

Leaf age and salinity influence water relations of pepper leaves

By

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(Received 7 May 1979; revised 24 August 1979)

Abstract

Plant growth is reduced under saline conditions even when turgor in mature leaves is maintained by osmotic adjustment. The objective of this study was to determine if young leaves from salt-affected plants were also osmotically adjusted. Pepper plants (*Capsicum annuum* L. cv. California Wonder) were grown in several levels of solution osmotic potential and various components of the plants' water relations were measured to determine if young, rapidly growing leaves could accumulate solutes rapidly enough to maintain turgor for normal cell enlargement.

Psychrometric measurements indicated that osmotic adjustment is similar for both young and mature leaves although osmotic potential is slightly lower for young leaves. Total water potential is also lower for young leaves, particularly at dawn for the saline treatments. The result is reduced turgor under saline conditions at dawn for young but not mature leaves. This reduced turgor at dawn, and presumably low night value, is possibly a cause of reduced growth under saline conditions. No differences in leaf turgor occur at midday.

Porometer measurements indicated that young leaves at a given salinity level have a higher stomatal conductance than mature leaves, regardless of the time of day. The result of stomatal closure is a linear reduction of transpiration.

Key words: Stomatal conductance, leaf water potential, leaf osmotic potential, leaf xylem pressure potential.

Introduction

Most plants are capable of adjusting osmotically to tolerate salinity. Typically, the osmotic potential of mature plant tissue is reduced by about the potential of the saline root medium (Bernstein 1961, 1963) as it must if the plant is to survive. Total water and osmotic potential measurements of mature leaf tissue indicate that the

pressure potential (turgor) of salt-affected plants is often equal to that for nonsaline plants (*i.e.*, Hoffman and Rawlins 1971, Cerda *et al.* 1977) or even higher (*i.e.*, Boyer 1965, Kirkham *et al.* 1974) if salination is not abrupt. A typical rate of osmotic adjustment in many plants is about 0.05 to 0.10 megapascals (MPa) per day (Bernstein 1963). Under normal field conditions, this rate is sufficient to keep pace with the usual change in soil salinity.

Although most plants exhibit this mechanism to maintain turgor, growth under saline conditions is less than normal. One possible reason for reduced growth is that young, rapidly growing leaves are not able to adjust as well osmotically as mature, slowly growing leaves. Measurements of leaf water potential have typically been confined to evaluating the water status of mature leaves because, in all but seedlings, mature leaves dominate plant leaf area and thus the anticipated response of leaf water potential to the environment or changes in internal stimuli.

There is some evidence that significant changes in water status may be occurring, undetected, in young leaves. Leaf age is known to influence plant-water relations because of its influence on stomatal diffusive conductance to water vapor. Brown and Rosenberg (1970) found that immature sugarbeet leaves had smaller conductance values than older leaves when exposed to solar radiation. Furthermore, conductance decreased first in lower (older) cotton leaves when the plant was subjected to increasing water stress, and stomatal closure proceeded from the oldest to the youngest leaves (Jordan *et al.* 1975). Jordan and coworkers also reported that young leaves had consistently higher values of stomatal diffusive conductance than older leaves at any given leaf total water potential.

Leaf water potential components and osmotic adjustment may also be influenced by leaf age. The cells of

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young leaves increase in volume much more rapidly than mature tissue. Consequently, under saline conditions the rate of solute accumulation may not keep pace with the volume change, resulting in a lack of osmotic adjustment and in low turgor (Greenway and Thomas 1965). Full turgor is essential for maximum cell enlargement of growing tissue (Lockhart 1965); thus, if any plant tissue under saline conditions is not osmotically adjusted, growth would be reduced.

The purpose of this study was to determine if young leaves from salt-affected plants were also osmotically adjusted. We hypothesized that stunted growth caused by salinity might be caused at least in part by the inability of young leaves to accumulate solutes rapidly enough for osmotic adjustment, causing turgor to be insufficient for normal cell enlargement. To test this hypothesis, we grew pepper plants at several levels of solution osmotic potential while leaf total water potential and osmotic potential were measured psychrometrically, transpiration was monitored continuously, and stomatal diffusive conductance to water vapor was measured periodically.

Materials and methods

Pepper plants (*Capsicum annuum* L. cv. California Wonder) were grown in aerated water cultures in one of the sunlit, temperature-controlled growth chambers located at The Volcani Center, Bet-Dagan, Israel. Seeds, planted on 12 July 1977, were germinated in shallow trays containing vermiculite in an artificially-lit room maintained at 25°C. After one month, eight seedlings were transplanted into each of the 16 plastic pots that contained five liters of nutrient solution. At 6 weeks of age, the plants were thinned to four per pot and moved to the growth chamber.

The air temperature of the growth chamber was maintained at $26.0 \pm 1^\circ\text{C}$ during the day (0800 to 1800 h) and at $20.5 \pm 1^\circ\text{C}$ during the night (2000 to 0600 h). Two hours were allotted for the change between day and night temperatures. Relative humidity, although not controlled, remained relatively stable, varying from $75 \pm 10\%$ during the day to $85 \pm 10\%$ at night. Solar radiation, monitored within 1 km of the growth chamber, averaged 2.1 MJ/m² daily with an average midday radiation level of 0.3 MJ/m² and hour during the last two weeks of the experiment.

Four salinity treatments, replicated four times, were established in a Latin square pattern within the growth chamber when the plants were two months old. The osmotic potentials of the treatment solutions ($^L\psi_0$) were -0.04, -0.24, -0.39, and -0.54 megapascals (MPa), including the -0.04 MPa osmotic potential of the modified half-strength Hoagland nutrient solution (Ca(NO₃)₂ - 5 mmol/l, KNO₃ - 5 mmol/l, MgSO₄ - 2 mmol/l, KH₂PO₄ - 1 mmol/l, micronutrients B-0.51 mg/l, Mn²⁺ - 0.50 mg/l, Cl⁻ - 0.65 mg/l, Zn²⁺ - 0.23 mg/l, Cu²⁺ - 0.25 mg/l, Mo⁺ - 0.01 mg/l, sequestrin Fe - 20 mg/l). The

three saline treatments were initiated by adding chemically equivalent amounts of NaCl and CaCl₂ to the nutrient solution at rates of -0.05, -0.09, and -0.12 MPa per day, respectively, over a 4-day period. After salination all the solutions were replaced weekly.

Leaf water potential ($^L\psi_t$) was measured on detached leaf discs with Peltier-type double-loop thermocouple psychrometers supplied by EMCO (Trade names and company names are included for the benefit of the reader and do not imply any endorsement or preferential treatment of the product by the U.S. Department of Agriculture). Both a young (< 50 mm long) and a mature (> 100 mm long) leaf were sampled from each of the sixteen pots just after dawn (between 0515 and 0600 h) on September 20, 21, 25, and 30. Likewise, samples were taken at midday (between 1145 and 1300 h) on September 18, 19, 26, and 28. All the leaves sampled were sunlit and near the top of the plant. Each leaf disc was taken midway between the midvein and the leaf edge and midway along the leaf blade. Secondary veins were avoided, if possible. The 10-mm diameter leaf disc was immediately sealed in a Teflon psychrometer unit (Hoffman and Herkelrath 1969) and placed in a constant-temperature water bath ($25 \pm 0.01^\circ\text{C}$) within 45 min after sampling. Leaf osmotic potential ($^L\psi_0$) was measured on each sample in the same psychrometer after dipping the leaf disc in liquid nitrogen to rupture the cell membranes. Leaf pressure potential ($^L\psi_p$) was calculated as the difference between $^L\psi_t$ and $^L\psi_0$.

Leaf xylem pressure potential ($^L\psi_x$) was measured with a pressure chamber (Scholander *et al.* 1965) immediately after sampling for $^L\psi_t$ on the same mature leaf. Young leaves were too small for measurements of $^L\psi_x$.

Stomatal diffusive conductance of water vapor (c_s) was measured on the adaxial leaf surface with a Lambda diffusion porometer using a horizontal sensor (Kanemasu *et al.* 1969). A mature, sunlit leaf was measured immediately after sampling for $^L\psi_t$ from all sixteen pots. Young leaves were sampled once at dawn (September 25) and three times at midday (September 19, 26, 28).

Water uptake by the plants in each pot was replenished continuously with demineralized water by a constant-level water device (Shalhevet *et al.* 1976) during the final two weeks of the experiment. Water lost from the pot was considered as transpiration because each pot was covered with a 10-mm-thick foam board. Transpiration was read during the morning and again in the afternoon as the water lost from a one liter buret attached to each constant-level water device. Earlier in the experiment, daily water loss was replenished manually.

At harvest on 2 October, the plants were divided into leaves, stems, fruit, and roots and weighed. Leaf area was calculated as the product of $0.635 \times \text{length} \times \text{width}$. The area factor was determined by measuring five leaf tracings of various sizes from half of the experimental plants. Dry weights were measured after drying at 70°C for several days.

Results and discussion

Plant growth. – The fresh weights of the various parts of 12-week-old pepper plants, grown at four levels of $s\psi_0$ for 3 weeks prior to harvest, are summarized in Table 1. Also given are leaf area and the ratios of shoot to root and leaf to stem. As expected, as $s\psi_0$ decreased, the weight of all plant parts decreased, except for the increase in root weight at the lowest salinity level ($s\psi_0 = -0.24$ MPa). Shoot to root ratio was consistently lower for saline than for the nonsaline treatment, Janes (1968) reported similar results for pepper. The preference for root growth during soil water stress has frequently been reported (*i.e.*, Begg and Turner 1976) and is probably an adaptive mechanism for stress (Hsiao and Acevedo 1974).

Decreases in $s\psi_0$ causes proportionally larger reductions in leaf area than in leaf weight. Also leaf to stem ratio increased as osmotic stress increased because of a proportionally larger decrease in stem weight. Leaf, stem, and root water contents (89, 88, and 93%, respectively) were not influenced by $s\psi_0$. Since at harvest the initial

fruit set was just beginning to enlarge, yields cannot be extracted from these data.

Water potential. – The average values of $L\psi_t$ and $L\psi_0$, determined psychrometrically, for young and mature leaves and $L\psi_x$, determined by pressure chamber, for mature leaves are given in Table 2. Also given are the calculated values of $L\psi_p$, ($s\psi_0 - L\psi_t$), and ($s\psi_0 - L\psi_0$). Values of $L\psi_t$, $L\psi_0$, and $L\psi_x$ all decrease linearly as $s\psi_0$ decreased regardless of time of measurement or leaf age (Table 3). Linear relationships for mature leaves based on psychrometric measurements have been reported previously (*i.e.*, Hoffman and Rawlins 1971, Hoffman and Jobes 1978).

At dawn, $L\psi_0$ was consistently about 0.1 MPa lower for young than for mature leaves but the difference is not statistically significant. Values of $L\psi_0$ decreased with a slope of about 0.8 at dawn for both young and mature leaves as $s\psi_0$ decreased; if perfectly adjusted osmotically the slope would be 1.0. The decrease in $L\psi_t$ as $s\psi_0$ decreased at dawn, however, was more rapid for young

Table 1. Influence of root medium salinity ($s\psi_0$) on the fresh weights of 12-week-old pepper plants. Also reported are leaf area and the ratios of shoot to root and leaf to stem.

$s\psi_0$ MPa	Fresh weight g/plant					Leaf area dm ² /plant	Fresh weight ratio	
	Leaf	Stem	Root	Fruit	Total		Shoot/root	Leaf/stem
-0.04	67	51	77	42	237	21	2.1	1.3
-0.24	67	45	87	38	237	19	1.7	1.5
-0.39	60	35	69	24	188	16	1.7	1.7
-0.54	51	22	57	22	152	13	1.7	2.3

Table 2. Total water, osmotic, and pressure potentials ($L\psi_t$, $L\psi_0$, $L\psi_p$), xylem pressure potential ($L\psi_x$), and the difference between the medium osmotic potential ($s\psi_0$) and $L\psi_t$ or $L\psi_0$ of young and mature pepper leaves at dawn and midday under four salinity treatments. Values expressed in MPa.

Leaf age	$s\psi_0$	$L\psi_t$	$L\psi_0$	$L\psi_x$	$L\psi_p$	$s\psi_0 - L\psi_t$	$s\psi_0 - L\psi_0$
<i>Dawn</i>							
Young	-0.04	-0.65	-1.07	–	0.42	0.61	1.03
	-0.24	-0.78	-1.15	–	0.37	0.54	0.91
	-0.39	-1.00	-1.30	–	0.30	0.61	0.91
	-0.54	-1.21	-1.48	–	0.27	0.62	0.94
Mature	-0.04	-0.58	-0.93	-0.23	0.35	0.54	0.89
	-0.24	-0.74	-1.13	-0.39	0.39	0.50	0.89
	-0.39	-0.77	-1.20	-0.52	0.43	0.38	0.81
	-0.54	-0.95	-1.39	-0.82	0.44	0.36	0.85
<i>Midday</i>							
Young	-0.04	-0.89	-1.21	–	0.32	0.85	1.17
	-0.24	-1.01	-1.34	–	0.33	0.76	1.10
	-0.39	-1.25	-1.61	–	0.37	0.86	1.22
	-0.54	-1.56	-1.93	–	0.37	1.02	1.39
Mature	-0.04	-0.74	-1.19	-0.46	0.45	0.70	1.15
	-0.24	-0.96	-1.40	-0.65	0.44	0.72	1.16
	-0.39	-1.16	-1.51	-1.00	0.35	0.77	1.12
	-0.54	-1.56	-1.92	-1.22	0.36	1.02	1.38

Table 3. Coefficients and correlations of linear equations relating pepper leaf total water potential (${}^L\psi_t$), osmotic potential (${}^L\psi_o$) and xylem pressure potential (${}^L\psi_x$) to the osmotic potential of the root medium (${}^S\psi_o$) as a function of leaf age and time of day. (${}^L\psi_t$, ${}^L\psi_o$, or ${}^L\psi_x = a + b {}^S\psi_o$).

Water potential component MPa	Time of day	Leaf age	Slope b MPa	Intercept a MPa	R ²
${}^L\psi_t$	Midday	Mature	1.59	-0.62	0.951
		Young	1.34	-0.77	0.934
${}^L\psi_t$	Dawn	Mature	0.64	-0.56	0.965
		Young	1.05	-0.58	0.980
${}^L\psi_o$	Midday	Mature	1.38	-1.09	0.916
		Young	1.45	-1.09	0.939
${}^L\psi_o$	Dawn	Mature	0.81	-0.91	0.987
		Young	0.76	-1.01	0.968
${}^L\psi_x$	Midday	Mature	1.58	-0.36	0.972
${}^L\psi_x$	Dawn	Mature	1.06	-0.16	0.971

(slope of 1.0) than for mature leaves (slope of 0.6) and the differences in ${}^L\psi_t$ for the two highest salinity treatments were statistically significant. Therefore, young leaves at dawn have a lower ${}^L\psi_p$ value in the salt treatments than the control, whereas the opposite is true for mature leaves. Thus, despite a reasonable osmotic adjustment, ${}^L\psi_p$ decreased as salinity increased in young leaves. Osmotic adjustment is apparently not a sufficient condition for maintaining turgor in young leaves at dawn. The low value of ${}^L\psi_p$ in young leaves at dawn in the high salt treatment may have been the result of leaf enlargement during the night, coupled with an inability of the cells to adjust osmotically to the increased cell volume. This low ${}^L\psi_p$ value at dawn, and presumably low night value, is possibly the cause of growth reduction under saline conditions. Turgor (${}^L\psi_p$) of mature leaves at dawn increased as ${}^S\psi_o$ decreased. This may have been caused by the more rigid mature cells not changing significantly in volume during the night, resulting in a lower vacuole osmotic potential and, consequently, a higher turgor.

Midday values of ${}^L\psi_t$ and ${}^L\psi_o$ were significantly lower than those at dawn for both young and mature leaves because of endogenous rhythm. The diurnal oscillation of ${}^L\psi_t$ and ${}^L\psi_o$ was about 0.2 MPa for the nonsaline treatment and increased as ${}^S\psi_o$ decreased to about 0.3 to 0.6 MPa for the most saline treatment, higher for mature than for young leaves. Diurnal oscillations of ${}^L\psi_t$ (with amplitude as large as 1.0 MPa) are common on sunny days and, typically, ${}^L\psi_o$ oscillates with similar amplitude (Hsiao *et al.* 1976).

At midday, ${}^L\psi_o$ was essentially independent of leaf age with ${}^L\psi_o$ decreasing with a slope of 1.4 as ${}^S\psi_o$ decreased. Under nonsaline conditions young leaves had lower ${}^L\psi_t$ values than mature leaves and, consequently, a lower ${}^L\psi_p$,

whereas under saline conditions ${}^S\psi_o$ negated the effect of leaf age.

The values ${}^L\psi_t$, independent of ${}^S\psi_o$ and time of day, were significantly higher for mature leaves than for young ($P > 0.98$). Differences in ${}^L\psi_o$ because of leaf age were not significant, although mean values of ${}^L\psi_o$ for mature leaves were consistently higher than those for young leaves for all but one salinity treatment at midday.

Measurements of ${}^L\psi_x$ and ${}^L\psi_t$ are compared in Figure 1. The dashed line indicates equipotential. Values of ${}^L\psi_x$ exceeded ${}^L\psi_t$ values with the difference decreasing from more than 0.3 MPa at high values to less than 0.2 MPa at low values. West and Gaff (1971) contended that ${}^L\psi_x$ should exceed ${}^L\psi_t$ by an amount equal to the ψ_o of the xylem sap. Unfortunately, we did not measure ψ_o but values range from less than -0.1 MPa (Boyer 1967) to -0.36 MPa for apple (West and Gaff 1971) or -0.65 MPa for safflower (Sepaskhah 1977). If the difference between ${}^L\psi_x$ and ${}^L\psi_t$ is attributed to ψ_o of the xylem sap alone, then our values ranged from -0.33 MPa for the nonsaline treatment to -0.19 MPa for the two highest salinity treatments. The reason the xylem sap had a smaller concentration of solutes (higher ψ_o) in the saline treatments than in the control is not clear.

Transpiration. — The influence of ${}^S\psi_o$ on transpiration is summarized in Table 4. Data are average values for 8 days during the final 2 weeks of the experiment. Midday transpiration was measured between 0930 and 1500 h on the average. Transpiration per unit leaf area or root

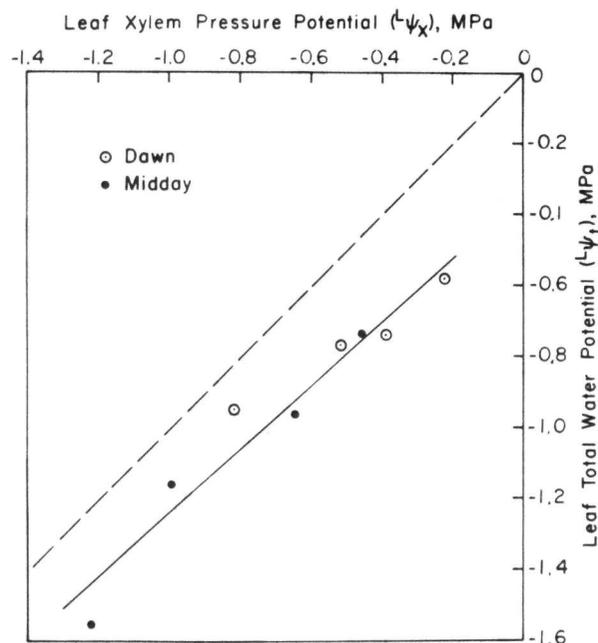


Figure 1. Comparison between xylem pressure potential measured with a pressure chamber and total water potential measured with thermocouple psychrometers. Comparisons made on the same mature pepper leaves at dawn and at midday.

Table 4. Effect of root medium salinity on the average daily and midday transpiration rates of pepper. Also given is plant conductance to water flow as a function of salinity.

$^s\psi_0$ MPa	Daily transpiration per			Midday transpiration rate per		
	plant ml plant ⁻¹	unit leaf area 1 m ⁻²	root fresh wt. 1 kg ⁻¹	plant ml plant ⁻¹	unit leaf area $\mu\text{l m}^{-2}\text{s}^{-1}$	root fresh wt. $\mu\text{l kg}^{-1}\text{s}^{-1}$
-0.04	260	1.2	3.4	28	36	100
-0.24	250	1.3	2.8	26	39	83
-0.39	170	1.1	2.5	18	31	72
-0.54	110	0.8	2.0	10	22	50

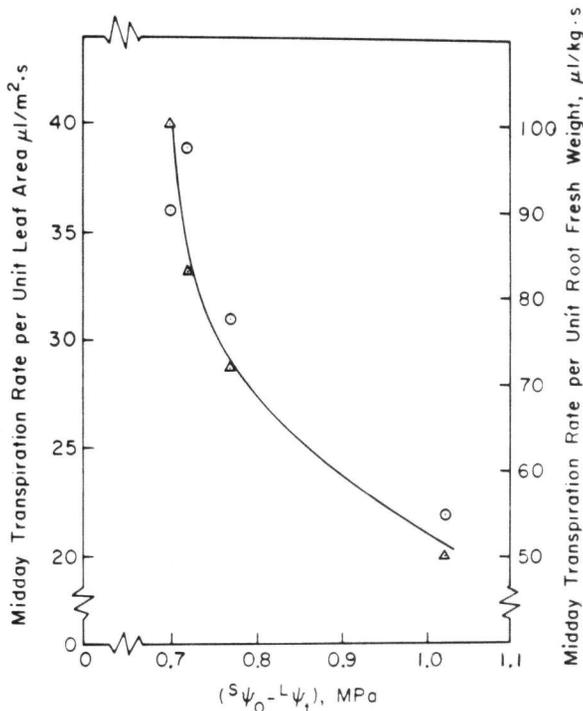


Figure 2. Midday transpiration rate per unit leaf area (circles) and per unit root fresh weight (triangles) as a function of the water potential difference between the salinated nutrient solutions ($^s\psi_0$) and mature pepper leaves ($^L\psi_t$).

weight is computed based on leaf area and root weight at harvest.

On a relative basis, transpiration was reduced more than leaf area as $^s\psi_0$ decreased below -0.24 MPa, indicating that the size of the transpiring surface is not the only factor limiting transpiration. As shown in the next section, decreasing $^s\psi_0$ below -0.24 MPa also reduces stomatal diffusive conductance to water vapor.

In contrast to the transpiration per unit leaf area, transpiration per unit root fresh weight at $^s\psi_0 = -0.24$ MPa was lower than that for the nonsaline treatment. This difference was caused by the enhancement of root growth at $^s\psi_0 = -0.24$ MPa discussed previously, showing that the absorbing area of the root may also be a limiting factor to water uptake and transpiration.

Figure 2 illustrates the relationship between the midday total potential difference between the root medium solution and mature leaves and transpiration per unit leaf area or per unit root fresh weight basis. The striking feature of the relationship is that both were negatively related with the potential difference. Generally, the relationship between flux and potential difference are explained by changes in root hydraulic conductance with changing salinity (Janes 1968). Shalhevet *et al.* (1976), however, found no change in the root conductance of tomato and sunflower under various salinity levels, using a technique which minimized changes in $^L\psi_t$ and stomatal conductance due to changes in $^s\psi_0$. Kirkham *et al.* (1969) using similar techniques obtained seemingly similar results, despite their different interpretation. Thus, the probable explanation for the negative relationship between flow and potential difference is the change in conductance of both the roots and stomata.

If the catenary theory of van den Honert holds, then the reduced transpiration should induce a proportional increase in leaf total water potential so that the potential difference between leaf and root medium will be compatible with the lower flow rate. Our measurements showed a larger difference in $^L\psi_t$ than needed for flow adjustment indicating that the measured equilibrium $^L\psi_t$ is not necessarily the driving force responsible for water movement to the transpiring surface. Under conditions of high salinity there is an increase in solute concentration of the vacuoles and a reduction in $^L\psi_0$. This reduction prevents drastic changes in leaf turgor. However, flow in the leaf takes place through cell walls where the potential difference may not depend on cell osmotic potential. The water potential measured on detached leaf discs is dependent on $^L\psi_0$ and, thus, may not represent the actual driving force responsible for transpiration. No clear evidence is available to support this speculation, but the explanation of the processes involved is cardinal to understanding plant response to salinity and deserves more attention.

Stomatal conductance. – The influence of salinity, time of day, and leaf age on stomatal diffusive conductance for water vapor (c_s) is presented in Figure 3. At dawn, leaf conductance is minimum and was lower for mature than

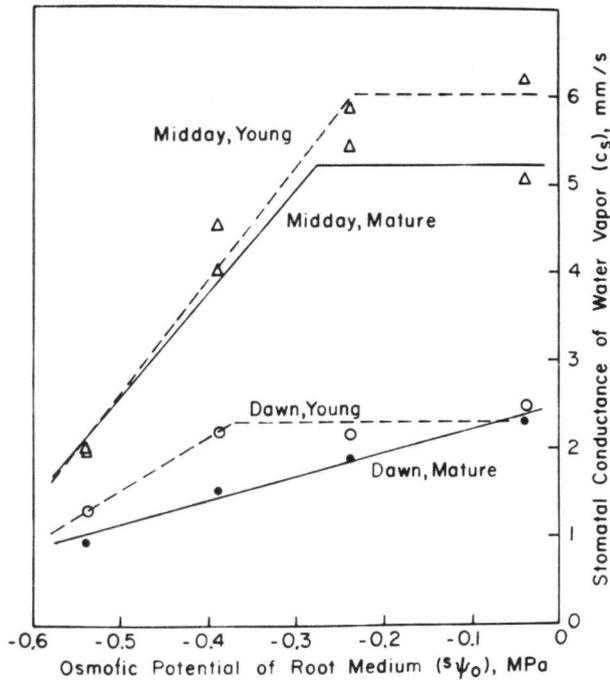


Figure 3. Influence of time of day and leaf age on the relationship between pepper leaf stomatal conductance to water vapor and the osmotic potential of the root medium.

for young leaves. For mature leaves, there was a linear reduction in c_s with decreasing $^s\psi_0$ (slope of about 2), young leaves did not show a reduction until $^s\psi_0$ was below -0.4 MPa. At midday, there was a plateau for both young and mature leaves with a threshold at about $^s\psi_0 = -0.25$ MPa. The threshold value for c_s of 5 to 6 mm/s presumably coincided with the maximum stomatal aperture for

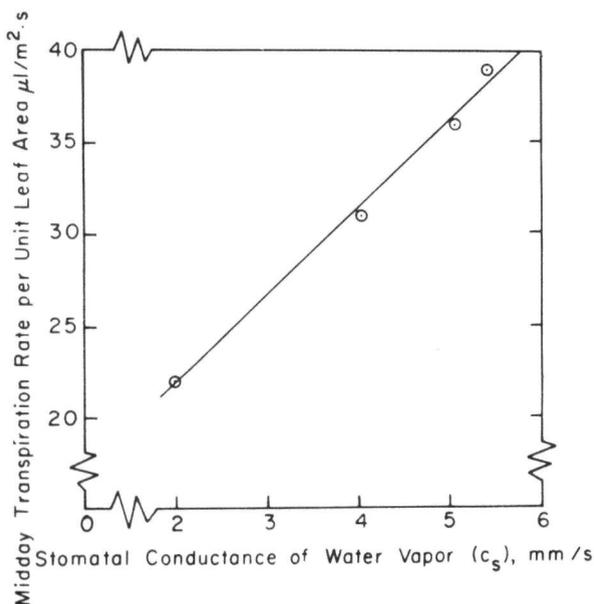


Figure 4. The effect of stomatal conductance of water vapor on the midday transpiration rate per unit leaf area for pepper under saline conditions.

the given environment. Beyond the threshold value, c_s is reduced linearly as $^s\psi_0$ decreases with a slope of about 12. As at dawn, c_s is higher for young than for mature leaves. The similarity in conductance between young and mature leaves at low $^s\psi_0$, and the much smaller diurnal oscillations show the predominance of high salinity over leaf age for c_s (Figure 3).

The increase in root medium salt concentration results in a reduction in stomatal diffusive conductance and presumably stomatal aperture. This is probably caused by a smaller osmotic adjustment in the guard cells as compared with other cells in the leaves. The result of stomatal closure is a linear reduction in transpiration (Figure 4).

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