Stomatal Response of Three Grapevine Cultivars (*Vitis vinifera* L.) to High Temperature

GONZALO SEPÚLVEDA[1] and W. MARK KLIEWER[2]

Potted Cardinal, Chardonnay, and Chenin blanc vines were subjected to heat stress of 40°C and 20°C (day and night temperatures, respectively) for periods of 0 (control), four, eight, and 12 days before returning the vines to optimal day temperature conditions of 25°C to 29°C in a greenhouse for an eight-day "recovery period". Root temperatures were maintained constant during the heat stress period by holding the pots in a water bath. Stomatal conductance, predawn leaf water potential, air and leaf temperatures, relative humidity, and photosynthetic active radiation were measured throughout the experiment. Heat stress markedly reduced stomatal conductance (Cs) in Chardonnay and Chenin blanc vines. Under optimal temperature conditions (25° to 29°C/15° to 16°C day/night temperatures), Chardonnay vines had the highest Cs, followed by Chenin blanc and Cardinal, whereas under heat stress (40°C), Chenin blanc had the highest Cs, followed by Chardonnay and Cardinal. However, Cardinal was the least affected of the three cultivars. Within one to four days after heat-stressed vines were returned to optimal day temperature conditions, Cs was similar to that of control vines.

Grapevine stomates are located primarily on the abaxial (lower) surface of the leaf laminae (31) with 10 000 to 15 000 stomata per square centimeter, averaging 10 to 13 microns in length and varying up to 5 microns in width according to their degree of openness (16).

The main function of stomates is to allow carbon dioxide uptake by leaves and the diffusion of water vapor, thus permitting the essential physiological processes of photosynthesis and transpiration. The measurement of stomatal conductance to water vapor with a porometer is usually correlated to CO_2 uptake by leaves, and hence may be an estimate of photosynthesis (20).

Extensive reviews on stomatal function and response to environmental factors have been done by Hsiao (11), Raschke (20), Hall, Schulze, and Lange (7), Sheriff (26), and Farquhar and Sharkey (3). Stomata respond to a number of environmental variables: temperature, photosynthetic photon flux density, vapor pressure deficit, carbon dioxide concentration, water stress, and a host of tissue cellular and subcellular processes involving solute membrane characteristics, hormones, *etc.* (12,13,20,30). The relations among the factors involved are complex and dynamic.

Studies on stomatal response to temperature have often yielded contradictory results; Heath and Orchard (9) and Heath and Meidner (8) observed stomatal closure with increasing temperature, while Hofstra and Hesketh (10), Drake *et al.* (1), Schulze *et al.* (23), Hall *et al.* (7), Rogers *et al.* (21), and Even-Chen *et al.* (2) found that stomata opened with increasing temperature. Also, maximum stomatal opening at an intermediate temperature has been reported (10,18,19).

Interactions between temperature and humidity may account for part of these conflicting results. Warrit *et al.* (29) concluded that there is no evidence that apple stomata are sensitive to temperature *per se*, but stomatal conductance is reduced by increasing leaf to air vapor pressure deficits. Similar conclusions were obtained by Schulze *et al.* (22,24,25) for apricots under desert conditions, adding that under these conditions, stomata respond to temperature and air humidity irrespective of a wide range of total water potential and internal CO_2 concentrations. However, Even-Chen *et al.* (2) reported that with prune trees stomatal conductance increased from 0.15 to 1.00 cm sec^{-1} when temperature increased from 25° to 40°C, despite a much larger vapor pressure deficit.

Kaufmann (12,13) concluded that temperature is not a significant independent variable controlling conductance in conifers under field conditions, provided that absolute humidity difference from leaf to air (DAH) is considered. He proposed a model which includes only photosynthetic photon flux density (PPFD) and DAH as the primary factors controlling stomatal function for plants growing in their native ranges. He considers temperature and water stress as secondary factors that affect conductance intermittently, except when the plants are growing outside their natural environments. Thorpe *et al.* (28) explained apple leaf conductance with an empirical model also having PPFD and DAH as components; however, their experiments were performed on potted saplings. Sheriff (26) states that the absence of an overall stomatal response to change in temperature could result from antagonism between the various feedback mechanisms (20) involved in stomatal regulation.

Information on grapevine leaf stomatal behavior has been mainly obtained through studies on photosynthesis (15,16) or plant water relations (15,17,27). Studies dealing with direct effects of environmental factors (temperature, humidity, light) on vine leaf stomatal response is scarce.

Korner *et al.* (14) reported values of maximum leaf diffusive conductance of 246 species and cultivars. Maximum leaf conductance was defined as the largest value of conductance observed in fully-developed (but not senescent) leaves of well-watered plants under optimal climatic conditions, natural outdoor CO_2 concentration, and suffi-

[1]Graduate Student and [2]Professor of Viticulture, Department of Enology and Viticulture, University of California, Davis, California 95616-5270.

The authors are grateful to Wendy Hall, Dr. J. Hatfield, and Mr. W. Pruitt for use of the porometer, infrared thermometer, and psychrometer, respectively.

Presented at the 33rd Annual Meeting of the American Society of Enologists, Anaheim, California (June 1982).

This research conducted at the University of California, Davis.

Manuscript submitted for publication 3 January 1983.

cient nutrient supply. Grapevine values ranged from 0.10 to 0.45 cm sec^{-1} for different cultivars, plant ages, and growing conditions.

Smart (27) reported values of stomatal conductance of 0.03 to 1.00 cm sec^{-1} for field-grown Shiraz grapevines under different irrigation regimes. Freeman *et al.* (4), working under natural conditions near Greenfield, California, measured stomatal conductance values of Chardonnay ranging from 0.10 to 1.00 cm sec^{-1}, with fog and wind being important environmental factors influencing stomatal behavior throughout the day. Stomatal conductance measurements made at Davis, California, using eight-year-old Carignane vines, resulted in values ranging between 0.10 to 0.40 cm sec^{-1}.

The main objective of this study was to examine the stomatal response of three vinifera grapevine cultivars (Chenin blanc, Chardonnay, and Cardinal) to high temperatures.

Materials and Methods

Three separate experiments were done during the summer of 1981, using a greenhouse and phytotron for conducting the work.

Experiment 1: Thirty-three four-year-old own-rooted, bearing Cardinal plants were used in this experiment between 23 June and 14 July 1981.

Experiment 2: Thirty-six four-year-old own-rooted, bearing Chardonnay plants were used. The experiment was conducted between 1 August and 22 August 1981.

Experiment 3: Thirty-six own-rooted, non-bearing two-year-old Chenin blanc plants were used between 5 September and 26 September 1981.

For each experiment, the plants were grown in 14-liter pots containing a sterilized mixture of soil, sand, and peat (2:2:1, v:v:v). Plants were maintained in a lath house covered with 2.5 cm mesh plastic bird netting before being transferred to a greenhouse for a one-week acclimation period prior to initiating each experiment. The bird netting had little or no effect on reducing the intensity of solar radiation.

One normal strength Hoagland nutrient solution was added to pots at weekly intervals until the initiation of each experiment. Thereafter, plants were irrigated daily or as needed with tap water. Insecticides and fungicides were applied at periodic intervals to control diseases and pests. Each plant was trained to one shoot with one cluster per shoot. Shoots with more than one cluster were thinned to one cluster shortly after budbreak.

The required number of plants for each experiment was selected for uniformity of size and divided into three groups representing tallest, medium-sized, and smallest plants. Each size category was considered as a block, and treatments were assigned randomly within a block prior to the initiation of the experiment. In all three experiments, vines were subjected to two temperature regimes ("high" and "normal" temperatures) for four, eight, and 12 days each, with and without a subsequent recovery period of eight days at the normal temperature regime. An individual plant was considered as the experimental unit.

The heat stress or high temperature treatment, corresponding to a day/night maximum/minimum temperature of 40°C/20°C was conducted inside a sunlit stationary phytotron room (32) with about 19 m^2 of utilizable area. Heat-stressed plants of each of the three experiments received six to seven hours of daily exposure to 40°C between 1100 h and 1800 h. Non-stressed plants (control) remained inside a greenhouse at maximum day temperatures between 25° and 29°C and minimum night temperatures from 15.5° to 16.5°C. This temperature regime will be referred to as "normal" temperature in this communication. The "recovery" treatment designates either removing the plants from the phytotron at the end of the high temperature exposure period (no recovery) or transferring the potted vines after various periods of time in the phytotron to the greenhouse for an eight-day period (with recovery). A typical curve showing diurnal changes in temperature of control and heat stress treatments over a 24-hour period is shown in Figure 1.

For root temperature control, the plants subjected to heat stress were set inside water baths, whereas control vines were set at floor level inside the greenhouse, and

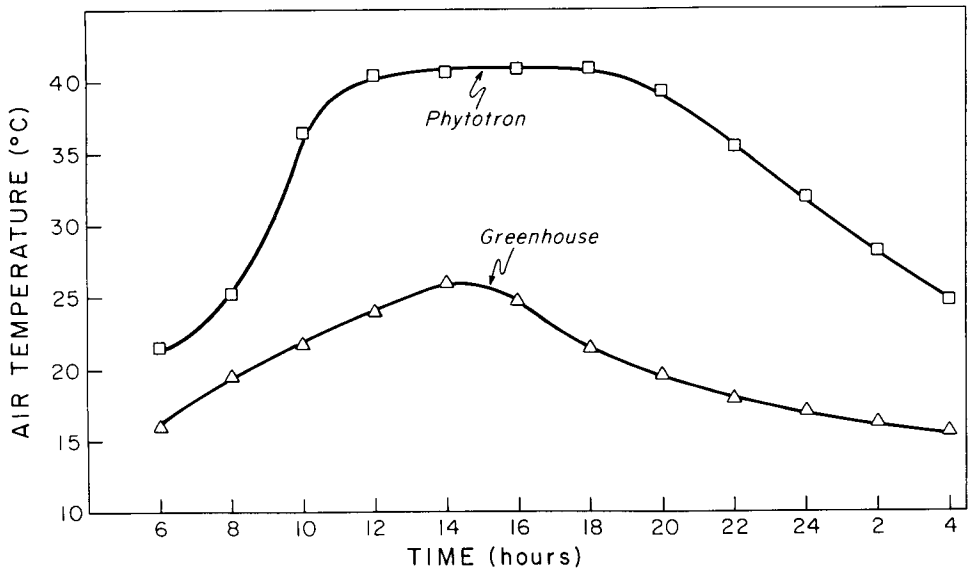

Fig. 1. Typical curve showing diurnal changes of air temperature in greenhouse and phytotron.

each pot was wrapped with aluminum foil paper to reflect incoming radiation. Root temperature was recorded on a thermograph using thermistor probes (20 cm long) inserted into both heat-stressed and control pots. Leaf resistance or conductance (reciprocal value) of the abaxial (lower) surface of a fully-expanded south-facing leaf, was measured with a diffusion porometer (Model LI-65, Li-Cor, Inc., Lincoln, NB). Readings were taken every other day between 1200 h and 1300 h. In addition, diurnal changes in stomatal conductance (Cs) was determined between 0600 h and 2100 h on days 3, 7, and 13 after Experiments 1, 2, and 3 had started, respectively. Readings in all cases were made at two- to three-hour intervals.

Leaf temperature values (T_l) were determined using an infrared thermometer (Raytex and Telatemp) pointed at a fully-expanded south-exposed leaf from a distance of about 20 cm. In most cases, Cs and T_l measurements were made on the same leaves. Readings were taken every other day between 1500h and 1600 h. Diurnal leaf temperature variation was established for Experiment 3 (day 7 of experiment) simultaneously with Cs determination.

Air temperature (T) and relative humidity (RH) were measured with a Psychrometer (Psychron, Model 566, Bendix Environmental Science Div., USA) at the time of stomatal resistance determinations. T was determined with the dry bulb thermometer, and RH was calculated from tables (at 30 in of pressure) as the depression of wet bulb thermometer at the corresponding air temperature.

Photosynthetically-active radiation (PAR) was determined simultaneously with Cs using a Quantum sensor (Model LI-190SB, Li-Cor Inc.) attached to a Li-Cor meter (Model LI-185B, Li-Cor Inc.). An overall value for each experimental site (greenhouse or phytotron) was obtained by locating the sensor next to the leaves used to determine stomatal conductance.

Leaf water potential ψ_l was measured with a portable pressure chamber (Model 600, PMS Instruments Co., Corvallis, OR) at predawn using a single fully-expanded leaf from each plant that was either being removed from or transferred to the greenhouse on that day, according to its treatment schedule. Readings were done within 30 seconds after the leaf was excised from the plant.

Results

Environmental parameters: Mean temperature (T), vapor pressure deficit (VPD), and PAR of the greenhouse and phytotron for each of the three experiments are presented in Table 1. Average T difference between the greenhouse and phytotron was 13°, 14.5°, and 17.8°C for Experiments 1, 2, and 3, respectively. T variability inside the greenhouse was higher than in the

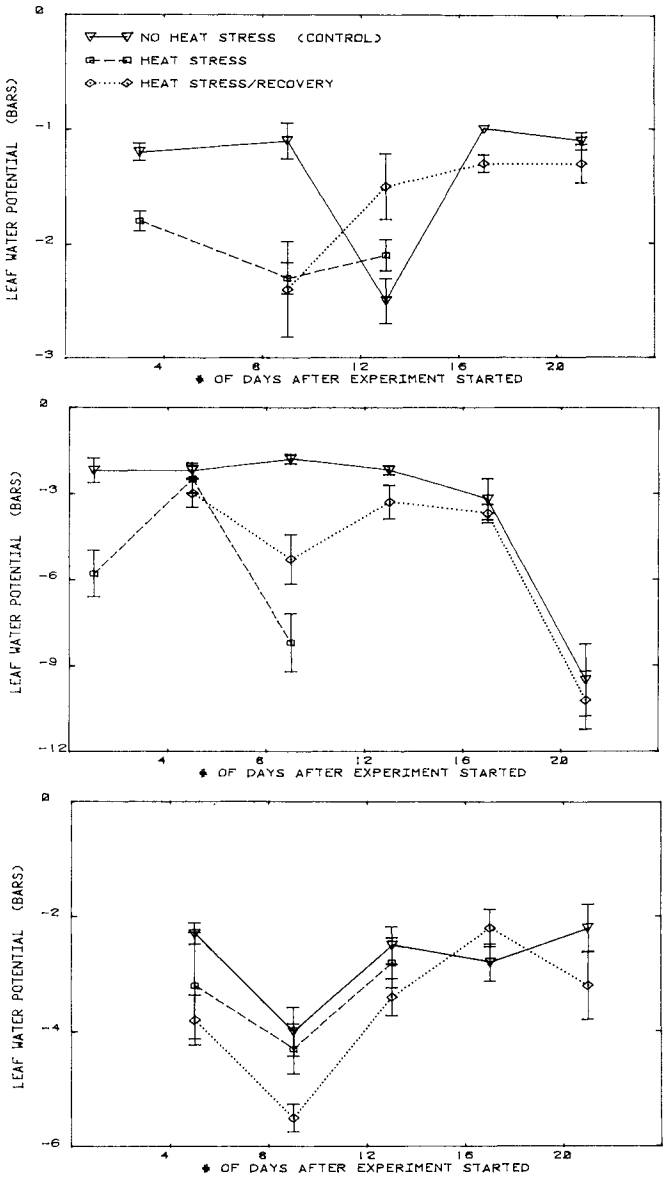

Fig. 2. Predawn leaf water potential of Cardinal (top), Chardonnay (middle), and Chenin blanc (bottom) grapevines subjected to no heat stress (control), heat stress, and heat stress/recovery over a period of 21 days. Brackets indicate ± SE. Each data point represents the average of measurements made on either three or six leaves. In all cases, vines were watered during the evening prior to the predawn ψ_l measurements.

Table 1. Average air temperature (T), relative humidity (RH), vapor pressure deficit (VPD), and photosynthetically-active radiation (PAR) of greenhouse and phytotron recorded for three different experiments. Measurements were made every second day during 21 days in the greenhouse and 13 days in the phytotron.

Experiment no.	Greenhouse T °C	RH %	VPD kPa	PAR $\mu E\ m^{-2}\ s^{-1}$	Phytotron T °C	RH %	VPD kPa	PAR $\mu E\ m^{-2}\ s^{-1}$
1	26.7 ± 3.0	66 ± 6.9	1.2 ± 0.4	587 ± 184.9	39.5 ± 1.3	49 ± 9.5	3.7 ± 0.8	883 ± 294.4
2	25.4 ± 2.1	74 ± 4.4	0.8 ± 0.2	567 ± 48.7	39.9 ± 1.5	43 ± 4.8	4.2 ± 0.6	1089 ± 145.7
3	24.0 ± 2.6	75 ± 5.0	0.7 ± 0.2	534 ± 117.4	41.8 ± 1.0	39 ± 1.8	4.9 ± 0.4	996 ± 56.7

± Indicates plus or minus one standard deviation.

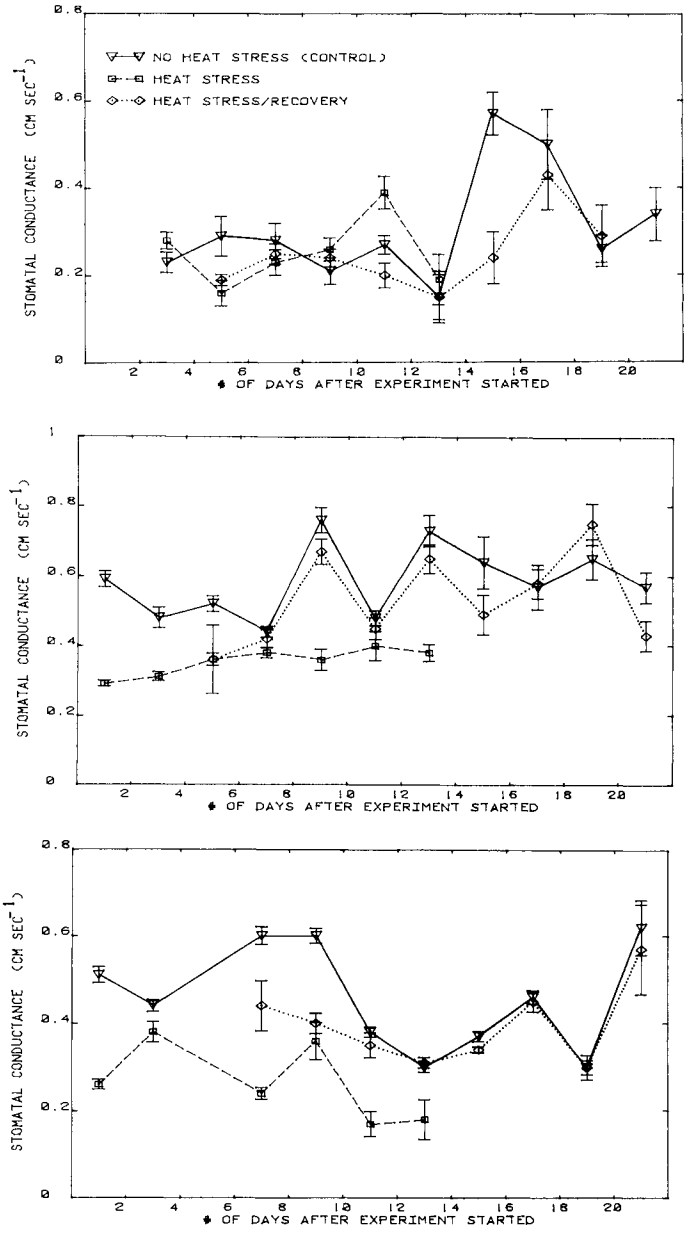

Fig. 3. Effect of heat stress and heat stress/recovery treatments on stomatal conductance of Cardinal (top), Chardonnay (middle), and Chenin blanc (bottom) grapevines. Brackets indicate ±SE.

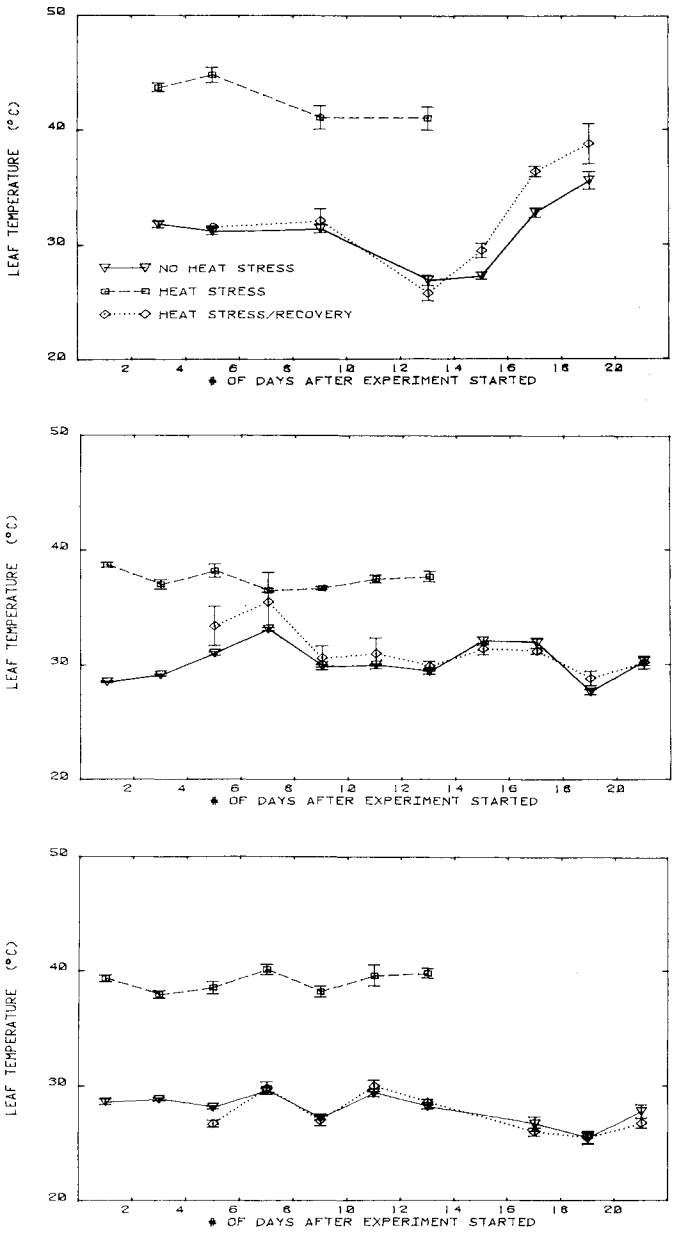

Fig. 4. Effect of heat stress and heat stress/recovery treatments on leaf temperature of Cardinal (top), Chardonnay (middle), and Chenin blanc (bottom) grapevines. Brackets indicate ±SE.

phytotron for all three experiments; however, mean T value and degree of variation for each experiment was about the same at each location.

Mean RH inside the greenhouse was higher (VPD lower) than in the phytotron for the three experiments (Table 1). RH variability inside the phytotron was greater than in the greenhouse for Experiment 1; however, the reverse was true for Experiment 3. There was almost no humidity variability between measurements for Experiment 2 (Table 1). For the three experiments, PAR was higher in the phytotron than in the greenhouse (Table 1); however, variation patterns in response to ambient changes were the same for both locations.

Leaf water potential: Mean predawn ψ_l values for heat-stressed Cardinal grapevines (Experiment 1) were significantly lower (more negative) than those for control vines, except on day 13 when ψ_l of control vines was −2.5 bars (Fig. 2A). Vines subjected to heat stress and then returned to the greenhouse for an eight-day recovery period (indicated in figures as heat stress/recovery) had ψ_l increasingly higher (less negative) during the treatment period. Significant differences from control vines were obtained on all but one occasion, day 21 (Fig. 2A).

Predawn ψ_l of control Chardonnay grapevines (Experiment 2) remained nearly constant up to day 17 (Fig. 2B); however, four days later, a predawn ψ_l value of −9.5 bars was recorded. This sharp decrease (more negative) was the consequence of vines inadvertently not receiving water the previous evening, but only early the same day. The plants, however, did not show visible signs of water

Table 2. Diurnal changes in air temperature (T), relative humidity (RH), vapor pressure deficit (VPD), and photosynthetically active radiation (PAR) in Experiments 1, 2 and 3.

		Greenhouse				Phytotron			
Cultivar and experiment	TIME hours	T °C	RH %	VPD kPa	PAR $\mu E\ m^{-1}s^{-1}$	T °C	RH %	VPD kPa	PAR $\mu E\ m^{-1}\ s^{-1}$
Cardinal, Expt. 1	6	17.2	83	0.3	6	23.3	61	1.1	65
	9	24.4	73	0.8	200	29.4	59	1.7	250
	12	30.0	66	1.4	325	36.7	70	1.9	1200
	15	29.4	62	1.6	600	41.1	61	3.1	750
	18	25.6	78	0.7	110	38.3	54	3.1	160
	21	20.6	85	0.4	0	35.6	55	2.6	0
	Mean	24.5	74.5	0.9		34.1	60.1	0.2	
	SD	5.0	9.2	0.5		6.5	5.6	0.8	
	Day 13 (3/13/81)								
Chardonnay, Expt. 2	6	16.7	89	0.2	0	22.8	57	1.2	0
	9	21.1	77	0.6	125	29.4	43.5	2.3	275
	12	23.9	82	0.5	550	40.6	37.5	4.8	775
	15	26.7	72	1.0	525	39.4	38.5	4.4	1050
	18	23.3	74	0.7	275	40.6	27.5	5.5	300
	21	20.6	72	0.7	0	37.2	34.5	4.2	0
	Mean	22.1	77.7	0.6		35.0	39.8	3.7	
	SD	3.4	6.7	0.3		7.3	10.0	1.6	
	Day 7 (9/11/81)								
Chenin blanc, Expt. 3	6	16.7	89	0.2	0	21.7	56	1.1	0
	9	23.3	47	1.5	125	24.4	70	0.9	250
	11	22.8	82	0.5	225	40.0	37	4.6	925
	12	26.1	75	0.8	500	42.2	37	5.2	1025
	13	26.1	75	0.8	500	43.3	36	5.6	1000
	15	27.8	72	1.0	475	43.3	38	5.4	850
	17	25.0	83	0.5	275	40.6	43	4.3	275
	19	22.8	82	0.5	7	40.0	39	4.5	27
	21	21.1	86	0.4	0	36.7	38	3.8	0
	Mean	23.5	76.8	0.7		36.9	43.8	4.0	
	SD	3.3	12.5	0.4		8.1	11.6	1.8	

stress at the time of measurement. Similar response was observed for heat stress/recovery plants, with an average ψ_l value of -10.2 on day 21 (Fig. 2B). Chardonnay grapevines subjected to heat stress had greater variation in the ψ_l than control and heat stress/recovery plants, and showed significantly lower (more negative) $\psi_l$than control vines on days 1 and 9. ψ_l of heat stress/recovery plants were significantly lower than the control only on days 9 and 13. Greater variability of the data within each recording date was observed for the heat stress and heat stress/recovery plants than for control vines (Fig. 2B).

Mean predawn ψ_l values of heat-stressed Chenin blanc plants (Fig. 2C), did not differ significantly from control vines even though the readings were always lower. However, heat stress/recovery vines had significantly lowerψ_l than control plants on days 5, 9, and 13. The ψ_l patterns of heat stress/recovery and control vines were similar (Fig. 2C).

Stomatal conductance: Cs values of heat-stressed Cardinal grapevines were significantly different than those of control vines on days 3, 5, and 11 (Fig. 3A). There was considerable variation in Cs over time, with values being lower or higher independent of temperature treatments, and mean Cs of control vines showing an opposite response pattern than stressed plants up to day 9 (Fig. 3A). Mean Cs values of heat stress/recovery vines were significantly lower than control vines on days 5, 11, and 15 (Fig. 3A). Within two days of returning the Cardinal vines subjected to heat stress back to the greenhouse, their Cs values were similar to control vines, and they continued to show a similar Cs response pattern to the control for the remainder of the experiment.

Cs values of heat-stressed Chardonnay leaves showed relatively little variation within each measuring date (Fig. 3B). Leaf Cs values of control plants in all cases were significantly higher than heat-stressed plants. Stomatal response with time showed less variation in heat-stressed Chardonnay vines than in the controls. From day 7 through day 13, control plants showed considerable variability in their Cs responses (Fig. 3B). The stomatal response pattern of heat stress/recovery Chardonnay vines closely followed control plants; however, significant differences between these two treatments occurred on days 5, 9, 15, and 21 after the experiment started (Fig. 3B). On day 5, Cs values of plants under heat stress were similar to vines which had completed their stress period the previous day but were now inside the greenhouse under much more favorable temperature conditions. Two days later (day 7), these same plants had identical mean Cs values as the control.

Cs values of control Chenin blanc grapevines were significantly higher than plants subjected to heat stress during the entire 13-day comparison period (Fig. 3C). Cs of plants exposed to heat stress and recovery treatments

showed a similar response pattern to control vines. However, significant differences between control and stress/recovery treatments were detected on days 7, 9, and 15 (Fig. 3C). Plants that were transferred from the phytotron to the greenhouse for an eight-day recovery period had Cs values similar to control vines within four days of the transfer.

Leaf temperature: T_1 values of Cardinal plants subjected to heat stress were significantly higher than control vines, whereas T_1 pattern of heat stress/recovery plants was similar to control grapevines (Fig. 4A). However, significant differences in T_1 were obtained on days 15 through 19, with temperature of heat stress/recovery leaves running higher than control leaves. For both treatments an increase in mean T_1 values was observed after day 13 of the experiment.

T_1 of Chardonnay vines exposed to heat stress was significantly higher than control plants (Fig. 4B) for the entire 13-day comparison period. Mean temperature values of heat-stressed leaves showed only small variations over the measurement period. For both temperature treatments, variation within each measuring date was small. Average T_1 of heat stress/recovery vines followed a pattern almost identical to control plants, but T_1 of heat stress/recovery plants was significantly higher than control vines on days 5 and 19.

T_1 of Chenin blanc plants subjected to heat stress, no heat stress, and heat stress/recovery varied little over time (Fig. 4C). T_1 values of plants subjected to heat stress and recovery showed significant differences from those of control vines only on day 5, whereas T_1 values of heat stress vines were significantly higher than values of control plants at all times.

Diurnal changes in T, RH, VPD, and PAR: Diurnal changes in air temperature (T), relative humidity (RH), vapor pressure deficit (VPD), and photosynthetically-active radiation (PAR) monitored between 0500 h and 2100 h for Cardinal, Chardonnay, and Chenin blanc in the greenhouse and phytotron are shown in Table 2.

Diurnal changes in stomatal conductance: Diurnal Cs values of Cardinal grapevines recorded on day 3 of the experiment showed significant differences between heat stress and control treatments at all times (Fig. 5A). Cs values of control plants increased sharply after 0600 h to reach a maximum value at 1200 h. During the late afternoon and evening, Cs decreased below that of the heat-stressed vines, reaching a minimal Cs value at 2100 h. Heat-stressed vines reached maximum Cs at 1500 h and continued to decline until 2100 h with Cs values running higher than control vines during this period.

Cs of heat-stressed Chardonnay plants reached a maximum value at 0900 h and then declined steadily throughout the remainder of the day (Fig. 4B). With the exception of the 2100 h conductance value, all other readings of heat-stressed plants were significantly lower that the control and stress/recovery vines. Cs values of control vines reached a maximum at 1500 h and then declined sharply. The stomatal response pattern of the heat stress/recovery vines was similar to the control (Fig. 5B); however, Cs of heat stress/recovery plants was

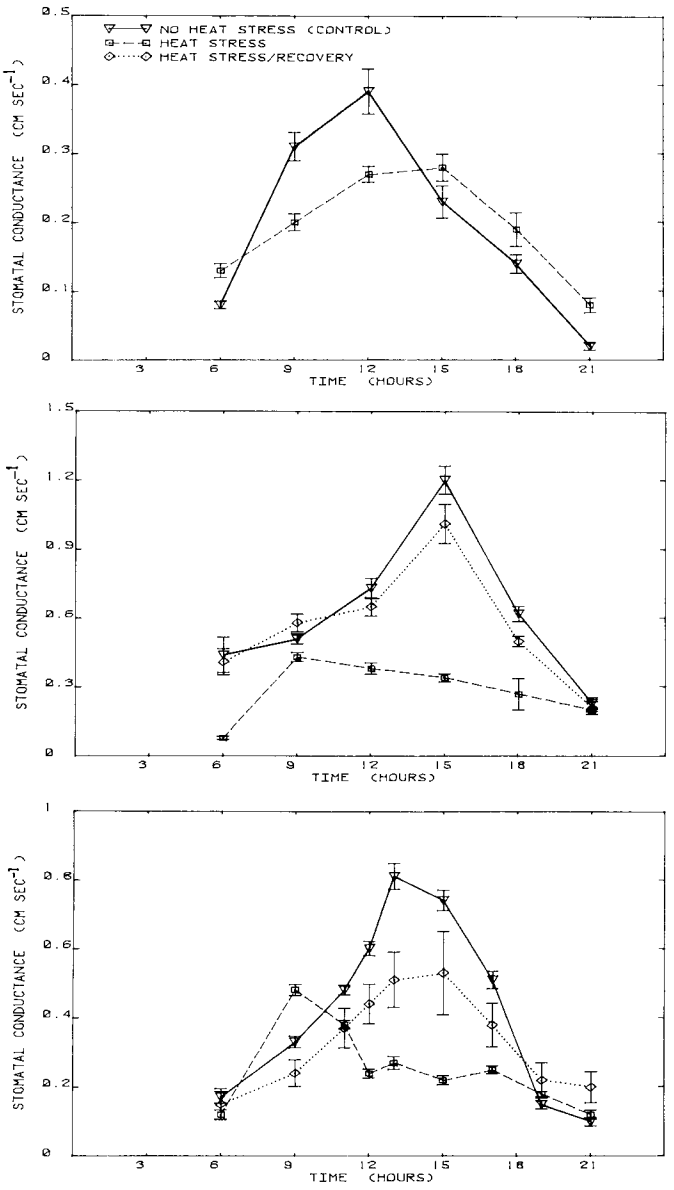

Fig. 5. Diurnal changes of stomatal conductance of Cardinal (top), Chardonnay (middle), and Chenin blanc (bottom) grapevines subjected to heat stress and heat stress/recovery. Brackets indicate ±SE.

significantly less than control plants at 1500 h and 1800 h.

Cs of Chenin blanc control plants increased sharply from 0600 h to 1300 h and then declined throughout the remainder of the afternoon and evening (Fig. 5C), whereas Cs values of heat-stressed plants increased steadily to 0900 h followed by a sharp decline until 1200 h and more slowly thereafter to a minimal value at 2100 h. Only at 0700 h and 2100 h did Cs control and heat-stressed Chenin blanc leaves not differ significantly. The heat stress/recovery Chenin blanc plants in Figure 4C were exposed to heat stress for four days before being transferred to the greenhouse, where they remained for three days before Cs determinations were made. The Cs pattern of the heat stress/recovery plants was similar to control plants, except values were consistently signifi-

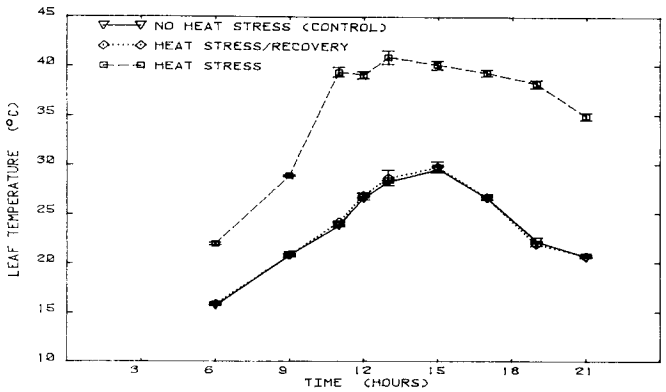

Fig. 6. Effect of heat stress and heat stress/recovery treatments on diurnal changes of leaf temperature of Chenin blanc grapevines. Brackets indicate ±SE.

cantly lower, with the exception of the 1900 h and 2100 h readings (Fig. 5C).

Diurnal changes in leaf temperature: T_l of Chenin blanc plants subjected to heat stress/recovery followed an identical pattern (no significant differences to control plants)(Fig. 6). Leaf temperatures of the other two cultivars were not determined but would be expected to follow similar patterns.

Discussion

Even though all plants in the three experiments were watered at the same time (during the early evening), vines under heat stress generally showed a lower (more negative) predawn ψ_l than the control (no heat stress); however, ψ_l values were not always significantly different (Fig. 2A, B, and C). This finding suggests an indirect effect of high temperature reducing the ability of the vines to recover from the stress condition developed during the day. This conclusion is supported by the ψ_l results of the heat stress/recovery vines, which were able to recuperate once they were put back into the greenhouse under moderate temperature conditions.

It is not known why heat stress/recovery Chenin blanc vines had lower ψ_l than heat-stressed plants. Possible factors involved could be the change in root temperature experienced by these plants when transferred to the greenhouse. The overall mean root temperatures for vines inside the phytotron and greenhouse were 27.8°C ±0.6° and 19.0°C ±2.6°, respectively. This difference of about 9°C may have been sufficient to cause a delayed stress effect which reduced the ability of roots to absorb water.

No significant correlation between the dawn ψ_l and the mid-day Cs was found in any of the three experiments. The overall average ψ_l obtained from the three experiments for each treatment (excluding extreme cases) was sufficiently high (less negative) to eliminate soil moisture as a factor influencing Cs in these experiments. Mid-day ψ_l levels were undoubtedly lower (more negative) than predawn ψ_l values, however, there was no indication that ψ_l and Cs values reached the critical level associated with stomatal closure by grapevines. ψ_l and Cs values associated with stomatal closure of grapevines are in the range of −12 to −16 bars and 0.03 to 0.04 cm sec^{-1}, respectively (15,17,27).

In each of the three experiments, stomatal response was not affected by the duration of the high temperature exposure (4, 8, and 12 days). When plants were transferred to a non-stressful environment for an eight-day recovery period, Cs values reached levels similar to control vines within one to four days, indicating that the stomatal apparatus was not permanently damaged (Fig. 3A, B, and C).

Cs values of heat-stressed plants of Chardonnay and Chenin blanc were significantly lower than control vines at all times. However, Cs values of heat-stressed Cardinal vines were higher than the control vines on some occasions. This discrepancy was probably a consequence of the day to day variation of environmental parameters influencing stomatal behavior. Consequently, stomatal response patterns presented in Figures 3A, B, and C are good examples of the complexity of the relationship existing between the factors governing stomatal action (20).

In order to interpret stomatal response to environmental factors over time, correlation and regression analyses of Cs on T_l, VPD, and PAR were determined for the three experiments using the data presented in Figures 2A, B, and C and the corresponding readings for T, RH, and PAR measured at each experimental location (data not presented).

The correlation between Cs and PAR for the duration of the experiments of all treatments was poor in Experiments 1 and 3, but slightly better in Experiment 2. However, in the three experiments a trend existed showing an increase in Cs with increase in PAR. This relationship is in agreement with other reports (7,26).

Correlation analysis of Cs versus RH and T over time showed no significant relationship existed for the three experiments, except for significant and positive Cs response of heat-stressed Cardinal vines to T. The opening of stomates at high temperature has been observed for many other plant species (2,7,21,23). The increased stomatal openings at high temperature are believed to be associated with enhanced evaporative cooling of leaves, reducing the likelihood of thermal damage to tissue (5).

An additional correlation was calculated for Chenin blanc between leaf to air vapor pressure deficit (D) as the independent variable and Cs. For calculation of D, T_l recorded at 1500 h was used even though Cs was measured three hours earlier. The average error involved in using this value were 1.1° and 1.0°C for no heat stress and heat stress/recovery treatments, respectively (*i.e.*, T_l between 1200 h and 1500 h increased on an average by that magnitude compared to the diurnal measurement taken on day 7) (Fig. 6). For the heat stress treatment there was a 0.8°C decrease in T_l between 1200 h and 1500 h.

A significant ($p < 0.05$) negative correlation coefficient ($r = 0.87$) was obtained only for Cs and D for the heat stress treatment, and can be described by the equation $Y = 0.89 - 0.59x$, where Y = Cs and x = D. This indicates that under high temperature Cs of Chenin blanc leaves decreased with an increase in D (values were between 3.3 and 4.6 kPa). In contrast, the control and

Table 3. Correlation coefficients (r) for stomatal conductance (Cs) on PAR (photosynthetically-active radiation), RH (relative humidity), T (air temperature), D (leaf to air vapor pressure deficit), T_1 (leaf temperature), and vapor pressure deficit (VPD) of diurnal measurements of Chenin blanc, Cardinal and Chardonnay grapevines.

Cultivar & experiment	Treatment	Dependent variable	Correlation coefficients (r) independent variables					
			PAR	RH	T	D	T_1	VPD
Chenin blanc, Expt. 3 Day 7	No heat stress	Cs	0.97***	−0.86**	0.82**	0.88**	0.88**	0.87**
	Heat stress	Cs	0.36	0.44	−0.11	0.05	0.09	−0.19
	Heat stress/recovery	Cs	0.97***	−0.92***	0.89**	0.87**	0.96***	0.93**
Cardinal, Expt. 1 Day 3	No heat stress	Cs	0.62	−0.81*	0.77	-	-	0.78*
	Heat stress	Cs	0.82*	0.62	0.50	-	-	0.20
Chardonnay, Expt.2 Day 13	No heat stress	Cs	0.85*	−0.23	0.81*	-	-	0.61
	Heat stress	Cs	0.62	−0.41	0.47	-	-	0.37
	Heat stress/recovery	Cs	0.82*	−0.19	0.76	-	-	0.55

*, **, *** Indicates significance of correlation coefficients (r) at 5%, 1% and 0.1% levels, respectively.

heat stress/recovery treatments showed the opposite trend, with Cs slightly increasing in response to increased D (values ranged from 0.9 to 1.9 kPa).

The drier conditions, together with the high air and leaf temperatures that existed in the phytotron compared to the greenhouse (Table 1), account for the greater D values obtained for the heat-stressed plants. These results are in agreement with the work done with apricots under desert conditions by Schulze *et al.* (22), as well as that of other workers (6,29). The negligible stomatal response to D obtained for control and heat stress/recovery treatments may be due to the lower D values as a consequence of the higher humidity and low to moderate T present in the greenhouse (Table 1) and to the lower T_1 of these plants (Fig. 4C). It is likely that under these conditions, the stomatal response is not governed by temperature and humidity, but by other feedback mechanisms controlling stomatal action, such as CO_2, water, or hormones (11,20). Work done by Warrit *et al.* (29) using apple trees, showed that Cs measured in a leaf chamber generally decreased with increasing D, regardless of temperature. However, in one of the cultivars which showed greater sensitivity to temperature, they found that the response was not consistent. In this cultivar, Cs increased with increasing D when T_1 was 17°C, decreased with increasing D when T_1 was 23° to 24°C, and remained more or less constant where T_1 was 27°C. In Experiment 3, average T_1 values for control and heat stress/recovery vines (Fig. 4C) were of about the same magnitude, *i.e.*, 27.9° and 27.6°C, respectively; thus, these results are in agreement with the findings of Warrit *et al.* (29).

Even though the three experiments were done at different periods, a comparison between Cs values among the three cultivars on a diurnal basis shows differences (Fig. 5A, B, and C). The control Chardonnay plants showed the highest Cs, followed by Chenin blanc and Cardinal. Under heat stress Chenin blanc had the highest Cs, followed by Chardonnay and Cardinal.

Diurnal Cs was correlated with T, VPD, and PAR in three experiments (Table 3). In addition, for Experiment 3, D was calculated (Table 3). In all experiments, Cs increased with increasing PAR as well as with T. However in most plants, stomata opened in response to T only up to a certain temperature threshold (which varied with each species) after which they closed (2,7,10,23). At extremely high T (*e.g.*, 40°C) Cs may decrease due directly to changes in leaf water status resulting from high transpiration rates, to increased intercellular CO_2 due to high temperature inhibition of photosynthesis, or to changes in endogenous abscisic acid levels resulting from plant water stress.

The nature of the response to humidity by the three cultivars differed depending on the temperature treatments. Stomates of plants subjected to heat stress opened in response to increased humidity, whereas Cs of control and heat stress/recovery plants decreased with increase in humidity. The increase in Cs in response to an increase in humidity is in agreement with that found in most species (6,22,26,29). However, the negative response to humidity found for control and stress/recovery vines probably was not of a direct nature but rather the result of stomatal closure in response to light; *i.e.*, low early morning and late evening light intensity apparently was the overriding factor, especially at high air humidity (7). In Experiment 3, D was directly correlated to Cs for control and heat stress/recovery treatments, but no significant correlation was found for the heat stress treatment, except when values of PAR obtained at 0600 h and 2100 h (no measurable light, Table 2C) were omitted from the correlation and regression analyses (Table 3). Then, a negative correlation between Cs and D was obtained (*i.e.*, Cs decreased with increase in D). This finding implies an overriding effect of light at sunrise and sunset on Cs and is in agreement with findings of Hall *et al.* (7).

Literature Cited

1. Drake, B. G., K. Raschke, and F. B. Salisbury. Temperatures and transpiration resistance of Xanthium leaves as affected by air temperature humidity and wind speed. Plant Physiol. 46:324-30 (1970).

2. Even-Chen, Z., S. A. Weinbaum, and R. W. Pearcy. High temperature effects on leaf resistance, leaf water potential and photosynthesis of non-bearing prune trees. J. Am. Soc. Hortic. Sci. 106(2):216-19 (1981).

3. Farquhar, G. D., and T. D. Sharkey. Stomatal conductance and photosynthesis. Ann. Rev. Plant Physiol. 33:317-45 (1982).

4. Freeman, B. M., W. M. Kliewer, and P. Stern. Influence of windbreaks and climatic region on diurnal fluctuation of leaf water potential, stomatal conductance, and leaf temperature of grapevines. Am. J. Enol. Vitic. 33(4):233-6 (1982).

5. Gates, D. M. Biophysical Ecology. pp 12-56. Springer Verlag, New York (1980).

6. Hall, A. E., and M. R. Kaufmann. Stomatal response to environment with *Sesamun indicum* L. Plant Physiol. 55:455-9 (1975).

7. Hall, A. E., E. D. Schulze, and O. L. Lange. Current perspectives of steady state stomatal response to environment. *In:* Water and Plant Life. O. L. Lange, L. Kappen, and E. D. Schulze (Eds.). Ecological Studies 19:167-88. Springer Verlag, Berlin (1976).

8. Heath, O. V. S., and H. Meidner. Effects of carbon dioxide and temperature on stomata of *Allium cepa* L. Nature 180:181-2 (1957).

9. Heath, O. V. S., and B. Orchard. Midday closure of stomata. Nature 180:180-1 (1957).

10. Hoftra, G., and J. D. Hesketh. The effect of temperature on stomatal aperture in different species. Can. J. Bot. 47:1307-10 (1969).

11. Hsiao, T. C. Plant responses to water stress. Ann. Rev. Plant Physiol. 24:519-70 (1973).

12. Kaufmann, M. R. Leaf conductance as a function of photosynthetic photo flux density and absolute humidity difference from leaf to air. Plant Physiol. 69:1018-22 (1982).

13. Kaufmann, M. R. Evaluation of season temperature, and water stress effects on stomata using a leaf conductance model. Plant Physiol. 69:1023-6 (1982).

14. Korner, C., J. A. Scheel, and H. Bauer. Maximum leaf diffusive conductance in vascular plants. Photosynthetica 13(1):45-82 (1979).

15. Kriedemann, P. E., and R. E. Smart. Effects of irradiance, temperature and leaf water potential on photosynthesis of vine leaves. Photosynthetica 5(1):6-15 (1971).

16. Kriedemann, P. E. Vineleaf photosynthesis. *In:* International Symposium on the Quality of the Vintage. pp 67-88. Oenological and Viticultural Research Institute, Stellenbosch (Ed.). South Africa (1977).

17. Liu, W. T., R. Pool, W. Wenkert, and P. E. Kriedemann. Changes in photosynthesis, stomatal resistance and abscisic acid of *Vitis labruscana* through drought and irrigation cycles. Am. J. Enol. Vitic. 29:239-46 (1978).

18. Losch, R. Responses of stomata to environmental factors. Experiments with isolated epidermal strips of *Polypodium vulgare*. Oecologia (Berlin) 29:85-97 (1977).

19. Neilson, R. E., and P. G. Jarvis. Photosynthesis in sitka spruce (*Picea sitchensis* (Bong) Car). VI. Responses of stomata to temperature. J. Appl. Ecol. 12:879-91 (1975).

20. Raschke, K. Stomatal action. Ann. Rev. Plant Physiol. 26:309-40 (1975).

21. Rogers, C., P. J. H. Sharpe, R. D. Powell, and R. D. Spencer. High-temperature disruption of guard cells of *Vicia faba*. Plant Physiol. 67:193-6 (1981).

22. Schulze, E. D., O. L. Lange, U. Buschbom, L. Kappen, and M. Evenari. Stomatal responses to changes in humidity in plants growing in the desert. Planta (Berlin) 108:259-70 (1972).

23. Schulze, E. D., O. L. Lange, M. Evenari, L. Kappen, and U. Buschbom. The role of air humidity and leaf temperature in controlling stomatal resistance of *Prunus armeniaca* L. under desert conditions. I. A simulation of the daily course of stomatal resistance. Oecologia (Berlin) 17:159-70 (1974).

24. Schulze, E. D., O. L. Lange, L. Kappen, M. Evenari, and U. Buschbom. The role of air humidity and leaf temperature in controlling stomatal resistance in *Prunus armeniaca* L. under desert conditions. II. The significance of leaf water status and internal carbon dioxide concentration. Oecologia (Berlin) 18:219-33 (1975).

25. Schulze, E. D., O. L. Lange, M. Evenari, L. Kappen, and U. Buschbom. The role of air humidity and temperature in controlling stomatal resistance of *Prunus armeniaca* L. under desert conditions. III. The effect on water use efficiency. Oecologia (Berlin) 19:303-14 (1975).

26. Sheriff, D. W. Stomatal aperture and the sensing of the environment by guard cells. Plant Cell Environ. 2:15-22 (1979).

27. Smart, R. E. Aspects of water relations of the grapevine (*Vitis vinifera* L.). Am. J. Enol. Vitic. 25:84-91 (1974).

28. Thorpe, M. R., B. Warrit, and J. J. Landsberg. Response of apple leaf stomata: A model for single leaves and a whole tree. Plant Cell Environ. 3:23-7 (1980).

29. Warrit, B., J. J. Landsberg, and M. R. Thorpe. Responses of apple leaf stomata to environmental factors. Plant Cell Environ. 3:13-22 (1980).

30. Watts, W. R. Field studies of stomatal conductance. *In:* Environmental Effects on Crop Physiology. J. J. Landsberg and C. V. Cutting (Eds.). pp 173-96. Academic Press, London (1977).

31. Winkler, A. J., J. A. Cook, W. M. Kliewer, and L. A. Lider. General Viticulture. University of California Press, Berkeley (1974).

32. Zscheile, F. P., S. M. Henderson, A. S. Leonard, L. W. Neubauer, and S. U. Sluka. A sunlight phytotron unit as a practical research tool. Hilgardia 36:493-565 (1956).