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

J. A. Adams, F. T. Bingham, M. R. Kaufmann, G. J. Hoffman, and D. M. Yermanos

ABSTRACT

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 80 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 Shradakov 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...
Because no petiole was present for mature leaves. Pressure was applied within 20 sec after removal of leaves from a branch. Tensiometers were placed singly in pots with the dome facing in the direction of gravity. After the water potential measurements, leaf osmotic potentials of the same samples were measured in the same psychrometers. A good correlation was found between the two measurements. Leaf water potentials were determined with Peltier-type thermocouple psychrometers with a design described by Hoffman and Herkelrath (1968). Leaf water potentials were determined with Peltier-type psychrometers to test the hypothesis that leaf water potential is a good indicator of plant water status. Leaf water potentials were determined for Del Mar and Aguanga plants measured on 20 November 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. Leaf water potentials for Del Mar were measured at 1000 and 1200 hours usually using three leaves with one-third to two-thirds of the lamina removed showed beyond the chamber sample holder. Comparisons made among leaves with one-third to two-thirds of the lamina removed so that the lamina tip would be visible before insertion into the sample holder of the pressure chamber, it was necessary to cut away about one-third of the base of the stem tips and adjacent trimmed leaves gave a good correlation of leaf water potential. Comparisons of the pressure chamber measurements with those from Peltier-type psychrometers indicated that leaf water 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. Leaf water potentials were determined as the difference between water and osmotic potentials. All sampling was done between 1000 and 1200 hours usually using three leaves per plant. When leaves were sampled for determination of leaf water potential, leaf osmotic potential was determined with Peltier-type psychrometers and leaf xylem pressure potential was measured with a Scholander pressure chamber apparatus to measure primarily matric potential. Measurements with soil thermocouple psychrometers were begun in September 1974. Psychrometer readings were made with a Keithley 148 nanovoltmeter. The psychrometers were calibrated with five perforated plates, each having a known resistance (Kanemasu et al., 1969). The plates were made of different materials having a known resistance (Kanemasu et al., 1969). The plates were placed in the psychrometers and the resistance was measured with the Keithley 148 nanovoltmeter. The porometer was calibrated with five perforated plates, each having a lithium chloride sensor (Elfving et al., 1972). The plates were made of different materials having a known resistance (Kanemasu et al., 1969). The plates were placed in the psychrometers and the resistance was measured with the Keithley 148 nanovoltmeter. The linear regression equation between leaf water potential (measured with Peltier-type psychrometers) and leaf xylem pressure potential was: 

\[ \text{leaf} = 1.25 \times \text{stem} + 3.03, \ r = 0.99. \]

The relationship between leaf water potential and turgor pressure potential is: 

\[ \text{leaf} = 1.25 \times \text{stem} + 3.03, \ r = 0.99. \]

Leaf xylem pressure potentials were determined with a Scholander pressure chamber apparatus to measure primarily matric potential. Leaf water potential was determined as the difference between water and osmotic potentials. All sampling was done between 1000 and 1200 hours usually using three leaves per plant. When leaves were sampled for determination of leaf water potential, leaf osmotic potential was determined with Peltier-type psychrometers and leaf xylem pressure potential was measured with a Scholander pressure chamber apparatus to measure primarily matric potential. Measurements with soil thermocouple psychrometers were begun in September 1974. Psychrometer readings were made with a Keithley 148 nanovoltmeter. The psychrometers were calibrated with five perforated plates, each having a known resistance (Kanemasu et al., 1969). The plates were made of different materials having a known resistance (Kanemasu et al., 1969). The plates were placed in the psychrometers and the resistance was measured with the Keithley 148 nanovoltmeter. The porometer was calibrated with five perforated plates, each having a lithium chloride sensor (Elfving et al., 1972). The plates were made of different materials having a known resistance (Kanemasu et al., 1969). The plates were placed in the psychrometers and the resistance was measured with the Keithley 148 nanovoltmeter. The linear regression equation between leaf water potential (measured with Peltier-type psychrometers) and leaf xylem pressure potential was: 

\[ \text{leaf} = 1.25 \times \text{stem} + 3.03, \ r = 0.99. \]
TABLE

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<th>Water</th>
<th>Osmotic</th>
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<tr>
<td>1.4</td>
<td>7.0</td>
<td>-24.6</td>
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RESULTS AND DISCUSSION

Soil Water Potentials

The average daytime leaf water potential observed in well watered plants was about --0.7 bars. With the exception of a few plants, these values were similar to the extremes of water potentials which averaged --20 bars and nighttime values ranged between --21 and --30.5 bars. These values are similar to the extremes of water potentials reported for cotton (Hsiao, 1973).

Leaf water potentials as low as --35 bars were measured in the salt stress experiment (Table 1). These values are comparable to turgor potentials determined in well watered plants in the Del Mar or Aguanga locations which ranged between --21 and --30.5 bars.

Leaf water potentials near --35 bars correspond to a soil water potential of about 15 to 20 bars, leaf turgor potential reached zero. Turgor potentials were negative when soil water potentials were below about 20 bars. Nix (1970) has shown the presence of negative turgor potentials (Slatyer, 1960; Grieve and Hellmuth, 1963) but some researchers have disputed the existence of negative turgor potentials (Slatyer, 1960; Grieve and Hellmuth, 1963). However, there is general agreement that negative turgor potentials are not associated with senescing leaves or senescing tissues. Negative turgor potentials (Slatyer, 1960; Grieve and Hellmuth, 1963) have been determined because of errors in measurement of vacuolar sap by water held by matric forces, whereas Kreeb (1965) and Walter (1963) argued that negative turgor potentials have been determined because of errors in measurement of vacuolar sap by water held by matric forces, whereas Kreeb (1965) and Walter (1963) argued that negative turgor potentials have been determined because of errors in measurement of vacuolar sap by water held by matric forces.

Halvorson and Patten (1974) reported that appreciable error could result from dilution and osmotic potentials of Del Mar and Aguanga plants. The linear regression equation for the data is:

\[ \text{turgor potential} = 0.42 \times \text{leaf water potential} + 14.47 \]

The turgor potential was a markedly nonlinear function of water potential, as approached --15 bars or less. Leaf water potentials decreased less rapidly than leaf turgor potentials. Gaff and Carr (1964) and Klepper (1963) argued that negative turgor potentials have been determined because of errors in measurement of vacuolar sap by water held by matric forces, whereas Kreeb (1965) and Walter (1963) argued that negative turgor potentials have been determined because of errors in measurement of vacuolar sap by water held by matric forces.
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. Barfs (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:

\[
\text{leaf water potential} = \text{leaf osmotic potential} = -18.69 + 0.64 \times (\text{root medium})
\]

where \( \text{leaf water potential} \) is the leaf water potential, and \( \text{leaf osmotic potential} \) is the 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:

\[
\text{leaf water potential} = -21.59 + 0.51 \times (\text{root medium})
\]

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.

Lea[ 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 measured maximum conductances for lower leaf surfaces of jojoba which were as high as 3.1 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...
desert species. For example, Van Den Driessche et al. have reported water potentials for some other species which are far below those typically associated with water stress (shown in Fig. 3) were found to have significantly increased growth rates of irrigated jojoba plants (in regions, but that the amount of water applied to main soils with matric potentials above --0.8 bar), the 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 potentials and stomatal closure may be affected by the rate of drying. However, similar pressure potentials were typically 3 or 4 bars lower than that for most shrub or tree crops. The effects of differing irrigation programs on seed yield and seedling development suggest that supplemental irrigation will greatly increase the growth rate of jojoba in arid regions. There have been reports that adaxial and abaxial stomata remain open during periods of drought and that they may be related more linearly to leaf water potential (Biscoe, 1972). Severe decreases in stomatal conductances were observed for plants under low soil water potentials (Kanemasu and Tanner, 1969; Rashke, 1970). The absence of indications of stress until considerable decreases in stomatal conductance to water vapor and CO2 fixation rate occur, as noted in Fig. 3, and leaf resistance has been viewed by Hsiao, 1973). In some cases, no threshold point occurs, as noted in Fig. 3, and leaf resistance has been viewed by Hsiao, 1973). In some cases, no threshold point for daytime stomatal closure is reached until reaching a threshold value of leaf water deficit has often been reported that stomata remain open below xylem pressure potentials of approximately --15 bars in an average of 8 days and reached --35 bars for jojoba plants in the field during the dry season. Estimated Transpiration Rates. Similar results were reported by Adams et al. (1977) using a double isotope porometer. Estimated Transpiration Rates. 

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

<table>
<thead>
<tr>
<th>Soil Water Potential</th>
<th>Upper Leaf Conductance</th>
<th>Lower Leaf Conductance</th>
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<tr>
<td>Soil above --15 bars</td>
<td>0.014</td>
<td>0.003</td>
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<tr>
<td>Soil below --15 bars</td>
<td>0.085</td>
<td>0.037*</td>
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* Upper and lower leaf conductances significantly different at the 5% level.
Engelmarm 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.

ElEving 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 annuus 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.

ElEving 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:

\[ \text{leaf} = \text{soil} - \text{(flux)} \times (\text{r}_{\text{soil to leaf}}) \]

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).