

Effects of manipulation of water and nitrogen regime on the water relations of the desert shrub *Larrea tridentata*

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Summary. Water and nitrogen regimes of *Larrea tridentata* shrubs growing in the field were manipulated during an annual cycle. Patterns of leaf water status, leaf water relations characteristics, and stomatal behavior were followed concurrently. Large variations in leaf water status in both irrigated and nonirrigated individuals were observed. Pre-dawn and midday leaf water potentials of nonirrigated shrubs were lowest except when measurements had been preceded by significant rainfall. Despite the large seasonal variation in leaf water status, reasonably constant, high levels of turgor were maintained. Pressure-volume curve analysis suggested that changes in the bulk leaf osmotic potential at full turgor were small and that nearly all of the turgor adjustment was due to tissue elastic adjustment. The increase in tissue elasticity with increasing water deficit manifested itself as a decrease in the relative water content at zero turgor and as a decrease in the tissue bulk elastic modulus. Because of large hydration-induced displacement in the osmotic potential and relative water content at zero turgor, it was necessary to use shoots in their natural state of hydration for pressure-volume curve determinations. Large diurnal and seasonal differences in maximum stomatal conductance were observed, but could not easily be attributed to variations in leaf water potential or leaf water relations characteristics such as the turgor loss point. The single factor which seemed to account for most of the diurnal and seasonal differences in maximum stomatal conductance between individual shrubs was an index of soil/root/shoot hydraulic resistance. Daily maximum stomatal conductance was found to decrease with increasing soil/root/shoot hydraulic resistance. This pattern was most consistent if the hydraulic resistance calculation was based on an estimate of total canopy transpiration rather than the more commonly used transpiration per unit leaf area. The reasons for this are discussed. It is suggested that while stomatal aperture necessarily represents a major physical resistance controlling transpiration, plant hydraulic resistance may represent the functional resistance through its effects on stomatal aperture.

Key words: *Larrea tridentata* – Water relations – Nitrogen fertilization – Stomata – Canopy transpiration

Since the introduction of the pressure-volume technique (Scholander et al. 1964), there have been numerous studies of changes in leaf water relations characteristics in plants subjected to drought. Many desert species exhibit a large degree of turgor maintenance through variations in the bulk leaf osmotic potential at which turgor loss occurs (Kappen et al. 1975; Nilsen et al. 1983, 1984). Turgor maintenance may occur via true osmotic adjustment in the form of a net accumulation of solutes per cell, a change in tissue elastic properties, or both (Tyree and Jarvis 1982). Recently, there have been efforts to partition turgor maintenance responses between their osmotic and elastic components (Pavlik 1984; Kikuta and Richter, 1986). In studies carried out under controlled conditions, changes in leaf osmotic and elastic properties can often be directly attributed to the water stress imposed (Cutler et al. 1980; Davies and Lakso 1979; Sobrado 1986). However, under natural conditions in the field, the influence of seasonal and intrinsic phenological factors may make it difficult to attribute changes in leaf water relations characteristics entirely to variations in plant water status (Monson and Smith 1982; Parker et al. 1982; Roberts et al. 1980).

Stomatal closure in a number of species subjected to declining soil moisture has been reported to occur at a threshold level of bulk leaf water potential (Hinckley et al. 1980; Parker et al. 1982; Syvertsen 1982; Turner et al. 1978). In some of these species it has been suggested that during acclimation to drought, observed drops in the water potential threshold for stomatal closure are related to a lowering of the leaf osmotic potential at the turgor loss point. More recently, however, stomatal conductance in a variety of woody and herbaceous species has been shown to be independent of short-term variations in bulk leaf water status and more closely associated with variations in soil and/or root water status (Bates and Hall 1981; Gollan et al. 1985; Kupperts 1984; Schulze 1986).

Larrea tridentata (DC.) Cov. (creosote bush) is an evergreen xerophytic shrub abundant in warm desert regions of the southwestern United States and Mexico. Its extreme drought-hardiness is exemplified by its ability to remain metabolically active and produce new leaves and shoots even under extremely dry conditions (Oechel et al. 1972; Sharifi et al. 1987). This can be partially attributed to its ability to maintain positive net photosynthesis at plant

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water potentials as low as -8 MPa (Odening et al. 1974) and to its ability to maintain fairly constant leaf turgor over a wide range of water potential (Meinzer et al. 1986).

In the present study, water and nitrogen regimes of *L. tridentata* shrubs growing under natural conditions in the field were manipulated in order to explore some of the factors responsible for control of stomatal opening in individuals subjected to different levels of soil drought. Of particular interest was the relative importance of factors such as bulk leaf water status, turgor, leaf water relations characteristics, and apparent soil or root water status in determining diurnal and seasonal patterns of stomatal behavior in droughted plants.

Materials and methods

The study site was a sandy wash woodland located in Living Desert Reserve near Palm Desert, California ($33^{\circ}44'$ N, $116^{\circ}23'$ W, elevation 60 m). Most of the 149 mm average annual precipitation is of frontal origin and falls between December and March. Late summer precipitation (July through September) occurs as localized thunderstorms and is highly variable from year to year. The average July maximum temperature exceeds 40° C and summer maximum temperatures $>47^{\circ}$ C are not uncommon.

Nine adult individuals were marked at the beginning of 1984 and three individuals were randomly assigned to each of the following treatments: 1) no irrigation, 2) irrigation only, 3) irrigation plus nitrogen added to the soil. Two 180° spray Microjet sprinklers per shrub wetted a 2 m radius under each shrub. In-line flow meters monitored delivery rates. Irrigation was applied to achieve field capacity in the upper 2 m of soil. Attainment of field capacity was assessed by monitoring one neutron probe access tube installed 1 m from the main stem of each plant. Irrigation was applied once a month from April through November 1984 and March through October 1985. For the added soil nitrogen treatment, NH_4NO_3 was applied to a 4 m diameter circle around each plant at a rate of 5 g N m^{-2} after the April 1984 and 1985 irrigations. An additional 2.5 g N m^{-2} was applied after the September 1984 and 1985 irrigations.

Predawn and midday leaf water potentials (ψ_L) were measured in the field with a pressure chamber (PMS Instrument Corp., Corvallis, Oregon) every 4–6 weeks. Two branches from each individual were excised into plastic bags which were rapidly sealed and held briefly in a darkened insulated box to minimize transpiration after excision and during the subsequent pressure chamber measurement (Turner and Long 1980). Immediately following predawn ψ_L measurements, an additional set of branch samples was excised for determination of leaf water relations characteristics by the pressure-volume method. Since hydration of cut shoots has been shown to cause large changes in the water relations characteristics of *Larrea* leaves (Meinzer et al. 1986), the samples were sealed in several layers of plastic and were not subjected to any hydration treatment. Pressure-volume curves were determined for these non-hydrated shoots in the laboratory the following day as described previously (Meinzer et al. 1986). For calculation of relative water content (RWC), turgid weights ($\text{RWC}=1$) of non-hydrated shoots were estimated by multiplying their dry weight by the turgid/dry weight ratio for parallel samples cut from the same individual on the same date and subjected to hydration (Meinzer et al. 1986). On some occasions pres-

sure-volume curves were also determined for fully hydrated samples. Pressure-volume curve data were not collected for individuals subjected to the irrigation plus soil nitrogen treatment.

On selected dates daily courses of ψ_L and leaf conductance (g) were monitored for two individuals from each of the three treatments (six individuals). Three branches were excised from each individual for each ψ_L determination. Leaf conductance measurements were made with a steady-state porometer (LI-1600, LICOR, Inc., Lincoln, Nebraska). Four samples, each oriented toward a different compass direction (N,S,E,W) were selected and labeled for each individual the previous day. A single set of 24 samples (8 per treatment) was thus used to characterize a given daily course of g. The samples consisting of 2–3 leaves each were excised at the end of the day and brought to the laboratory for area determination with an area meter (LI-3100, LICOR). To obtain transpiration rates, ambient vapor pressure was estimated by measuring relative humidity and temperature with the porometer chamber held open next to the foliage. Leaf-to-air vapor pressure difference (VPD) was obtained by subtracting ambient vapor pressure from saturation vapor pressure at the leaf temperature in the porometer chamber. For calculation of transpiration rates on a whole plant basis, total canopy area of each individual was estimated on a regular basis throughout the experiment (Sharifi et al. 1987).

Results

Throughout most of the experimental period, predawn and midday ψ_L was lower in nonirrigated individuals than in individuals receiving irrigation or irrigation plus soil N (Fig. 1). The maximum difference in predawn ψ_L between irrigated and nonirrigated individuals was 0.85 MPa during July, 1984. Predawn ψ_L of individuals receiving irrigation plus soil N was not significantly different from that of individuals irrigation only. These data are not shown in Fig. 1 because the symbols would be largely superimposed on those of irrigation treatment. At midday, however, the irrigation plus soil N plants always had a slightly to moderately lower ψ_L than the irrigated plants. The large seasonal fluctuations in ψ_L even in irrigated individuals were due to a combination of relatively long intervals between irrigations (1 month), large seasonal changes in evaporative demand, and heavy precipitation which occurred during August and December 1984. Differences in ψ_L between irrigated and nonirrigated individuals tended to diminish either after a significant precipitation event or at the end of an irrigation cycle just prior to a new irrigation.

Bulk leaf osmotic potential at zero turgor (ψ_{π}^z) was highly correlated with predawn ψ_L in both nonirrigated and irrigated *Larrea* shrubs (Fig. 2). If a threshold for zero turgor is defined as a 1:1 relationship between ψ_{π}^z and predawn ψ_L , then predawn turgor can be estimated from the distance between this 1:1 line and the measured relationship between ψ_{π}^z and predawn ψ_L . Thus it can be seen in Fig. 2 that high levels of predawn turgor were maintained over the large range of ψ_L observed during the experimental period. The decline in bulk leaf osmotic potential at full turgor (ψ_{π}^{100}) with declining predawn ψ_L was relatively small (Fig. 2) as were changes in total symplast solute content (data not shown). However, while ψ_{π}^{100} decreased by only 0.35 MPa over the range of predawn ψ_L measured,

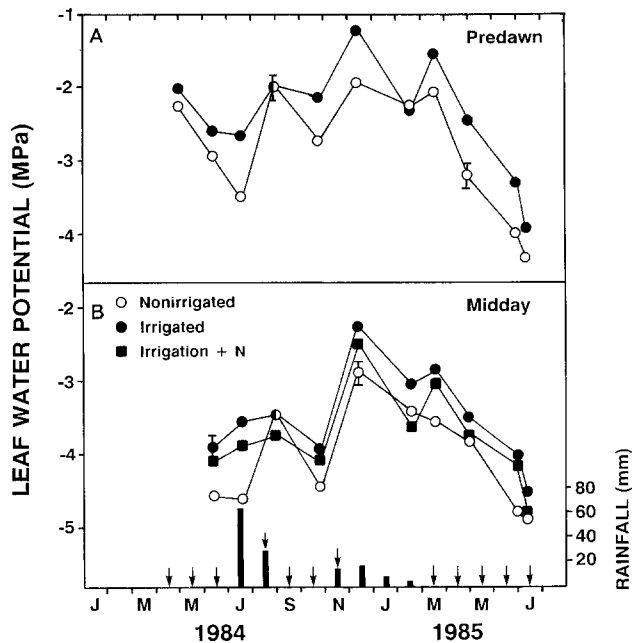


Fig. 1A, B. Seasonal course of predawn and midday leaf water potential. Predawn water potentials of shrubs subjected to the irrigation plus soil nitrogen treatment were nearly equal to those of the irrigation only treatment and are not shown. Each point represents the mean of six samples. Largest standard errors of the mean are shown. Irrigation dates are indicated by arrows

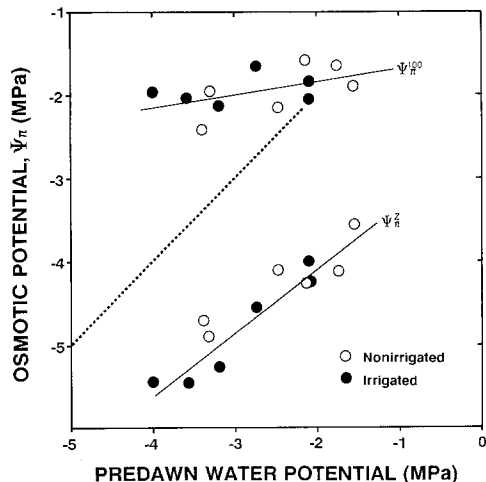


Fig. 2. Leaf osmotic potential at full turgor (ψ_{π}^{100}) and at the turgor loss point (ψ_{π}^z) in relation to predawn water potential for irrigated and nonirrigated shrubs. Measurements were made on six dates during 1984–85. Points are means of estimates obtained from 2–4 pressure-volume curves determined on the same date. The solid lines represent least squares regressions fitted to the points (ψ_{π}^z , $r=0.93$; ψ_{π}^{100} , $r=0.48$). The broken line represents the threshold for zero turgor ($\psi_{\pi}^z = \text{predawn water potential}$)

the difference between ψ_{π}^{100} and ψ_{π}^z increased from 2 MPa at high ψ_L to about 3.6 MPa at low ψ_L . This suggested that of the 2 MPa net decrease in ψ_{π}^z approximately 1.6 MPa may have been mostly attributable to tissue elastic changes.

The possibility that turgor maintenance in *Larrea* leaves was due largely to tissue elastic changes was investigated further by analysis of individual pressure-volume curves determined for shoots excised from a single nonirrigated indi-

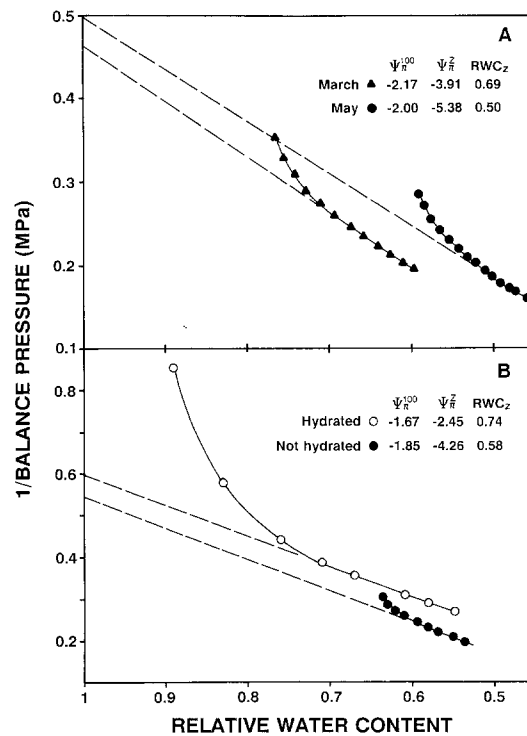


Fig. 3A, B. Representative pressure-volume curves determined for shoots cut from a single nonirrigated individual. A nonhydrated shoots cut during March and May 1985; B two shoots cut on the same day, one of which was subjected to a hydration treatment

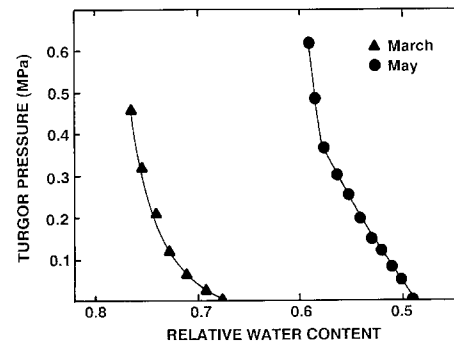


Fig. 4. The relationship between turgor pressure and relative water content calculated from the pressure-volume curves shown in Fig. 3A

vidual. Between March and May 1985 predawn ψ_L for this individual decreased from -1.70 to -2.87 MPa. The resulting decrease in ψ_{π}^z was 1.47 MPa while ψ_{π}^{100} changed only slightly (Fig. 3A). Tissue relative water content at zero turgor (RWCz), however, dropped from 0.69 to 0.50. Experiments conducted with shoots cut from the same individual on a single day indicated that the changes in ψ_{π}^z and RWCz induced by variations in shoot water status were rapidly reversible. In one such experiment subjecting a shoot to a 24 h hydration treatment with its cut base under water caused its ψ_{π}^z and RWCz to increase by 1.81 MPa and 0.16 respectively, when compared with a nonhydrated shoot (Fig. 3B). There was a small 0.18 MPa difference in ψ_{π}^{100} between the nonhydrated and hydrated shoots. Further analysis of the pressure-volume curves shown in Fig. 3A to determine the relationship between bulk leaf turgor pressure and RWC (Fig. 4) again suggested that tis-

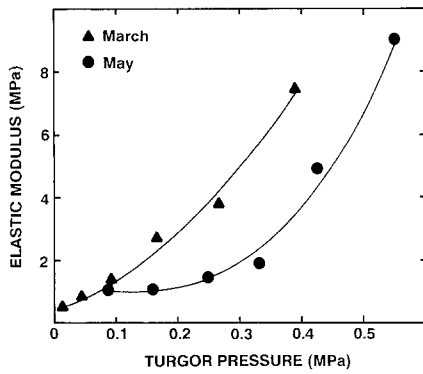


Fig. 5. The turgor dependence of the bulk tissue elastic modulus calculated from the pressure-volume curve data shown in Fig. 3A

stule elasticity increased between March and May when predawn ψ_L dropped from -1.7 to -2.87 MPa. Calculation of the turgor dependence of the bulk tissue elastic modulus ($\bar{\epsilon}$) confirmed this (Fig. 5). A graphical approach described by Tyree (1981) was used to calculate the values of $\bar{\epsilon}$ shown in Fig. 5, since it was not possible to describe the turgor pressure versus RWC plots in Fig. 4 with a single mathematical function (Kikuta and Richter 1986). It was not possible to calculate asymptotic values of $\bar{\epsilon}$ near full turgor, since hydration treatments caused large changes in tissue water relations characteristics (Fig. 3B).

Courses of g , ψ_L , and VPD during three days are shown in Fig. 6. On these days and an additional day (data not shown) g was generally lowest in nonirrigated individuals. There were no significant differences in g between individ-

uals receiving irrigation only and irrigation plus soil N. Patterns of ψ_L for the three treatments were similar to those presented in Fig. 1 with irrigated individuals having the highest, nonirrigated individuals having the lowest, and plants receiving irrigation plus soil N having intermediate values of ψ_L . An exception was 30 August 1984, which was preceded by a severe thunderstorm with heavy precipitation. Some of the variation in g between treated individuals could be loosely ascribed to differences in ψ_L . However, much of the seasonal variation in g and even diurnal variation in some cases (30 August 1984) could not easily be attributed to the influence of ψ_L . For example, while the data for 20 July 1984 suggest a role for ψ_L in modulating g , patterns of g and ψ_L for 30 August 1984 and 2 May 1985 suggest lack of such a role. Examination of all the g and ψ_L measurements revealed no close correlation between patterns of maximum g and indices such as predawn ψ_L ($r^2=0.08$), minimum ψ_L ($r^2=0.04$) or calculated predawn turgor ($r^2=0.07$).

In view of reports that root and soil rather than shoot water status are key factors in modulating g , the soil and root system moisture environment of individual *L. tridentata* shrubs was characterized. Total soil/root/shoot hydraulic resistance was calculated as an index of the differential ability of root systems to supply shoots with transpirational water. Hydraulic resistance calculated from the slope of the relationship between ψ_L and transpiration per unit leaf area (Fig. 7A) as $\Delta\psi_L/\Delta$ transpiration. Hydraulic resistance was typically highest in nonirrigated individuals and lowest in plants receiving irrigation only (Fig. 7A). Hydraulic resistance of plants receiving irrigation plus soil N was higher than that of plants receiving irrigation only.

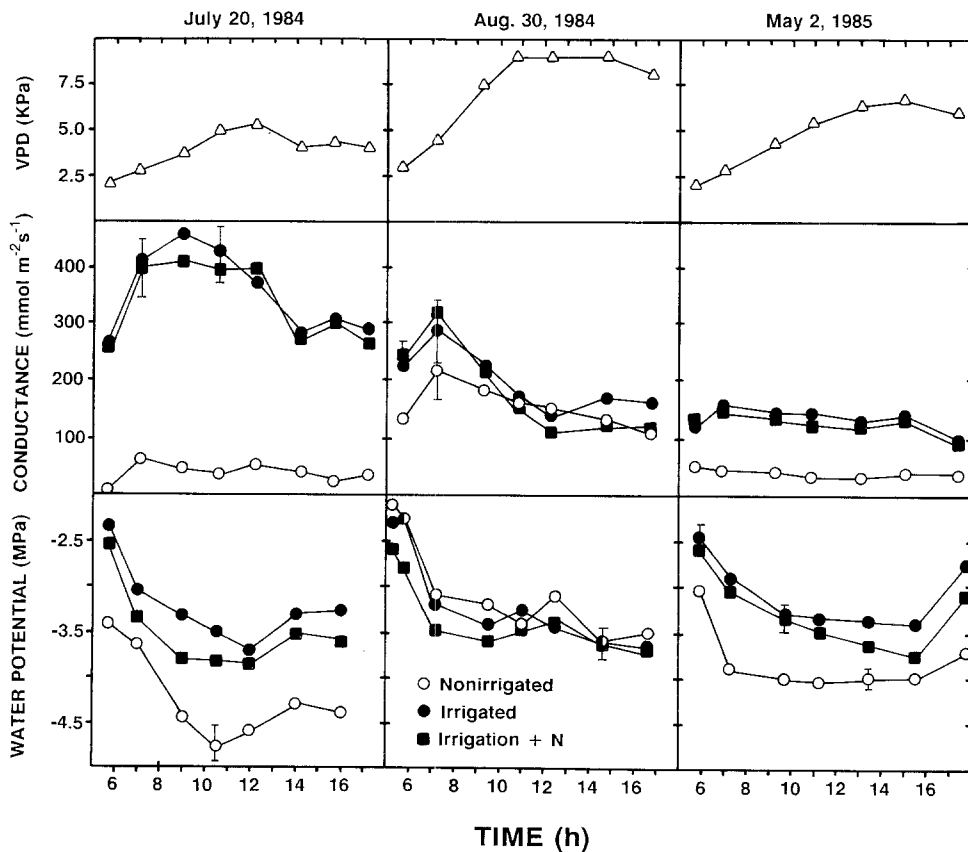


Fig. 6. Daily courses of leaf water potential, stomatal conductance and leaf-to-air vapor pressure difference for shrubs in the three treatment groups described in the text. Largest standard errors of the mean are shown

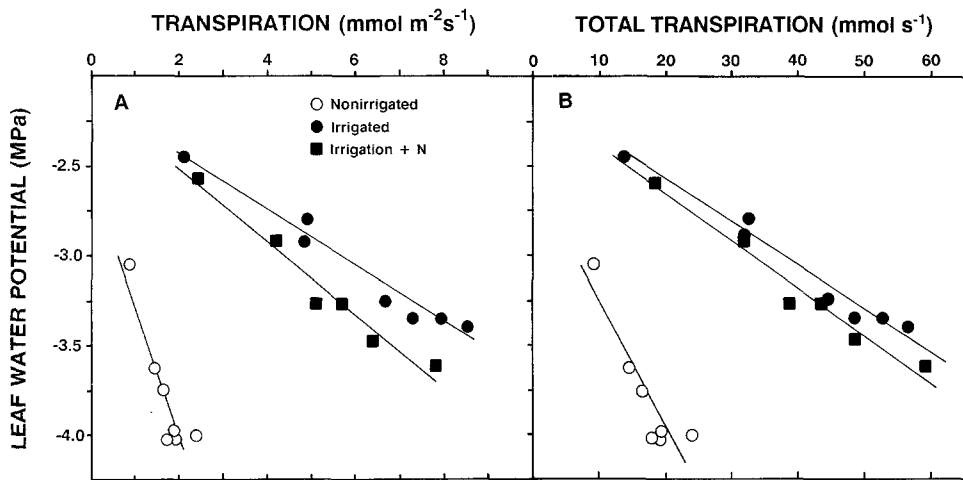


Fig. 7A, B. The relationship between leaf water potential and transpiration for three shrubs on the same data. Slopes of the least squares regression lines were used to calculate hydraulic resistance. A transpiration expressed on a unit leaf area basis; B transpiration expressed on a whole canopy basis

Table 1. Seasonal changes in total canopy leaf area of six *L. tridentata* shrubs. A + B were the two individuals from each treatment for which daily courses of stomatal conductance and leaf water potential were monitored

Treatment	Individual	Leaf area (m^2)			
		Jul 84	Aug 84	Dec 84	Jun 85
Nonirrigated	A	1.90	3.46	4.04	7.46
	B	7.43	22.05	21.93	12.95
Irrigation	A	9.76	27.83	26.46	7.77
	B	6.01	11.87	13.22	5.56
Irrigation + N	A	27.80	56.72	19.19	4.40
	B	4.16	17.39	27.07	10.83

Since g and therefore per unit leaf area transpiration rates were similar for individuals receiving these two treatments (Fig. 6), this ranking of hydraulic resistance was usually reflected in the patterns of midday ψ_L for the irrigation and irrigation plus soil N treatments (Fig. 1). However, large seasonal and treatment-related variations in total canopy leaf area occurred during the experiment (Table 1). When hydraulic resistance was calculated on a total canopy transpiration basis using data from Table 1, differences in resistance between individuals receiving irrigation and those receiving irrigation plus soil N diminished while nonirrigated individuals still had the highest resistance (Fig. 7B). For individual shrubs on all measurement dates higher maximum g appeared to be correlated with lower hydraulic resistance calculated on a total canopy transpiration basis (Fig. 8). The relationship appeared to conform with an exponential decay model ($y = e^{-bx}$) yielding an r^2 of 0.85.

Discussion

The apparent mechanism for turgor maintenance in *L. tridentata* leaves is of interest although bulk leaf turgor appeared to have little influence on stomatal aperture in individuals subjected to drought. Adjustment of ψ_π^z over a wide range of ψ_L appeared to be almost entirely attributable to tissue elastic changes. This was evident in the relationship between ψ_π^z and RWCz (Fig. 3), turgor and RWC (Fig. 4), and in the turgor dependence of $\bar{\epsilon}$ (Fig. 5). Previous work

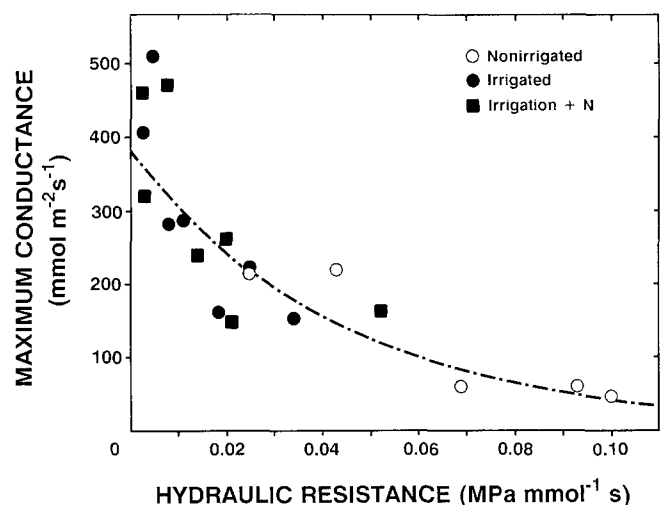


Fig. 8. Maximum daily stomatal conductance in relation to hydraulic resistance for individual shrubs during the course of the study. Estimated total canopy transpiration was used to calculate hydraulic resistance. The broken line represents a least squares regression fitted to the points ($y = 381e^{-21.544x}$; $r^2 = 0.85$)

by Meinzer et al. (1986) which showed that lower values of ψ_π^z were associated with higher osmotic water fractions in *L. tridentata* leaves also points to a significant role for tissue elastic changes in turgor regulation in this species. The turgor maintenance response in a number of woody and herbaceous species has been reported to have a significant elastic component (Davies and Lakso 1979; Pavlik 1984; Robichaux et al. 1986). The physiological basis of this response is unclear, but may involve metabolically reversible changes in cell wall composition. Turgor regulation via elastic adjustment in *L. tridentata* may present certain advantages over sole reliance on a mechanism such as osmotic adjustment. For instance, transport and synthesis of solutes involved in osmotic adjustment may be energetically more costly than metabolically reversible changes in cell wall characteristics. Limitations on the rates of solute accumulation and loss by mature leaves may also limit the effectiveness of osmotic adjustment as a mechanism for turgor regulation in this shallow rooted desert shrub which experiences large, relatively rapid fluctuations in its water status (Hinckley et al. 1980, 1983).

The rapid elastic adjustment in *L. tridentata* leaves upon hydration precluded use of the graphical analysis proposed by Kikuta and Richter (1986) to quantitatively partition turgor adjustment between osmotic and elastic components. In their study, elasticity of wheat leaves was higher during drought and decreased rapidly following relief from drought. However, Melkonian et al. (1982) using values of ϵ obtained from pressure-volume curves concluded that water deficits decreased the elasticity of wheat leaves. Similarly, in a previous study of *L. tridentata* in which $\bar{\epsilon}$ was determined by fitting a mathematical function to pressure-volume curves it was concluded that tissue elasticity was higher in fully hydrated shoots (Meinzer et al. 1986). In the present study, the pattern seen in Fig. 4 suggested that it was not possible to describe the relationship between turgor and RWC with a single mathematical function. However, when a graphical approach was used to calculate $\bar{\epsilon}$ (Tyree, 1981), it could be seen that tissue elasticity was actually higher in more dehydrated shoots (Fig. 5). These observations plus occasional unusual patterns of turgor dependence of the elastic modulus when calculated from pressure-volume curves (Roberts et al. 1981; Robichaux et al. 1986) point to the need for alternate approaches in characterizing changes in tissue elastic properties during drought and their role in turgor maintenance.

Both short and long-term variations in ψ_L and leaf water relations characteristics played a minor role in determining maximum levels of stomatal opening in *L. tridentata*. Daily and seasonal patterns of g for individuals subjected to different water and N regimes were correlated with levels of plant hydraulic resistance. Conventional estimates of soil and root water status such as predawn ψ_L have been used with success by some workers to predict daily maximum g (Running 1976; Ullmann 1985). However, predawn ψ_L will only reflect soil ψ if transpiration has been at or near zero sufficient time for true equilibrium to be attained. Even under these conditions predawn ψ_L in some species may only reflect the ψ of roots in contact with the wettest portions of the soil and not the ability of the roots to supply the shoot with transpirational water during the day when evaporative demand is high. In *L. tridentata* predawn ψ_L is not a reliable indicator of soil water status due to high nighttime VPD and incomplete nighttime stomatal closure which result in significant nocturnal transpiration (Fig. 6). Predawn ψ_L of *L. tridentata* shrubs can often be increased by 1 MPa simply by covering them with plastic bags during the night (Meinzer, unpublished observations).

Our results and those of Goldstein et al. (1987) suggest that hydraulic properties calculated on a whole canopy transpiration or total leaf area supplied basis ($\text{mmol H}_2\text{O s}^{-1}$) rather than the more commonly used transpiration per unit leaf area basis ($\text{mmol H}_2\text{O m}^{-2} \text{s}^{-1}$), may be more appropriate for evaluating stomatal conductance-hydraulic conductance relationships. For example, hydraulic resistance of *L. tridentata* shrubs subjected to the irrigation plus soil N treatment was nearly always higher than that of irrigated shrubs when transpiration per leaf area was used in its calculation (Fig. 7A). Since g and transpiration rates per leaf area were typically similar for these two treatments, the difference in hydraulic resistance resulted from a larger daily fluctuation in ψ_L in the irrigation plus soil N treatment (Fig. 6). When the greater canopy leaf area of the irrigation plus N-treated shrubs was taken into account (Table 1), hydraulic resistances and the relationship between daily

maximum g and hydraulic resistance for all shrubs receiving irrigation were similar (Fig. 7B).

Caution should be exercised in comparing estimates of hydraulic properties based on extrapolation of individual leaf transpiration measurements to the whole canopy level (Jarvis and McNaughton 1986). Coupling between stomatal movements and transpiration varies with canopy and stand structure, but it is usually high for plants such as *L. tridentata* which grow as isolated individuals (Jarvis 1985). Because of the assumptions involved in the extrapolation of transpiration measurements, the hydraulic resistance values presented here should be interpreted only as relative values for use in comparisons between individuals of the same species. Lysimetric or sap flow velocity techniques would be needed to obtain absolute values under field conditions.

Evidence for an effect of changing soil/root/shoot hydraulic properties on stomatal aperture has been obtained with other woody species (Kuppers 1984; Sanchez-Diaz and Mooney 1979). In all of these species lower g was associated with lower hydraulic conductivity. In a more direct demonstration of this effect, Teskey et al. (1983) showed that wounding of root or stem xylem or cooling of *Abies amabilis* roots caused rapid stomatal closure independent of evaporative demand, ψ_L , or root water status. From the rapidity of the effect, they concluded that the stimulus was physical rather than chemical. Although there is much evidence that changes in root water status control stomatal conductance (Schulze 1986), the observations of Teskey et al. suggest that a hydraulically based measure of the ability of the root system to supply the shoot with water may provide a more appropriate basis for predicting stomatal aperture of plants subjected to variations in their moisture regime. Thus, while resistance to water loss in the vapor phase comprises the major physical resistance controlling transpiration, plant hydraulic resistance may represent the functional resistance through its effects on stomatal aperture and therefore vapor phase resistance. This would be a feedforward form of regulation in that nearly constant ψ_L could be maintained over a range of soil ψ .

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