

STUDENT AWARD PAPER

DIURNAL TRENDS IN WATER STATUS, TRANSPIRATION, AND PHOTOSYNTHESIS OF SALT CEDAR

by

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ABSTRACT

Relative water content (RWC), water potential (Ψ), and gas exchange were measured on saltcedar at the Bernardo, New Mexico, lysimeter site. RWC and Ψ were closely correlated; but, water potential measurements, taken with a pressure bomb, were more convenient and reliable. RWC and Ψ decreased sharply from sunup until about 0900, when minimum values of about -26 bars Ψ or 80% RWC were reached. Water status then remained constant or improved slightly through late afternoon. Transpiration rates typically remained high until about noon and then began a steady, gradual decrease that continued throughout the afternoon. The data suggest that water stress may be a factor in initiating stomatal closure; however, transpiration continued to decline despite a constant or improved leaf water status. Maximum net photosynthetic rates occurred by 0900, and depressions throughout the remainder of the day were largely accounted for by increased leaf temperatures. Afternoon depressions in transpiration and photosynthesis occurred in twigs held at constant temperature and relative humidity, suggesting that a diurnal rhythm may be involved in control of gas exchange. Water status of plants growing on the lysimeters was comparable to that of plants in adjacent natural stands; gas exchange rates were slightly higher for the lysimeter-grown plants.

INTRODUCTION

Saltcedar (*Tamarix chinensis* Lour.) is an introduced tree or shrub that covers over 1.3 million acres along the permanent and transient waterways of the southwestern United States. It is of economic concern because of its high consumptive water use, which is estimated to be over five million acre-feet per year (Robinson, 1965). Saltcedars are hydrohalophytic; their roots extend to the ground water table and they are able to tolerate a wide range of soil salinities (Waisel, 1972).

Studies conducted during June, 1975, at the Bernardo, New Mexico, lysimeter site indicated that, under typical summer conditions, a significant afternoon depression of transpiration and photosynthesis occurred. Transpiration depression could result from a direct effect of high temperatures or low relative humidity on the stomatal mechanism (Lange, et al., 1971; Schulze, et al., 1973), or from water stress imposed by the transpirational demand. The present study was undertaken to assess diurnal trends in the water status of saltcedar, to determine if depressions of transpiration and photosynthesis occurred in twigs held at constant temperature and relative humidity, and to determine if changes in transpiration and photosynthesis were correlated with changes in water status. In addition, water status and gas exchange of plants growing on and off the Bernardo lysimeters was compared to ascertain that saltcedar stands on the lysimeters were not atypical.

METHODS

Relative water content (RWC) (Slatyer and Barrs, 1965) was measured on 7 cm saltcedar cuttings that were made with a sharp razor blade and immediately weighed on a Mettler balance to determine fresh weight (FW). The cuttings were placed in 25 ml beakers that contained 5 ml distilled water to which a non-ionic surfactant (Triton X-100) was added (0.1 ml surfactant/100 ml water) to overcome surface tension effects. The twigs were propped against the sides of the beakers to insure that only the cut surface would be immersed. The beakers were set in a tray filled to a depth of 8 mm with water. The tray had a close fitting cover and served as a humidity chamber. Cuttings were allowed to saturate at room temperature in subdued light for two hours and were then removed and blotted with tissue to remove external water. Care was taken to avoid contact between the cut surface and the tissue. Following visual inspection to insure that there was no externally adhering water, saturated weight (SW) was determined. Samples were then dried in an oven for 12 hours at 100°C. Dry weights (DW)

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were determined, and RWC calculated according to the formula:

$$RWC = \frac{FW - DW}{SW - DW} \times 100$$

Plant water potential was measured on excised twigs using the Scholander pressure bomb method (Waring and Cleary, 1967).

The methods for measuring transpiration and photosynthesis are described in a companion paper in this volume (Anderson, 1977).

RESULTS AND DISCUSSION

MEASUREMENT OF PLANT WATER STATUS

Relative water content has proven to be a sensitive, reliable, and convenient means for studying plant water status, and has been used successfully with whole leaves (Anderson and McNaughton, 1973), leaf discs (Slatyer and Barrs, 1965), and conifer needles (Hellkvist, 1973). Because water potential measurements may be less sensitive to small changes in water status when plants are well supplied with water (Slatyer, 1967), we thought the technique might detect small changes in the water status of saltcedar that would not be detected by other methods.

In initial attempts to determine RWC of saltcedar, as much as 40% of the sampled twigs failed to saturate. We considered cutting the stems under water as suggested by Decker and Wien (1960) to avoid introduction of air into the xylem; however, the overlapping nature of the scale-like leaves, which tends to trap a lot of water, and the possibility of hydrating the surface salt crystals, seemed to preclude immersing the twigs. Addition of the surfactant to the solutions improved saturation to near 100% with not more than one twig in a sample of 12 failing to saturate. Twigs that did not gain weight in the saturation chamber were eliminated from the sample.

Saturation curves showed a rapid uptake of water during the first hour with minimal changes over the next two hours. Results within the first three hours were consistent with the water uptake curves of Slatyer and Barrs (1965). There was no significant difference between 2- and 3-hour saturation weights ($t = 0.38$; $P > 0.5$), and a 2-hour saturation time was selected for convenience.

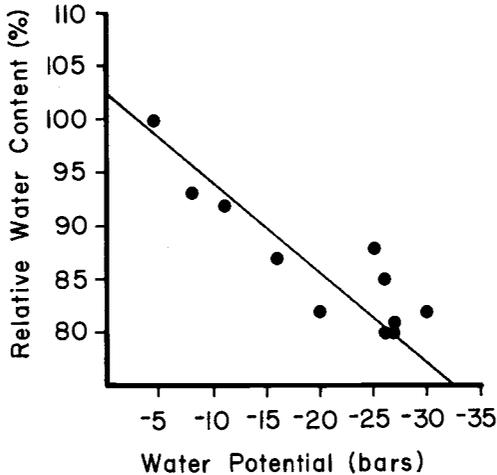


Figure 1. Relationship between relative water content and water potential for saltcedar twigs. Each point is the mean of 10-12 RWC determinations paired with the mean of several water potential determinations taken in the same stand at the same time of day.

Twig saturation times greater than three hours frequently resulted in significant losses in leaf weight, indicating that twigs were losing water in the saturation chambers. We suspected that weight losses beyond three hours might result from changes in the osmotic balance of the saturating solution due to movement of the solutes from the

leaves or leaf surfaces into the medium. However, samples returned to the laboratory and tested with a conductance bridge, a refractometer, and a chloridometer failed to reveal any consistent osmotic changes that would explain the water loss. Thus, the explanation of the weight losses with longer saturation times remains unknown.

RWC values were closely correlated with water potential (Figure 1), suggesting that RWC would provide a valid indication of water status in saltcedar. Despite the care taken in handling samples, however, within sample variability of RWC determinations was quite high. Of 46 samples of 12 twigs each, two-thirds had standard deviations of the mean RWC values of 3 or less. Standard deviations of the remaining samples was greater than 3, with a few as high as 6.7. Because of the sample variability, RWC was less sensitive to small changes in water status than the pressure bomb technique. Systematic errors were also apparent when RWC data were collected by different investigators. In order to achieve reliable and consistent estimates, all RWC determinations had to be made by the same person. In addition to the difficulties encountered, the RWC technique proved to be tedious and very time consuming. Therefore, the technique cannot be recommended for saltcedar studies. In contrast, pressure bomb data could be collected and interpreted very quickly, and the water potential data appeared to be more reliable. Minimum water potential values of -25 to -30 bars are very low for plants with an adequate water supply, however, and these values are about 10 bars lower than pressure bomb values for the same saltcedar stand at comparable times determined with a different instrument (D. Davenport, personal communication). Thus, we suspect that there may have been a systematic error in our pressure bomb data. This question will be resolved by further study, but it should not affect the general patterns and interpretations which follow.

DIURNAL WATER STATUS AND GAS EXCHANGE PATTERNS

Diurnal patterns of twig water potential, net photosynthesis, and transpiration are shown in Figure 2. Within one-half hour after sunup, water potential decreased from near zero to -17 bars. This decrease continued until about 0900 at which time near minimum water potential values of about -26 bars were observed. Diurnal curves

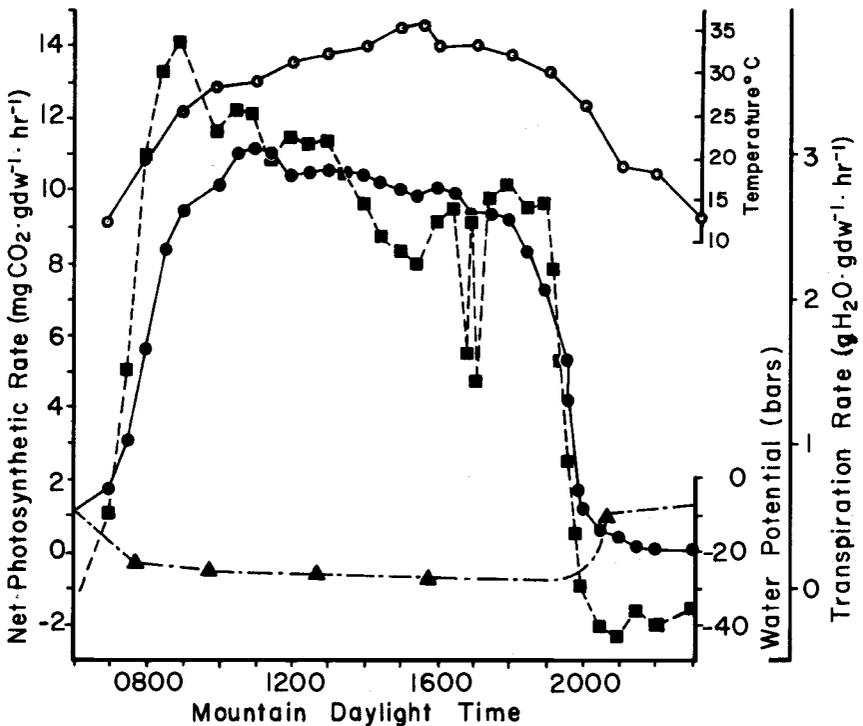


Figure 2. Diurnal patterns of air temperature (○) and transpiration (●), net photosynthesis (■), and twig water potential (▲) for saltcedar on a lysimeter at Bernardo, New Mexico, June 10-11, 1976.

for RWC are similar, with minimum values near 80%. After reaching these minimal values, water potential and RWC usually varied little (± 4 bars; $\pm 2\%$ RWC) throughout the remainder of the day. Water status improved rapidly after sunset, and full turgidity was reached between midnight and 0500. Although the water potential data shown in Figure 2 indicate a slight decline from 0930 to 2000, the actual mean values do not differ significantly. Data for several other days indicate that water status tends to remain constant or even improve slightly during the afternoon (see Figure 3).

Transpiration increased rapidly following sunup, presumably because of stomatal opening, and then continued to increase as air temperature increased until about 1030. Although air temperature continued to increase after 1030, transpiration leveled off and then gradually decreased throughout the remainder of the day, dropping sharply at dusk. Using an energy budget analysis, Gay, *et al.* (1976) reported that transpiration from saltcedars fell below potential values during the afternoon, and they attributed this decline to increased canopy resistance. In separate experiments (Anderson, 1977), we found that stomatal resistance increased linearly with temperature. This would contribute to the decline in transpiration observed (Figure 2).

Photosynthesis reached its maximum by 0900, while air temperatures were relatively cool (Figure 2). Separate experiments showed that the optimum photosynthetic temperature was 23-28°C and that photosynthesis was typically reduced by about 20% at leaf temperatures of 35°C (Anderson, 1977). Thus, the decline in net photosynthesis after 0900 can largely be accounted for by increases in air temperature. The maximum midday depression of photosynthesis correlates closely with the highest air temperature, and the recovery of photosynthetic rates after 1530 corresponds to decreases in ambient temperature. The two sharp depressions in photosynthesis between 1630 and 1700 were caused by passing cumulus clouds that decreased light intensity about 66%.

CONSTANT TEMPERATURE AND RELATIVE HUMIDITY EXPERIMENTS

In an effort to determine if afternoon depressions of gas exchange were caused only by the effects of temperature and/or the leaf-air humidity gradient, experiments

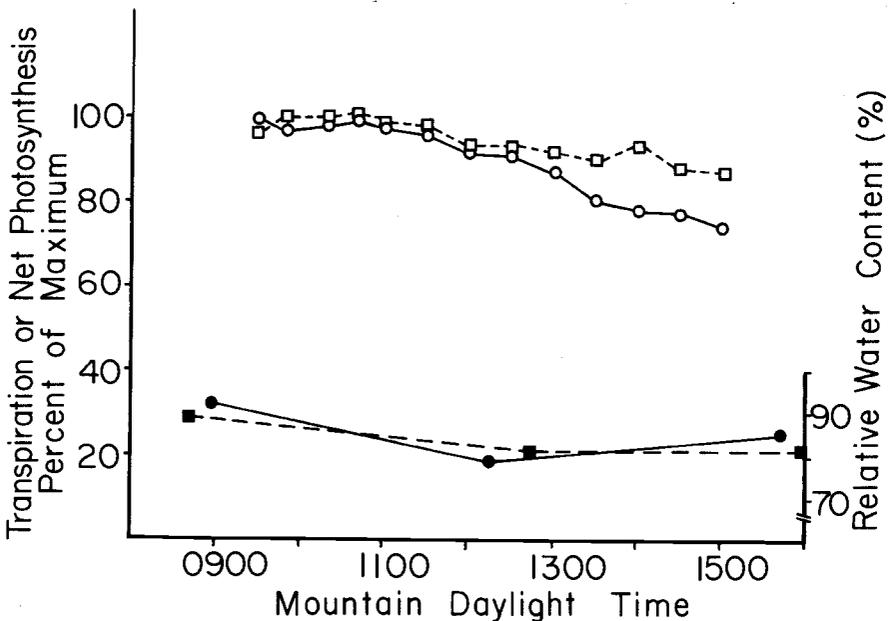


Figure 3. Upper curves: Transpiration (○) and net photosynthesis (□), expressed as percentages of the maximum rates observed, for a saltcedar twig held at constant temperature (30°C) and relative humidity (45%). The plant was growing on lysimeter no. 5.

Lower curves: Relative water content for plants growing on lysimeter no. 5 (●) and in an adjacent natural stand (■). All data were taken on June 8, 1976.

were conducted with those factors held constant. Afternoon depressions occurred in twigs maintained at 30°C and 45% relative humidity (Figure 3). Therefore, increased diffusive resistance during the afternoons does not result entirely from temperature or humidity effects. Water stress may be a factor in initiating stomatal closure; but, while water status remains constant or improves slightly, transpiration and photosynthesis continue to decline. If stomatal resistance was regulated primarily by the water status of the plant, one would expect transpiration to reach a steady state, or to increase with improved leaf water status, under constant environmental conditions. This is clearly not the case. On one occasion when the sky remained overcast until 1130 and air temperatures remained below 30°C throughout the afternoon, depressions that were practically identical to those shown in Figure 3 occurred. Under those conditions, it is unlikely that much water stress developed; yet, the typical transpiration decline was evident by early afternoon. These observations indicate that afternoon depressions in gas exchange cannot be totally accounted for by water stress, temperature, or relative humidity. It is possible that the rates might be depressed by a diurnal rhythm in stomatal resistance, but the reasons for such a rhythm are not at all obvious. At Bernardo, saltcedars growing both on and off the lysimeters are well supplied with water from a 1.5 m water table.

ON-OFF LYSIMETER COMPARISONS

Water status, transpiration rates, and net photosynthetic rates for saltcedars growing on the lysimeters were compared to the same parameters for plants growing off, but in the immediate vicinity. No significant differences in water status were observed (Figure 3). Transpiration rates for plants on lysimeter no. 5 (3.3 g H₂O g dry weight leaf⁻¹ h⁻¹) were significantly ($t = 3.1$ with 10 d.f.; $P < 0.02$) higher than rates for plants in the immediate vicinity (2.6 g H₂O g dry weight leaf⁻¹ h⁻¹). Similarly, photosynthesis for lysimeter-grown plants (14.3 mg CO₂ g dry weight leaf⁻¹ h⁻¹) was significantly ($t = 3.3$ with 10 d.f.; $P < 0.01$) higher than for plants growing off the lysimeter (11.2 mg CO₂ g dry weight leaf⁻¹ h⁻¹). Rates for plants growing on lysimeter no. 6 were very similar to those for off-lysimeter plants. The reasons for these differences are not apparent, but the differences are not large and it seems safe to conclude that the saltcedar stands on lysimeters 5 and 6 are quite typical of natural stands in the vicinity.

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