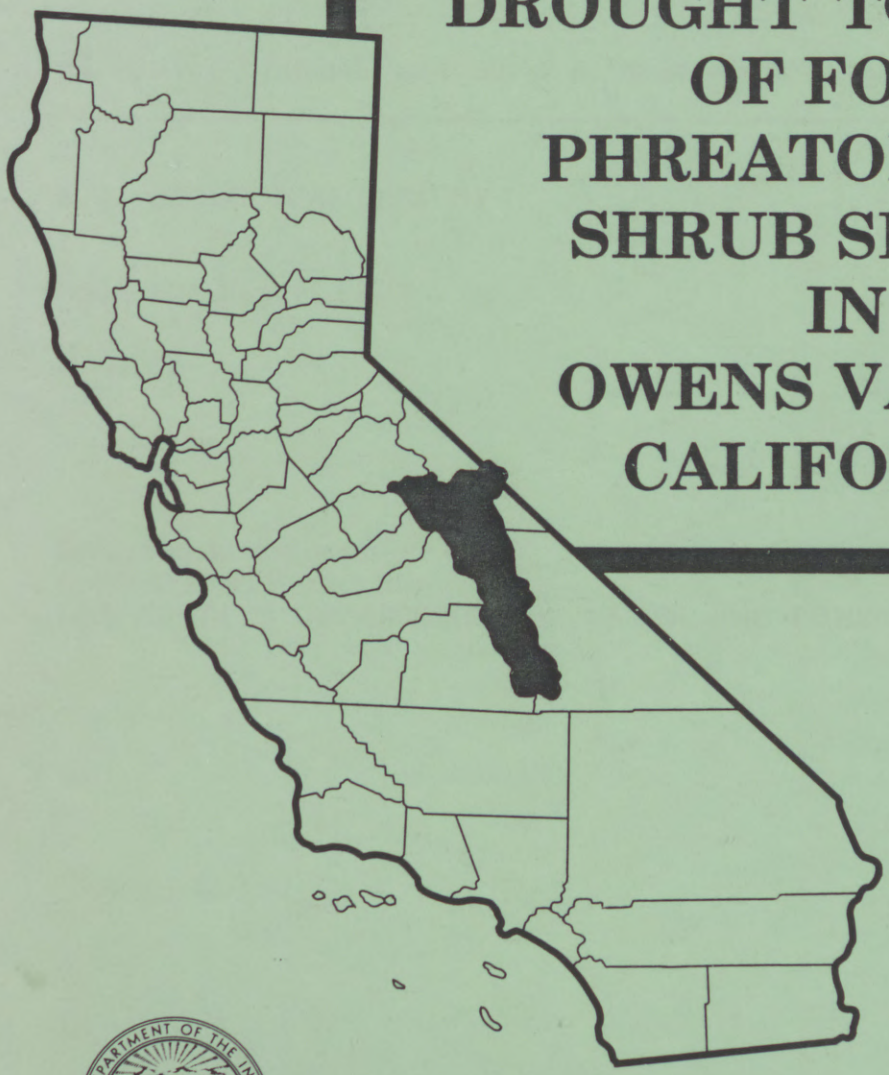
OSMOTIC POTENTIAL AND PROJECTED DROUGHT TOLERANCE OF FOUR PHREATOPHYTIC SHRUB SPECIES IN OWENS VALLEY, CALIFORNIA



U.S. GEOLOGICAL SURVEY
Open-File Report 88-77

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Prepared in cooperation with
INYO COUNTY and the LOS ANGELES DEPARTMENT OF WATER AND POWER

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With a section on PLANT-WATER RELATIONS

By *Peter D. Dileanis* and *David P. Groeneveld*

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LOS ANGELES DEPARTMENT OF WATER AND POWER

Sacramento, California
1988

DEPARTMENT OF THE INTERIOR

DONALD PAUL HODEL, Secretary

U.S. GEOLOGICAL SURVEY

Dallas L. Peck, Director

For additional information
write to:

District Chief
U.S. Geological Survey
Federal Building, Room W-2234
2800 Cottage Way
Sacramento, CA 95825

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SYMBOLS USED IN TEXT

ψ_g	Gravitational potential	ψ_π^i	Osmotic potential at initial hydration
ψ_w^i	Initial water potential	ψ_π^z	Osmotic potential at turgor loss
ψ_m	Matric potential	ψ_w	Total water potential
E	Modulus of elasticity	R_a	Apoplastic fraction
ψ_p	Pressure potential	RWC	Relative water content
ψ_π	Osmotic potential		

CONVERSION FACTORS

For use of readers who prefer inch-pound units, conversion factors for terms used in this report are listed below.

Multiply	By	To obtain
meter (m)	3.281	feet
centimeter (cm)	0.3937	inch
millimeter (mm)	0.039	inch
kilometer (km)	0.6214	mile
megapascal (MPa)	0.1	bar
	1.45038	pound per square inch
milligram (mg)	0.00003527	ounce

Temperature is given in degrees Celsius (°C), which can be converted to degrees Gahrenheit (°F) by the following equation:

$$°F=1.8(°C)+32.$$

Sea Level: In this report, "sea level" refers to the National Geodetic Vertical Datum of 1929 (NGVD of 1929)--a geodetic datum derived from a general adjustment of the first-order level nets of both the United States and Canada, formerly called Mean Sea Level of 1929.

OSMOTIC POTENTIAL AND PROJECTED DROUGHT TOLERANCE OF FOUR PHREATOPHYTIC SHRUB SPECIES IN OWENS VALLEY, CALIFORNIA

By *Peter D. Dileanis* and *David P. Groeneveld*[1]

ABSTRACT

A large part of the water used by plant communities growing on the floor of Owens Valley, California, is derived from a shallow unconfined aquifer. Fluctuations in the water table caused by ground-water withdrawal may result in periods when this water supply is not accessible to plants. The capacity of the plants to adapt to these periods of water loss depend on the availability of water stored in the soil and on physiological characteristics related to the ability of the plants to resist dehydration and wilting.

Osmotic adjustment occurred in four phreatophytic shrub species at sites near Bishop, California, where the water table had been lowered by a system of pump-equipped wells installed in the vicinity of vegetation transects. The pressure-volume technique was used to determine osmotic potential and cell-wall elasticity between March 1985 and September 1986 for *Atriplex torreyi*, *Chrysothamnus nauseosus*, *Sarcobatus vermiculatus*, and *Artemisia tridentata*. Although not usually classified as a phreatophyte, *Artemisia tridentata*, where it grows on the valley floor, is apparently dependent on the depth to the water table.

During late summer, osmotic potentials were 0.37 to 0.41 megapascal lower in plants growing on the site where the water table had been lowered compared to an adjacent site where the water table remained at its natural levels. Measurements of soil matric potential at the two sites indicated that osmotic adjustment occurred in response to stress caused by lowering the water table.

A theoretical lower limit of osmotic adjustment was determined by comparing initial cell osmotic potentials with initial xylem water potentials. These experimentally derived limits indicated that *A. torreyi* and *S. vermiculatus* may maintain leaf cell turgor at significantly lower cell water potentials (about -4.5 megapascals) than *C. nauseosus* or *A. tridentata* (about -2.5 megapascals) and allows them to function in dryer soil environments.

[1]David P. Groeneveld, Inyo County Water Department, Bishop, California.

INTRODUCTION

The drought tolerance of many plants growing in arid environments is reflected in their water potential components, particularly osmotic potential (Monson and Smith, 1982; Calkin and Pearcy, 1984; Bowman and Roberts, 1985; Bennert and Mooney, 1979). The ability to decrease cell osmotic potential by the accumulation of solutes is termed osmotic adjustment.

Osmotic adjustment is a mechanism that allows plants to maintain cell water balance during periods of depleted soil water. For those plant species that possess this mechanism, a determination of the degree of osmotic response in relation to other cell water balance characteristics may indicate their relative drought tolerance. This concept is applicable for Owens Valley, California, where the relative drought tolerance of several phreatophytic shrub species would be useful knowledge for effective land and water management. Phreatophytic plants derive a significant part of their water requirements from the shallow unconfined aquifer and the capillary fringe above the water table (Meinzer, 1927). These species form most of the vegetation in the zone of influence surrounding existing or potential well fields developed to extract ground water for export to the city of Los Angeles. Short- or long-term changes in the depth of the subirrigating water table due to ground-water withdrawals may induce changes in the amount of vegetation cover.

This study was accomplished as part of a much larger effort. In 1982 the U.S. Geological Survey, in cooperation with Inyo County and the Los Angeles Department of Water and Power, began a series of comprehensive studies to define the ground-water system in Owens Valley and to determine the effects of ground-water withdrawals on native vegetation. These studies are discussed more fully by Hollett (1987). The results of the studies, as well as a comprehensive summary, are presented in a U.S. Geological Survey Water-Supply Paper series as the interpretive products of the studies become available. The series consists of eight chapters as follows:

A. A summary of the hydrologic system and soil-water-plant relations in Owens Valley, California, 1982-87, with an evaluation of management alternatives,

B. Hydrogeology and water resources of Owens Valley, California,

C. Estimating soil matric potential in Owens Valley, California,

D. Osmotic potential and projected drought tolerances of four phreatophytic shrub species in Owens Valley, California, with a section on plant-water relations (this report),

E. Estimates of evapotranspiration in alkaline scrub and meadow communities of Owens Valley, California, using the Bowen-ratio, eddy-correlation, and Penman-combination methods,

F. Influence of changes in soil water and depth to ground water on transpiration and canopy of alkaline scrub communities in Owens Valley, California,

G. Vegetation and soil water responses to changes in precipitation and depth to ground water in Owens Valley, California, and

H. Numerical simulation and system analysis of the ground-water-flow system in Owens Valley, California.

Purpose and Scope

The purpose of this report is to define a physiological response of vegetation to a lowered water table through an understanding of the osmotic components of water balance of four phreatophyte shrub species common to the shallow ground-water environment of the Owens Valley floor and to define the relative drought tolerance of the species.

Between March 1985 and September 1986, measurements of the water-potential components of three of the species were made on samples collected at a site where the water table had been lowered by a specially designed well system. Comparison was made with samples collected from an adjacent site unaffected by pumping. Likewise, a comparison was made for a fourth species between two

sites that were affected by varying distance along a depth-to-water-table gradient away from another well system constructed for the project. Cell osmotic potential was measured by using the pressure-volume curve technique (Scholander and others, 1964; Tyree and Hammel, 1972), and both predawn and midday xylem pressure potential were measured by using a pressure chamber (Scholander and others, 1964; Ritchie and Hinckley, 1975). These data were obtained during 1985 and 1986 and were combined to represent plant responses through a growing season.

A separate section titled "Plant-Water Relations" has been included beginning on page 35 for the reader unfamiliar with the concepts and terminology currently used in the field of plant physiology. Its purpose is to provide sufficient technical background for a comprehensive reading of this report.

Description of the Study Area

Owens Valley is between the Sierra Nevada and the White and Inyo Mountains near the eastern border of California (fig. 1). The long, narrow valley floor slopes gently to the south, and altitudes range from 1,250 m at Bishop to 1,095 m to the southeast at Owens Lake. The valley floor is composed primarily of alluvial deposits, broken by basalt flows and igneous intrusions in several locations. Alluvial fans emanating from the Sierra Nevada and the White and Inyo Mountains intersect the valley floor along the valley margins (Lee, 1906).

The valley is a hydrologically closed basin and all natural drainage flows into Owens Lake. Most surface flow in the basin is diverted to the aqueduct system operated by the Los Angeles Department of Water and Power for export to the Los Angeles metropolitan region 370 km to the south.

The climate of the valley is arid, owing to the rainshadow of the Sierra Nevada. Annual precipitation is variable and averages 100 to 150 mm depending on location. Most of the precipitation falls between the months of November and March. Summers are hot and dry with occasional thundershowers.

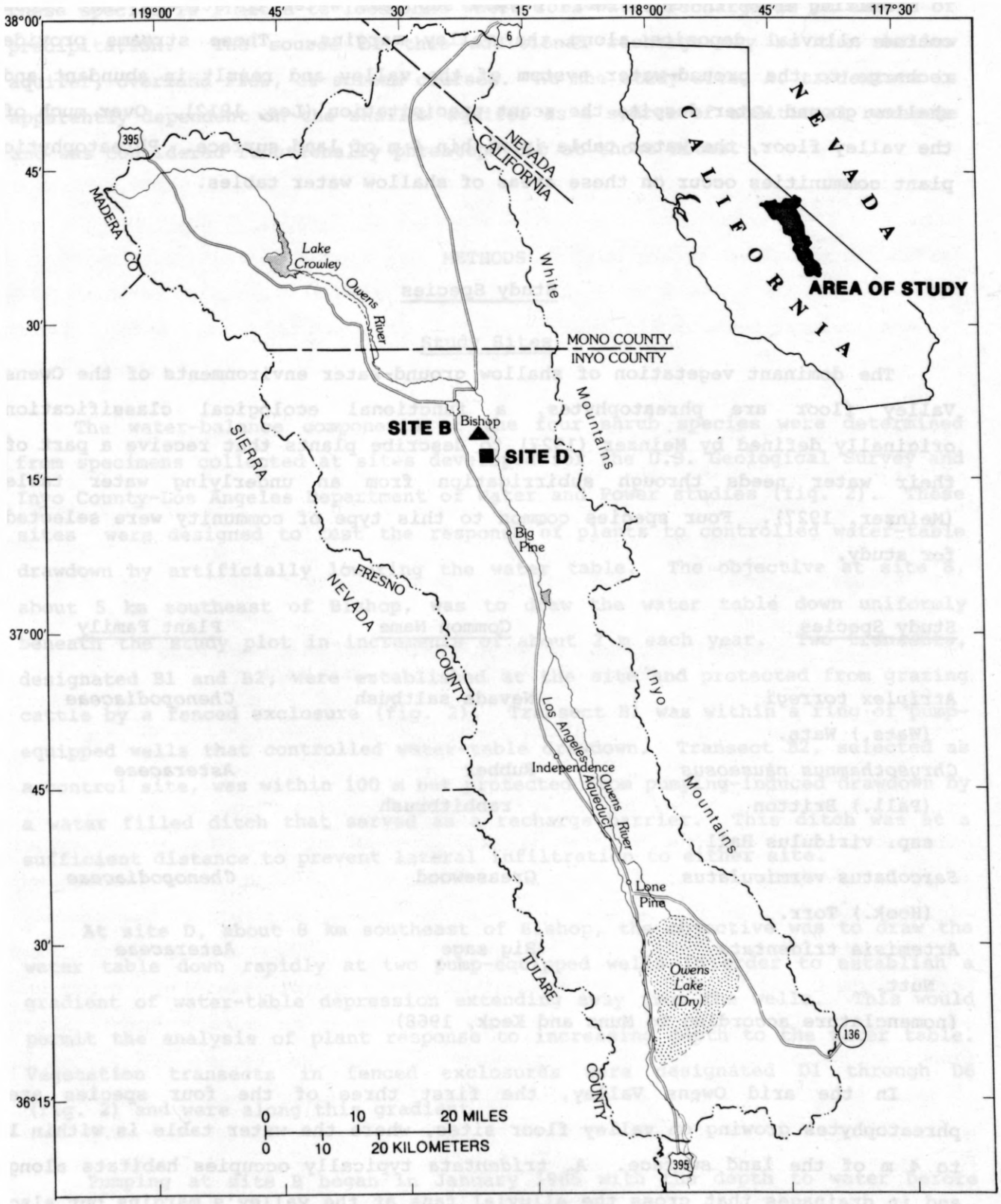

FIGURE 1.—Location of study area and sites.

Melting snow in the Sierra Nevada supplies water to streams that cross coarse alluvial deposits along the valley margins. These streams provide recharge to the ground-water system of the valley and result in abundant and shallow ground water despite the scant precipitation (Lee, 1912). Over much of the valley floor, the water table is within 4 m of land surface. Phreatophytic plant communities occur on these areas of shallow water tables.

Study Species

The dominant vegetation of shallow ground-water environments of the Owens Valley floor are phreatophytes, a functional ecological classification originally defined by Meinzer (1927) to describe plants that receive a part of their water needs through subirrigation from an underlying water table (Meinzer, 1927). Four species common to this type of community were selected for study.

Study Species	Common Name	Plant Family
Atriplex torreyi (Wats.) Wats.	Nevada saltbush	*Chenopodiaceae*
Chrysothamnus nauseosus (Pall.) Britton ssp. viridulus Hall	Rubber rabbitbrush	*Asteraceae*
Sarcobatus vermiculatus (Hook.) Torr.	Greasewood	*Chenopodiaceae*
Artemisia tridentata Nutt.	Big sage	*Asteraceae*

(nomenclature according to Munz and Keck, 1968)

In the arid Owens Valley, the first three of the four species are phreatophytes growing on valley floor sites, where the water table is within 1 to 4 m of the land surface. *A. tridentata* typically occupies habitats along and in drainages that cross the alluvial fans at the valley's margins but also may be in valley floor locations, where the soils are coarse textured and low in salinity. Perhaps due to the arid environment, the presence of all four of

these species is limited to locations where soil-water recharge is in excess of precipitation. The source of this additional recharge may be the shallow aquifer, overland flow, or stream courses. At the study site, *A. tridentata* is apparently dependent on the shallow aquifer as a source of additional recharge and was considered functionally phreatophytic at those sites.

METHODS

Study Sites

The water-balance components of the four shrub species were determined from specimens collected at sites developed for the U.S. Geological Survey and Inyo County-Los Angeles Department of Water and Power studies (fig. 2). These sites were designed to test the response of plants to controlled water-table drawdown by artificially lowering the water table. The objective at site B, about 5 km southeast of Bishop, was to draw the water table down uniformly beneath the study plot in increments of about 2 m each year. Two transects, designated B1 and B2, were established at the site and protected from grazing cattle by a fenced exclosure (fig. 2). Transect B1 was within a ring of pump-equipped wells that controlled water-table drawdown. Transect B2, selected as a control site, was within 100 m but protected from pumping-induced drawdown by a water filled ditch that served as a recharge barrier. This ditch was at a sufficient distance to prevent lateral infiltration to either site.

At site D, about 8 km southeast of Bishop, the objective was to draw the water table down rapidly at two pump-equipped wells in order to establish a gradient of water-table depression extending away from the wells. This would permit the analysis of plant response to increasing depth to the water table. Vegetation transects in fenced exclosures were designated D1 through D6 (fig. 2) and were along this gradient.

Pumping at site B began in January 1985 with the depth to water before pumping at about 2 m below land surface at transect B1. From March 1985 through September 1986, the water table was about 3.5 m below land surface,

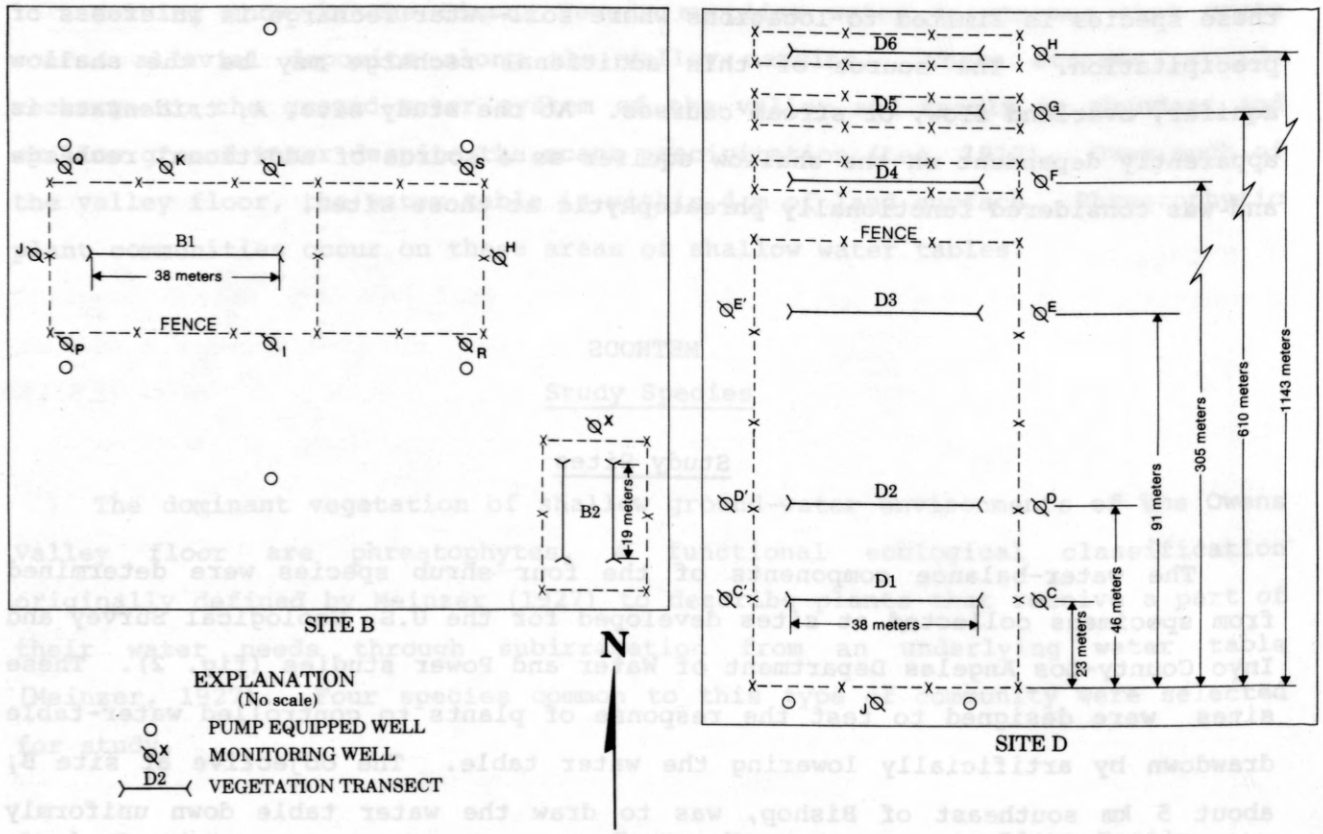

FIGURE 2.—Well placement and sampling locations at sites B and D. Letters identify individual wells. Distance between transects not to scale.

representing a drawdown close to 1.5 m. The water table at the adjacent control transect, B2, was maintained close to the starting depth of about 2.5 m below land surface. Samples of *C. nauseosus*, *S. vermiculatus*, and *A. torreyi* were analyzed from plants at transects B1 and B2. The sampled shrubs grew adjacent to, but not on the transects, which were established to measure plant cover for other studies.

The *A. tridentata* samples were obtained from plants at transects D1 and D3, which experienced water-table drawdown of about 4 and 3 m, respectively. The initial static water level at site D was about 2.7 m, when pumping began in October 1984.

The two study sites were considered to be representative of the vegetation that exists over a broad expanse of the valley. The coarse-textured soils at these sites were more representative of those in the northern part of the valley floor. The soil matric potentials were measured during the study to permit comparison of the plant responses directly to the energy state of the water in the soil.

Pressure Chamber

One of the most informative single measurements of water stress is the pressure potential of the water in the xylem of the shoots because it integrates the water-potential components involved in the development of water deficit and is a direct measure of the force exerted for water uptake from the soil (Ritchie and Hinckley, 1975; Kramer, 1983). This potential was measured by using a pressure chamber (Scholander and others, 1964, 1965), which required that a leafy stem be removed from the plant, transferred rapidly to a pressure chamber, and mounted with the leafy material inside and the cut stem protruding to the atmosphere. Under field conditions usually encountered, the water in the xylem is under tension arising from the water potential gradient and

combined resistances between the leaves and the root and soil system. When the stem is cut, the water columns in the xylem vessels snap apart due to the rise to atmospheric pressure at the cut surface.

The pressure chamber measures the original degree of tension of the water column by applying pressure on the leafy part of the stem to force the water column back down the xylem to just reach the cut surface of the stem. With reversal of sign, this balancing point represents the tension of the sap within the xylem at the time of excision. The pressure potential derived from pressure-chamber measurements commonly is used to estimate bulk cellular (symplastic) water potential. Under equilibrium conditions, the water potential in the apoplast is equal to the water potential in the symplast. The osmotic component of the apoplastic fraction usually is assumed to be negligible; accordingly, the pressure component is a reasonably accurate estimation of the total water potential (ψ_w) of the shoot.

Predawn and midday estimates of xylem pressure potentials were obtained monthly during the 1986 growing season using a pressure chamber for comparison to the components of plant water potential obtained from the samples collected before dawn on the three sampling dates.

Pressure-Volume Curves

Plant-water status can be more fully described by determining the osmotic potential (ψ_π) and pressure potential (ψ_p) components of ψ_w. The relation between water potential and water content in the form of a pressure-volume curve is used to estimate these components. Measurements made with the pressure chamber provide estimates of the shoot water potentials that occur as the water content of the shoot is progressively lowered. The reciprocal of the balancing pressure is plotted against relative water content (RWC), which is a measure of the hydration of the specimen relative to its initial weight. This graphical representation of the relation between water potential and water content is called a pressure-volume curve (Scholander and others, 1964). A representative pressure-volume curve is shown in figure 3.

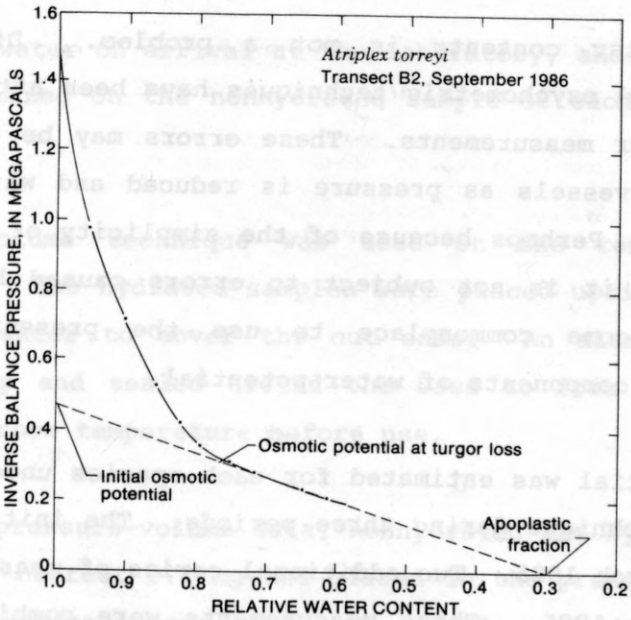

FIGURE 3.—Relation between the reciprocal of balance pressure and relative water content.

A pressure-volume curve usually has two regions; an upper exponential part that represents the combined ψ_p and ψ_π and a linear region that represents the ψ_π component only (Scholander and others, 1964; Tyree and Hammel, 1972; Richter, 1978). The point of divergence between the two curves represents the osmotic potential at which turgor pressure is lost (ψ_π^z). The slope of the line representing the relation between ψ_π and RWC can be extrapolated to any RWC to allow the estimation of the ψ_π and ψ_p for a range of water content. Using this approach, the linear part of the curve was used to estimate the osmotic potential at the point of turgor loss (ψ_π^z) and the osmotic potential at the initial hydration (ψ_π^i) (RWC=1.00) of the plant material when the measurements began. The fraction of water partitioned within the plant but outside living cells is called the apoplastic fraction (Ra) and is estimated by the point where the extrapolated linear part of the pressure volume curve crosses the abscissa.

Only the pressure-volume curve technique was used to estimate ψ_π. Other methods, such as cryoscopy and psychometric techniques, result in a disruption of cell contents that could induce solute contamination from salty glandular hairs covering the epidermis of *A. torreyi*, inducing large errors. Errors from dilution of cell contents by apoplastic water also have been reported. The pressure-chamber method used intact leaves and branchlets and contamination or

dilution of cellular contents is not a problem. Discrepancies between pressure-chamber and psychometric techniques have been attributed to errors in the pressure-chamber measurements. These errors may be due to embolisms developing in xylem vessels as pressure is reduced and water moves from xylem into the symplast. Perhaps because of the simplicity of the pressure chamber and the fact that it is not subject to errors caused by the disruption of cells, it has become commonplace to use the pressure chamber for the measurement of the components of water potential.

Osmotic potential was estimated for each species under study by using the pressure-volume technique during three periods. The initial measurements were obtained during March 1985. Two additional series of measurements were made in June and September 1986. These measurements were combined to represent the plant responses through a seasonal period.

The original pressure-volume technique involved overnight hydration of the plant material (Boyer, 1969; Roberts and Knoerr, 1977; Cheung and others, 1975). This hydration was done for all the March 1985 analyses. Meinzer and others (1986) compared hydrated and nonhydrated stems of *Larrea tridentata* and documented significant differences in estimated values of ψ_π between the two methods. Bowman and Roberts (1985) reported similar effects for hydrating samples of chaparral species. To test the effects of hydration, duplicate samples were collected and one of each pair was hydrated before the pressure-volume curve procedure was begun. The other sample of each pair was nonhydrated. The pressure-volume measurements of March 1985 used only hydrated plant material. In all other respects, the techniques used during the March determinations were identical to those used during June and September 1986. Two stems were collected from each of three or more individuals of each species at each of the study sites before dawn on the sampling day. The specimens were selected to represent average leafy stems of a size that would fit within the pressure chamber with an extra 20 cm of stem included to permit trimming. Each branch was then re-cut closer to the desired length with the stem under water in order to re-establish the hydraulic continuity of the water in the xylem. These were then sealed in an aluminum foil envelope and placed in a cooler equipped with a moist paper towel to reduce water loss during the 20-min transport to the laboratory. An additional 3 cm of stem was again trimmed from

all the stems under water on arrival at the laboratory, and the pressure-volume data was then determined on the nonhydrated sample of each pair as rapidly as possible.

The pressure-volume technique was used on the remaining stem after overnight hydration. The hydrated samples were placed upright in plastic cups filled with enough water to cover the cut ends. An aluminum foil tent was placed over each cup and sealed around the base to form a humid chamber to remain overnight at room temperature before use.

To measure the pressure-volume data, nonhydrated and hydrated samples were first weighed to the nearest 0.1 mg and placed in the pressure chamber for the initial balancing pressure measurement. The sample was then removed from the chamber and allowed to lose water at room conditions from 5 to 40 min depending upon the rate of weight loss. This method of reducing water content has been referred to as bench drying. The samples were then reweighed and placed in the pressure chamber to determine a new balance point at that water content. The cycle of water loss, weighing, and finding the new balance point was repeated until sufficient points were obtained to define a pressure-volume curve. This generally required from 10 to 15 measurements.

After the data for the pressure-volume curves were obtained, the samples were oven dried overnight at 55 °C and reweighed. The dry weight was used in the calculation of relative water content:

$$RWC=W-W_d/W_i-W_d, \quad (1)$$

where

RWC is the relative water content,
W is the weight at the balance point,
W_d is the dry weight, and
W_i is the initial saturated weight.

For the nonhydrated samples, a weight at full saturation was not available so the initial weight of the sample was substituted. The pressure-volume data for each sample was then plotted on a graph with RWC on the abscissa and the reciprocal of the balance point on the ordinate. Linear regression was used to establish the formula for the linear phase of the curve. Most of the correlation coefficients (r values) were typically close to 1.00 and averaged greater than 0.95.

Cell-Wall Elasticity

Cell-wall elasticity affects the cell water balance during osmotic adjustment because the pressures exerted by solute accumulation for turgor maintenance would tend to be negated if the cell wall were to deform. Under conditions of osmotic adjustment, cell-wall elasticity either remains relatively constant or decreases (Pavlik, 1984; Jones and Turner, 1978; Wilson and others, 1980). Cell-wall elasticity can be measured as the elastic modulus (E), defined in the following equation (Zimmerman, 1978):

$$E=(\Delta\psi_p/\Delta V)*V, \qquad (2)$$

where

E is the modulus of elasticity,

$\Delta\psi_p$ is the difference in pressure potential (turgor), and

ΔV is the corresponding difference in cell-water volume.

The modulus of elasticity (E) can be calculated substituting RWC-R_a for V, where R_a is the apoplastic water fraction (Robichaux, 1984). Pressure potential (ψ_p) and relative RWC derived from the pressure-volume curves of rehydrated samples were used to estimate E in this study. Pressure potentials were determined by subtracting ψ_π from ψ_w for points on the curvilinear part of each pressure volume curve. Differences in ψ_p and RWC represent differences between two successive points on the pressure-volume curve. The maximum values of E for each curve at or near full hydration were used for comparison purposes.

Soil Matric Potential

Soil matric potentials were measured several times during each growing season to characterize changes in soil water potential encountered by the plants under study. Soil matric potential is a good measure of water availability because it represents the water retention force that must be overcome to induce water flow from soil into the roots.

Soil matric potential was measured using the filter-paper method of McQueen and Miller (1972). By use of a hand driven barrel type auger, a continuous series of soil samples were collected from the soil surface to just above the water table. Each 10-cm increment of soil core was sealed in a plastic bag along with a piece of filter paper. The bag was then sealed in a metal can to prevent evaporative loss of water. After equilibrating with the soil sample, the moisture content of the filter paper was measured and used to determine matric potential using calibration curves that relate filter-paper water content to matric potential of the soil sample.

EFFECTS OF SAMPLE REHYDRATION

Shoot samples were tested for the effect of overnight hydration by comparing the pressure-volume analysis results of paired hydrated and nonhydrated samples. No comparison was possible for *A. tridentata* in September because late summer water potentials of nonhydrated samples were below the range of the instrument. At 8 to 10 MPa of pressure, pressure-chamber seals failed before a sufficient number of points to adequately describe the pressure-volume relation could be measured.

Mean values and standard errors of initial osmotic potential, osmotic potential at turgor loss, and the apoplastic water fraction determined by the pressure-volume technique are shown in table 1. Differences in mean osmotic potential at turgor loss between hydrated and nonhydrated sample pairs are shown in table 2. In all comparisons, the ψ_{π}^{z} for hydrated samples were higher

Table 1. Mean and standard error for initial osmotic potential (ψ_π^i), osmotic potential at turgor loss (ψ_π^z), and apoplastic water fraction (R_a), determined by the pressure-volume technique

[Osmotic potentials, in megapascals; apoplastic water fraction is dimensionless; --, no data]

		March 1985		June 1986		September 1986	
		Mean	Standard error	Mean	Standard error	Mean	Standard error
Atriplex torreyi							
Transect B1							
nonhydrated	ψ_π^i	--	--	-3.972	0.468	-4.206	0.696
	ψ_π^z	--	--	-4.524	.386	-4.372	.593
	R_a	--	--	.02	.04	.54	.21
hydrated	ψ_π^i	-2.241	0.234	-2.813	.200	-2.682	.227
	ψ_π^z	-3.731	.248	-3.386	.324	-3.331	.082
	R_a	.59	.11	.06	.05	.27	.09
Transect B2							
nonhydrated	ψ_π^i	--	--	-4.158	.310	-4.020	.275
	ψ_π^z	--	--	-4.468	.289	-4.979	.213
	R_a	--	--	.02	.05	.35	.13
hydrated	ψ_π^i	-2.393	.324	-2.468	.248	-2.117	.068
	ψ_π^z	-3.717	.344	-3.068	.262	-2.937	.172
	R_a	.57	.05	.03	.03	.09	.08

Table 1. Mean and standard error for initial osmotic potential (ψ_π^i), osmotic potential at turgor loss (ψ_π^z), and apoplastic water fraction (R_a), determined by the pressure-volume technique--Continued

[Osmotic potentials, in megapascals; apoplastic water fraction is dimensionless; --, no data]

		March 1985		June 1986		September 1986	
		Mean	Standard error	Mean	Standard error	Mean	Standard error
Chrysothamnus nauseosus							
Transect B1							
nonhydrated	ψ_π^i	--	--	-2.365	0.220	-2.206	0.262
	ψ_π^z	--	--	-2.689	.213	-2.648	.158
	R_a	--	--	.20	.14	.29	.19
hydrated	ψ_π^i	-1.420	0.006	-2.172	.165	-1.910	.206
	ψ_π^z	-2.255	.089	-2.586	.227	-2.227	.172
	R_a	.49	.04	.23	.20	.42	.9
Transect B2							
nonhydrated	ψ_π^i	--	--	-2.275	.110	-2.413	.172
	ψ_π^z	--	--	-2.648	.248	-2.737	.186
	R_a	--	--	.26	.24	.21	.10
hydrated	ψ_π^i	-1.489	.082	-1.910	.062	-1.393	.179
	ψ_π^z	-2.331	.220	-2.406	.082	-1.820	.124
	R_a	.34	.05	.38	.07	.22	.13

Table 1. Mean and standard error for initial osmotic potential (ψ_π^i), osmotic potential at turgor loss (ψ_π^z), and apoplastic water fraction (R_a), determined by the pressure-volume technique--Continued

[Osmotic potentials, in megapascals; apoplastic water fraction is dimensionless; --, no data]

		March 1985		June 1986		September 1986	
		Mean	Standard error	Mean	Standard error	Mean	Standard error
Sarcobatus vermiculatus							
Transect B1							
nonhydrated	ψ_π^i	--	--	-4.393	0.248	-5.544	0.806
	ψ_π^z	--	--	-5.068	.423	-5.779	.413
	R_a	--	--	.25	.11	.38	.28
hydrated	ψ_π^i	-1.779	0.158	-4.055	.200	-4.455	.172
	ψ_π^z	-2.193	.303	-4.627	.324	-5.317	.124
	R_a	.09	.06	.04	.07	.14	.05
Transect B2							
nonhydrated	ψ_π^i	--	--	-4.475	.082	-4.965	.331
	ψ_π^z	--	--	-4.862	.206	-5.268	.413
	R_a	--	--	.11	.13	.07	.04
hydrated	ψ_π^i	-1.724	.124	-3.468	.337	-4.372	.231
	ψ_π^z	-2.137	.179	-4.110	.200	-4.944	.198
	R_a	.06	.05	.09	.06	.20	.08

Table 1. Mean and standard error for initial osmotic potential (ψ_π^i), osmotic potential at turgor loss (ψ_π^z), and apoplastic water fraction (R_a), determined by the pressure-volume technique--Continued

[Osmotic potentials, in megapascals; apoplastic water fraction is dimensionless; --, no data]

		March 1985		June 1986		September 1986	
		Mean	Standard error	Mean	Standard error	Mean	Standard error
Artemisia tridentata							
Transect B1							
nonhydrated	ψ_π^i	--	--	-2.682	0.062	--	--
	ψ_π^z	--	--	-2.903	.282	--	--
	R_a	--	--	.09	.08	--	--
hydrated	ψ_π^i	-1.337	0.082	-1.986	.096	-2.737	0.489
	ψ_π^z	-1.606	.062	-2.434	.172	-3.275	.517
	R_a	.21	.13	.14	.04	.25	.18
Transect B2							
nonhydrated	ψ_π^i	--	--	-2.744	.172	--	--
	ψ_π^z	--	--	-2.772	.124	--	--
	R_a	--	--	.12	.10	--	--
hydrated	ψ_π^i	-1.344	.117	-1.882	.186	-1.986	.110
	ψ_π^z	-1.613	.096	-2.165	.124	-2.331	.131
	R_a	.09	.11	.15	.13	.27	.11

Table 2. Differences in mean osmotic potential at turgor loss between hydrated and nonhydrated sample pairs in 1986

[Asterisk (*) indicates significant differences at 0.95-confidence level or greater using two-sided t-tests; --, no data]

Species	Transect	Difference in mean osmotic potential at turgor loss, in megapascals	
		June	September
Atriplex torreyi	B1	1.139*	1.041*
	B2	1.402*	2.043*
Chrysothamnus nauseosus	B1	.246	.417*
	B2	.101	.916*
Sarcobatus vermiculatus	B1	.441	.462
	B2	.752*	.319
Artemisia tridentata	D1	.465	--
	D3	.605*	--

than that of nonhydrated samples. The results of t-tests show differences were statistically significant in 8 of the 14 comparisons. Significant differences ranged from about 0.4 to 2.0 MPa and were highest in *A. torreyi*.

The increase in ψ_{π}^{z} in the hydrated samples may be due to osmotic adjustment during hydration, although differences in the method of calculation also may have had some effect. RWC is usually calculated using the fully saturated weight of the sample. This weight is the initial weight of the hydrated samples. The initial weight of the nonhydrated samples would be less than the fully saturated weight in all but the wettest soil conditions. The samples could not be rehydrated to saturation after pressure volume curves had been made. This was probably because of embolisms in the xylem following repeated pressure chamber measurements. Efforts to estimate the weight from the ratio of saturated and dry weight of the paired hydrated samples also were unsuccessful due to the large variation in the data. Because we were unable to determine a fully saturated weight, the initial weight also was used to calculate RWC in the nonhydrated samples.

Although sample hydration has been used often in previous studies, recent work has shown that the method may result in underestimation of ψ_{π}^{z} in some California chaparral species (Bowman and Roberts, 1985) and in creosote bush (*L. tridentata*) (Meinzer and others, 1986). Theoretically, the point of turgor loss (ψ_{π}^{z}) should not change, given constant molality of solutes and constant cell-wall properties. Meinzer and others (1986), analyzing paired hydrated and nonhydrated samples, found what appeared to be a movement of solutes from symplast to apoplast as a result of hydration. Their data also indicated that plastic deformation of cell walls had occurred due to abnormal hydrostatic pressure developed during hydration. Whatever the cause, the possibility of differences in estimation of osmotic potentials because of hydration should be kept in mind when comparing data from pressure-volume curves.

SOIL WATER CONDITIONS

Profiles of soil matric potential at each of the study sites are shown in figure 4. Following the drawdown of the water table, soils drained to field capacity (about 0.01 to 0.03 MPa depending on texture; Hillel, 1971) in the deeper parts of soil profiles at transects B1, D1, and D3. Marked decreases of soil matric potential below field capacity approaching 3 m deep were measured at transect B1. The relative dryness of the soil in that region indicates the effect of root extraction following the loss of capillary recharge from the underlying water table. Measurements of root density at an area adjacent to the site indicate that this drying zone reflects the distribution of roots (D.P. Groeneveld, Inyo County Water Department, oral commun., 1986). Though the water table was adjusted to a point 4.5 m below the initial static level at D1, soil matric potentials below 1 m were consistently greater than the 0.2 MPa estimate of field capacity. At D3, about 70 m farther from the wells, the water table was adjusted to a point about 3.5 m deeper than the initial level (because the water level declined below the bottom of the observation wells at this site, the decline in water table is estimated). The profiles of soil matric potential at D3 showed limited evidence of soil-water depletion by October 1986.

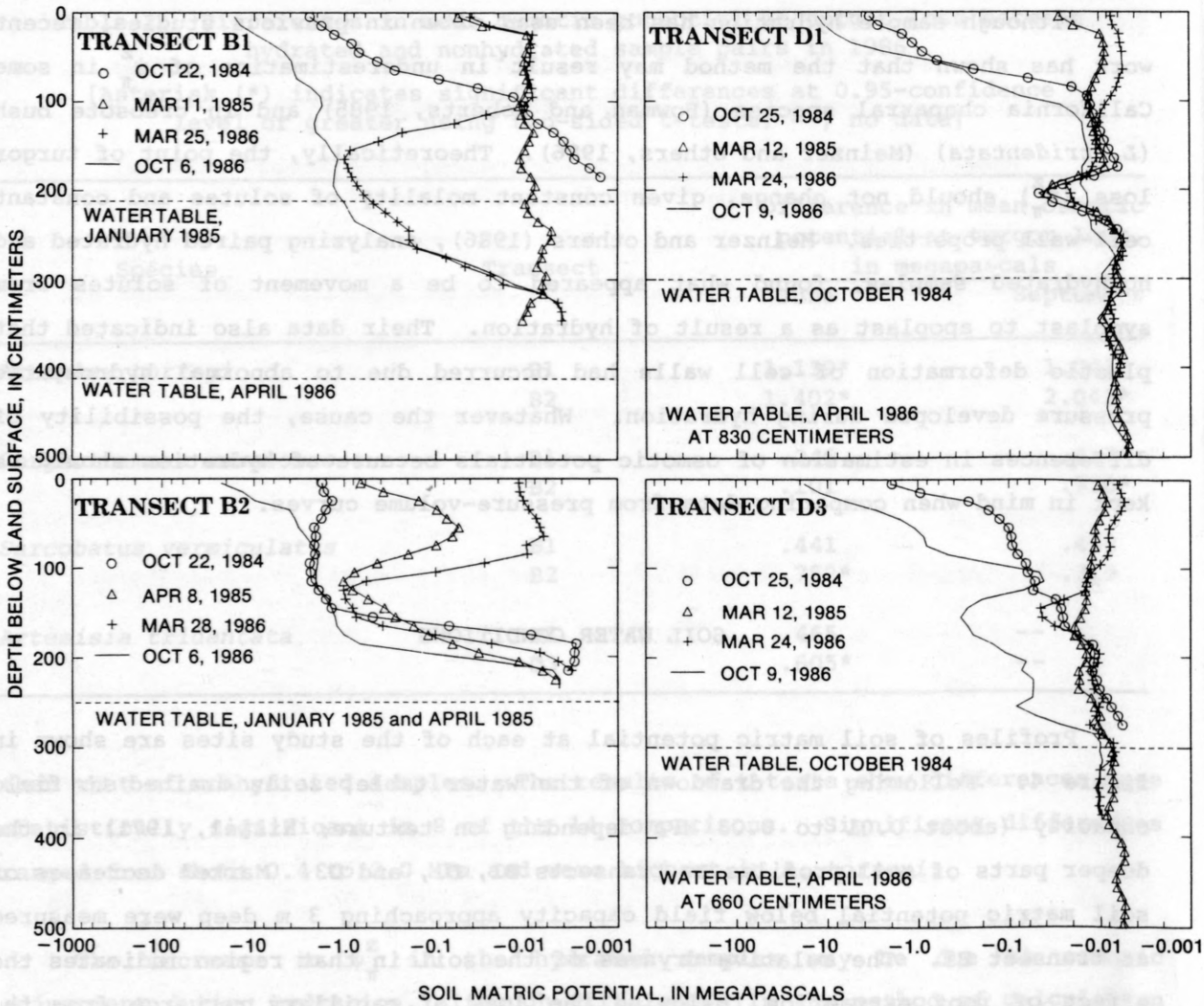

FIGURE 4.—Profiles of soil matric potential at study transects. Measurements were made at 10-cm-depth increments using the filter-paper method (McQueen and Miller, 1972; Sorenson and others, 1988).

A seasonal fluctuation of soil matric potential occurred in the top 1 m of each of the sampled soils due to winter and spring precipitation recharge. Decreasing soil matric potentials during late summer indicated water depletion by transpiring plants combined with evaporation from the soil surface.

COMPARISONS OF OSMOTIC POTENTIAL AMONG SITES, SPECIES, AND SEASONS

A series of t-tests and analysis of variance (Steel and Torrie, 1980) were used to determine the differences between sites, species, and seasons for the hydrated plant samples. The data derived from hydrated samples were used for these comparisons because data from nonhydrated samples were not available from the March 1985 sampling and because the methods used for the hydrated samples were consistent with those of most previous studies. Because the plant samples were all treated alike during the hydration and analysis, comparisons using the data from hydrated samples are considered valid.

Differences in Osmotic Potential at Turgor Loss Between Plants Growing at B1 and B2

The effect of soil-water depletion on plant osmotic responses was investigated for plants at transects B1 and B2. These two transects were selected because the soil matric potential at B1 decreased significantly during the study and the matric potential in the deeper parts of the profiles at B2 remained relatively constant owing to the presence of the water table. As a consequence of lower matric potentials at B1, less water was available for plant use.

For each of the three species, the difference in mean osmotic potential at turgor loss (ψ_π^z) was compared by two-sided t-tests between the two transects per season (table 3). No differences in ψ_π^z were visible during the March measurements. During the June measurement, *S. vermiculatus* at B1 showed significantly lower ψ_π^z. By September, *A. torreyi* and *C. nauseosus* also showed significantly lower ψ_π^z at B1 than at B2 suggesting that osmotic adjustment occurred at B1 relative to B2. The difference in ψ_π^z between plants at the two

Table 3. Differences in mean osmotic potential at turgor loss between plants growing at B1 and B2

[Asterisk (*) indicates significant differences at the 0.95-confidence level using two-sided t-tests]

Species	Mean osmotic potential at turgor loss, in megapascals		
	March 1985	June 1986	September 1986
Atriplex torreyi	0.016	0.322	0.393*
Chrysothamnus nauseosus	.072	.183	.411*
Sarcobatus vermiculatus	.055	.519*	.372*

transects corresponds to the difference in soil-water availability. Because this study was limited to one treatment site, no statistical inferences can be made concerning the lowered water table and the plants physiological response. However, the data presented provides evidence that lowered water tables can affect vegetation when the lowered water table results in lower matric potentials in the plants root zone.

Differences in Osmotic Potential at Turgor Loss Among the Four Species

Analysis of variance was used to evaluate ψ_{π}^{z} among species derived from the hydrated samples from transects B2 and D3. These transects were selected for comparison because they had soil water profiles that were relatively undisturbed by water-table decline and therefore yielded the most valid comparison of species responses under more or less natural conditions. The September data were selected for the analysis because late summer is the period that water deficit stress would exert the strongest effect within sites under natural regimes of soil water following the typically hot and dry summers that occur in Owens Valley. The 95-percent confidence intervals plotted around each of the mean values of ψ_{π}^{z} for the four species provided a visual assessment of their relative values (fig. 5). F-test results indicate that there were significant differences between means ($p>0.99$). Multiple comparisons at the

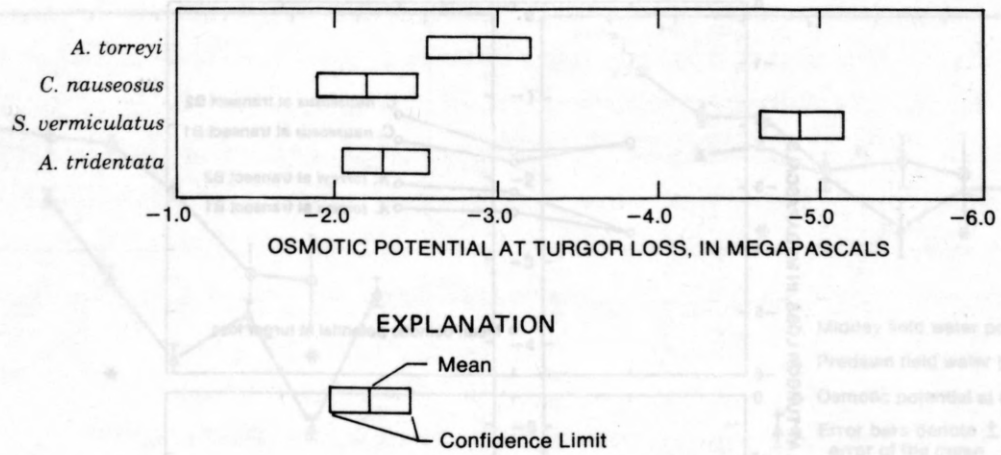

FIGURE 5.—Means and 95-percent confidence intervals for osmotic potential at turgor loss obtained in September 1986 at transect B2 from hydrated samples.

95-percent confidence level were made using Fisher's Least Significant Difference tests in order to rank the species relative to each other. *A. tridentata* and *C. nauseosus* were equivalent and showed significantly higher ψ_π^z than the other two species. Values of ψ_π^z for *S. vermiculatus* were the lowest of the four species and significantly lower than *A. torreyi*.

Seasonal Changes in Osmotic Potential at Turgor Loss

The seasonal progression of ψ_π^z estimated from hydrated samples for the four species at each of the study sites are shown in figure 6. Two patterns of change for ψ_π^z can be seen through the summer period. Statistically significant decreases in ψ_π^z were evident for *S. vermiculatus* and *A. tridentata*. *C. nauseosus* and *A. torreyi* showed no significant changes of ψ_π^z between the June and the September measurements.

The seasonal distribution of ψ_π^z indicates that *C. nauseosus* and *A. torreyi* maintained a fairly constant osmotic potential throughout the season, with minimal decrease in ψ_π^z and that turgor was maintained by an initial osmotic accumulation that remained constant through the period of measurement. In contrast, *S. vermiculatus* and *A. tridentata* began the growing season with relatively high ψ_π^z, which declined as soil water decreased during the season.

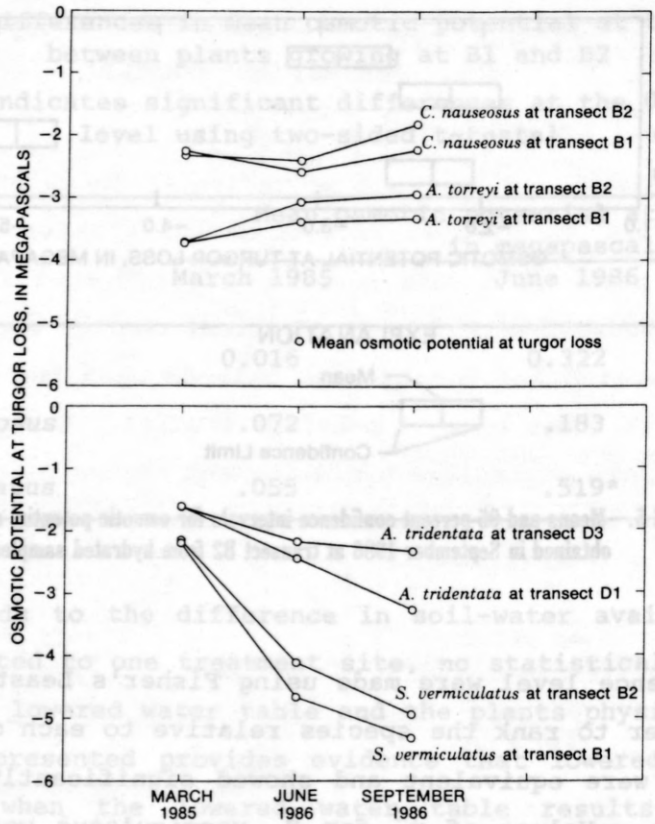

FIGURE 6.—Seasonal progression of mean osmotic potential at turgor loss developed from hydrated samples.

SEASONAL CHANGES IN MIDDAY AND PREDAWN XYLEM PRESSURE POTENTIAL

Monthly field measurements of predawn and midday shoot pressure potentials were obtained by pressure chamber for each of the species. Plots of these data are combined with the values for ψ_{π}^{z} derived in the laboratory from nonhydrated samples (except for *A. tridentata* where hydrated data are presented for the September measurements). They show a seasonal progression of decreasing predawn and midday water potentials that followed the diminishing soil water availability in the upper levels of the soils at each transect (fig. 7). Lower values for pressure potentials are believed to be related to greater drought tolerance (F.A. Branson, U.S. Geological Survey, written commun., 1987).

The predawn ψ_w for *A. torreyi* at B1 and B2 were equivalent through the growing season (fig. 7). The midday ψ_w were significantly lower in July and

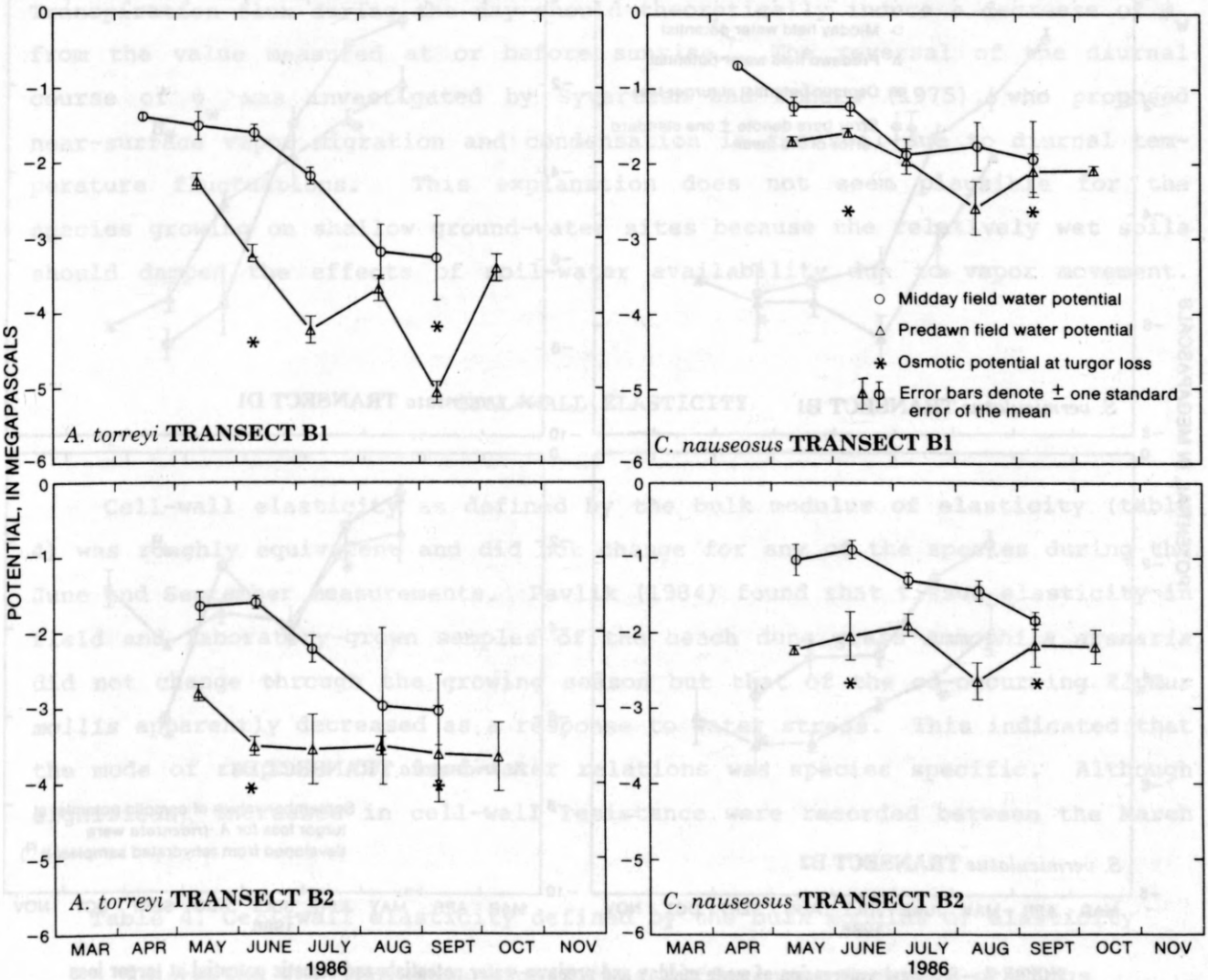

FIGURE 7.—Seasonal progression of mean midday and predawn water potentials and osmotic potential at turgor loss developed from nonhydrated samples collected before dawn.

September at B1, which had greater depth to water table and lower soil water potentials due to the experimental pumping. The August measurements of ψ_w were obtained under an overcast sky, which may explain why the data for midday were higher than expected at B1. Bennert and Mooney (1979) found that the minimum daily ψ_w for *Atriplex hymenelytra* were related to cloud cover, especially in specimens stressed by water deficit.

In the September *A. torreyi* measurements, the midday ψ_w at B1 was about 1 MPa less than the ψ_π^z measured from the samples. Because the samples were

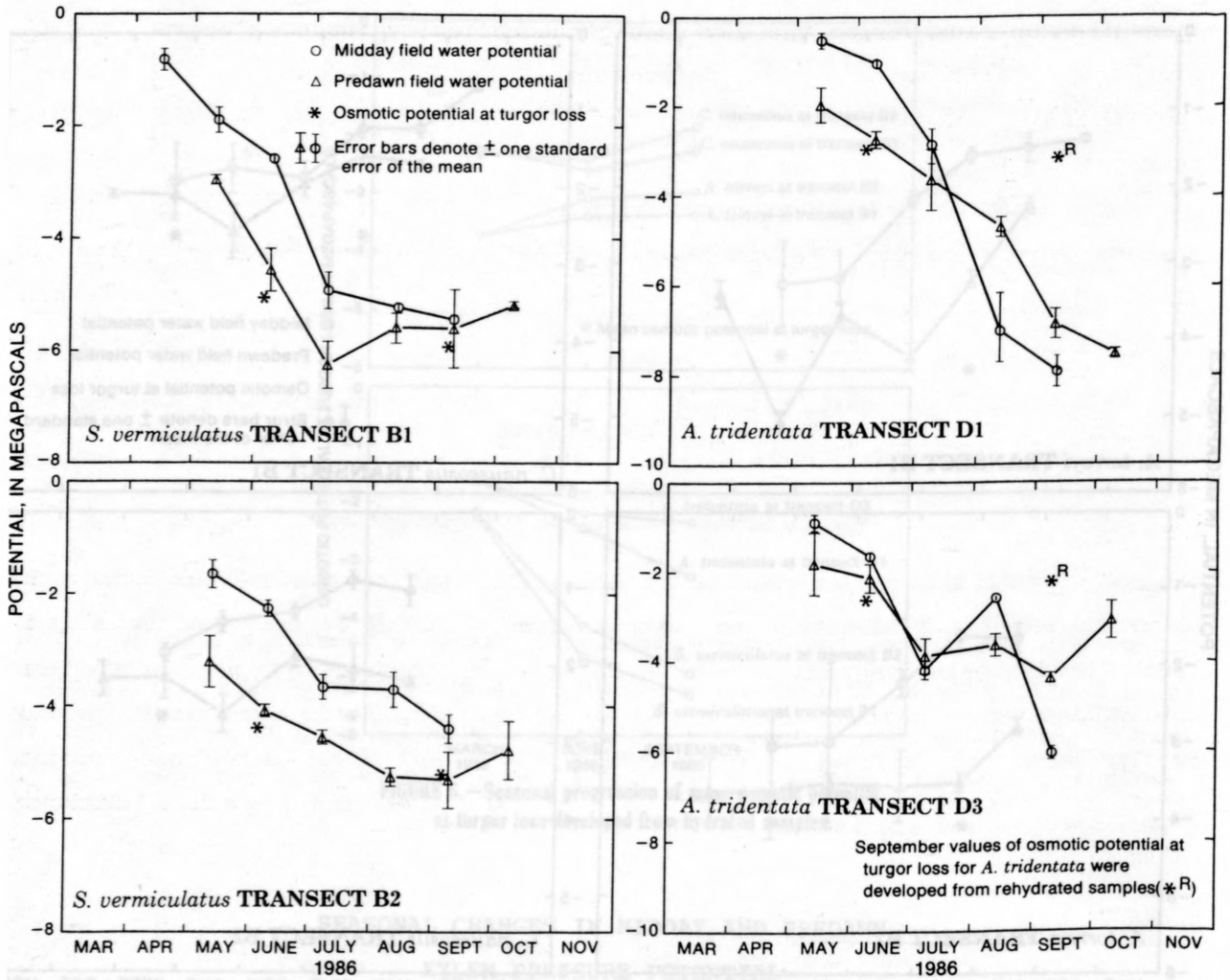

FIGURE 7.—Seasonal progression of mean midday and predawn water potentials and osmotic potential at turgor loss developed from nonhydrated samples collected before dawn — Continued.

obtained prior to dawn but are compared to midday ψ_w, this could be the result of negative turgor (Monson and Smith, 1982; Nilsen and others, 1984) or more probably, diurnal adjustment of ψ_π (Bowman and Roberts, 1985; Bennert and Mooney, 1979).

The seasonal decrease in midday and predawn ψ_w were roughly parallel for each of the species except *A. tridentata*, which displayed higher midday estimates of ψ_w than predawn ψ_w during the latter two measurements of the season. This anomalous response has been found for *A. torreyi*, *C. nauseosus*, and *S. vermiculatus* under conditions of relatively abundant soil water (D.P. Groeneveld, Inyo County Water Department, written commun., 1986).

Transpiration flux during the day should theoretically induce a decrease of ψ_w from the value measured at or before sunrise. The reversal of the diurnal course of ψ_w was investigated by Syvertsen and others (1975), who proposed near-surface vapor migration and condensation in the soil due to diurnal temperature fluctuations. This explanation does not seem plausible for the species growing on shallow ground-water sites because the relatively wet soils should dampen the effects of soil-water availability due to vapor movement.

CELL-WALL ELASTICITY

Cell-wall elasticity as defined by the bulk modulus of elasticity (table 4) was roughly equivalent and did not change for any of the species during the June and September measurements. Pavlik (1984) found that tissue elasticity in field and laboratory-grown samples of the beach dune grass *Ammophila arenaria* did not change through the growing season but that of the co-occurring *Elymus mollis* apparently decreased as a response to water stress. This indicated that the mode of response for leaf-water relations was species specific. Although significant increases in cell-wall resistance were recorded between the March

Table 4. Cell-wall elasticity defined by the bulk modulus of elasticity

[Asterisk (*) indicates significant differences from the previous sampling at the 0.95-confidence level using two-sided t-tests]

Species	Elasticity, in megapascals					
	March 1985		June 1986		September 1986	
	Mean	Standard error	Mean	Standard error	Mean	Standard error
Atriplex torreyi	6.8	3.6	12.4	6.8	7.8	9.4
Chrysothamus nauseosus	2.6	2.1	7.3*	3.1	6.2	2.8
Sarcobatus vermiculatus	6.3	2.5	14.7*	5.1	8.4	3.7
Artemisia tridentata	6.0	3.3	5.9	2.3	5.6	5.4

and June measurements for the winter deciduous *S. vermiculatus* and *C. nauseosus*, these differences may have resulted from physical hardening of the cell walls in the developing shoots during March growth initiation rather than a set response. Bulk elastic modulus did not increase in the evergreen *A. torreyi* and *A. tridentata*.

DROUGHT TOLERANCE INFERRED BY OSMOTIC AND WATER POTENTIAL MEASUREMENTS

The data for the pressure-volume curves were derived from three sampling periods that represented comparatively well watered conditions in the early part of the growing season and diminishing soil-water availability as the season progressed. The data from each of the sampling periods were combined for an analysis to determine how the initial osmotic potential (ψ_π^i) was related to the osmotic potential at turgor loss (ψ_π^z) and the initial pressure potential (ψ_w^i) as estimated by the initial balancing pressure.

Initial osmotic potential (ψ_π^i) is compared to osmotic potential at turgor loss for hydrated and nonhydrated samples in figure 8. The ψ_π data, initial and at turgor loss, were first separated into data groups that were derived from the samples that were either hydrated or nonhydrated. The relation between these data indicated that strong linearity existed for both comparisons with slopes of unity and with intercepts that described the ψ_π^z at between 0.4 and 0.8 MPa below the ψ_π^i. Both slopes and intercepts were statistically equivalent (tests according to Kleinbaum and Kupper, 1978), so one line was used to describe the data sets for nonhydrated and hydrated samples.

$$\psi_\pi^z = 0.973\psi_\pi^i - 0.581 \quad (r=0.963). \tag{3}$$

Although the data for each species did not occupy the entire range between the two variables, the values for the species represented a continuum along the calculated line. These results are similar to data of Monson and Smith (1982), which compared ψ_π^i and ψ_π^z calculated from rehydrated samples for seven Sonoran

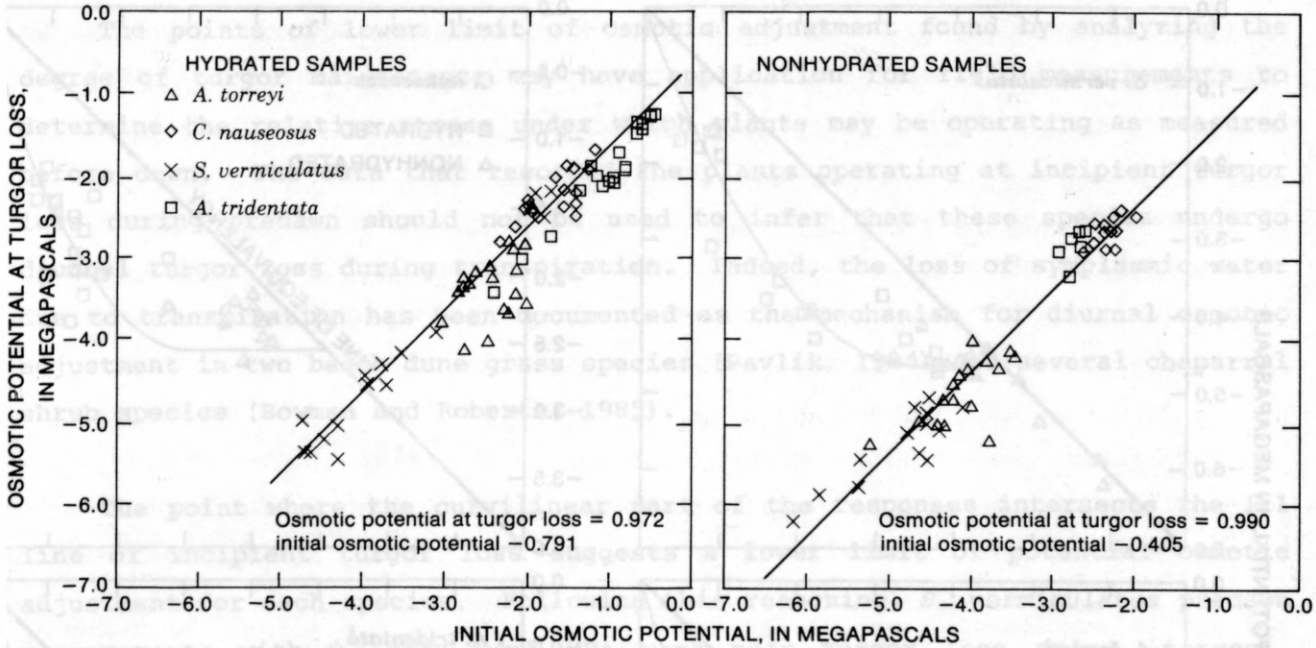

FIGURE 8.—Relation between initial osmotic potential and osmotic potential at turgor loss for hydrated and nonhydrated samples. The curves are statistically equivalent, indicating constant slope for the relation of water potential compared to relative water content among species.

Desert species that occupied different ecologic niches from xeric to phreatic. The slope of the linear relation they calculated also was equivalent to one but predicted ψ_π^z at 1.2 MPa lower than ψ_π^i.

The relation between initial osmotic potential (ψ_π^i) and initial water potential (ψ_w^i) for each species is shown in figure 9. This relation may be used to track the turgor response of each species over the range of field values of ψ_w^i. Because rehydration did not induce changes in the slope of the line between ψ_π^i and ψ_π^z in these plants, ψ_π^i and ψ_w^i pairs from both hydrated and nonhydrated samples were combined. The relation describes the turgor pressure under the hydration of the sample with respect to the line of equivalency between the initial ψ_w and ψ_π. Theoretically, when ψ_w^i and ψ_π^i are equal, the plant cells are at a state of incipient turgor loss. The plot for *S. vermiculatus* presents the most ideal response of the four species. Visible on this plot is a curve with two regions, an initial curvilinear response, which then intersects and assumes the 1:1 line of incipient turgor loss. The curvilinear part was modeled with a polynomial as shown on the graphs.

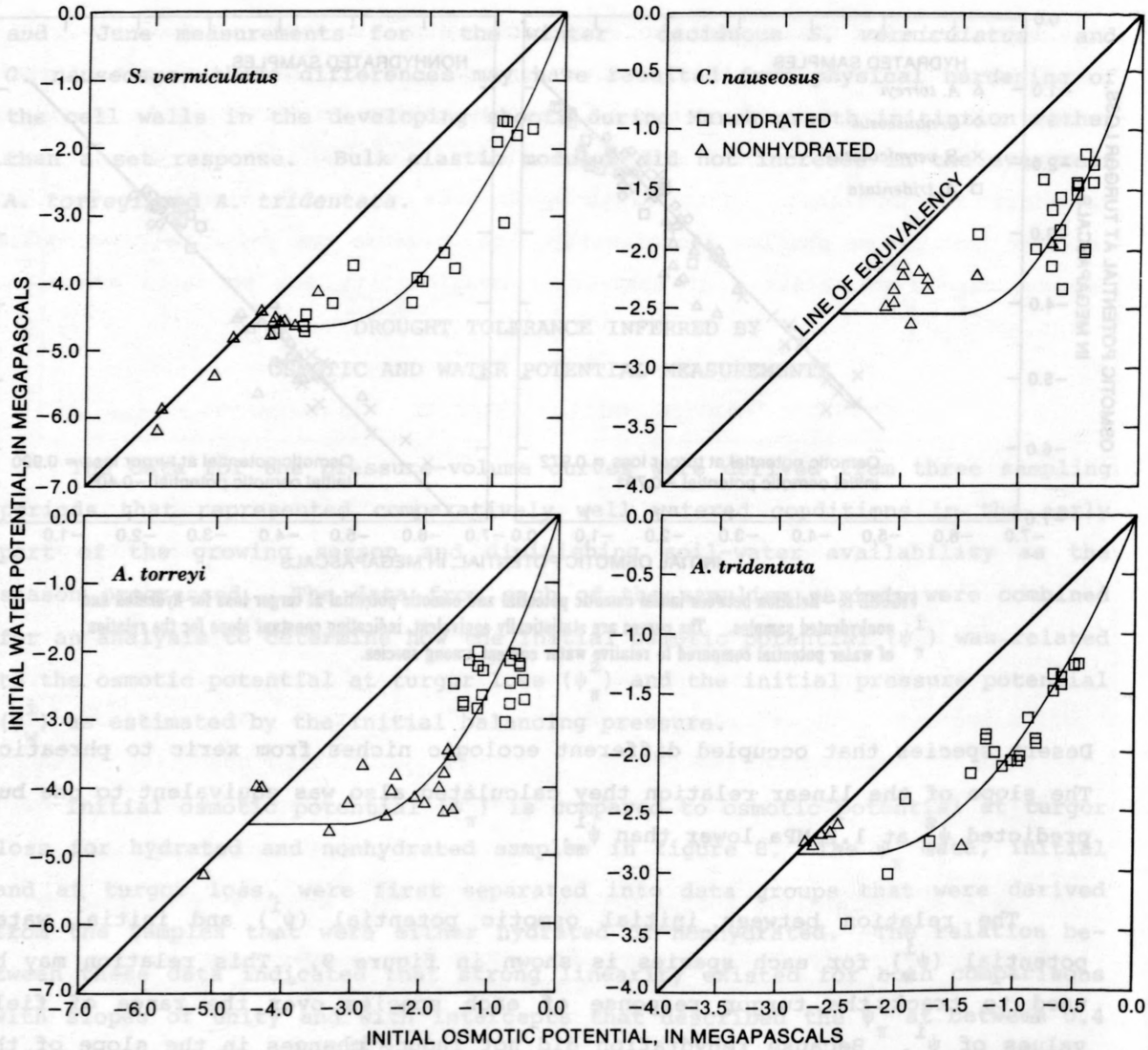

FIGURE 9.—Relation between initial osmotic potential and initial water potential of each of the shrub species.

The data developed using the nonhydrated samples recorded incipient turgor loss where ψ_π^i was equal to ψ_w for *A. torreyi*, *S vermiculatus*, and *A. tridentata*. Bennert and Mooney (1979) also found that *A. hymenelytra* and *L. tridentata* operated with turgor pressures near zero under conditions of limiting soil water. This suggests that the species were at a state of hydration near turgor loss under field conditions as sampled before dawn.

The points of lower limit of osmotic adjustment found by analyzing the degree of turgor maintenance may have application for field measurements to determine the relative stress under which plants may be operating as measured before dawn. The data that recorded the plants operating at incipient turgor loss during predawn should not be used to infer that these species undergo diurnal turgor loss during transpiration. Indeed, the loss of symplasmic water due to transpiration has been documented as the mechanism for diurnal osmotic adjustment in two beach dune grass species (Pavlik, 1984) and several chaparral shrub species (Bowman and Roberts, 1985).

The point where the curvilinear part of the responses intersects the 1:1 line of incipient turgor loss suggests a lower limit of potential osmotic adjustment for each species. Following this reasoning, *S. vermiculatus* predawn measurements with ψ_w^i near -4.5 MPa were near turgor loss and *A. torreyi*, *A. tridentata*, and *C. nauseosus* predawn measurements of ψ_w^i were near the point of turgor loss at -4.5, -2.8, and -2.5 MPa, respectively. This treatment of the data also suggests a natural division of the four species into two groups by the degree of osmotic response that parallel their phylogenetic relations. The two aster family species apparently have much less ability to maintain turgor at low water potentials than the two chenopods.

SUMMARY

The components of water potential were examined for four phreatophytic shrub species in Owens Valley, California; Nevada saltbush (*Atriplex torreyi*), rubber rabbitbrush (*Chrysothamnus nauseosus*), greasewood (*Sarcobatus vermiculatus*), and big sagebrush (*Artemisia tridentata*). The pressure-volume technique was used to estimate water potential components of leafy stems sampled from plants growing on sites where the water table had been artificially lowered and on a control site where the water table remained in its natural state. The osmotic component of water potentials were used to determine a significant physiological response of the plants to a lowered water table and to indicate their relative drought tolerance.

Soil matric potentials were monitored periodically throughout the study. Midday and predawn plant water potentials were measured in the field monthly by using a pressure chamber.

The common procedure of hydrating samples prior to pressure-volume measurements was evaluated by comparing data developed from split samples; one-half at field hydration and one-half hydrated overnight in the laboratory. Hydration resulted in higher estimates of osmotic potential.

Compared to plants growing above a naturally high water table, significantly lower osmotic potentials were measured during late summer in the plants growing above an artificially lowered water table. Measurements of soil matric potential indicated that osmotic adjustment occurred in response to reduced soil-water availability. Low osmotic potentials theoretically permit the maintenance of positive hydrostatic pressure (turgor) in the cell under conditions of low soil-water availability. Because turgor pressure is important for growth and metabolic processes, its maintenance is important for drought resistance under conditions of water deficit.

Osmotic potentials declined markedly through the growing season for *A. tridentata* and *S. vermiculatus*. The osmotic potentials for *A. torreyi* and *C. nauseosus* remained relatively constant throughout the period of monitoring.

The bulk modulus of elasticity determined from the hydrated samples indicated that the cell-wall properties for resisting the tensions developed during osmotic adjustment remained relatively constant through the mid- to late-growing season for all four species.

A theoretical lower limit of osmotic adjustment was determined for combined hydrated and nonhydrated samples by comparing the estimated osmotic potentials with initial water potentials determined at the beginning of the pressure-volume measurements. This comparison indicated a natural division of the plant species into two groups that paralleled their phylogenetic relations. As measured from the predawn samples, *A. torreyi* and *S. vermiculatus* were

capable of adjusting osmotic potentials to about -4.5 MPa and *A. tridentata* and *C. nauseosus* only achieved osmotic adjustment to about -2.5 MPa. These experimentally derived limits indicate that simple field measurement of predawn water potential may be used to indicate whether a plant may be operating near the point of turgor loss and, therefore, near the limit of its capability to withstand further drought stress.

PLANT-WATER RELATIONS

This section presents concepts and terminology currently used in the field of plant physiology. It was written for the reader unfamiliar with this field in order to provide sufficient technical background for a comprehensive reading of this report.

Water is in constant motion around and within living plants. In order to maintain sufficient water content for life processes, terrestrial plants must balance water intake from the soil with water lost through transpiration. Water movement in plants may be described by a form of the general transport law:

$$\text{flux} = \text{driving force}/\text{resistance} \qquad (4)$$

Flux, or flow, is the volume of water transpired as a function of time. The flow is moderated by a series of resistances occurring in the soil and plant system that are determined by characteristics of the conducting medium. The driving force for water movement can be expressed as a difference or gradient in the chemical potential of water between two points. The chemical potential of water is usually referred to in terms of water potential (ψ_w). Water potential is a measure of the ability of water to do work in terms of its free energy and volume compared to pure water at standard pressure and temperature. Water moves in response to differences in water potential with the direction of movement from higher to lower potential. Energy and volume units are more conveniently expressed as equivalent pressure units such as the megapascal (MPa). One MPa equals 10 bars, which equals 10^6 newtons per square meter.

In plants, ψ_w the whole plant water potential, is the sum of four components:

$$\psi_w = \underset{(1)}{\psi_p} + \underset{(2)}{\psi_\pi} + \underset{(3)}{\psi_m} + \underset{(4)}{\psi_g} \quad (5)$$

(1) Pressure potential (ψ_p) is the hydrostatic pressure. An increase in pressure increases water potential and a decrease in pressure decreases water potential. Pressure potential can be either positive or negative.

(2) Osmotic or solute potential (ψ_π) is the reduction in free energy of a solution due to the addition of solutes to pure water. As the concentration of dissolved solutes increases, the potential of the solution decreases.

(3) Matric potential (ψ_m) results from the weak molecular bonding between polar water molecules and surfaces of the medium such as are in the soil particles or the cellulose and organic compounds of plant tissues. In unsaturated soil, matric potential also can refer to hydrostatic pressure resulting from the cohesive nature of water.

(4) Gravitational potential (ψ_g) is the force exerted on water due to its position in the Earth's gravitational field. Though ψ_g can be a significant factor in moving water up a tall tree or a very deep root system, the magnitude of ψ_g is insignificant compared to the other potential components for the short vertical distances that water moves in shrubs.

At equilibrium, the ψ_w that results from the additive effect of the four components in the plant cell is equal to the tension that exists in the xylem adjacent to the leaf cells.

Most of the water in a plant is in its living cells. Cell water content affects many primary metabolic processes in the cells, and so affects the functioning of the entire plant. Plant cells consist of a cell wall surrounding an aqueous protoplast. The cell wall is a porous matrix of cellulose capable of elastic expansion. Under normal conditions, a positive pressure

exists in the cell caused by the resistance of the cell wall to expansion of the water swollen protoplast. This pressure, called turgor pressure, is dependent on the relative volume of the protoplast, which is a function of its water content.

The interior elements of living cells (protoplast) are bounded by a differentially permeable membrane, which allows water molecules to pass through relatively unhindered but restricts or controls the movement of solutes (Kramer, 1983). Dissolved solutes are concentrated in the protoplast in membrane bound regions called vacuoles. Plants may control location and concentration of solutes to control the water potential in the cell and thus affect intercellular water movement (Zimmerman, 1978).

A net flow of water into or out of cells occurs when there are differences of ψ_w within the cell and outside of the cell membrane. The significant water potential components within the cell are ψ_π caused by dissolved solutes concentrated within vacuoles and ψ_p resulting from turgor. Matric potential is usually ignored because, in saturated conditions, it is usually low and remains relatively constant for short periods of time. Turgor is developed when the cell ψ_π is lower than ψ_w of the water outside the cell. Water will flow into the cell causing turgor pressure to increase until the sum of the negative ψ_π and the positive ψ_p (turgor pressure) are equal to ψ_w outside the cell. The water within a plant is considered to be partitioned between the living cells (symplast) and outside of the cells (apoplast).

As water is lost from leaves during transpiration, matric forces lower the water potential in leaf tissues, creating a water-potential gradient that draws water from the xylem. Xylem is a water-conducting tissue that serves as a low resistance pathway for water movement from the roots to the leaves. Owing to the cohesive nature of water, the decrease in potential is transferred throughout the plant to induce the uptake of water from the soil by roots. When the water potential in the xylem becomes lower than that of the water held in the soil, water and dissolved nutrients move from the soil into the root, and are drawn through the xylem to the leaves. In the leaves, water moves from the xylem into cell walls and intercellular spaces replacing the water lost by transpiration (Van den Honert, 1948; Slatyer and Taylor, 1960; Oertli, 1976).

Water-vapor loss takes place through openings in the leaf (stomata), which has specialized guard cells that control the aperture and thus gas diffusion into and out of the leaf. Because of the steep water potential gradient between the atmosphere and the leaf and the presence of a relatively impervious epidermal cuticle, the primary control of water vapor diffusion and flow through the soil, plant, atmosphere continuum is through the stomata (Milburn, 1979; Kramer, 1983).

As water vapor moves out of the leaf, carbon dioxide diffuses into the leaf through the open pores of the stomata to provide the raw material for photosynthesis and carbohydrate production. Though the water lost during the gas exchange for photosynthesis benefits the plant by inducing the flow of water and nutrients from the soil, the development of water deficit due to uncontrolled water loss would be detrimental to growth and viability particularly in an arid environment. Stomatal control of leaf conductance therefore attempts to balance the production of carbohydrate through uptake of CO_2 and the detrimental effects that are induced by concomitant losses of water.

Stomatal aperture is a function of guard cell turgidity, which is highly affected by the water status of the plant (Hsiao, 1973; Jarvis, 1980; Davies and others, 1981). Stomata also may react to other stimuli; temperature, relative humidity, light, and intercellular CO_2 concentration, but with the overall function is to adjust leaf conductance so that carbon gain (photosynthesis) is optimized for minimal water loss (Cowan and Farquhar, 1977).

Water deficit develops when a plant loses more water by transpiration than is absorbed from the soil by roots. Water stress occurs when the deficit is sufficient to disturb normal functions (Kramer, 1980). Limited water deficit is often a diurnal occurrence during midday due to high rates of evaporation (Kramer, 1937). Such short-term water stress may occur even in relatively wet soils (Tazaki and others, 1980). During the night when transpiration processes generally cease, gradual uptake of water by the roots adjusts the water potential between the plant and soil toward an equilibrium.

Extreme or long-term deficits may have many deleterious effects on plant growth and function (Hsiao, 1973; Kozlowski, 1978, 1981; Bradford and Hsiao, 1982). Strain due to the stress of water deficit is the largest single cause of lost productivity in agricultural crops (Kramer, 1980). On a larger scale, the availability of soil water is a major factor that controls the occurrence of native plant communities (Lange and others, 1976).

Changes in turgor have been implicated as the mechanism by which water deficits are manifested as changes in metabolism (Hsiao, 1973; Hsiao and others, 1976). Turgor pressure controls the process of cell elongation which is required for plant growth (Acevedo and others, 1971). In addition, the maintenance of turgor pressure within stomatal guard cells ensures gas exchange for photosynthesis. Turgor maintenance at low water potentials therefore permits the plant to survive periods of low water availability (Hsiao and others, 1976).

Turgor pressure at any given water content depends on the cell osmotic potential being lower than the potential of the water in the xylem. Low cellular osmotic potential therefore achieves turgor maintenance under conditions of water deficit. Some plants accumulate solutes within their cells, thus decreasing their osmotic potential. This process is called osmotic adjustment (Turner and Jones, 1980). Osmotic adjustment has been noted for plants within both diurnal and seasonal time scales (Bowman and Roberts, 1985; Pavlik, 1984; Bennert and Mooney, 1979; Nilsen and others, 1984; Hinckley and others, 1983; Monson and Smith, 1982). The degree of the osmotic adjustment that can be achieved by a plant under conditions of water deficit therefore may be used as an indicator of the drought tolerance of a species.

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GLOSSARY

Apoplast.--One of two water systems in a plant. The apoplast includes the xylem, cell walls, and all space that exists outside the cell protoplasts, as opposed to symplast.

Cellulose.--A complex carbohydrate forming the submicroscopic fibers that are the principal structural component of plant cell walls.

Cryoscopy.--The determination of solute concentration or solute potential by measurement of the freeze point depression of a solution.

Cuticle.--A water resistant waxy layer covering the outside surface of leaves.

Deciduous.--Plants that lose their leaves at the end of their growing season, as opposed to evergreen.

Differentially permeable membrane.--A membrane that permits water molecules to pass through freely, but inhibits or restricts the movement of dissolved solutes.

Elastic modulus.--A measure of the elasticity of a cell wall.

Gravitational potential.--The component of water potential resulting from position in a gravitational field.

Guard cells.--Specialized cells bordering stomata. Changes in turgor of these cells result in changes in shape that cause stoma to open or close.

Metabolism.--The chemical processes of living cells.

Osmotic adjustment.--The active accumulation of solutes within cells in response to water deficit stress.

Osmotic potential.--Also referred to as solute potential. The component of water potential resulting from the addition of solutes to pure water. It is always negative in sign.

Photosynthesis.--The production of carbohydrates from carbon dioxide and water using energy from light.

Phreatophyte.--An ecologic classification designating a plant that receives at least part of its total water requirements directly from a water table or the capillary zone above it.

Pressure chamber.--A device used to measure xylem and leaf water potential. A leafy stem is sealed inside the chamber with the cut end of the stem protruding through a gas tight compression gasket. Compressed air or nitrogen is metered into the chamber slowly raising the its pressure. The magnitude of the pressure at which fluid begins to exude from the stem is considered equal to the tension (negative pressure) that existed in the stem when it was cut and is regarded as an estimate of leaf tissue water potential. A single leaf also may be used.

Pressure potential.--The component of water potential due to positive or negative hydrostatic pressure.

Protoplast.--The living contents of a cell within the cell membrane.

Stoma (plural, stomata).--Small openings in the leaf (and sometimes stem) epidermis that facilitate gas exchange and transpiration between plant and atmosphere.

Subirrigation.--Water supplied to the root zone from below the roots.

Symplast.--The water system consisting of all the cell protoplasts.

Transpiration.--The loss of water vapor from plants, primarily through stoma.

Turgor.--The positive pressure in plant cells caused by the resistance of the cell wall to expansion of the protoplast. This pressure results in much of the cells structural rigidity and in the maintenence of the cells interior organization.

Vacuole.--A membrane-bound region within the protoplast which functions as a storage for dissolved and undissolved materials and in the maintenance of cell water balance.

Water potential.--A measure of the thermodynamic free energy state (Gibbs free energy) of a given mass of water compared to pure water at standard pressure and isothermal conditions. The different physical and chemical factors that affect water potential can be expressed as water potential components whose algabraic sum is equal to the water potential. In plant water relations, the most significant components are the pressure potential, osmotic potential, and matric potential. Differences in water potential are the driving forces for water movement from soil to plant to atmosphere and for water movement into and out of plant cells.

Xylem.--The principal water conducting tissue in plants. Mature xylem consists of dead elongated and hollow cells and associated living cells, which run longitudinally throughout the plant and function as conduits for water and mineral transport from the roots to the leaves.

Xylem lumina.--The interior of the xylem tissue's water conducting elements.

Xylem pressure potential.--The water potential within the xylem elements as measured by the pressure chamber. In equilibrium conditions, it is also a measure of leaf tissue water potential.