stress periods. Trees preconditioned to water stress exhibited a greater tolerance to stress with less negative leaf water potential and greater stomatal conductances (Davies and Lakso 1979a). For this reason responses to a slow stress could differ from responses to a rapid stress.

Studies of the growth and water status parameters were believed essential to identifying parameters best suited for developing irrigation schedules. The thesis was developed in two sections with the general objective to assess the potential of various growth and water stress parameters as indicators of water stress. The specific objective of Section I was to characterize the growth responses of 'Red-haven' peach trees under a rapid water stress and a slow water stress. The objective of Section II was to study the diurnal responses of stomatal conductance, transpiration, leaf water potential, and trunk growth during a cycle of water stress and recovery.



SECTION I. EFFECT OF A RAPID WATER STRESS AND A
SLOW WATER STRESS ON THE GROWTH OF
'REDHAVEN' PEACH TREES



ABSTRACT

A rapid water stress (RWS) and recovery treatment and two levels of a slow water stress (SWS) treatment (rewatering at 50 and 25% of the control) were applied to potted one-year-old peach trees (Prunus persica, L., Batsch, cv. 'Redhaven'/'Halford') in a greenhouse. Growth, growth rates, leaf water potential components, and stomatal conductance were observed. Occurrence of statistical differences between treatments was used to determine sensitivity to stress. Total leaf water potential was 0.18MPa less than control for the stress trees after one week of RWS. Leaf emergence was more sensitive than leaf or shoot growth; however, leaf growth rates recovered fastest after rewatering. Leaf emergence, leaf length, and shoot length were reduced by 80, 77, and 65%, respectively. Available soil water declined to 40 and 20% of the control for the 50 and 25% SWS treatments. Leaf emergence was more sensitive than trunk or shoot growth, while leaf growth rates were more sensitive than leaf emergence, trunk, or shoot growth rates. Leaf emergence, leaf growth, shoot extension, and trunk diameter were reduced by 58, 82, 56, 76, and 64% for the 50% treatment, and 50, 75, 36, 57, and 39% for the 25% treatment, respectively. Significant reductions in stomatal conductance followed with the reductions in growth within 2-7 days for the SWS experiment.

Introduction

In the last 20 years the advent of trickle irrigation has made irrigation feasible in peach orchards, where previously irrigation has yielded marginal economic benefit. As the technology in trickle irrigation progresses, the demand for efficient, effective, and economical schedules for peach orchards increases. Scheduling irrigation according to Class A pan evaporation (Epan) or soil water status are relatively easy methods (Elfving 1982); however, these methods may not accurately reflect the amount of soil water available to the root system because only a portion of the root system is wetted with a trickle irrigation system. In addition Epan and soil water measurements do not account for growth, physiological status, or water needs of the tree. Incorporating parameters of growth and water status could improve the efficacy of an irrigation schedule.

Parameters used to develop an irrigation schedule should reliably represent tree growth and water status, and the data should be easy to obtain. Trunk or limb diameter and leaf water potential measurements are possible candidates. Trunk growth has been highly correlated with shoot growth and other parameters of growth and size (Khatamian and Hilton 1977, Chalmers and Wilson 1978). Trunk cross-sectional area (TCA) was believed to be a satisfactory indicator of tree vigor (Khatamian and Hilton 1977, Westwood and Roberts 1970). Diurnal contraction and swelling of the trunk reflected the sensitivity

of diameter changes in response to water loss and retention due to stomatal opening and closure (Kozlowski 1968, Powell 1976). Trunk diameters are easily measured with vernier calipers and millimeter micrometers and recorded using dendrometers or linear transducers (Chalmers and Wilson 1978, Kozlowski 1968, Powell 1976).

When peach trees were subjected to drought stress, plant water potential became more negative (Proebsting and Middleton 1980, Xiloyannis et al. 1980, Tan and Buttery 1982, Young et al. 1981). As an indicator of stress, plant water potential was most reliable before dawn (Xiloyannis et al. 1980) because midafternoon water potentials tended to reflect the hot, dry environment more than the stressed status of the tree (Proebsting and Middleton 1980, Xiloyannis et al. 1980). Pressure bomb techniques for determining leaf and xylem water potential are well described (Davies and Lakso 1978, Scholander et al. 1965, Slavik 1974), and the measurements are easily made in the field. Leaf position, leaf age, time of day and season, and environmental factors were shown to influence leaf water potential, and therefore, must be considered when interpreting the results (Klepper 1968, Proebsting and Middleton 1980, Stanley et al. 1983).

The production of soil water conditions in a pot similar to field conditions has been questioned. Wilting and soil water depletion occurred in seven to ten days after watering was terminated in several experiments with potted plants (Davies and Lakso 1979, Tan and Buttery 1982, Young et al. 1981). Soil water depletion can require four weeks in an orchard (Cullinan and Weinberger 1931, Hendrickson 1926, Xiloyannis et al. 1980). Some preconditioning may occur in trees



which experience slowly developing or intermittent water stress periods. Trees preconditioned to water stress exhibited a greater tolerance to stress with less negative leaf water potentials and greater stomatal conductances (Davies and Lakso 1979a). For this reason, responses to a slow stress could differ from responses to a rapid stress.

The goal of this study was to characterize some of the growth responses of 'Redhaven' peach trees under a rapid and a slow stress. Understanding these growth responses could aid in developing trickle irrigation schedules for peach orchards. 'Redhaven' peach trees were selected because of the commercial importance of this cultivar (Childers 1978).

Materials and Methods

General. Two groups of one-year-old grafted peach trees (Prunus persica, L., cv. 'Redhaven'/'Halford') were grown in 19 liter containers filled with 2 soil: 1 sphagnum moss: 1 sand (v:v:v) soil mixture in a greenhouse. Group I was potted in September 1981 and group II in April 1982. Each tree was pruned to two branches. The experiments were begun six weeks later, after 10-15 leaves had unfolded. High irradiation density lamps, cooling fans, and steam radiator heat were used to maintain a 15h photoperiod, a night temperature of $17\pm 2^{\circ}\text{C}$ and a day temperature of $30\pm 5^{\circ}\text{C}$. A water-soluble fertilizer (20-20-20) at 250ppm N was applied with alternate waterings. Miticides and fungicides were applied sparingly as needed.



The number of leaves (no.), leaf length (mm), shoot length (cm), and trunk diameter (mm) were the growth parameters measured. The number of leaves were counted from the base and included every leaf longer than 2mm. Leaf length was measured from the petiole base to the leaf tip. Shoot length was measured from the base of the shoot to the tip of the newest emerging leaf or tip of the terminal bud. Trunk diameter was measured with a digital micrometer (Mitutoyo, Japan, Model 193-101, range $0-25 \pm 0.05\text{mm}$) at marked locations on the trunk 10-12 cm above the graft union.

Cumulative increases in number of leaves, shoot length, and trunk diameter were calculated based on the measurement made on day 1 of each experiment (Equation 1, Table 1).

Equation 1: Cumulative increase in growth

$$C = M_n - M_1$$

where: C = cumulative increase in the parameter measured
(mm, cm, or no.)

M_n = measurement on day_n (mm, cm, or no.)

M_1 = measurement on day₁ (mm, cm, or no.)

Rates of leaf emergence, shoot extension, and trunk diameter change were calculated for two- to four-day intervals for each experiment (Equation 2).

Table 1. Initial number of leaves, shoot length, and trunk diameter measurements for the rapid water stress (RWS) and slow water stress (SWS) experiments used for calculating cumulative increases in growth.

Parameter	Treatment	Measurement on day 1 ^z
Rapid Water Stress		
No. of Leaves	Control	24.1 ± 3.1
	Stress	28.3 ± 3.2
Shoot Length (cm)	Control	26.8 ± 7.1
	Stress	38.2 ± 9.4
Slow Water Stress		
No. of Leaves	100%	32.0 ± 4.4
	50%	31.9 ± 3.7
	25%	32.8 ± 3.0
Shoot Length (cm)	100%	54.7 ± 14.5
	50%	51.3 ± 13.8
	25%	53.5 ± 8.2
Trunk diameter (mm)	100%	9.98 ± 0.24
	50%	9.71 ± 1.13
	25%	9.76 ± 0.65

^zEach measurement represents an average of 4 trees.

^yMeans within parameters are not statistically different (LSD, 5% level).

Equation 2: Growth rate

$$R = \frac{M_c - M_p}{n}$$

where: R = growth rate (mm, cm, or no. day⁻¹)

M_c = current measurement (mm, cm, or no.)

M_p = previous measurement (mm, cm, or no.)

Water status was monitored with stomatal conductance and water potential measurements. Stomatal conductance was determined with a steady-state porometer (Li-cor, Inc., Lincoln, Nebraska, Model 1600) on the abaxial side of a recently expanded leaf. The same leaf was used for total leaf water potential (ψ_1) measurements using a pressure bomb (PMS, Corvallis, Oregon) and the technique of Scholander et al. (1965). The leaf was sealed in a 'Ziploc' bag, kept in the dark in a cooler and frozen to -20°C two hours later. The osmotic potential (ψ_s) was determined by dewpoint hygrometry (Wescor, Inc., Logan, Utah, micro-voltmeter, Model HR-T 33 and chamber, Model C-52) using one thawed 5mm disc from each leaf and a 15-minute equilibration time in the chamber.

The data were analyzed as a randomized, complete block with four replications. The trees were blocked by trunk diameter size. Each date was analyzed separately. For the analysis, a value for each one tree plot was calculated from the average of two measurements per tree, one from each branch. Only one trunk diameter measurement was made

per tree. Significant differences between treatments were determined by a least significant difference (LSD) statistic at the 0.05 level (Steele and Torrie 1980).

Rapid Water Stress Experiment (RWS). A rapidly induced water stress situation was created by withholding water until the leaves wilted and the soil water tension approached 60kPa. The number of leaves, leaf length, and shoot length were recorded beginning at 0800h every three to four days during the prestress period, day 1-5 (October 15-19, 1981), during the stress period, day 6-16 (October 20-30, 1981), and during the recovery period, day 17-33 (October 31-November 16, 1981). For the leaf length measurements, leaves emerging on day 1, 12, and 22 were collectively named Leaf Group (LG) A, B, and C, respectively. Plant water potentials were determined at 1300h every three to four days during the stress period.

Slow Water Stress Experiment (SWS). A simulation of gradual soil water depletion was created by watering some of the trees with 50 or 25% of the volume of water retained per watering period by the fully watered trees. Every tree received 2 liters of water every two to three days for two weeks. The water drained after 24h was measured and the volume subtracted from 2 liters to determine the amount of water retained. An average volume of water retained per day for the two-week period was calculated to be 400 ± 50 ml. Of this volume 50 to 25% (i.e., 200ml and 100ml) was applied every two to three days to the stress treatments, while the control trees continued to receive



2 liters. After 16 days the volume of water applied to all trees was adjusted for growth and increased transpiring surface based on an average volume of water retained per day by the control trees during the 16-day period.

The number of leaves, leaf length, shoot length, and trunk diameter were recorded beginning at 0800h every two to three days from day 1 (May 20, 1982), two days before the stress treatments were started, and were continued until day 29 (June 19, 1982), when the stress was relieved. For the leaf length measurements, leaves emerging two weeks before day 1, on day 1, and on day 12 were collectively named Leaf Group (LG) A', B', and C', respectively. Stomatal conductance and transpiration were measured at 1000 and 1400h three times during the stress period and one day after rewatering.

Results

Rapid Water Stress Experiment. Plant water potential was used as an indicator of the stressed status of the trees (Table 2). On day 6, the first day of the stress period, no statistical differences between treatments for ψ_p , ψ_s , or ψ_1 were observed. Three days later, ψ_s differed significantly, but ψ_p and ψ_1 did not. After one week with no additional water ψ_p and ψ_1 differed significantly, however, ψ_s did not.

The net result of the RWS treatment was reduced increases in the number of leaves, shoot length, and leaf length of emerging (LG-B) or rapidly expanding (LG-A) leaves (Fig. 1, 2, 3). The length of leaves emerging after rewatering (LG-C) was not affected by the stress (Fig. 2).



Table 2. Effect of rapid water stress (RWS) and time (days) on the osmotic potential (ψ_s), turgor potential (ψ_p), and total leaf potential (ψ_l), of 'Redhaven' peach leaves.

Time ^z (days)	Treatment	ψ_s^y (MPa)	ψ_p^y (MPa)	ψ_l^y (MPa)
6	Control	-2.98	1.58	-1.40
	Stress	-2.87	1.06	-1.71
9	Control	-2.38 a	1.08	-1.42
	Stress	-2.80 b	0.98	-1.82
13	Control	-2.60	1.42 a	-1.28 a
	Stress	-2.82	0.98	-1.81 b

^zNumber of days after initiation of experiment. Water was withheld between day 6 and 16.

^yMean separation within time by LSD, 5% level.



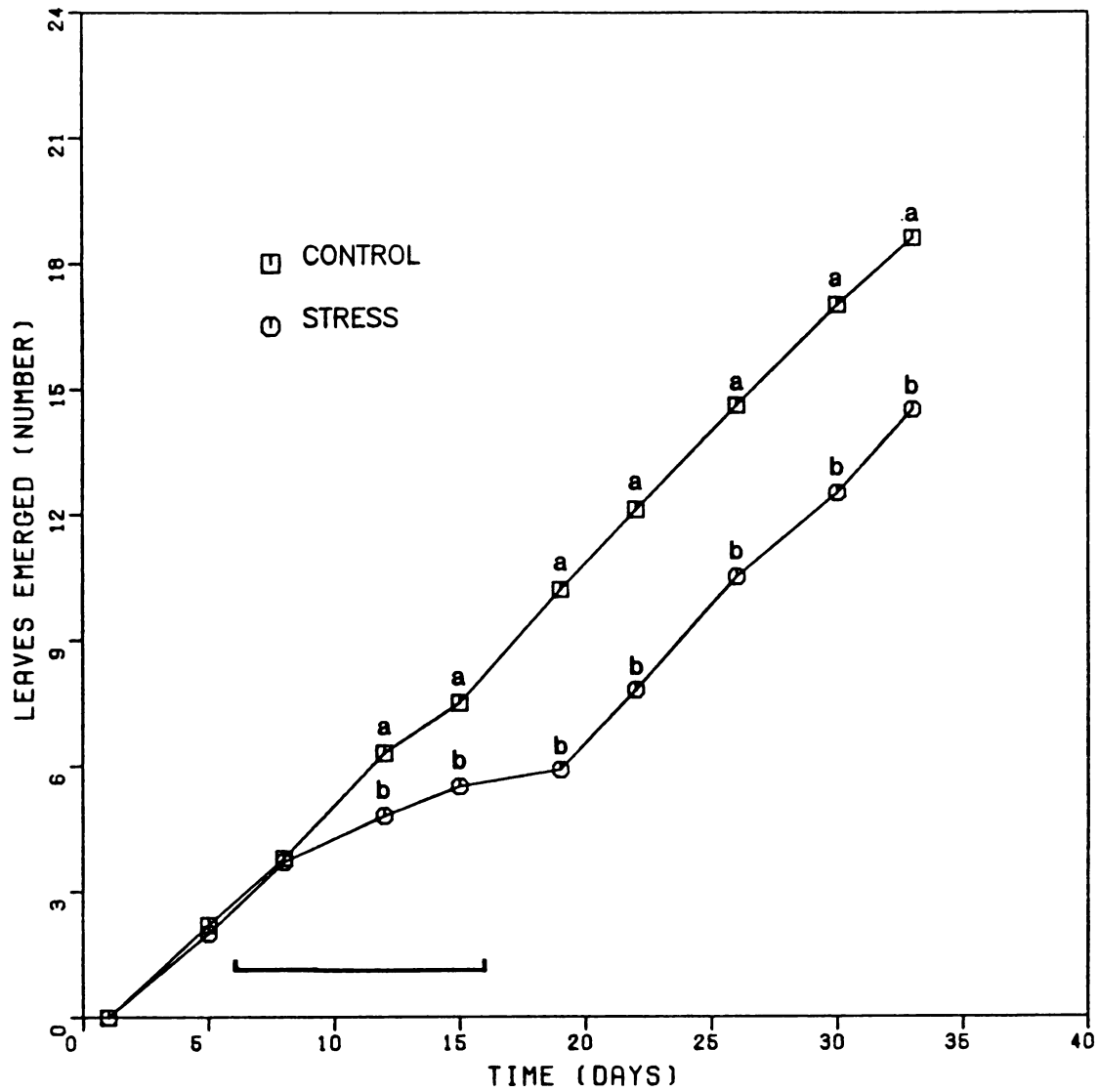


Figure 1. Effect of rapid water stress, rewatering, and time (days) on leaf emergence of 'Redhaven' peach. Mean separation within time by LSD, 5% level.



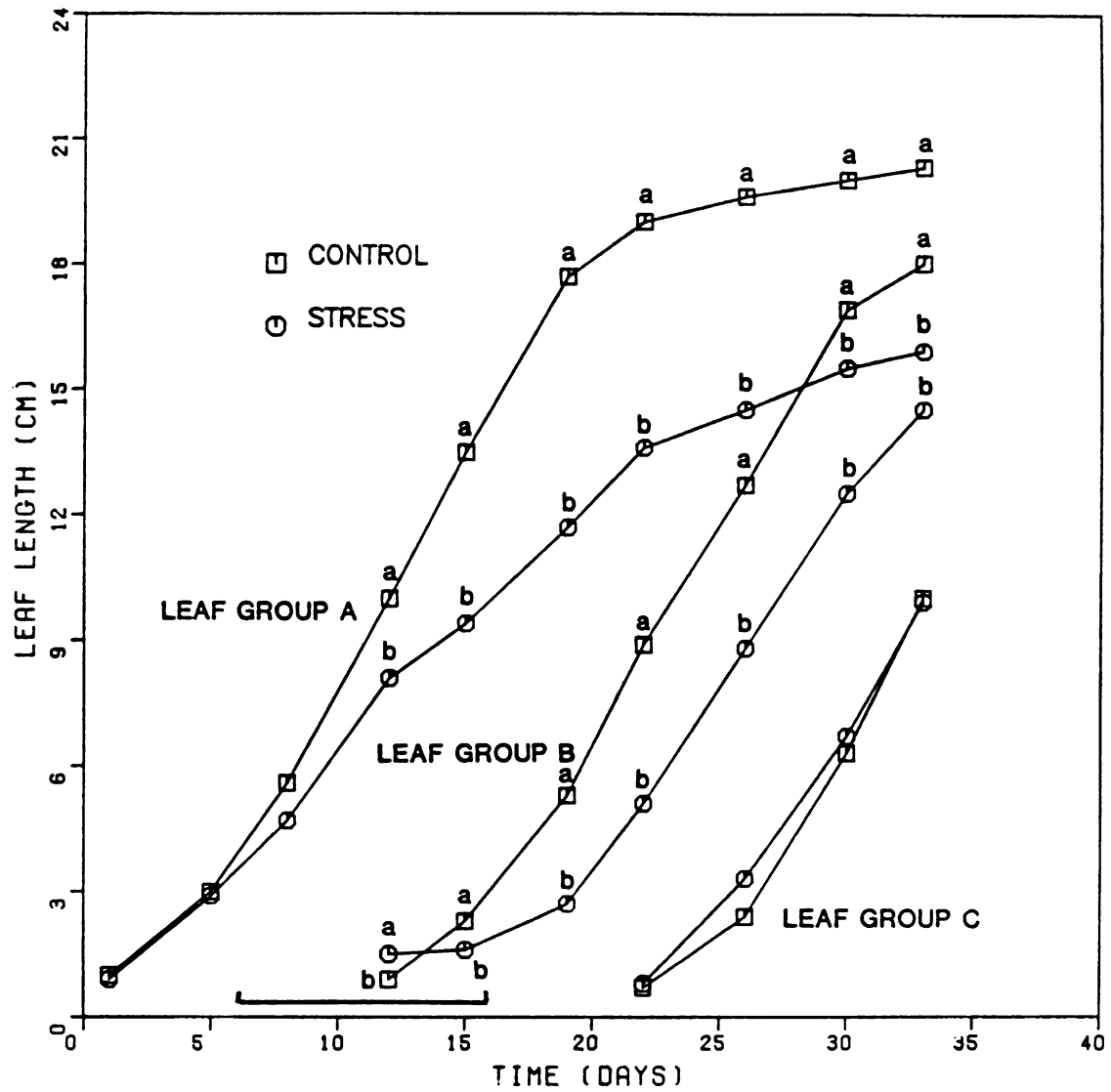


Figure 2. Effect of rapid water stress (RWS), rewatering, and time (days) on the length of 'Redhaven' peach leaves. Mean separation by LSD, 5% level.

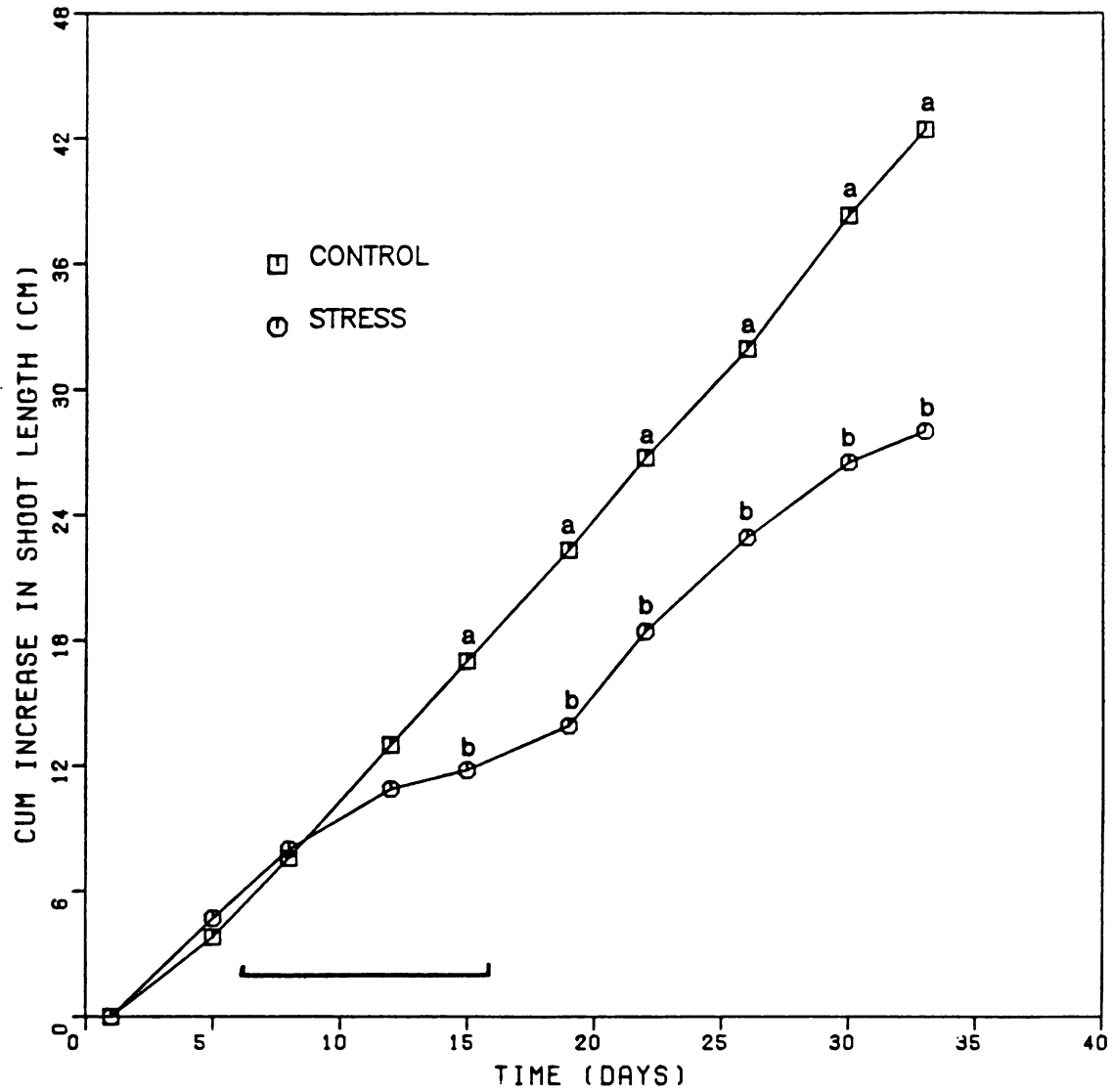


Figure 3. Effect of rapid water stress, rewatering, and time on the cumulative increase in shoot length of 'Redhaven' peach trees. Mean separation within time by LSD, 5% level.



The effect of water stress and recovery on the growth rates and the occurrence of statistical differences between treatments was used to determine the sensitivity of these growth parameters to water stress (Table 3 and 4). Leaf emergence rate was more sensitive to water stress than leaf or shoot growth rate. The growth rate for leaves emerging during the stress period (LG-B) was more sensitive than the growth rate for leaves rapidly expanding at the same time (LG-A). After rewatering, leaf growth rate recovered faster than leaf emergence or shoot growth rate; however, the recovery of leaf emergence rate was more complete. About two weeks elapsed after rewatering before the shoot growth rate for stressed and control trees were similar. The growth rate of leaves emerging three days after rewatering (LG-C) were unaffected by the stress.

Slow Water Stress Experiment. The amount of water available at field capacity was determined to be 4000 ± 150 ml per pot. The 50 and 25% watering treatments resulted in a progressive decrease in available water (Fig. 4). By day 24 the available water had decreased to approximately 40 and 20% of the control for the 50 and 25% treatments, respectively.

Growth was significantly reduced for all stress treatments except shoot growth for the 50% treatment. The significant effects of the SWS on the increase in growth were first observed 12-16 days after treatments were initiated (Figs. 5, 6, 7, and 8). From most to least sensitive, the order of sensitivity to the stress was leaf emergence, trunk growth, shoot extension. The duration of the stress was

Table 3. Effect of rapid water stress (RWS), rewatering, and time (days) on the rates of leaf emergence, leaf expansion, and shoot extension.

Treatment	Time After Initiation of Experiment (days) ^z						
	5	8	12	15	19	22	30
	Leaf Emergence (No. day ⁻¹) ^y						
Control	0.58 ^y	0.53	0.63a	0.37	0.70a	0.63	0.80
Stress	0.50	0.53	0.25b	0.20	0.10b	0.63	0.60
	Leaf Group A (cm day ⁻¹) ^y						
Control	0.50	0.65	1.05	1.67a	1.03	0.43	0.28
Stress	0.53	0.60	0.85	0.43b	0.58	0.63	0.25
	Leaf Group B (cm day ⁻¹) ^y						
Control		0.47a	0.75	1.20	0.80	0.95	1.05
Stress		0.03b	0.28	0.80	0.93	0.93	0.93
	Leaf Group C (cm day ⁻¹) ^y						
Control						0.65	0.85
Stress						0.40	0.98
	Shoot Extension (cm day ⁻¹) ^y						
Control	0.95	1.27	1.33	1.33a	1.33a	1.57a	1.58
Stress	1.18	1.10	0.80	0.30b	0.48b	0.57b	1.13

^zWater was withheld between day 6 and 16.

^yMean separation within time by LSD, 5% level.



Table 4. Time (days) of occurrence of statistical differences^Z between treatments for the growth rate and water potential parameters measured during the rapid water stress (RWS) experiment.

Parameter	Time (days) After Initiation of RWS Experiment ^{Z,Y}						
	1	5	10	15	20	25	30
Stress Period							
Growth Rates							
Leaf Emergence			*	*	*	*	*
Leaf Group A			*				
Leaf Group B			*				
Leaf Group C			*				
Shoot Extension				*	*	*	*
Water Potential							
Total Leaf Potential							
Osmotic Potential		*		*			
Turgor Potential				*			

^Z* designates the days on which statistical differences (LSD, 5% level) occurred.

^Y* designates the days on which the leaf emergence rate of the stressed trees exceeded the rate for the control trees.

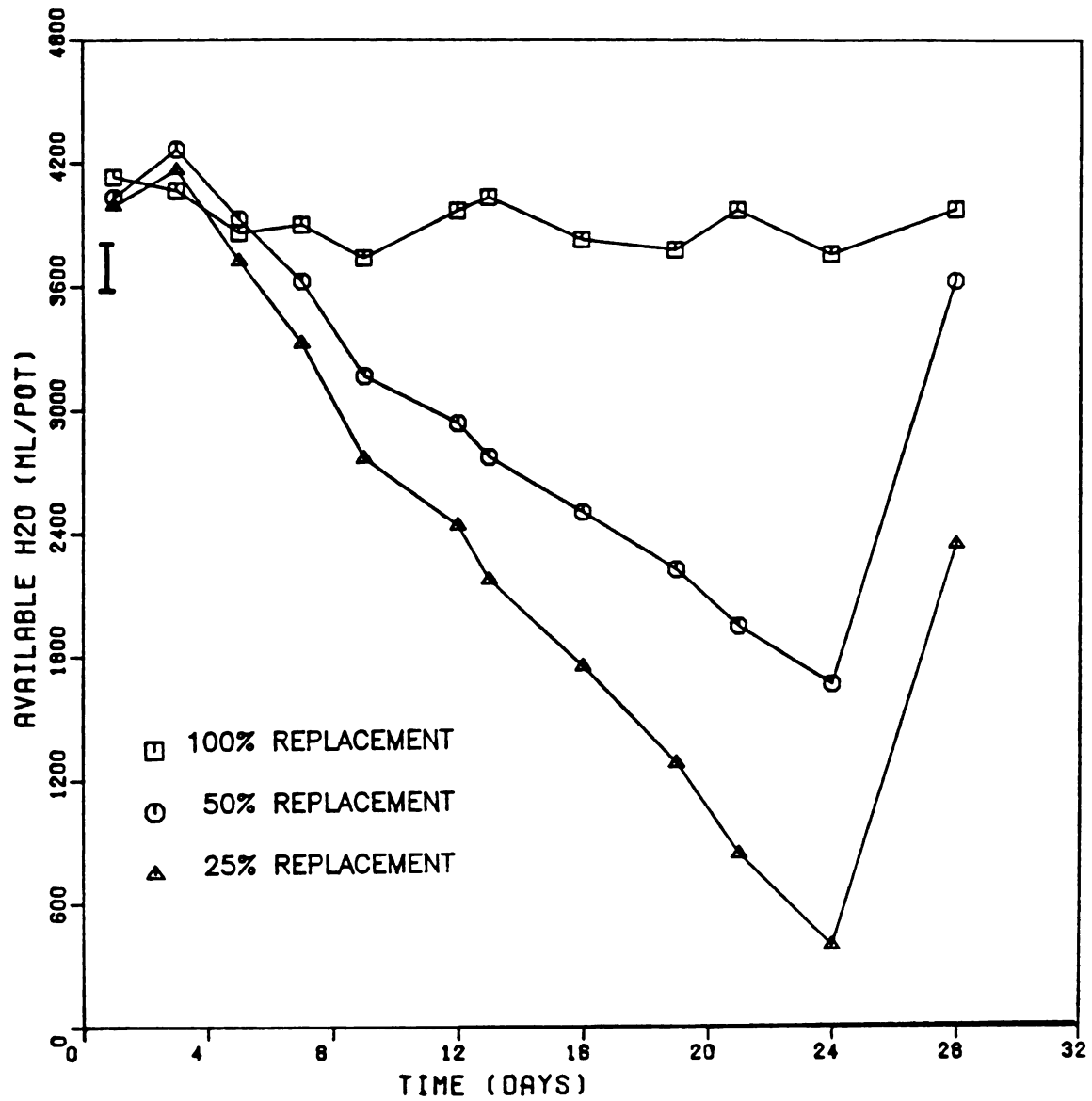


Figure 4. Calculated available water (ml/pot) for the 100, 50, and 25% treatments.

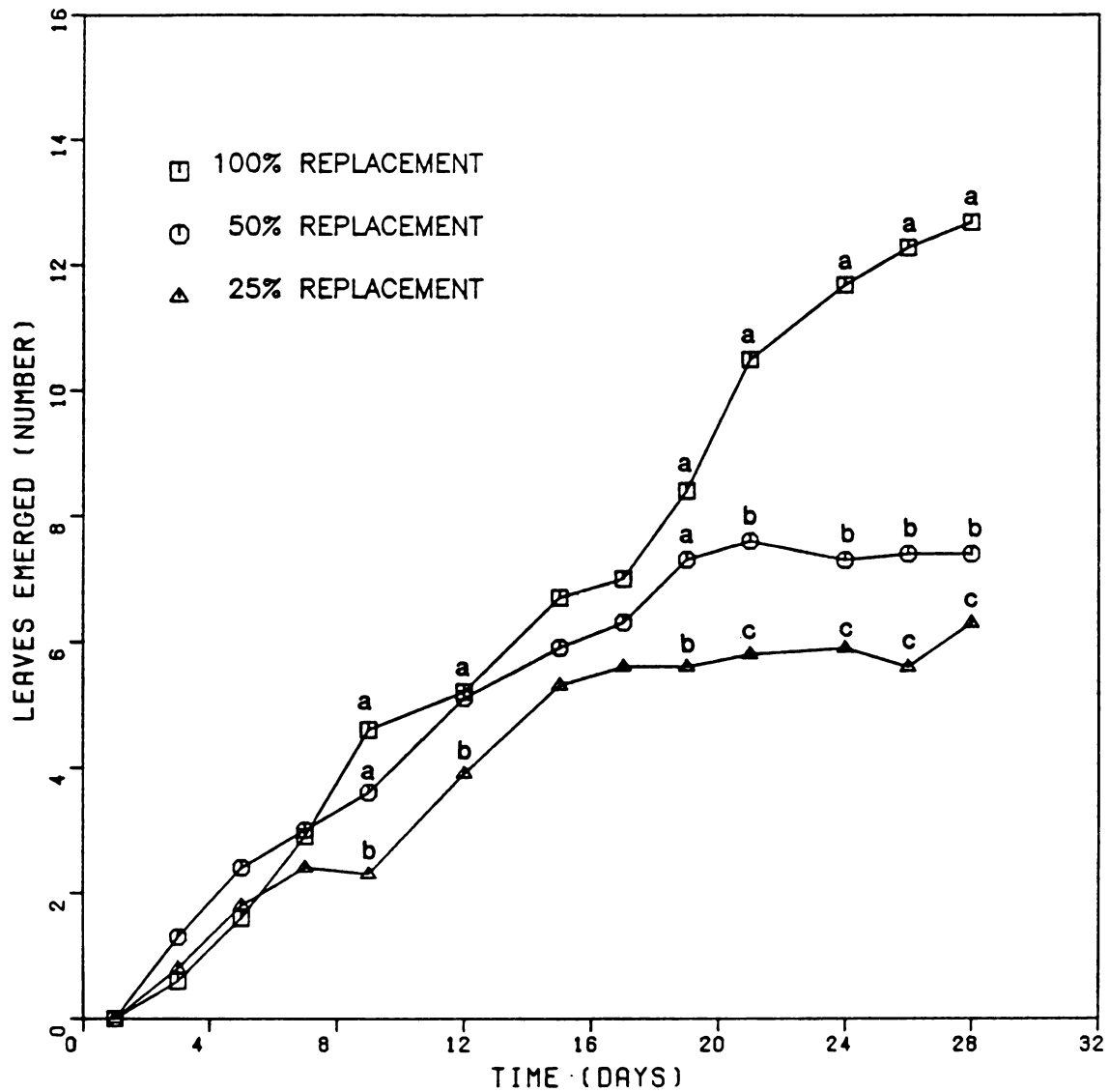


Figure 5. Effect of three levels of replacement of water used (100, 50, and 25%) and time (days) on leaf emergence of 'Redhaven' peach leaves. Mean separation by LSD, 5% level.

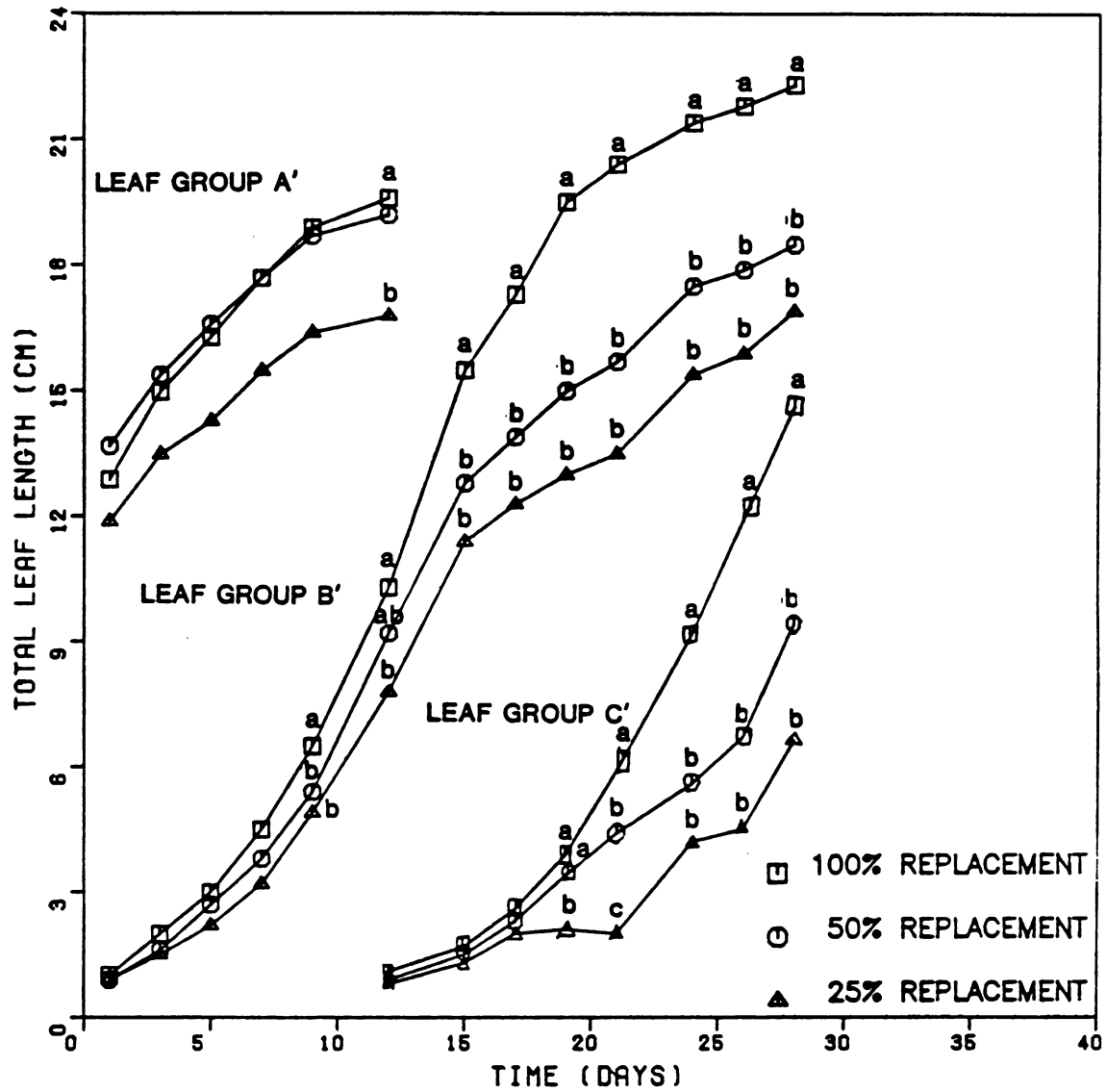


Figure 6. Effect of three levels of replacement of water used (100, 50, and 25%) and time (days) on length of 'Redhaven' peach leaves. Mean separation by LSD, 5% level.



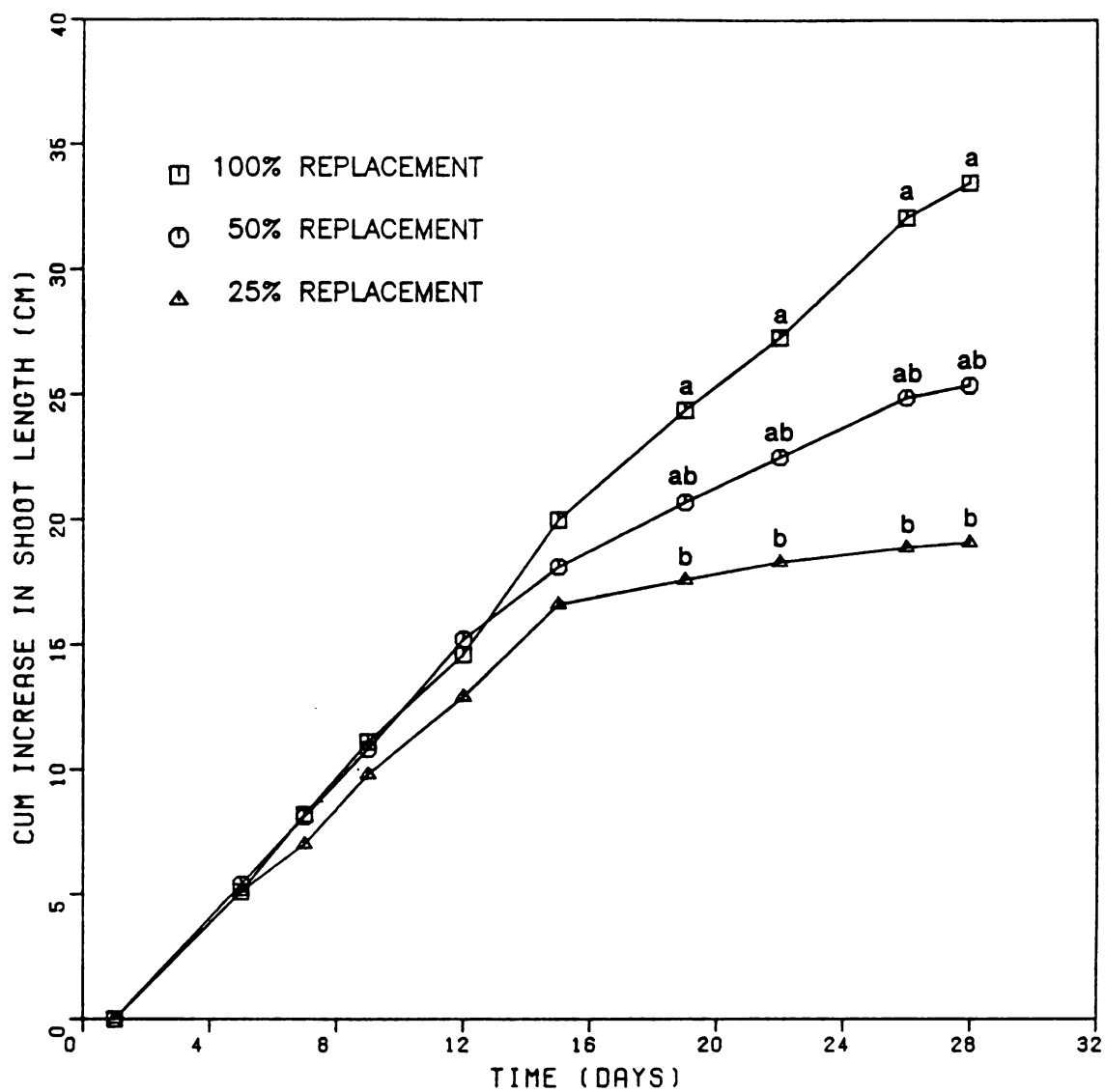


Figure 7. Effect of three levels of replacement of water used (100, 50, and 25%) and time (days) on the cumulative increase in shoot length of 'Redhaven' peach trees. Mean separation within time by LSD, 5% level.



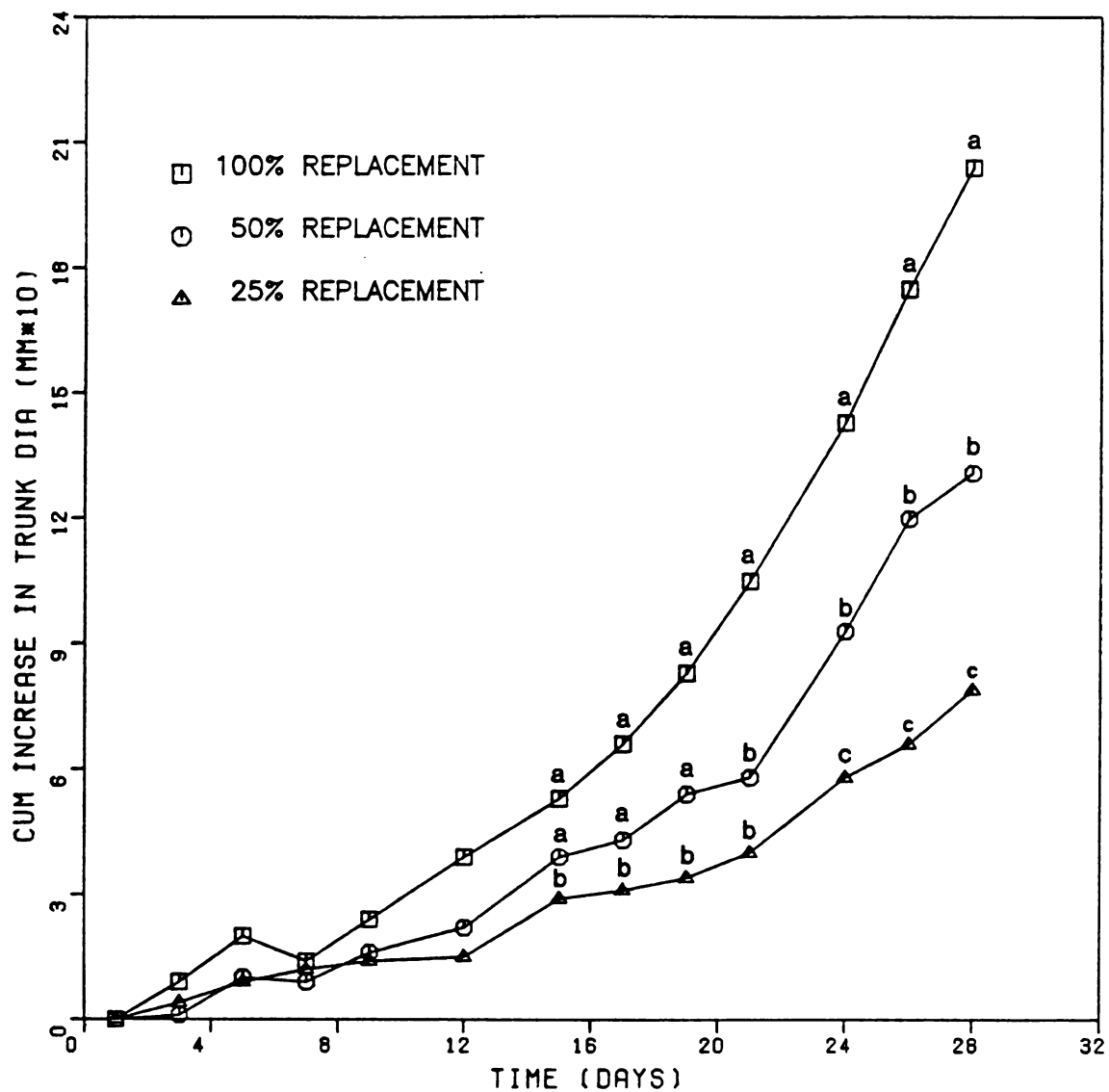


Figure 8. Effect of three levels of replacement of water used (100, 50, and 25%) and time (days) on the cumulative increase in trunk diameter of 'Redhaven' peach trees. Mean separation within time by LSD, 5% level.

sufficient to halt leaf emergence for both stress treatments, and shoot growth for the 25% treatment. The rapidly expanding phase of leaf growth became irregular and shorter for the stressed trees.

The order of sensitivity of the growth rates in response to SWS was unlike the order for a RWS. For the SWS, the order was LG-B' and C' (for the 25 and 50% treatments), leaf emergence and trunk diameter (25% treatment), trunk diameter (50% treatment), shoot extension (25% treatment), leaf emergence (50% treatment), shoot extension (50% treatment) (Tables 5 and 6). Although LG-C emerged nine days after treatments were begun, it was ranked highly sensitive because a significant reduction in rate occurred within five to seven days after emergence. A similar response was observed for LG-B'.

After the growth of the stressed trees was beginning to differ from the control trees, differences in stomatal conductance were also observed (Tables 6 and 7). On day 17, 1000h stomatal conductances were significantly less for the 25% treatment. At 1400h both the 25 and 50% treatments were significantly different. One day after rewatering there were no differences in stomatal conductance.

A comparison of the effects of the two stress situations was simplified because growth rates for the control trees were similar for both experiments (Table 8). Further generalized comparisons among parameters, between treatments and between experiments were made by expressing the data from each parameter as a percent of the control for selected times in each experiment (Tables 9 and 10). An estimate of internode length was derived from a ratio of shoot

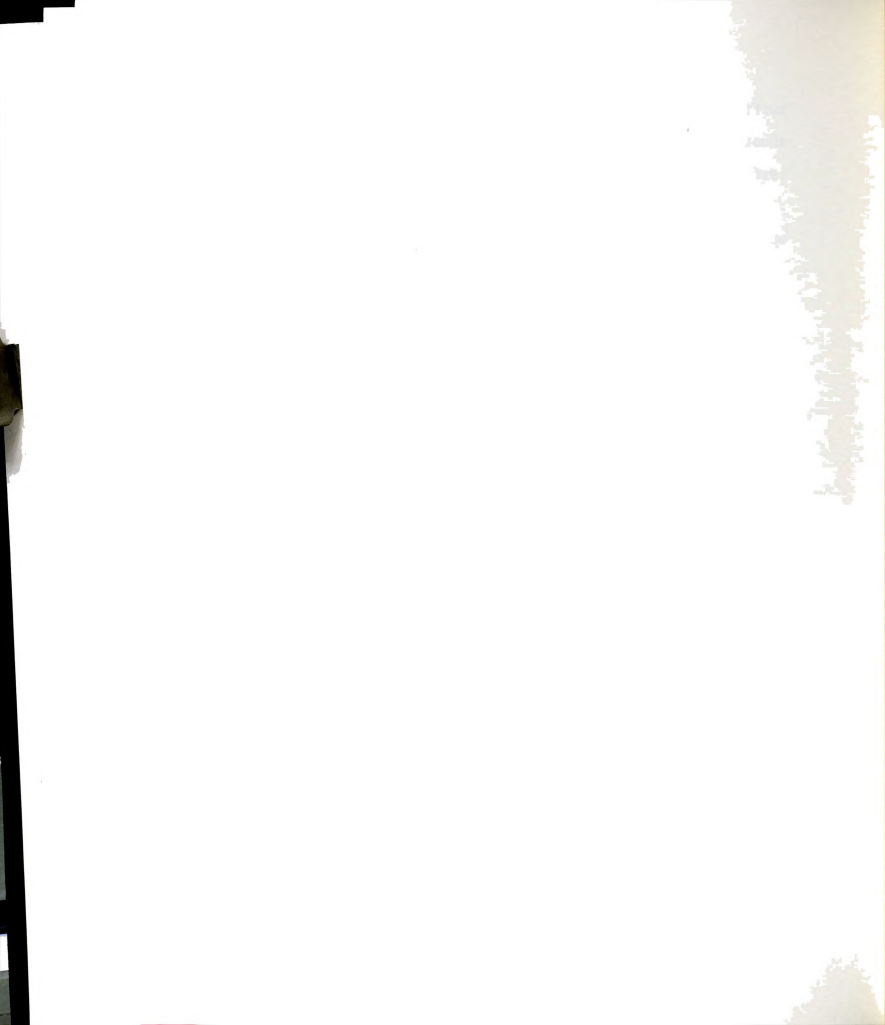


Table 5. Effect of three levels of replacement of water used (100, 50, and 25%) and time (days) on the rates of leaf emergence, leaf expansion, shoot extension, and trunk diameter change of 'Redhaven' peach trees.

Treatment	Time After Initiation of Experiment (Days) ²											
	3	5	7	9	12	15	17	19	21	24	26	28
Leaf Emergence (No. day ⁻¹)												
100%	0.30a ^y	0.65	0.50	0.00b	0.73a	0.60	0.25	0.75a	0.90a	0.50a	0.25a	0.30a
50%	0.65b	0.55	0.30	0.45a	0.43b	0.27	0.30	0.40ab	0.20b	0.00b	0.05b	0.00b
25%	0.40a	0.50	0.30	0.00b	0.53a	0.47	0.20	0.00b	0.05b	0.10b	0.00b	0.20a
Leaf Group A' (cm day ⁻¹)												
100%	0.80	0.65	0.55	0.60	0.30a							
50%	0.90	0.65	0.60	0.55	0.13b							
25%	0.80	0.40	0.55	0.50	0.17ab							
Leaf Group B' (cm day ⁻¹)												
100%	0.25b	0.55a	0.80a	1.05a	1.27	1.77a	0.90a	0.60a	0.55a	0.30b	0.20	0.25
50%	0.35a	0.55a	0.55b	0.75b	1.27	1.20b	0.55b	0.55ab	0.35ab	0.60a	0.30	0.30
25%	0.30ab	0.35b	0.50b	0.75b	0.97	1.20b	0.45b	0.35b	0.25b	0.73a	0.35	0.50
Leaf Group C' (cm day ⁻¹)												
100%						0.20	0.45	0.60a	1.00a	1.07a	1.20a	1.25
50%						0.20	0.25	0.40ab	0.40b	0.67ab	0.60b	0.85
25%						0.17	0.30	0.20b	0.20b	0.43b	0.30b	0.80
Shoot Extension (cm day ⁻¹)												
100%		1.00	1.55a	1.45	1.17	1.87a		1.75a	1.37a		1.20a	0.75a
50%		1.35	1.35a	1.30	1.47	0.97b		0.68b	0.57b		0.63b	0.25b
25%		1.35	0.90b	1.35	1.23	1.17b		0.38c	0.23c		0.15b	0.15b
Trunk Diameter Change (mm day ⁻¹ x 10)												
100%	0.45a	0.40	0.05	0.40	0.53a	0.43	0.65a	0.85a	1.05a	1.27a	1.67a	1.20ab
50%	0.05b	0.45	0.00	0.35	0.23ab	0.53	0.35b	0.60a	0.15b	1.30a	0.00b	1.90a
25%	0.30b	0.10	0.05	0.35	0.30b	0.47	0.10c	0.15b	0.03a	0.60b	0.40b	0.40b

Table 6. Time (days) of occurrence of statistical differences^y between treatments for growth rates and stomatal conductance measured during the slow water stress (SWS) experiment.

Parameter	Treatment	Time (days) after Initiation of SWS Experiment ^z ,y									
		1	5	10	15	20	25	30			
<hr/>											
Stress Period											
<hr/>											
Growth Rates											
Leaf Emergence	50	*			*	*	*	*	*	*	
	25		*			*	*	*	*	*	
Leaf Group A'	50										
	25			*		*					
Leaf Group B'	50		*		*	*	*	*	*	*	
	25		*		*	*	*	*	*	*	
Leaf Group C'	50					*	*	*	*	*	
	25					*	*	*	*	*	
Shoot Extension	50				*	*	*	*	*	*	
	25				*	*	*	*	*	*	
Trunk Diameter	50	*				*	*	*	*	*	
	25	*			*	*	*	*	*	*	
<hr/>											
Stomatal Conductance											
1000h	50				*						
	25				*						
1500h	50				*						
	25				*						

^zTreatments were initiated on day 3.

^y*designates days on which the first statistical differences occurred (LSD, $p = 0.05$).

Table 7. Effect of three levels of replacement of water used (100, 50, and 25%) and time (days, h) on the stomatal conductance of 'Redhaven' peach leaves.

Time (days) ^z	Treatment	Stomatal conductance (cm s ⁻¹) ^y	
		Time (h)	
		1000	1500
1	100%	1.60	1.75
	50%	1.70	1.76
	25%	1.76	1.77
12	100%	1.94	2.06
	50%	1.97	1.88
	25%	1.89	1.94
17	100%	1.63a	1.93a
	50%	1.60ab	1.57b
	25%	1.30b	1.16b
28	100%	2.13	1.72
	50%	2.15	1.83
	25%	2.09	1.75

^zTreatments were begun on day 3; stress relieved on day 29.

^yMean separation within time (day) and time (h) by LSD, 5% level.



Table 8. Growth rates for the control trees in the rapid water stress (RWS) and slow water stress (SWS) experiments.

Growth parameter	Growth rate ^z (mm, cm, or no. day ⁻¹)
Rapid Water Stress Experiment	
Leaf emergence	0.61 leaves
Leaf group A	0.97 cm
Leaf group B	0.99 cm
Leaf group C	0.98 cm
Shoot extension	1.35 cm
Slow Water Stress Experiment	
Leaf emergence	0.50 leaves
Leaf group A'	1.18 cm
Leaf group B'	1.16 cm
Leaf group C'	1.13 cm
Shoot extension	1.35 cm
Trunk diameter	0.055 mm

^zGrowth rates were determined from the average rate during the 10-12 day period of rapid leaf expansion.



Table 9. Growth and growth rates, expressed as percent of control, for the rapid water stress (RWS) trees at the end of the stress and recovery periods.

Parameter	End of Stress	End of Recovery
Cumulative Growth (% of control)		
Leaf emergence	73.3	80.3
Leaf Group A	61.6	77.7
Leaf Group B	5.0	77.2
Leaf Group C	--	103.3
Shoot extension	60.9	65.3
Growth Rates (% of control)		
Leaf emergence	54.0	126.0
Leaf Group A	25.7	185.7
Leaf Group B	6.4	181.1
Leaf Group C	--	--
Shoot extension	22.6	83.9



Table 10. Growth and growth rates, expressed as percent of control, slow water stress (SWS) for the trees (50 and 25% trts.) on the day responses were statistically different and at the end of the stress period.

Parameter	Treatment	Day of Response		End of Stress	
		50%	25%	50%	25%
Cumulative Growth (% of Control)					
Leaf Emergence				58.3	49.6
Leaf Group A'				98.0	85.7
Leaf Group B'				82.5	74.9
Leaf Group C'				56.3	36.3
Shoot Extention				75.8	57.0
Trunk Diameter				64.2	38.7
Growth Rate (% of Control)					
Leaf Emergence		22.0	5.0	0.0	66.0
Leaf Group A'		43.3	56.7	43.3	56.7
Leaf Group B'		68.8	63.6	115.7	194.1
Leaf Group C'		40.0	3.3	67.2	61.7
Shoot Extension		51.9	62.6	33.3	20.0
Trunk Diameter		53.8	5.7	158.3	33.3



length to number of leaves (Table 11). For the RWS experiment, the estimated internode lengths were reduced by 19%. The internode lengths for the 50% treatment were unaffected, while those for the 25% treatment were reduced by 7%. The effect of water stress on shoot vs. trunk growth relationships was examined (Fig. 9). A change in the relationship was observed.

Discussion

The effect of water stress on the relationships among leaf emergence, leaf growth, shoot extension, and trunk expansion were illustrated by this study. Internode length, estimated by the ratio of shoot length to number of leaves, was reduced as a result of the RWS treatment and the 25% SWS treatment. Water availability and leaf emergence rate were potential factors which controlled shoot and internode growth. A comparison of leaf emergence and shoot extension patterns for the SWS experiment suggested that shoot extension ceased as new leaves stopped emerging (Figs. 5 and 7). However, the percent reduction in shoot length was greater than the percent reduction in leaf emergence for the RWS experiment and 25% SWS treatments (Table 8). Since cell expansion is dependent in part on turgor pressure (Hsiao 1973), water availability probably exhibited greater control over shoot length and internode length than leaf emergence.

The rapid phase of shoot growth began about three to four weeks before the rapid phase of trunk growth. A similar pattern was reported by Kozlowski (1958) and Khatamian and Hilton (1977). In the SWS experiment the relationship appeared to vary among treatments,

Table 11. Effect of rapid water stress (RWS) and slow water stress (SWS) on the final shoot length to final leaf number ratio, and the treatment effects expressed as percent of control.

Treatment	Shoot Length ^z (cm)	% of Control	No. of Leaves ^z	% of Control	Shoot : Leaf (cm : Leaf)	% of Control
Rapid Water Stress Experiment						
Control	81.0	100	48.6	100	1.67	100
Stress	54.8	68	40.4	83	1.36	81
Slow Water Stress Experiment						
100%	95.1	100	46.7	100	2.04	100
50%	80.2	84	39.3	84	2.04	100
25%	72.6	76	38.3	82	1.90	93

^zRepresents an average of four trees.



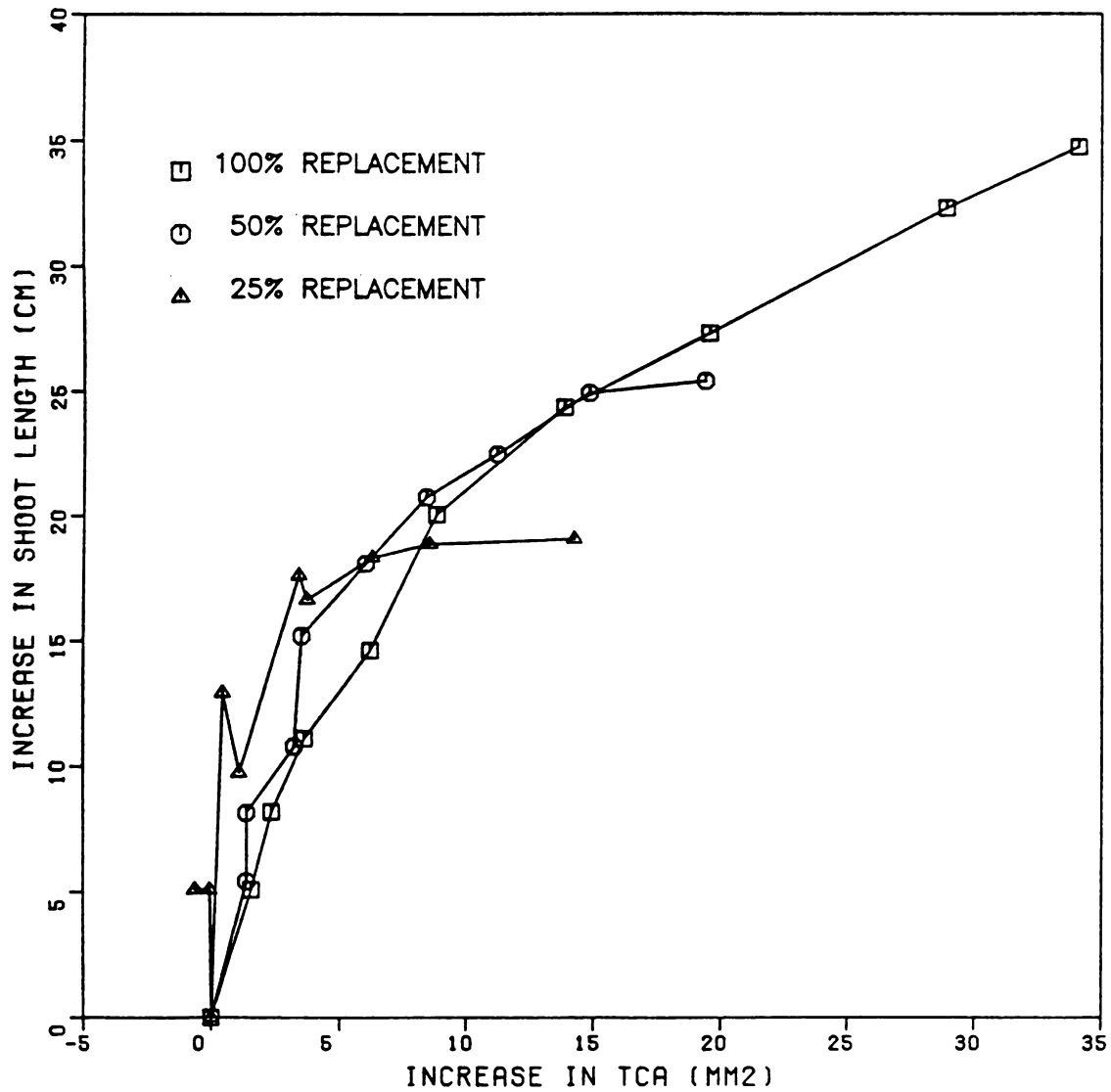


Figure 9. Increase in trunk cross-sectional area (TCA) vs. increase in shoot length of 'Redhaven' peach trees for three levels of water replacement 100, 50, and 25%.

indicating a change in the relationship between shoot and trunk growth as a result of the water stress (Fig. 9). This response was expected because trunk growth was shown to be more sensitive to water stress than shoot extension by the order of sensitivity and greater reduction in growth (Table 8), thus offsetting the normal shoot growth to trunk growth relationship.

The RWS and SWS experiments had different effects on the growth and growth rates of peaches. In the RWS experiment, the number of newly emerged leaves was reduced immediately, while the leaf emergence rates were not significantly different until three days after the stress period began. A SWS also caused a reduction in leaf emergence, but these differences were not significant until after day 10. The RWS and the 25% treatment reduced shoot extension more than leaf emergence; whereas the opposite was observed for the 50% treatment, SWS for both cumulative growth and growth rates (Tables 8 and 9). An extended period of SWS was necessary before increases in shoot extension and shoot growth rates were reduced to the same extent as those under RWS. Regardless of the duration or severity of the stress, leaf growth was very sensitive to water stress, recovered quickly after rewatering and achieved 75-80% of the potential length even as water supplies slowly diminished.

Stomata of 'Redhaven' peach leaves closed sooner under a rapid stress than a slow stress. In a similar experiment (Section II) stomatal conductance differed at 1100 and 1400h within three days after withholding water. After 11 days of the slow stress, neither morning or afternoon stomatal conductances differed; after 11 days of

the rapid stress, trees were watered to relieve the stress. Tan and Buttery (1982b) reported a similar decline in stomatal conductance after three days of stress, and reported that stomatal conductance was 80% of the control after only one-half of the root system had received water for three weeks. The stomatal sensitivity to stress observed in this study was similar to results obtained for field-grown trees (Cullinan and Weinberger 1932, Jones 1931, Xiloyannis et al. 1980). Stomata closed earlier in the day for the water stressed trees. Peach stomata appeared to be more sensitive to water stress than apple, which have been reported to remain open under stress (Davies and Lakso 1979, Powell 1976).

In addition to available water, other factors must be considered in analysis of cumulative growth and growth rates. Linear growth measurements provide only a general view of the performance of the tree; whereas dry weight measurements more accurately reflect photosynthetic productivity (Causton and Hill 1981). The more rapid rates of leaf growth for the control trees of the SWS experiment (Table 8) were probably due to slightly warmer temperatures and increased radiation, since peach leaf growth rate was influenced by temperature and available radiation (Haun and Coston 1983). Diurnal changes in growth can lead to faulty measurements of real growth, if measurements are not made at similar times each time (Powell 1976, Klepper 1968, Kozlowski 1968). Even irregular timing of watering relative to measuring growth can lead to erroneous measurements of treatment effects. In the SWS experiment the rates of leaf emergence and trunk diameter

changes were affected after rewatering even with 50% or less of the water needed. In preliminary experiments with trunk diameter measurements using a linear transducer, small but measurable increases in trunk radius were detected within minutes after rewatering (unpublished results, M. E. Olien and J. A. Flore). Frequent manipulation of leaves and shoots for growth measurements may inflict damage and affect growth (Causton and Hill 1981); however, Haun and Coston (1983) have developed a scale for rating leaf emergence based on the "morphologic changes during leaf unfolding" which could minimize the physical damage.

In temperate regions, the ability to reduce growth via water management may only be possible during droughty periods of considerable length during DWII. Early wet periods are needed to establish good leaf area development. Exploiting the sensitivity of leaf emergence during this period may prove detrimental to the current crop. Adequate drought to reduce growth during DWII is most likely to occur if there is a period of excessive evaporative demand or if DWII is longer than the drought period. The duration of fresh weight stage II (FWII), which has been shown to be similar in length to DWII (Chalmers and Van Ende 1975), can vary 5-42 days depending on the season and variety (Tukey 1933). Therefore, this system may only work with long season varieties. Irrigation after harvest may be neglected for economical reasons; however, this may be advantageous time to irrigate for the benefit of trunk growth and carbohydrate storage if the current production has been low.

Scheduling irrigation according to trunk diameter changes is appealing. Trunk diameter changes are relatively easy to measure, the parameter is sensitive to water stress, and when expressed as trunk-cross-sectional area, it is an adequate measure of vigor for mature trees (Khatamian and Hilton 1977, Westwood and Roberts 1970). Further studies of the relationship of trunk growth to canopy growth, water stress development in the tree, the soil water conditions and the climatic conditions are necessary to determine the suitability of scheduling irrigation based on trunk diameter fluctuations.

Conclusions

Water stress reduced growth in 'Redhaven' peach trees. Two weeks of the SWS were required before a reduction in growth similar to the RWS was observed. Under RWS conditions, leaf emergence was more sensitive than leaf or shoot growth. Leaf growth rate for the RWS recovered fastest, while shoot growth rate recovered slowest. Under the SWS conditions, leaf emergence was more sensitive than leaf, trunk or shoot growth; however, leaf growth rate was more sensitive than leaf emergence, trunk growth, or shoot growth rate.

Trunk growth was selected as the best parameter to monitor tree water status in research experiments for irrigation scheduling. Although leaf emergence and leaf growth rates were more sensitive, these parameters were not as suited to frequent and rapid sampling. Shoot growth did not appear sensitive enough. Trunk growth fluctuations were relatively easy to observe in the field, and the parameter was sensitive to water stress.



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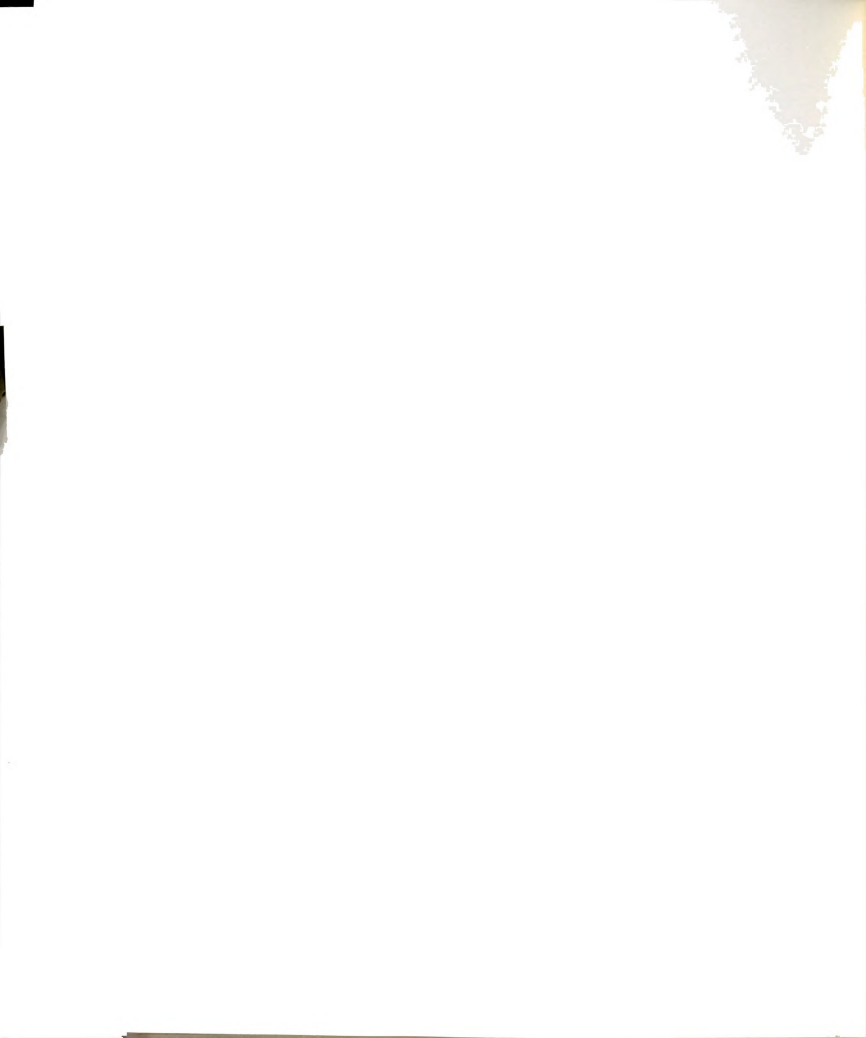
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SECTION II

DIURNAL RESPONSES OF 'REDHAVEN' PEACH TREES UNDER WATER STRESS AND DURING RECOVERY

ABSTRACT

Diurnal responses of 'Redhaven' peach trees (Prunus persica, L., Batsch) were observed during a two-week water stress period in a greenhouse environment. Late morning and afternoon stomatal conductance and transpiration readings were lower for stressed plants during the stress period. Early morning stomatal conductance and transpiration readings differed after one week of the stress period. Leaf water potentials of stressed plants were at least 0.34MPa more negative than those of nonstressed plants. Osmotic potentials of stressed trees were significantly less in early stages of stress, and turgor potentials varied only 0.12MPa during the stress period. Trunk diameters increased 5.5% for the stressed trees compared with 6.5% for the nonstressed trees. No treatment differences were observed after rewatering, indicating recovery from stress.



Introduction

The diurnal variations in plant growth, water status, and stomatal functions are well documented for a variety of fruit trees (Chalmers et al. 1975, Davies and Lakso 1978, Goode and Higgs 1973, Klepper 1968, Xiloyannis et al. 1980, Young et al. 1981). Diurnal responses have been correlated with the following environmental factors: light, temperature, and humidity. Trunk diameter is at a maximum before sunrise and a minimum in the afternoon (Kozłowski 1968). Stomatal conductance reaches a maximum before noon and a minimum by midafternoon (Davies and Lakso 1978, Young et al. 1981); whereas the peak in transpiration generally occurs aftermidday, when temperatures and vapor pressure deficits are the greatest (Kramer 1967). Similarly, plant water potential becomes most negative between 1000 and 1600h and least negative overnight (Klepper 1968, Young et al. 1981, Goode and Higgs 1973). Water flux in and out of the plant is the primary regulator of these diurnal curves; however, environmental factors and position in the canopy (Klepper 1968) can affect the extent and duration of the change.

The diurnal patterns observed for photosynthesis, stomatal conductance, leaf water potential, and limb shrinkage have been characterized for several cultivars of peach under watered and stressed conditions (Chalmers 1975, 1983, Xiloyannis et al. 1980, Young et al. 1981). The use of one of these parameters in planning irrigation schedules



for peach would be desirable, and requires the characterization of the response to water stress. 'Redhaven' peaches are highly recommended for commercial planting in most peach producing areas in the United States (Childers 1978). The sensitivity of this cultivar to stress and its ability to recover after rewatering are important to planning the physiological aspects of scheduling.

The objective of this research was to study the diurnal responses of these parameters: stomatal conductance, transpiration, leaf water potential, and trunk growth of 'Redhaven' peach trees during a cycle of water stress and recovery, and to assess their potential as indicators of water stress.

Materials and Methods

One-year-old peach trees, Prunus persica, L., cv. 'Redhaven'/'Halford', were potted in 19 liter containers in a soil mix of 2 soil:1 sphagnum moss:1 sand (v:v:v), and were pruned to two branches. The trees were maintained in an open-ended quonset greenhouse which provided an outdoor environment protected from rain. Air temperature and relative humidity (Table 1) were similar to the prevailing conditions; however, the available photosynthetically active radiation (Table 1) was reduced to 60% of the available radiation. This level, $700\text{--}1000 \mu\text{E m}^{-2} \text{ s}^{-1}$, was above saturation for 'Redhaven' peach leaf photosynthesis (Kappel et al. 1983) between 1000 and 1500h on most days. Stomatal conductance and transpiration were measured on the abaxial side of one recently expanded leaf from each branch on each tree four times per day with a steady state porometer (Licor Inc.,



Table 1. Air temperature ($^{\circ}\text{C}$), relative humidity (RH, %), and available photosynthetically active radiation (PAR, $\mu\text{E m}^{-2} \text{s}^{-1}$) values recorded at the time of the stomatal conductance measurements

Date	Parameter ^z	Time of Day (hr)			
		0800	1100	1400	1700
June 8	Temp.	24.8		32.8	32.2
	R.H.	49.0		31.5	30.4
	PAR	657		908	855
June 11	Temp.	21.8	25.9	29.9	28.9
	R.H.	43.7	32.8	28.1	29.4
	PAR	626	819	998	548
June 17	Temp.	18.0	23.5	29.3	26.4
	R.H.	50.1	39.8	33.5	38.7
	PAR	381	837	938	238
June 21	Temp.	19.0	22.2	25.9	26.4
	R.H.	56.3	48.5	37.3	34.7
	PAR	436	711	754	705
June 29	Temp.	22.8	24.8	28.5	25.7
	R.H.	72.7	59.9	46.1	48.2
	PAR	259	727	440	135

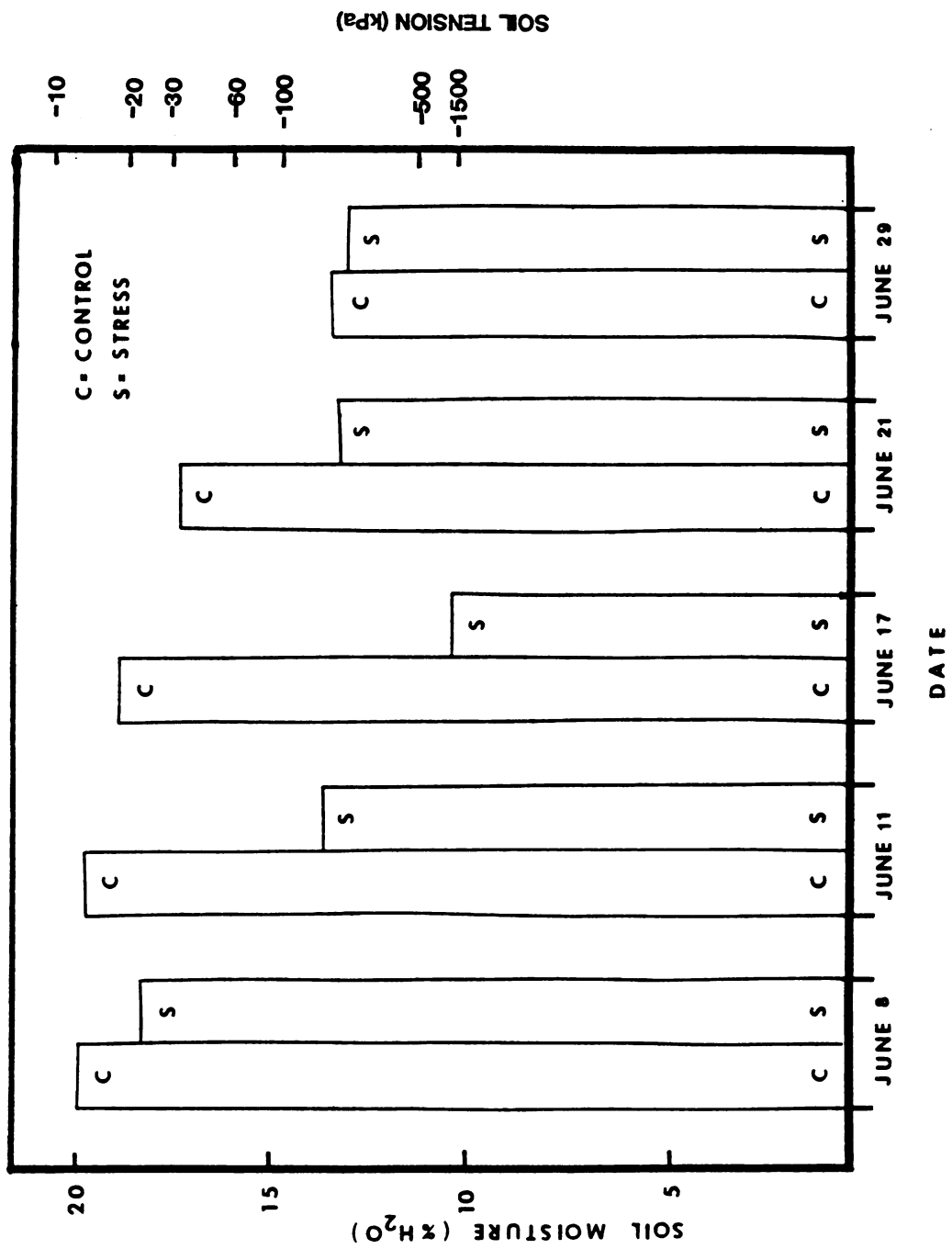
^zEach value represents the mean of 32 measurements.

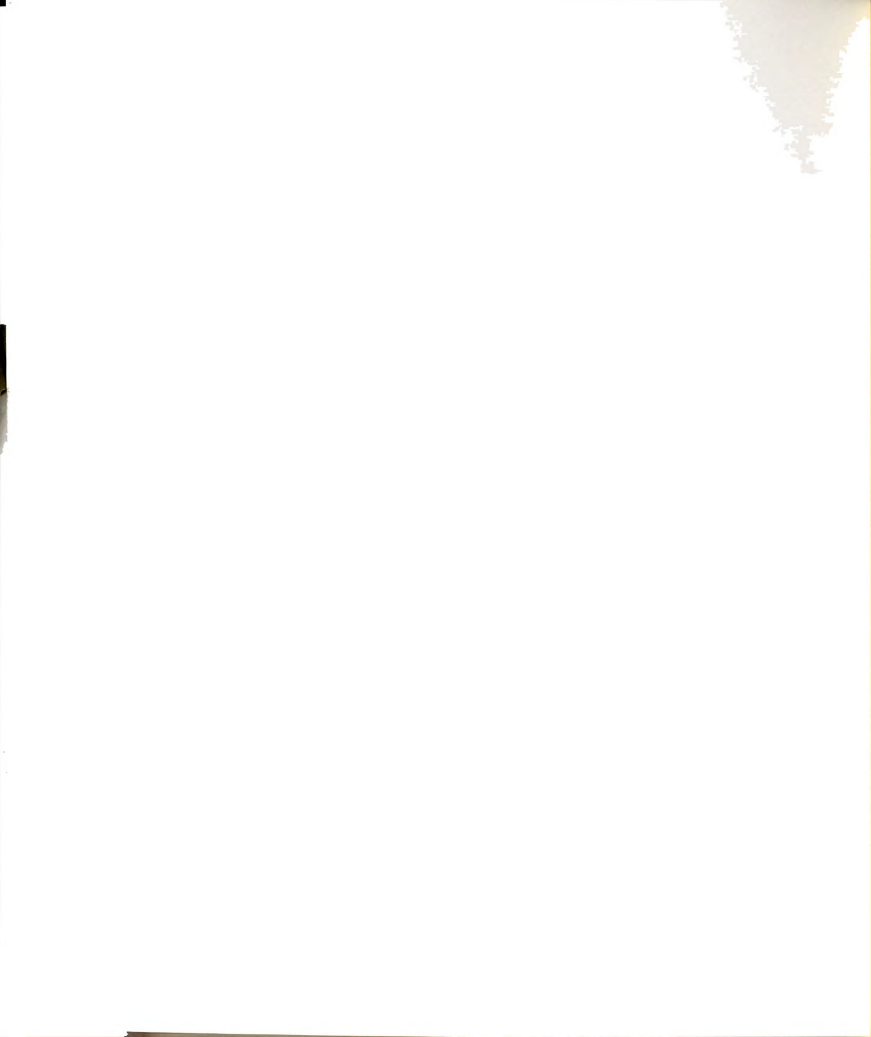


Model 1600). These same leaves were used for leaf water potential measurements. Total leaf water potential was determined two times per day with a pressure bomb (PMS, Corvallis, Oregon) according to the technique of Scholander et al. (1965). The leaves were then sealed in airtight bags and frozen to -20°C for later osmotic potential measurements, which were determined by dewpoint hygrometry (Wescor, Inc., C-52 Chambers and HR-T33 microvoltmeter) (Slavik 1974). Trunk diameters were determined with a millimeter micrometer (Mitutoyo Instruments, Model 193-101, range $0-25 \pm 0.01\text{mm}$). Samples for soil moisture were taken at the end of the day and the percent water determined gravimetrically (Slavik 1974). A soil moisture release curve, relating soil water content to soil water potential was determined by recording soil water content at a series of applied pressures (Richards 1947). At field capacity, the soil contained 20% water by weight (soil water potential = 2 kPa) and at wilting contained 13% water (soil water potential = 100 kPa) (Fig. 1).

Water stress was induced by withholding water until wilting occurred. The stress period began on June 8 and ended on June 26. The control trees were watered to field capacity every two to three days. The experiment was arranged as a randomized complete block with eight replications per treatment. Blocks were arranged by trunk diameter size. Measurements were determined on June 8, 11, 17, 21, and 29, 1982. At least significant difference (LSD) statistic ($P = 0.05$) was used to determine statistical differences between treatments for all parameters except trunk diameters, which was not analyzed (Steele and Torrie 1980).

Figure 1. Percent soil water and soil water tension (kPa) of control and stress treatments during the experiment. Mean separation by LSD, 5% level.





Results

Leaf water potential of the stressed leaves was always more negative than the control leaves on the dates tested (Fig. 2). Significant differences existed on June 17 and 21 at 0800 and 1400h. The effects of water stress on 0800h osmotic and turgor potentials appeared as differences in osmotic potential on June 11 and 17, and as differences in turgor potential on June 17 and 21 (Table 2). Treatment effects were not detected after rewatering for leaf water potential.

Stomatal conductance decreased between 0800 and 1100 h for both treatments (Fig. 3, a-e); 1400h stomatal conductances were always less than the 1000h values. Midday differences in stomatal conductance existed on June 11, 17, and 21. Differences between treatments at 0800 and 1700h occurred on June 17 and 21 when drought was the most severe. After rewatering all trees responded similarly.

Transpiration rates (Table 3) were significantly reduced for the stressed trees between 1000 and 1400h on June 11, and between 0800 and 1700h on June 17 and 21. The amplitude of the diurnal variation of transpiration rate was less in the trees under stress. No differences between treatments were observed after rewatering.

Trunk growth occurred in all trees; however, the increase in growth of the stressed trees was 5.5% compared with 6.5% for the control trees (Fig. 4). Normal late afternoon trunk expansion appeared to begin sooner for the stress trees, even after rewatering.

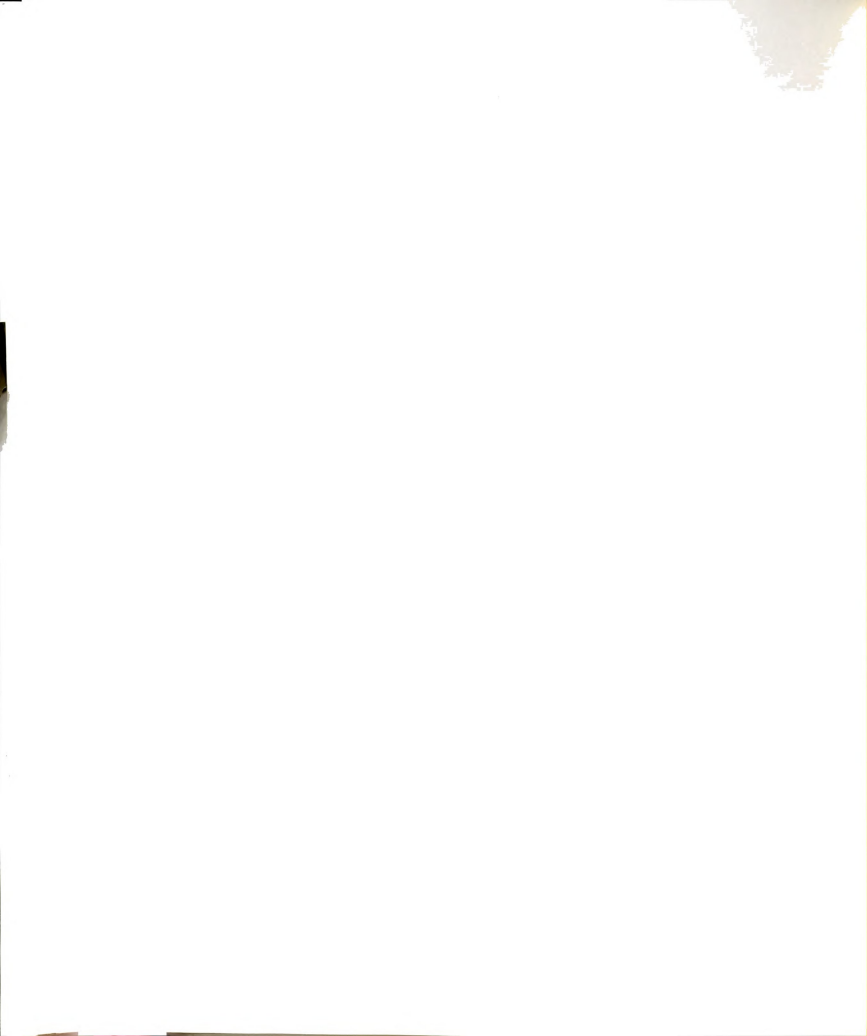


Figure 2. Effect of water stress and recovery on leaf water potential (MPa) of 'Redhaven' peach leaves at 0800 and 1400h. Mean separation by LSD, 5% level.

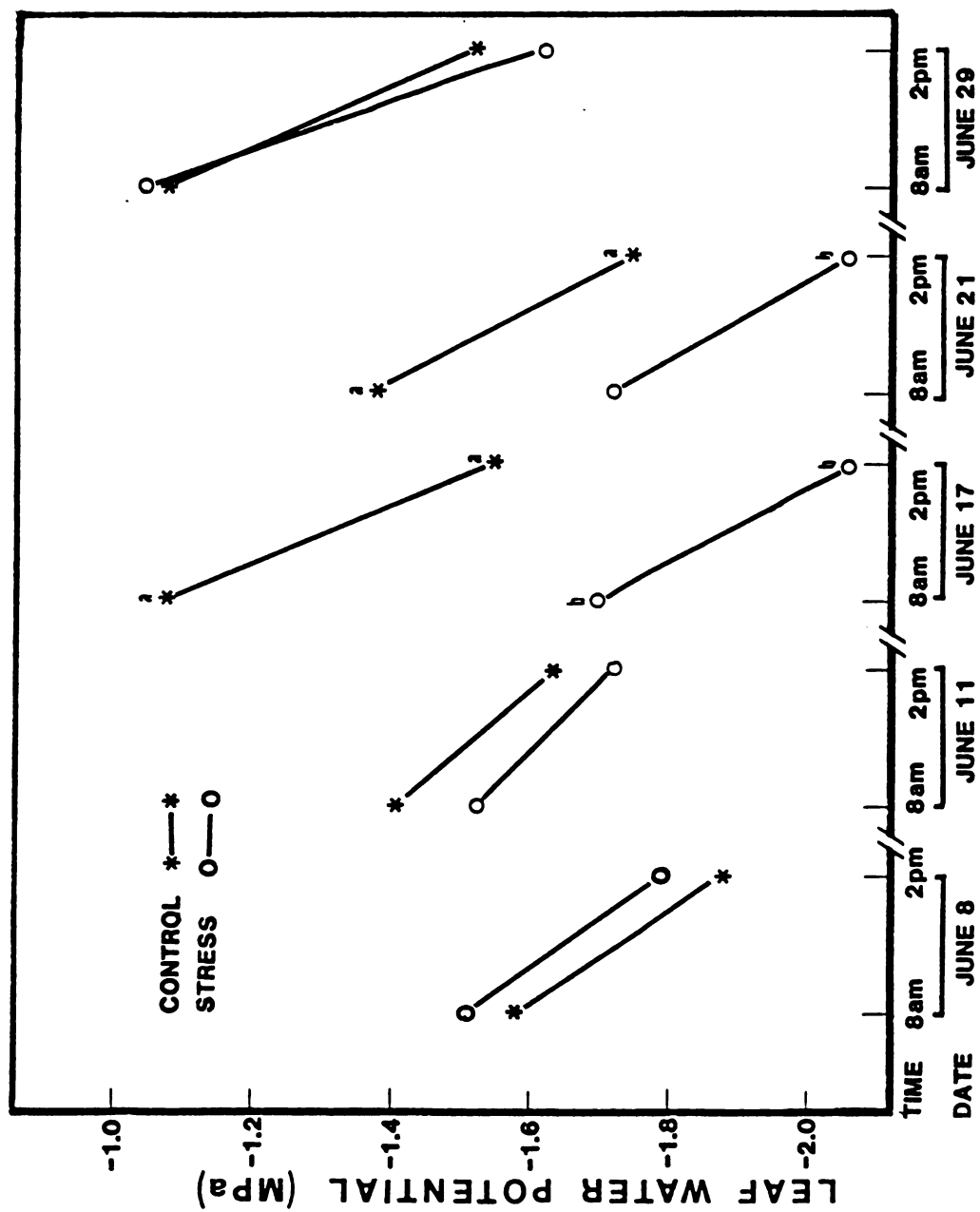


Table 2. Effect of water stress on the 0800h osmotic, turgor, and total leaf water potential (MPa) of 'Redhaven' peach leaves.

Treatment	Dates			
	June 8	June 11	June 17	June 21
Osmotic Potential (MPa) ^z				
Control	-3.01	-2.75 a	-2.85	-2.98
Stress	-2.93	-2.89 b	-3.07	-3.01
Turgor Potential (MPa) ^z				
Control	1.44	1.34	1.77 a	1.61 a
Stress	1.41	1.37	1.37 b	1.29 b
Total Leaf Water Potential (MPa) ^z				
Control	-1.58	-1.41	-1.08 a	-1.38 a
Stress	-1.51	-1.52	-1.70 b	-1.72 b

^zValues followed by different letters are statistically different (LSD, 5% level).

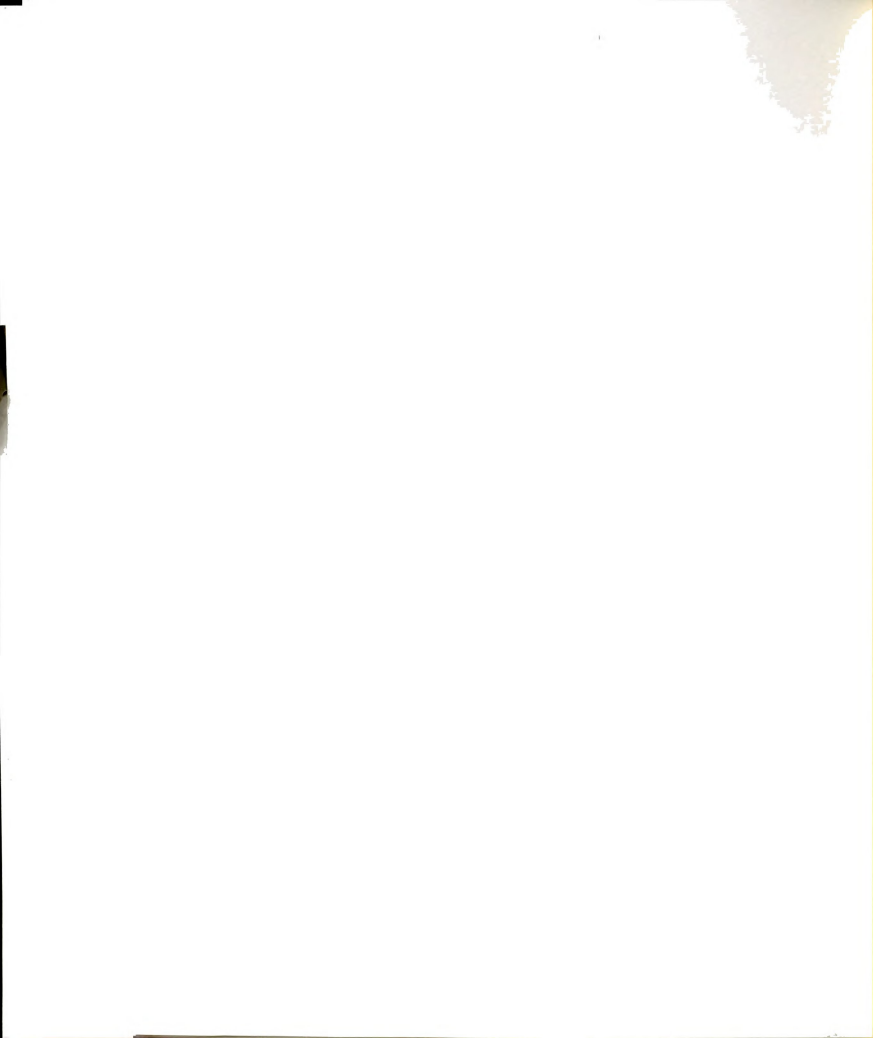
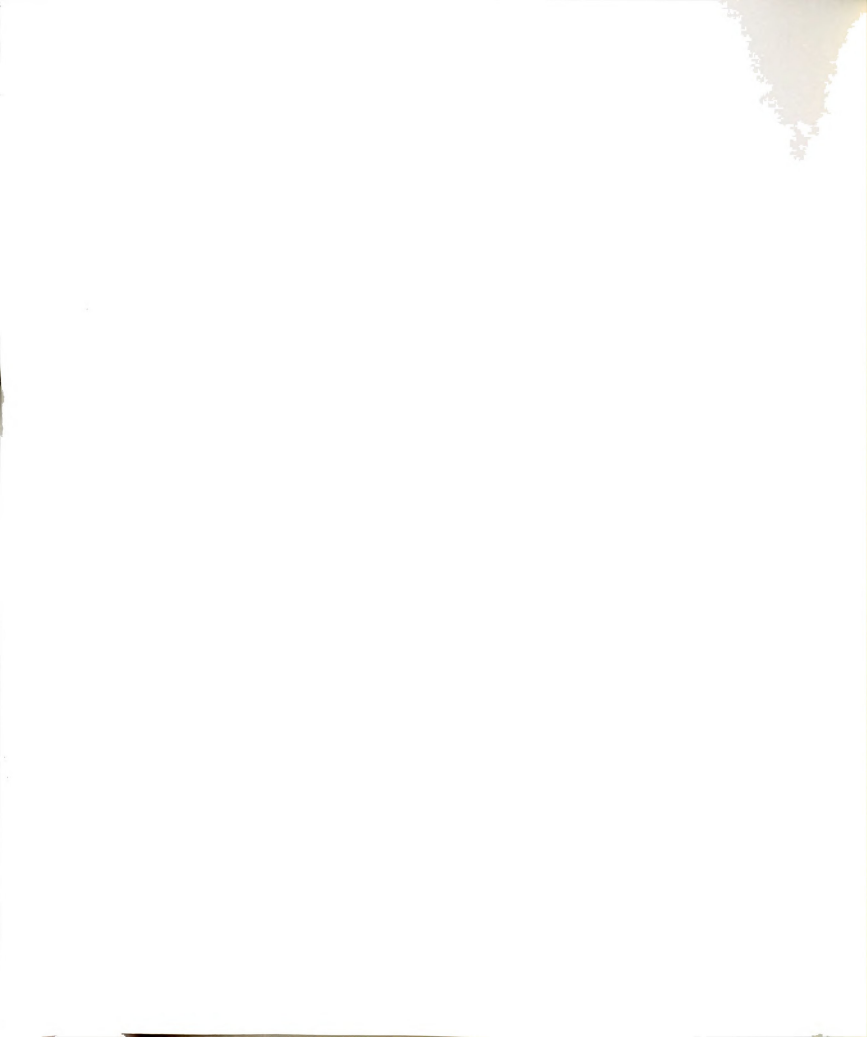
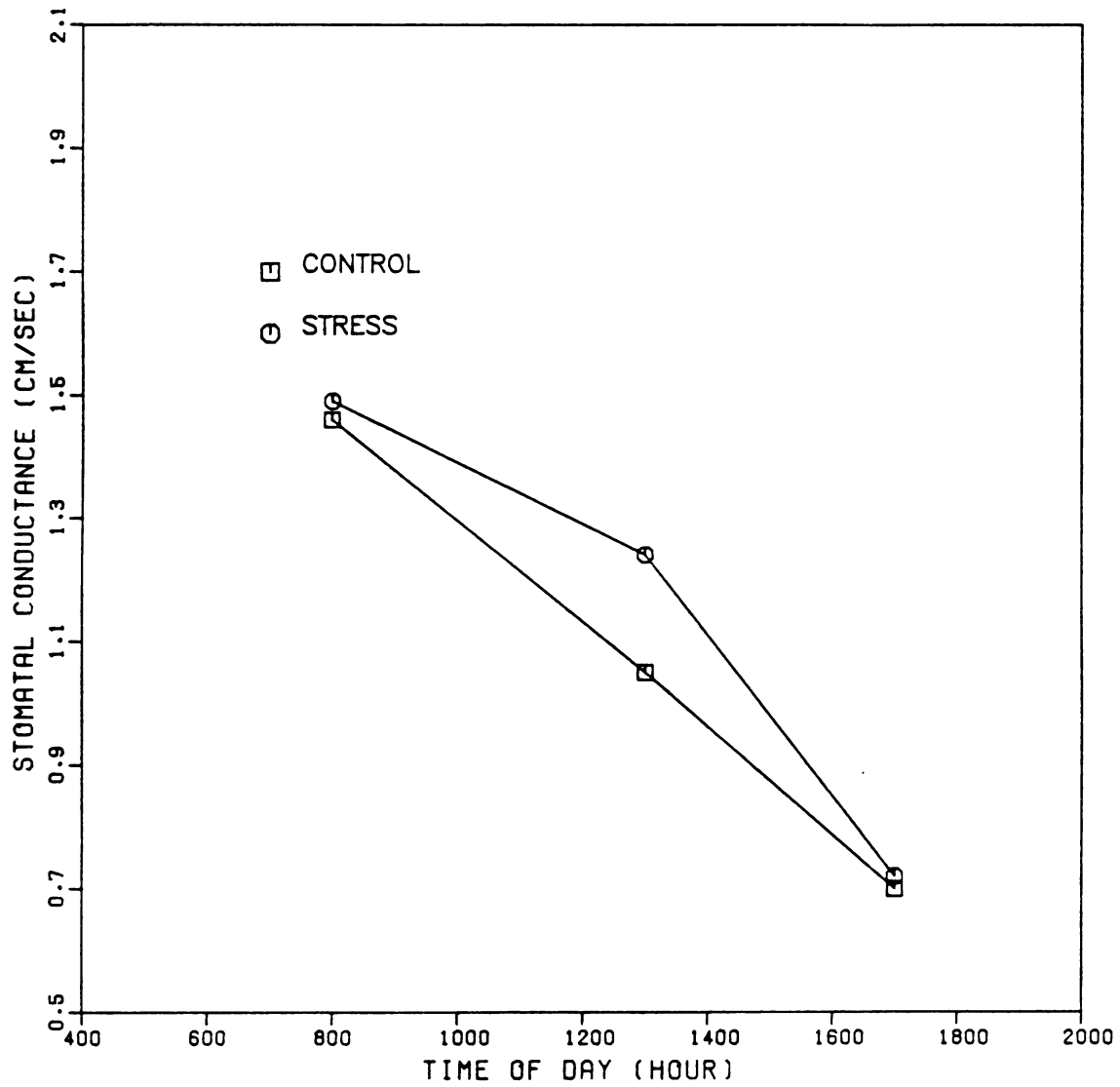


Figure 3.a-e. Effect of water stress and recovery on the diurnal changes in stomatal conductance (cm sec^{-1}) of 'Redhaven' peach leaves. Mean separation by LSD, 5% level.

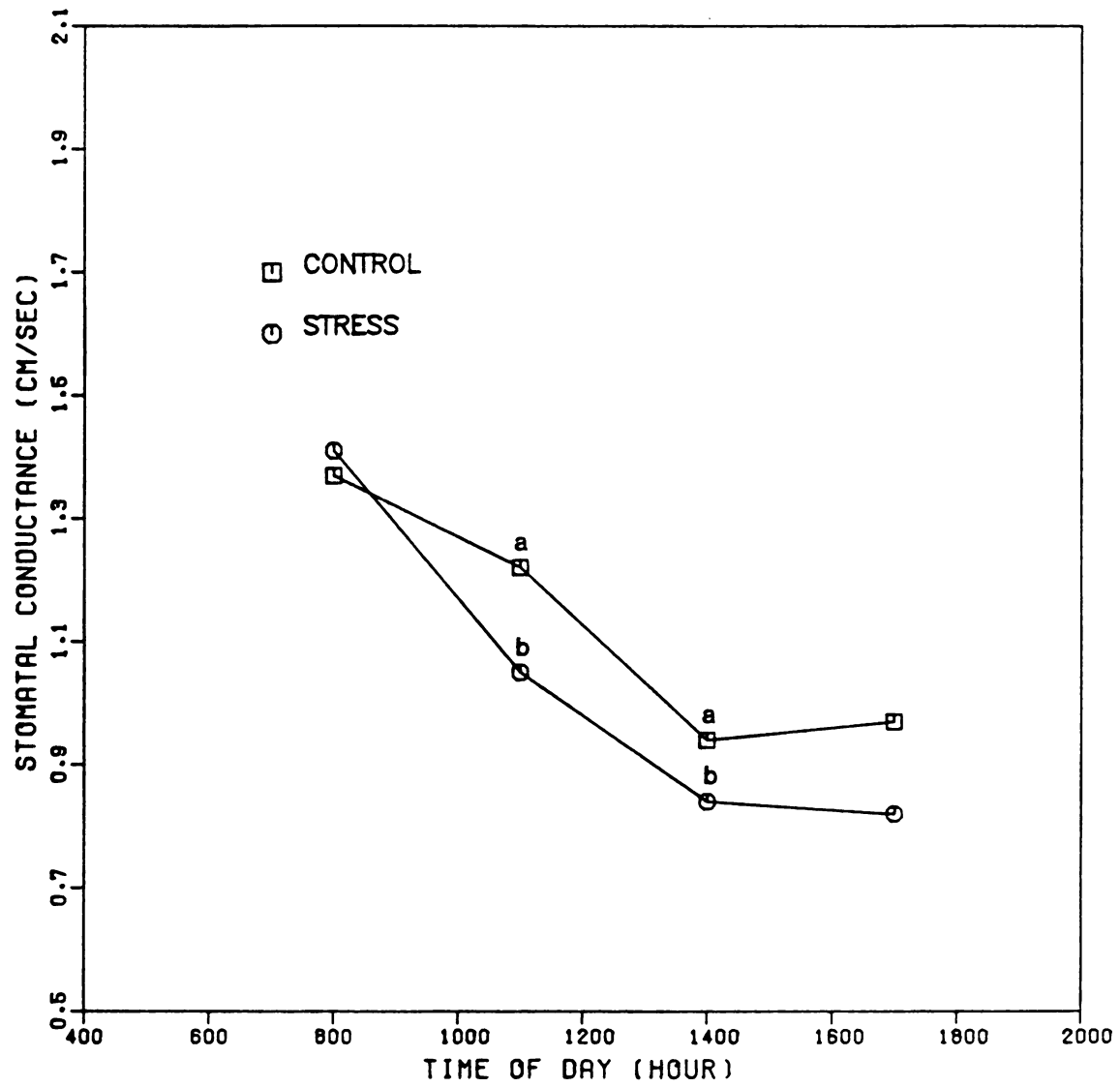
- a. June 8, 1982
- b. June 11, 1982
- c. June 17, 1982
- d. June 21, 1982
- e. June 29, 1982





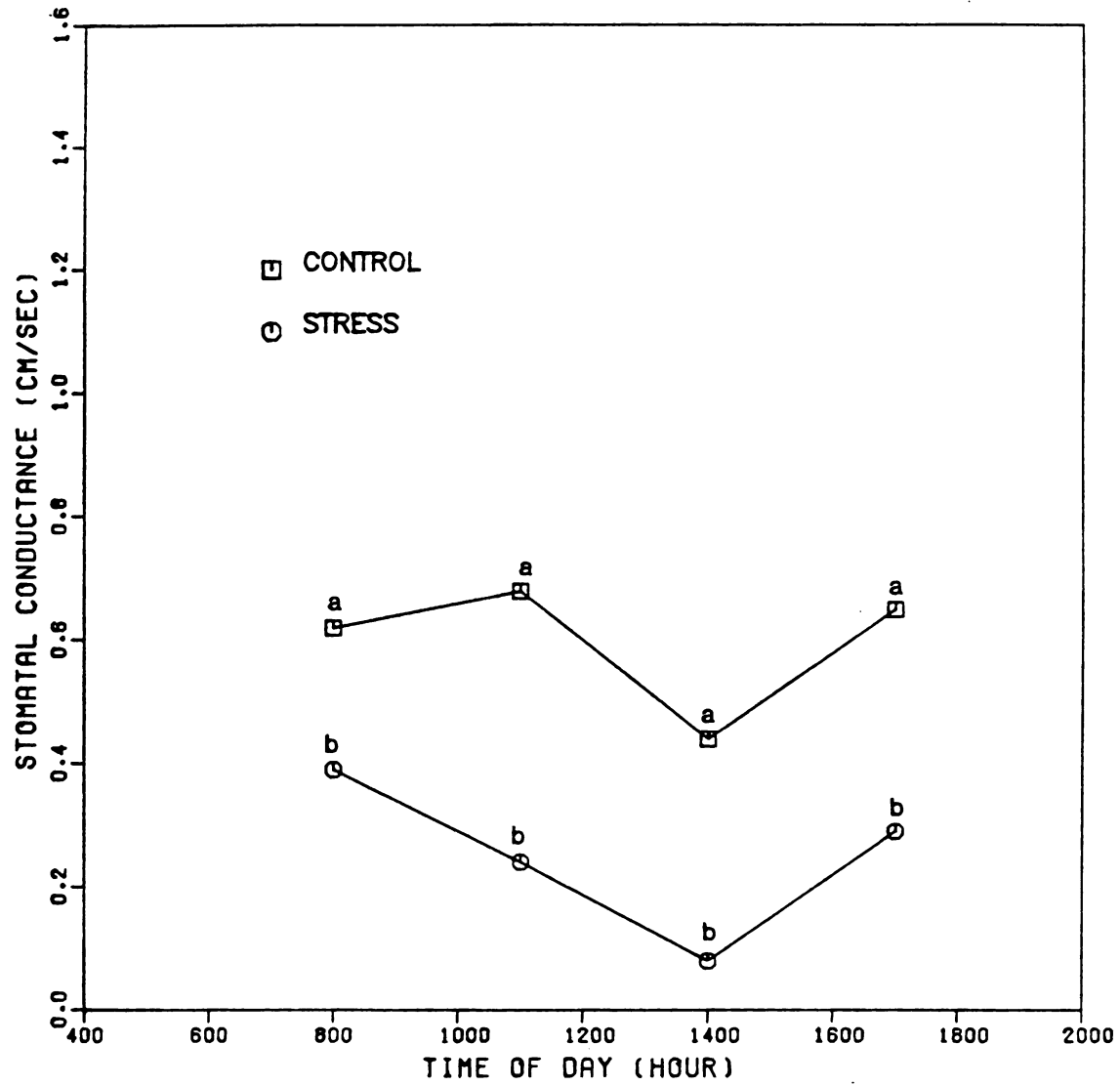
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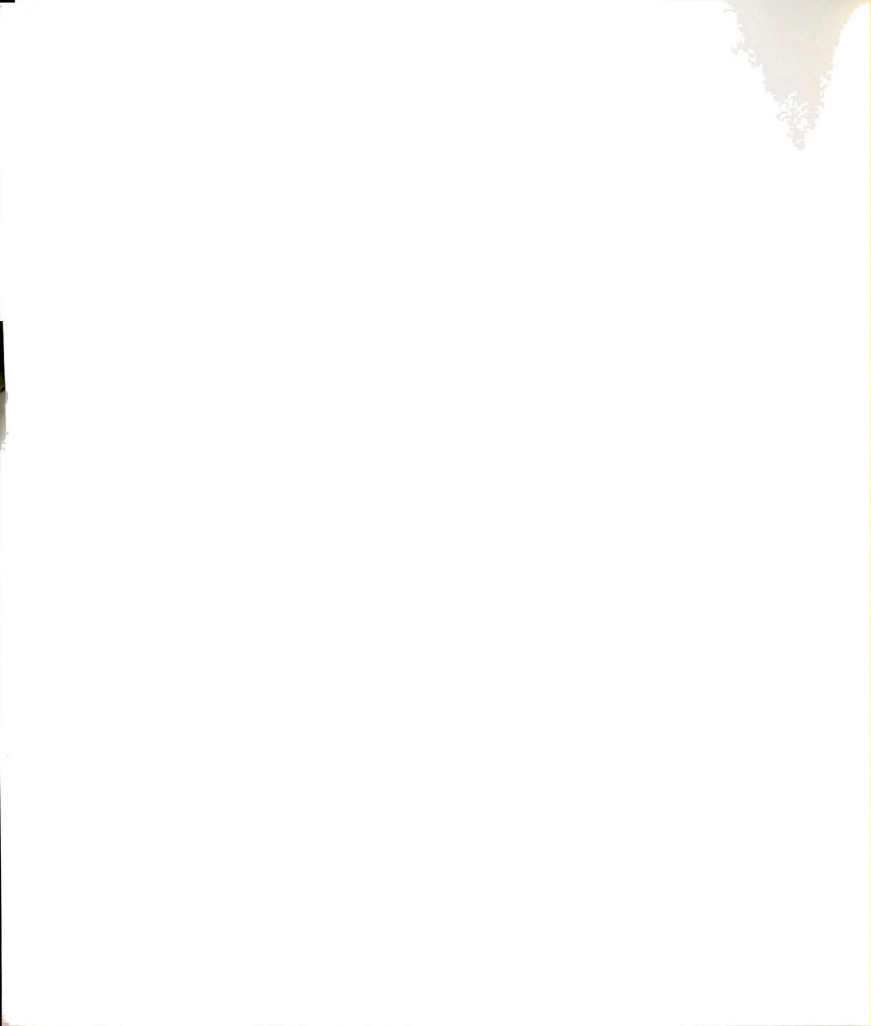


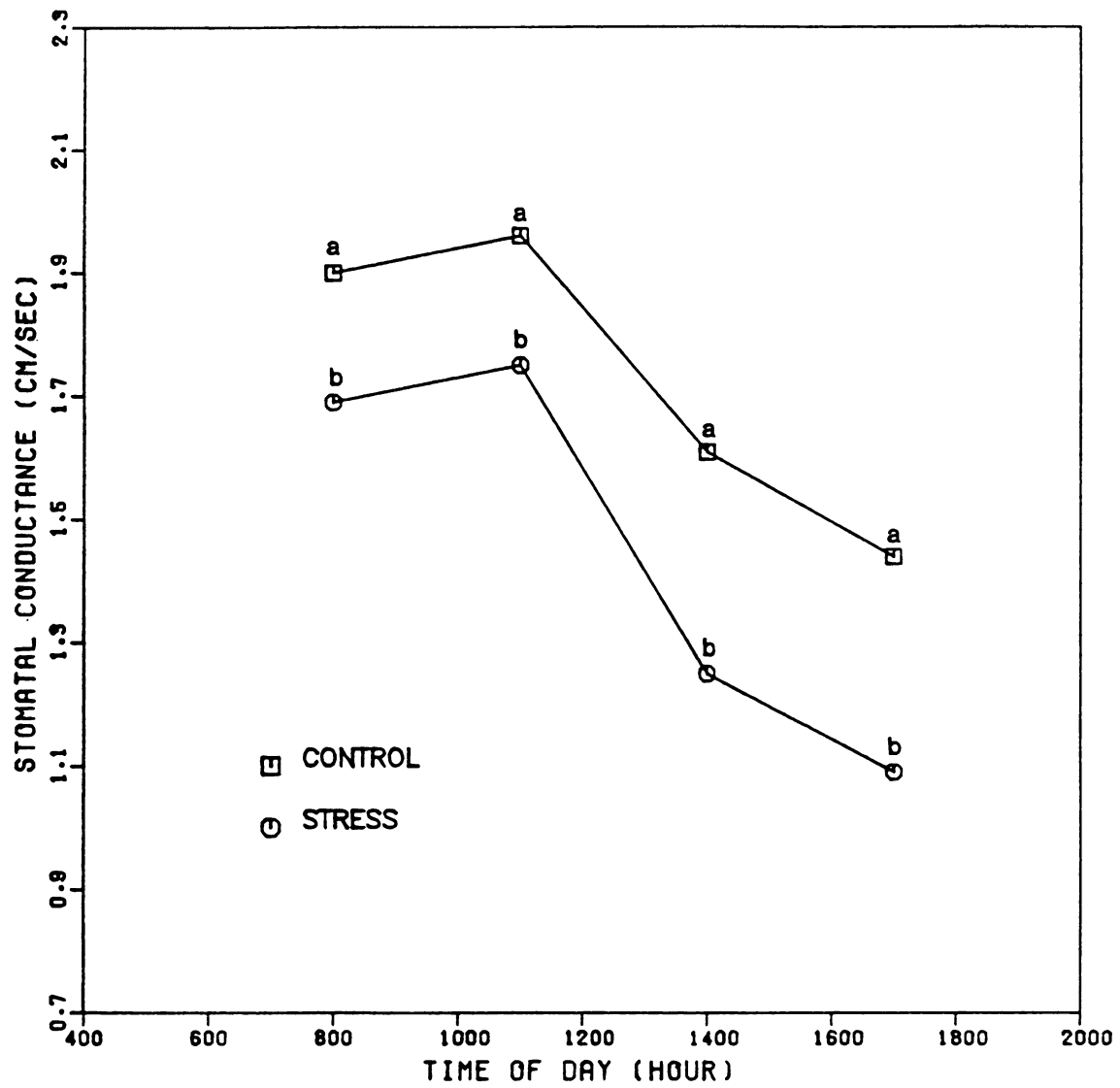
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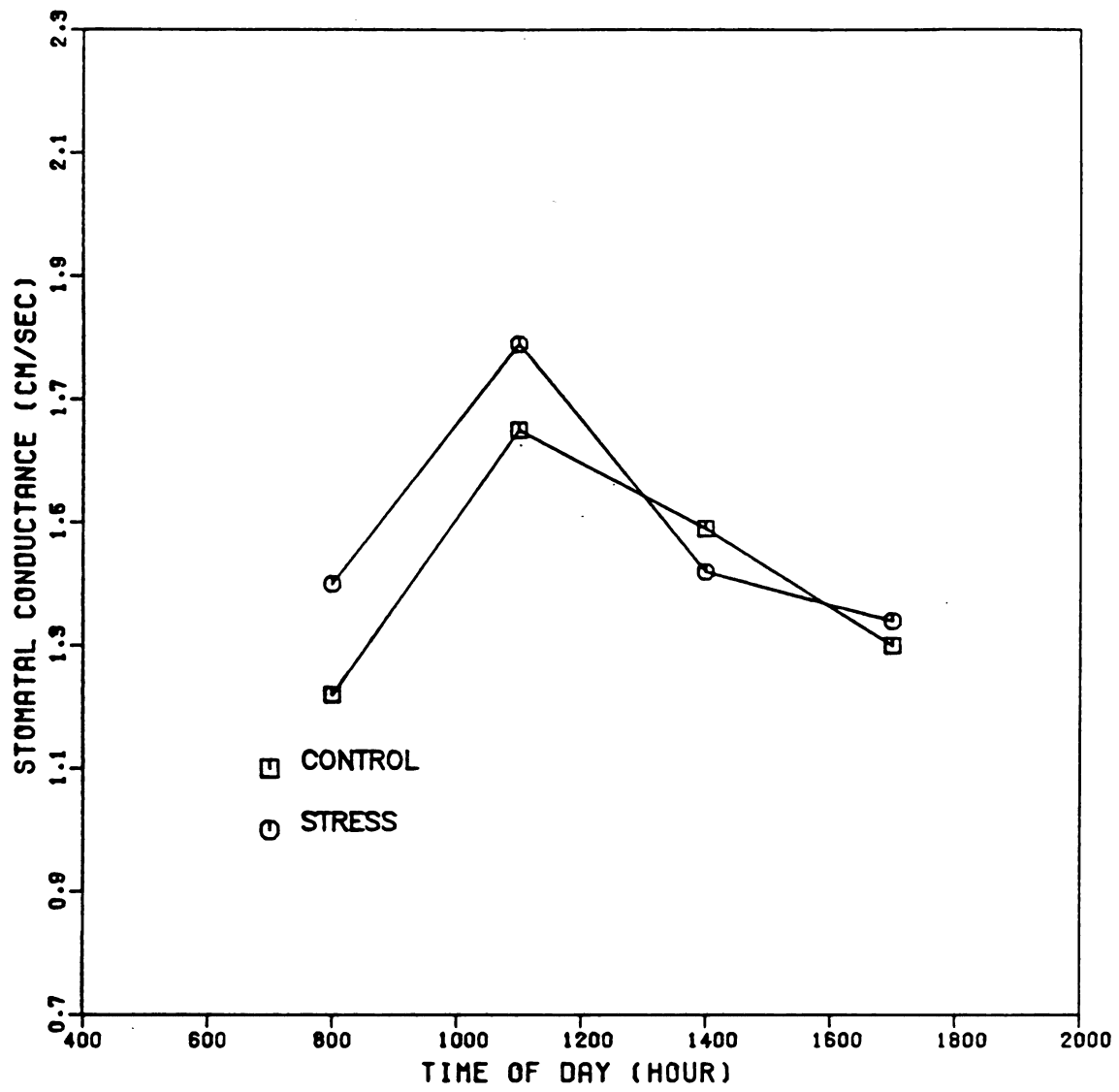
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June 21, 1982





June 29, 1982

Table 3. Effect of water stress and recovery on the diurnal changes in transpiration rate ($\mu\text{g H}_2\text{O mm}^{-2} \text{s}^{-1}$) of 'Redhaven' peach leaves.

Date	Treatment	Transpiration Rate ($\mu\text{g H}_2\text{O mm}^{-2} \text{s}^{-1}$) ^z			
		Time (hr)			
		0800	1100	1400	1700
June 8	Control	26.49		33.5	20.3
	Stress	26.93		39.81	19.59
June 11	Control	23.0	27.22a	31.34a	24.95
	Stress	21.9	22.74b	22.89b	20.99
June 17	Control	5.95a	10.15a	8.50a	11.6a
	Stress	3.05b	3.45b	2.0b	4.16b
June 21	Control	24.2a	36.12a	36.41a	34.8a
	Stress	18.31b	30.1b	27.64b	23.62b
June 29	Control	8.31	28.88	29.39	22.98
	Stress	12.31	27.57	29.05	20.94

^zMean separation within date and time by LSD, 5% level.



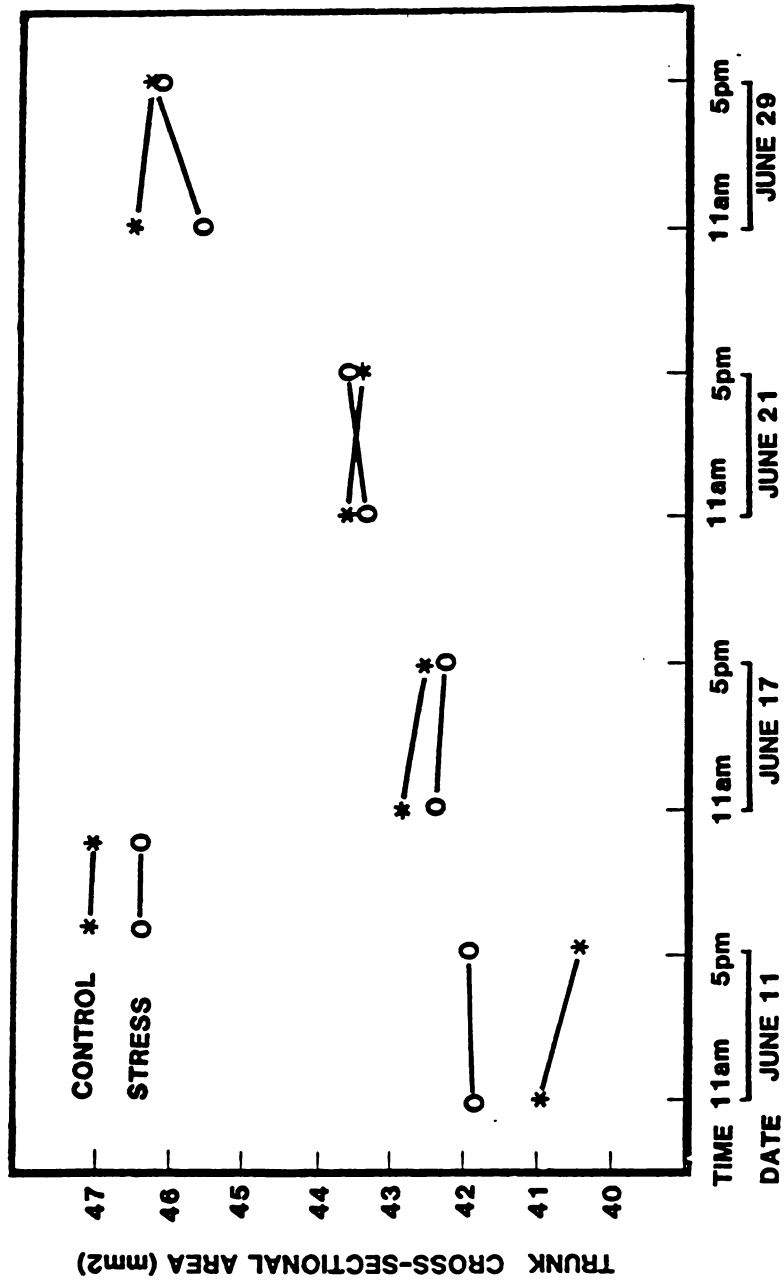
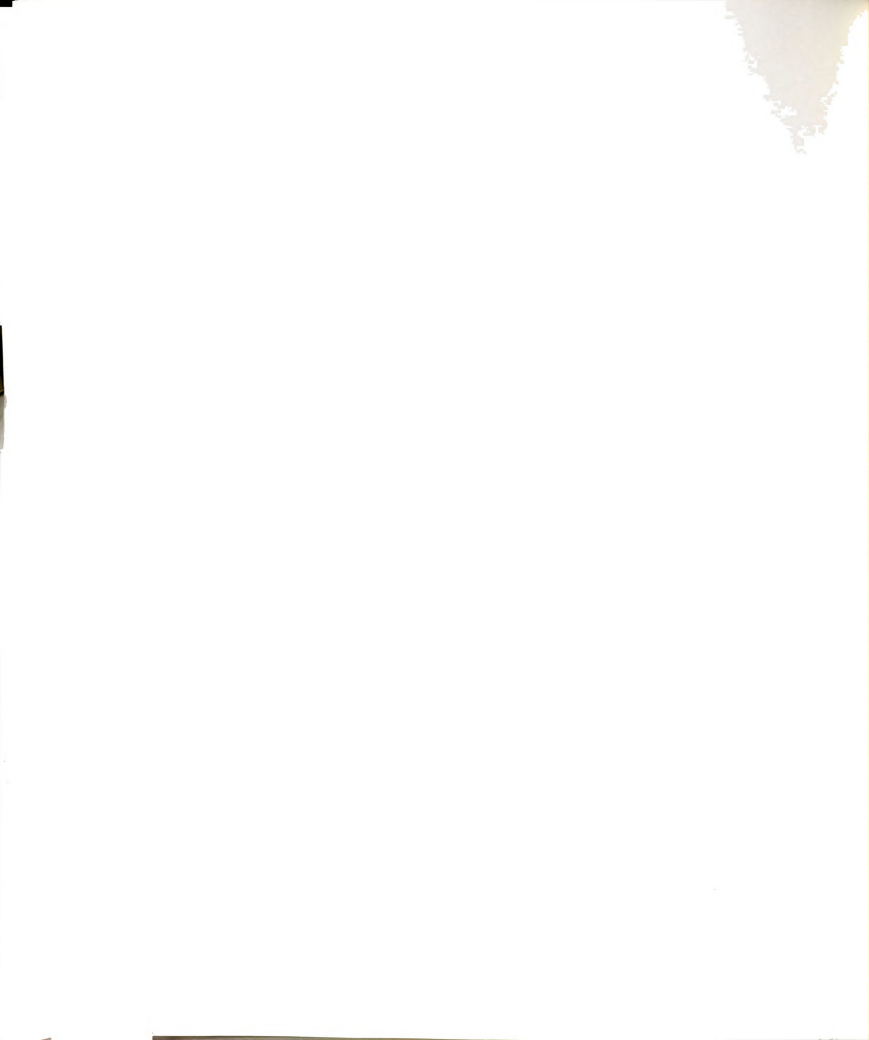


Figure 4. Effect of water stress and recovery on the trunk growth (mm^2) of 'Redhaven' peach trees.



Discussion

Osmotic adjustment has been demonstrated in stressed apple trees (Davies and Lakso 1979, Goode and Higgs 1973), and it has been proposed for peach trees (Young et al. 1982). The water potential data (Table 2) implied that osmotic adjustment may be a factor in moderating turgor loss in stressed peach trees. In the early stages of stress, the stressed trees had significantly less negative osmotic potentials and the calculated turgor potentials varied only 0.12 MPa during the stress period. Similar results were obtained for 'Redhaven' peach in an earlier experiment (Sec. 1). Verification of this mechanism would require more frequent sampling of total water and osmotic potential under stressed and nonstressed conditions. It has been suggested that determination of osmotic potential by the tissue-freezing method should be calibrated against the pressure volume curve (Brown and Tanner 1983). Errors associated with freezing and thawing of the leaf tissue may lead to overestimating the potential for osmotic adjustment (Brown and Tanner 1983).

The stomatal responses observed agreed with other published data on peach stomatal behavior. The diurnal pattern was similar to field results (Xiloyannis et al. 1980) and measurements of stomatal aperture (Hendrickson 1926). The effects of increasing evaporative demand, created by the interactive effects of temperature and humidity, was believed to be largely responsible for changes in stomatal conductance and transpiration rate observed throughout the day. The statistical analysis of the stomatal conductance (Fig. 3), transpiration (Table 3),

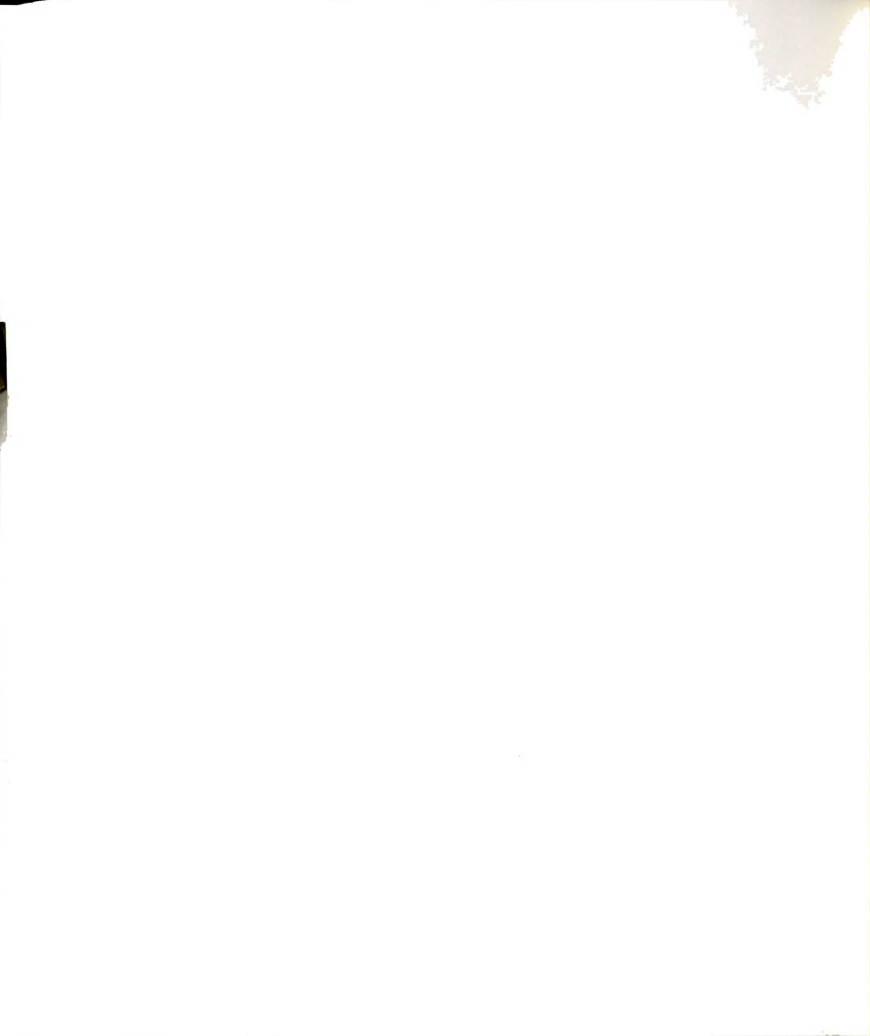


and the stomatal conductance data reported earlier (Sec. I) indicated that 'Redhaven' peach stomata were responsive to mild stress conditions even though leaf water potential did not differ and the percent of available soil water was above 50%. This response to a mild stress was viewed as part of a mechanism to conserve water and stabilize the plant water status.

Recovery in response to rewatering is dependent upon the duration and severity of the water stress imposed (Ludlow et al. 1980) and may be related to an adaptive mechanism. Leaf water potentials have recovered to prestress levels within 24 hours of rewatering (Ludlow et al. 1980, Tan and Buttery 1982b); however, stomatal conductance required one to five days (Hsiao 1973, Tan and Buttery 1982b, Ludlow et al. 1980), and was less than 100% of the prestress values. The recovery results presented here were obtained three days after rewatering and are in agreement with those reported previously (Tan and Buttery 1982b). Stomatal conductances for peaches subjected to a slowly progressing stress (Sec. I) were not different from the well-watered control 24 hours after rewatering. Adaptation via preconditioning probably occurred as the stress progressed and perhaps eliminated the "after effect" (Hsiao 1973) of reduced stomatal conductance. Davies and Lakso (1979), Tan and Buttery (1982b), and unpublished results on 'Montmorency' cherry (M. E. Olien and J. A. Flore) have demonstrated that stomatal conductance was greater and the ability to tolerate subsequent drought periods was improved for trees preconditioned to water stress. The potential for preconditioning could be expected for 'Redhaven' peach trees.

Conclusion

This study illustrated some of the adaptive responses of 'Red-haven' peach trees experiencing water stress. Under mild stress, stomatal conductance declined earlier and osmotic adjustment appeared to have a role. These mechanisms moderated the potential for water loss and aided in maintaining turgor. The ability to recover from water stress was indicated by the lack of statistical differences between treatments for stomatal conductance and leaf water potential.



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SUMMARY



Summary

Water stress reduced growth in 'Redhaven' peach trees. Two weeks of the SWS were required before a reduction in growth similar to the RWS was observed. Under RWS conditions, leaf emergence was more sensitive than leaf or shoot growth. Leaf growth rate for the RWS recovered fastest, while shoot growth rate recovered slowest. Under the SWS conditions, leaf emergence was more sensitive than leaf, trunk, or shoot growth; however, leaf growth rate was more sensitive than leaf emergence, trunk growth, or shoot growth rate.

Trunk growth was selected as the best parameter to monitor tree water status in research experiments for irrigation scheduling. Although leaf emergence and leaf growth rates were more sensitive, these parameters were not as suited to frequent and rapid sampling. Shoot growth did not appear sensitive enough. Trunk growth fluctuations were relatively easy to observe in the field, and the parameter was sensitive to water stress.

This study illustrated some of the adaptive responses of 'Redhaven' peach trees experiencing water stress. Under mild stress, stomatal conductance declined earlier and osmotic adjustment appeared to have a role. These mechanisms moderated the potential for water loss and aided in maintaining turgor. The ability to recover from water stress was indicated by the lack of statistical differences between treatments for stomatal conductance and leaf water potential.



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