Responses of Stomata and Water, Osmotic, and Turgor Potentials of Jojoba to Water and Salt Stress[1]

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ABSTRACT

Jojoba (*Simmondsia chinensis* (Link) Schneider) is a desert shrub which can provide a much needed substitute for sperm whale oil. Because of the absence of soil-plant-water data for jojoba and the limited amount of such information for desert plants in general, selected plants were water- and salt-stressed in greenhouse soil and sand culture experiments. Responses of leaf water, osmotic, and turgor potentials to stress and associated stomatal behavior were studied.

Leaf water potentials of well watered jojoba plants (measured with thermocouple psychrometers) averaged —20 bars in the daytime and were generally below —10 bars at night, very low in comparison to most mesophytic plants. The recovery of plants which were water stressed to leaf water potentials below —50 bars (soil water potentials below —40 bars) indicates great drought tolerance. Turgor potential decreased linearly with decreasing leaf water potential, showing a lack of osmotic adjustment as leaf water potentials fall below about —30 bars. Turgor potential reached zero at a leaf water potential of about —35 bars, and dropped as low as —10 bars under the most severe water stress without wilting of mature leaves. Plants in the salinity experiment showed osmotic adjustment down to a root medium osmotic potential of —9 bars.

Values of leaf conductance decreased markedly only at very low xylem pressure potentials (pressure chamber measurements) and soil water potentials (—40 bars and —20 bars, respectively), corresponding to about the same values at which turgor potential reached zero. Stomatal closure was continuous with increasing water stress, rather than occurring abruptly at a threshold. There was no significant decrease in leaf conductance at root medium osmotic potentials as low as —9 bars in the salinity experiment.

Conductances of well watered plants to water vapor on lower leaf surfaces were typically similar or greater in value than those of upper leaf surfaces, whereas plants under water stress showed significantly higher conductances on their upper leaf surfaces rather than lower leaf surfaces.

Leaf xylem pressure potentials decreased with increasing transpiration rate under non-limiting soil water conditions and decreased below values predicted for well watered plants at the same transpiration rate as soil water potentials decreased. Thus it was possible to make an estimate of edaphic limitations of water absorption based on leaf xylem pressure potentials despite variation in the pressure potentials in response to microclimatic changes.

Additional index words: **Conductance to water vapor, Diffusion resistance for water vapor, Soil water potential, Xylem pressure potential, Transpiration rate, Soil-plant-atmosphere continuum.**

JOJOBA [*Simmondsia chinensis* (Link) Schneider], a dioecious shrub in the Buxaceae family, is native to the dry foothills and mesas of southwestern North America. The plant is an unusual desert species because it has persistent, broad leaves, unlike those of most associated plants in the Sonoran desert. Jojoba has special interest as a possible commercial crop because the seeds contain a liquid wax which can be used as a substitute for sperm whale oil (Yermanos, 1974).

Jojoba is well adapted to drought, soil salinity, and extreme temperatures. It is native to areas where the annual rainfall ranges from 100 to 450 mm and daily temperatures can vary from 0 to 35 C, with temperatures as high as 45 C. Although the plant seems to be well adapted to drought, McGinnies and Arnold (1939) reported that jojoba has a water requirement about three times greater than perennial grasses. Gentry (1958) reported that jojoba grows best in areas with more than 30 cm of annual rainfall, but is limited ecologically to sites receiving runoff where annual rainfall is less than 12.5 cm. Yermanos et al. (1967) reported no symptoms of major salt injury at soil salinity levels as high as 13.6 mmhos/cm in the soil saturation extract.

Al-Ani et al. (1972) reported that positive apparent photosynthetic rates were measured in the field for plants with leaf water potentials (determined with the Shardakov dye method) as low as —70 bars. They suggested that populations of jojoba form ecotypes with differing adaptations to drought depending upon available moisture in their natural environments.

Because of the interest in cultivating jojoba, and uncertainties regarding jojoba's responses to drought and salinity, we undertook the present study of seedlings taken from two quite different ecosystems in southern California. The study focused upon substrate-plant potential stomatal behavior relationships.

Stomatal conductance was compared to water stress to determine if there was a continuous increase in stomatal closure with increasing stress or if closure occurred abruptly at a threshold. Comparisons were made between conductance of upper and lower leaf surfaces to contrast their response to water stress. The effect of transpiration rates on leaf xylem pressure potentials was studied to evaluate the use of leaf xylem pressure potential measurements as an indication of soil water availability.

METHODS

Water Stress Experiment

Air-dried Domino silt loam (Xerollic calciorthid: 11 kg/pot) was placed in 50 11.4-liter pots, lined with plastic bags to prevent drainage. About 0.75 g N, 0.66 g P, and 0.62 g K were added in a deionized water application to each pot. To decrease genetic heterogeneity, seedlings of jojoba originating from a single plant

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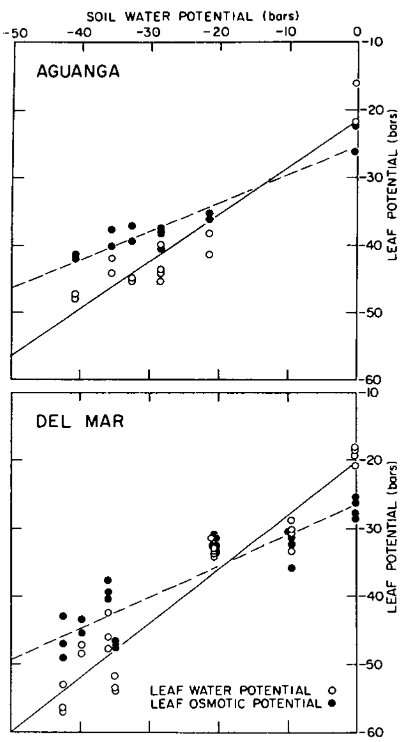

Fig. 1. Comparison between soil water potential at a depth of 15 cm and leaf water potential and leaf osmotic potential for Aguanga and Del Mar jojoba plants.

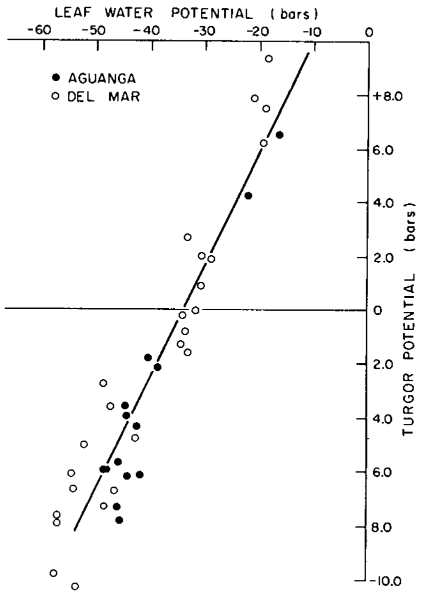

Fig. 2. Comparison between leaf water potential and turgor potential for Del Mar and Aguanga plants measured on leaf discs with Peltier-type psychrometers.

growing on the cliffs above the beach near Del Mar, Calif. and cuttings obtained from a plant growing near Aguanga, Calif., were planted singly in plots in November 1973. Pots were randomly placed in a greenhouse ventilated with charcoal-filtered air. The nighttime temperature was controlled at about 27 C, and daytime temperatures on the warmest days reached 33 to 35 C.

The Domino soil had a pH (saturated paste) of 7.5, a cation exchange capacity of 14me/100 g, and an electrical conductivity (EC_e) of the saturation extract of 0.8 mmhos/cm. The organic C content of the soil was about 1.4%. Mica and montmorillonite were the dominant layer silicates in the clay fraction. Soils were covered with about 2.5 cm of pea-size gravel to minimize evaporation of soil water. Tensiometers were placed singly in pots with their tips located about 15 cm below the surface of the soil (total depth was 20 cm).

Measurements with soil thermocouple psychrometers were begun in September 1974. Psychrometer readings were made with a Keithley 148 nanovoltmeter. The psychrometers were initially placed about 15 cm below the soil surface, but later, additional soil psychrometers were placed about 7.5 cm below the soil surface. Psychrometers were read several hours after placing pots in a darkroom to allow soil and psychrometers to reach thermal equilibrium. Plants were subjected to several cycles of water stress down to soil water potentials below —15 bars before measurements of leaf potentials and stomatal conductance were made.

Electrical conductivities of saturation extracts (EC_e), determined for soils collected at the end of the experiment in January 1975, showed that the average EC_e for soils of four well watered plants was 0.8 mmhos/cm and that for soils of eight water-stressed plants was 0.9 mmhos/cm. At water contents fivefold less than saturation, the osmotic potential (OP) of the soil would be higher (less negative) than —2 bars, since OP $\approx -0.36 \times$ mmhos/cm. Thus, the psychrometers were assumed to measure primarily matric potential.

Leaf Xylem Pressure Potential. Leaf xylem pressure potentials were measured with a Scholander pressure chamber apparatus (Scholander et al., 1965) using fully expanded, recently mature leaves. Pressure was applied within 20 sec after removal of leaves from a branch. Because no petiole was present for insertion into the sample holder of the pressure chamber, it was necessary to cut away about one-third of the base of the lamina. Sufficient material was not available to insert small branches into the pressure chamber; however, a comparison between stem tips and adjacent trimmed leaves gave a good correlation:

$$\psi\text{leaf} = 1.25\ \psi\text{stem} + 3.03,\ r = 0.99.$$

Plants with the smallest leaves had more than one-third of the lamina removed so that the lamina tip would be visible beyond the chamber sample holder. Comparisons made among leaves with one-third to two-thirds of the lamina removed showed only small differences in xylem pressure potential.

Leaf Water Potential. Leaf water potentials were determined with Peltier-type thermocouple psychrometers with a design described by Hoffman and Herkelrath (1968). Leaf water potentials for the water stress experiment were determined on 2 and 11 Dec. 1974. The average temperature and relative humidity (mean of measurements preceding and following sampling) were 27.5 C and 52% on 2 December and 27.7 C and 43% on 11 December. After the water potential measurements, leaf osmotic potentials of the same samples were measured in the same psychrometers several hours after immersing the leaf discs in liquid N to rupture the cell membranes. Turgor potential was calculated as the difference between water and osmotic potentials. All sampling was done between 1000 and 1200 hours usually using three or four leaves per plant. When leaves were sampled for determination of leaf water potentials with psychrometers, opposite leaves were removed for measurement of leaf xylem pressure potential with a pressure chamber.

Comparisons of the pressure chamber measurements with those from Peltier-type psychrometers indicated that xylem pressure potential was somewhat lower than water potential but that leaf xylem pressure potential measurements provided excellent evidence for changes in plant water stress among the treatments. The linear regression equation between leaf water potential (measured with Peltier-type psychrometers) and leaf xylem pressure potential is:

$$\psi \text{ leaf water potential} = 1.02\ (\psi \text{ leaf xylem pressure potential}) + 3.48,\ r = 0.98.$$

Such a relationship between leaf xylem pressure potential and leaf water potential has been reported in other species (Kaufmann, 1968a, b).

Leaf Resistance. Leaf resistance was measured with a diffusion porometer having a lithium chloride sensor (Elfving et al., 1972). The porometer was calibrated with five perforated plates, each having a known resistance (Kanemasu et al., 1969). The plates

Table 1. Water, osmotic, and turgor potentials of Del Mar and Aguanga jojoba leaves as a function of root medium salinity.

Osmotic potential of root medium	No. of samples	Water potential	Osmotic potential	Turgor potential
bars			bars	
		Del Mar		
−0.3	12	−18.6 a*	−26.1 a	+7.5
−2.7	12	−21.0 b	−27.0 a	+6.0
−7.6	16	−22.6 b	−28.6 b	+6.0
−8.9	13	−25.0 c	−31.3 c	+6.3
		Aguanga		
−0.2	13	−18.4 a	−27.5 a	+9.1
−1.0	7	−24.6 cd	−31.9 b	+7.3
−2.3	7	−23.7 c	−31.7 b	+7.9
−6.1	22	−27.2 d	−31.5 b	+4.3
−7.4	7	−22.7 bc	−30.6 ab	+7.8

* Means followed by the same letter in each column for Del Mar or Aguanga plants are not significantly different at the 5% level as determined by the Newman-Keuls test.

were lightly coated with silicone to prevent capillary rise of water and were placed over wet filter paper. Calibration was done at three temperatures representative of the greenhouse at the time of data collection. The porometer was recalibrated after completion of the resistance measurements.

Measurements were obtained from 27 Sept. 1974 to 26 Oct. 1974. Resistance values were determined for upper and lower surfaces of leaves. Leaf-air temperature differences were determined with thermocouples, one of which could be clamped on leaves. Relative humidity, determined with a wet and dry bulb psychrometer, was normally 40 to 60% during the daytime.

Salinity Experiment

Plants from Del Mar and Aguanga, Calif. were also used in the salt stress experiment. The Aguanga plants were seedlings originating from different parental plants than those used in the water stress experiment. One-year-old plants which had been grown outdoors were placed in a greenhouse for 2 months and then were transplanted from small pots into sand cultures in September 1973. Four salinity levels (with osmotic potentials of about —0.7, —3, —6, and —9 bars), replicated five times, were established in April 1974 by adding NaCl and $CaCl_2$ to a complete nutrient solution at a rate which decreased the osmotic potential of the nutrient solution (full strength Hoagland solution; Hoagland and Arnon, 1950) 1 bar every other day until the desired salinity level was reached. The ratio of moles of NaCl to $CaCl_2$ was 1.4 to 1.0. Each replication consisted of four porcelain containers with the walls lined with plastic and filled with about 12 kg of quartz sand. Two plants from Del Mar and two from Aguanga (one plant per container) constituted a replication. The four containers were placed on top of a tank containing 100 liters of the salt solution and were filled automatically by pump for 20 min, eight times daily.

Leaf water potential measurements were made on the Del Mar plants on 26, 27, and 29 Nov. 1974 and the Aguanga plants were sampled on 14, 15, and 16 Jan. 1975. The average temperature and relative humidities during the sampling periods were 29.4 C and 31%, and 28.3 C and 35% for the Del Mar and Aguanga plants, respectively.

RESULTS AND DISCUSSION

Daytime Comparison of Leaf Potentials and Soil Water Potentials

Figure 1 shows the decrease in leaf water and osmotic potentials (measured with Peltier-type psychrometers on detached leaf discs) as soil water potential at a 15-cm depth decreased. Soil water potentials measured at 7.5 cm typically averaged several bars higher than those at 15 cm. The heterogeneity with depth complicates correlation of soil water potential and plant response. Halvorson and Patten (1974) measured daytime pressure potentials at three field locations which ranged between —21 and —30.5 bars for well watered plants, whereas plants under the most intense water stress had values below —50 bars. These values are similar to the extremes of water potential values shown for sunny days in Fig. 1. The plants exposed to soil water potentials below —40 bars did not show any visual evidence of water stress, indicating the extreme drought tolerance of jojoba. Leaf water potentials as low as —57 bars were measured without any visual evidence of wilting. Even well watered plants had low daytime leaf water potentials which averaged —20 bars and nighttime values of leaf water potential were typically below —10 bars. No marked differences were noted between Del Mar and Aguanga plants in Fig. 1. Leaf osmotic potential decreased less rapidly than leaf water potentials as soil water potential decreased, indicating the lack of osmotic adjustment as soil water potentials approached —15 bars or less.

Figure 2 shows the relationship between leaf turgor potential and leaf water potential. No appreciable difference is apparent between Del Mar and Aguanga plants. The linear regression equation for the data is:

$$\text{turgor potential} = 0.42 \text{ leaf water potential} + 14.47 \quad (r = 0.94).$$

In contrast, turgor potential in other plants may be a markedly nonlinear function of water potential, as reported for cotton (*Gossypium hirsutum* L.) by Gardner and Ehlig (1965). For well watered plants, the turgor potential (calculated as the difference between osmotic and water potentials) for both Del Mar and Aguanga plants was about 5 to 8 bars. The turgor potentials observed in well watered plants in the water stress experiment were similar to those of plants in the salinity experiment (Table 1). These values are comparable to turgor potentials determined in leaves of some well watered mesophytic plants, which are about 5 to 9 bars (Hsiao, 1973). The turgor potential decreased as soil water potential decreased, and at a soil water potential of —15 to —20 bars, leaf turgor potential reached zero. Turgor potentials were negative when soil water potentials were below about —20 bars. When leaf water potentials decreased below approximately —35 bars, turgor potential reached values as low as —10 bars. Positive turgor potential is believed to be required for growth (Hsiao, 1973), so leaf water potentials near —35 bars (corresponds to leaf xylem pressure potential of approximately —38 bars) may be associated with severe growth depression.

There are many published reports of negative turgor potentials (Slatyer, 1960; Grieve and Hellmuth, 1970; Noy-Meir and Ginzburg, 1969), but some researchers have disputed the existence of negative turgor potentials. Gaff and Carr (1964) and Klepper (1963) argued that negative turgor potentials have been determined because of errors in measurement of leaf osmotic potentials. Gaff and Carr (1964) reported that appreciable error could result from dilution of vacuolar sap by water held by matric forces, whereas Kreeb (1965) and Walter (1963) argued

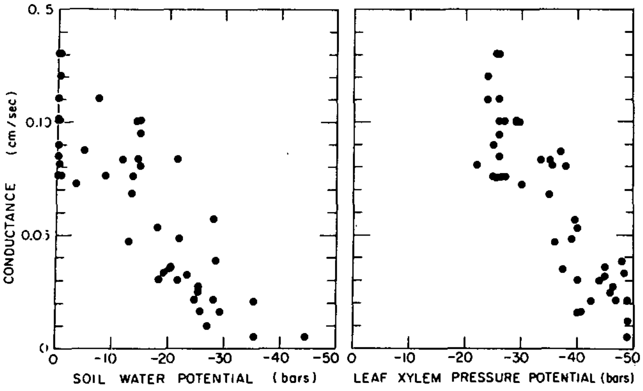

Fig. 3. Comparison of conductances with soil water potentials and leaf xylem pressure potentials. Soil potentials higher than —0.8 bar were matric potentials.

that dilution of cell sap with water from the cell walls and other free space after killing tissues would have a negligible effect. Leaves of jojoba contain secretory canals (Yermanos et al., 1967) which may produce substances causing low matric potentials. Barrs (1968) cautioned that negative turgor potentials, calculated from the difference between leaf water potentials and osmotic potentials, are not unquestionably established and that estimates of turgor potential should be made cautiously, especially when negative turgor potentials are determined.

Comparison of Leaf Potentials and Salinity Stress

The effects of salinity on water, osmotic, and turgor potentials of leaves are shown in Table 1. Standard deviations of leaf water potentials were generally larger than those for leaf osmotic potentials, as was also noted by Hoffman and Rawlins (1971) for beet (*Beta vulgaris* L.), onion (*Allium cepa* L.), and radish (*Raphanus sativus* L.). The maximum stress from salinity was much less than the severe water stress imposed in the preceding experiment. Linear regression equations for Del Mar plants are:

$$\psi\text{leaf} = -18.69 + 0.64\ (\psi\ \text{root medium}),\ r = 0.96,$$
$$\psi_o\text{leaf} = -25.70 + 0.52\ (\psi\ \text{root medium}),\ r = 0.93,$$

where ψ_{leaf} is leaf water potential, and ψ_o is leaf osmotic potential. This type of relationship has been reported for onion and beet by Hoffman and Rawlings (1971).

The data from Aguanga plants were less consistent. Linear regression equations for Aguanga plants are:

$$\psi\text{leaf} = -21.59 + 0.51\ (\psi\ \text{root medium}),\ r = 0.50,$$
$$\psi_o\text{leaf} = -29.70 + 0.22\ (\psi\ \text{root medium}),\ r = 0.41.$$

Water and osmotic potentials of Aguanga leaves decreased from the nonsaline treatment (—0.2 bars) to the lowest salinity level (—1.0 bars), but they had very similar values with further increases in salinity, except for the —6.1 bar treatment.

Turgor potential was essentially unchanged with increasing salinity for Del Mar and Aguanga plants, indicating osmotic adjustment. Plants irrigated with saline water had markedly thickened leaves, but generally did not show leaf burn symptoms. With increases in root medium salinity, there were typically small changes in leaf water potential and leaf osmotic potential. The small adjustment of leaf osmotic potential to added salinity compared to the adjustment in other species is unusual although it is consistent with the results of Yermanos et al. (1967), which suggest that jojoba is tolerant to relatively high levels of salinity.

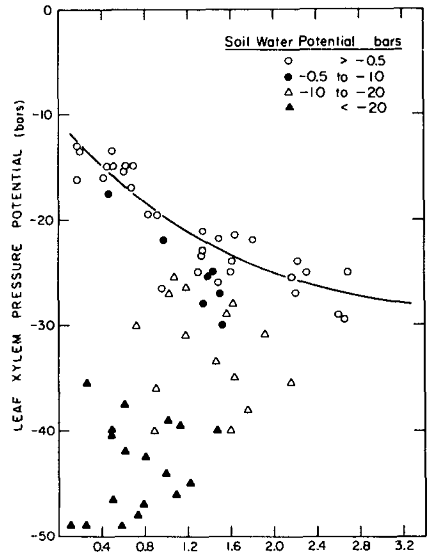

Fig. 4. Comparison of calculated transpiration rates with leaf xylem pressure potentials at various soil water potentials. Soil potentials higher than —0.8 bar were matric potentials. Line represents soil matric potentials higher than —0.5 bar.

Leaf Conductance Measurements. The highest conductance measured on a sunny day for a lower leaf surface was 0.13 cm/sec. The highest conductances calculated for both leaf surfaces in parallel were greater than 0.25 cm/sec, somewhat low in value compared to conductances reported for some other desert and mesophytic woody species (Holmgren et al., 1965; Whiteman and Koller, 1967; Bull, 1969). Adams et al. (1977) and Reyes-Manzanares[3] measured maximum conductances for lower leaf surfaces of jojoba which were as high as 0.33 and 0.25 cm/sec, respectively, but the Adams et al. (1977) measurements were made outside the greenhouse with a double isotope porometer where the illuminance was greater. Ehrler (1975) reported that the maximum conductance for jojoba plants calculated from transpiration measurements in a growth chamber was 0.12 cm/sec. The minimum conductance was 0.011 cm/sec.

Figure 3 shows a comparison of daytime conductance of the lower leaf surface with soil water potential and leaf xylem pressure potential. The graphs reveal a more or less continuous decrease in conductance with decrease in soil water and xylem pressure potentials. Marked decreases in stomatal conductance occurred when soil water potentials and xylem pressure potentials dropped to about —20 and —40 bars, respectively. This coincides approximately with the leaf water potentials and soil water potentials at which

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[3] D. Reyes-Manzanares. 1975. Effects of soil aeration and soil temperature on physiology of tomato, sunflower, and jojoba. Ph. D. Disser. Univ. of California, Riverside.

turgor potentials reached zero (Fig. 1, 2), since xylem pressure potentials were typically 3 or 4 bars lower than leaf water potentials. Negative turgor potentials were associated with incomplete stomatal closure. Adams et al. (1977) measured significant decreases in conductance to water vapor and CO_2 fixation rate below xylem pressure potentials of approximately —40 bars and soil water potentials of —20 bars. It has often been reported that stomata remain open until reaching a threshold value of leaf water deficit after which dramatic stomatal closure occurs (reviewed by Hsiao, 1973). In some cases, no threshold occurs, as noted in Fig. 3, and leaf resistance has been related more linearly to leaf water potential (Biscoe, 1972). Severe decreases in stomatal conductances were observed when soil water potential or leaf xylem pressure potentials dropped as low as —30 or —50 bars, respectively (Fig. 3). Halvorson and Patton (1974) measured xylem pressure potentials below —50 bars for jojoba plants in the field during the dry season.

The absence of indications of stress until considerable drying has occurred as well as enormously increased growth rates of irrigated jojoba plants (increases in fresh weight as great as 2,000% in 6 months for plants which were 1 year old at the start of the experiment) suggest that supplemental irrigation will greatly increase the growth rate of jojoba in arid regions, but that the amount of water applied to maintain a significantly increased growth rate may be less than that for most shrub or tree crops. The effects of differing irrigation programs on seed yield and vegetative growth rate (especially considering interactions with supply of mineral nutrients) should be investigated with field experiments.

The Del Mar plants dried the soil from —0.2 to —15 bars in an average of 8 days and reached —35 bars, approaching the lowest soil water potentials of the experiment, in about 2 more days. The Aguanga plants dried the soil to —15 and —35 bars in an average of 16 and 21 days, respectively. The variability in rate of drying may have caused some variability in the data because the relation between leaf xylem pressure potential and stomatal closure may be affected by the rate of drying (Biscoe, 1972). However, the marked difference in rate of drying caused no noticeable differences between stomatal conductance and water stress of Del Mar and Aguanga plants (the data are pooled in Fig. 3).

Conductance values at the lowest soil water potentials and xylem pressure potentials were greater than 0.02 cm/sec in many cases (Fig. 3). Nighttime conductance values were sometimes less than 0.002 cm/sec, indicating that daytime stomatal closure is incomplete under conditions of greatest water stress in this experiment. Plants subjected to the greatest water stress (shown in Fig. 3) were found to have values of conductance as high as non-stressed plants when measured the day after watering.

Stomata remain open in jojoba at leaf potentials which are far below those typically associated with stomatal closure in mesophytic plants and which would be fatal to many mesophytes. However, similar relations between stomatal closure and leaf and soil water potentials have been reported for some other desert species. For example, Van Den Driessche et al. (1971) reported that there is still significant gaseous exchange in acacia (*Acacia harpophylla* F. Muell.) at a leaf water potential of —50 bars. Wendt et al. (1968) observed that transpiration of mesquite (*Prosopis glandulosa* var. *glandulosa* (Torr.) Cockr.) was not reduced by soil matric potentials as low as —15 bars.

Table 2. Comparison of soil water potentials and upper and lower stomatal conductances.

Leaf surface	Stomatal conductance Soil above −15 bars	 Soil below −15 bars
	cm/sec	
Daytime		
Upper	0.085	0.037*
Lower	0.091	0.030*
Nighttime		
Upper	0.014	0.005
Lower	0.014	0.004

* Upper and lower leaf conductances significantly different at the 5% level.

Contrast of Conductance of Upper and Lower Leaf Surfaces. The effects of soil drying on the stomatal conductance of the upper and lower leaf surfaces were determined. When soil water potential was greater than —15 bars (most of these plants were in soils with matric potentials above —0.8 bar), the average daytime conductance for lower surfaces was 7.5% greater than for upper surfaces (Table 2). Plants in soil with water potentials below —15 bars (average was —25.5 bars) had an average daytime conductance which was 23% greater on upper surfaces than lower surfaces. At night no difference in upper and lower conductance was observed for plants under low soil water stress.

There have been reports that adaxial and abaxial leaf surfaces may differ in stomatal response to water stress (Kanemasu and Tanner, 1969; Rashke, 1970) while in other cases no differences have been reported (Sanchez-Diaz and Kramer, 1971). A higher level of conductance on the upper leaf surface has not been reported frequently and could indicate a mechanism for greater cooling on the upper surface. Jojoba leaves may be 1 mm or more thick, and appreciable temperature differences could result under high radiation loads.

Leaf Resistance Measurements in Relation to Salinity Stress. No significant difference in daytime stomatal conductance was measured in relation to root medium osmotic potentials ranging from —0.7 to —9 bars. Similar results were reported by Adams et al. (1977) using a double isotope porometer.

Comparison of Leaf Xylem Pressure Potentials with Estimated Transpiration Rates. Figure 4 shows the relationships between calculated transpiration rates and leaf xylem pressure potentials for jojoba. Calculated transpiration rates were determined by dividing vapor pressure gradient (calculated from measurement of relative humidity, leaf temperature, and air temperature) by mean leaf diffusion resistance:

$$\frac{1}{(\text{r lower surface})} + \frac{1}{(\text{r upper surface})} = \frac{1}{(\text{r mean})}$$

Evidence for citrus (Camacho et al., 1974a) and for

Engelmann spruce (*Picea engelmanni*) (M. R. Kaufmann, unpublished data) indicates that the ratio of absolute humidity gradient to leaf diffusion resistance provides a reasonable estimate of transpiration. Data were obtained during sunny days, cloudy days, and at night for well watered plants. Nighttime xylem pressure potentials were below —10 bars, even for well watered plants. Data from sunny and cloudy days are shown for the water-stressed plants. Soil matric potentials greater than —0.5 bars were used to plot a curve of the relationship with adequate soil water. As soil water potentials became lower, leaf xylem pressure potentials generally decreased below values observed for similar transpiration rates at high matric potentials. The high variability of the data in Fig. 4 probably results largely from inaccuracies in adequately characterizing soil water potential and perhaps from natural variation in leaf conductances and water potentials in unmeasured portions of the shoot. No apparent differences occurred between plants from Del Mar and Aguanga. Significant departures from the potentials predicted for well watered soil at the same transpiration rates generally occurred where soil water potentials were below —15 bars, indicating that edaphic conditions limited water uptake considerably in this range.

Elfving et al. (1972), Hinckley and Bruckerhoff (1975), and Camacho et al. (1974a, b) determined that leaf water potentials or xylem pressure potentials of several well watered woody species decreased with increasing transpiration rates, whereas Camacho et al. (1974a) reported that in three herbaceous species [sunflower (*Helianthus anuus* L. 'Mammoth Russian'); pepper (*Capsicum frutescens* L. 'Yolo Wonder'); and sesame (*Sesamum indicum* L. 'Glauca')] no such decrease in leaf water potential occurred with increasing transpiration rate. Camacho et al. (1974a) suggested that the decrease in water potentials observed in woody plants at high rates of transpiration may be due to physical limitations of plant structure.

Elfving et al. (1972) interpreted the relationship between flux and plant water potential with a submodel of the soil-plant-atmosphere continuum based on work of Huber (1924), Gradmann (1928), and van den Honert (1948). The model assumes that water flux in the soil-plant-atmosphere continuum may be described by a series of steady states. Leaf water potential was considered to be dependent on soil water potential, transpirational flux of water through the system, and resistance to flow between the soil and leaf:

$$\psi_{\text{leaf}} = \psi_{\text{soil}} - (\text{flux})\ (r_{\text{soil to leaf}}).$$

Therefore, leaf water potential will decrease as soil water potential decreases, transpiration rate increases, or resistance from soil to leaf increases. Note that the formula is not used to provide a rigorous mathematical model, but a conceptual model. Because simultaneous changes in various environmental factors often make it difficult to learn how leaf water potential is influenced by soil and atmospheric factors, the model is useful to determine edaphic conditions that limit water absorption in a natural environment where leaf water potential varies in response to climatic changes (Kaufmann and Hall, 1974).

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