TOLERANCES OF PLANTS TO DROUGHT AND SALINITY IN THE WESTERN UNITED STATES

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CONVERSION FACTORS

For use of readers who prefer inch-pound units rather than the metric (International System) units used in this report, the following conversion factors may be used:

Multiply metric unit	*By*	*To obtain inch-pound unit*
meter (m)	3.281	feet
centimeter (cm)	0.3937	inch
megapascal (MPa)	0.1	bar

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ABSTRACT

Differing capacities of plant species to tolerate drought and salinity are causative factors for presence of species and communities in various habitats. It is proposed that minimum xylem pressure potentials are indicative of drought tolerance and that minimum cell osmotic potentials are indicative of salt tolerances of plant species.

Of 85 species measured, Nuttall saltbush *Atriplex nuttallii nuttallii* was found to be the most drought tolerant. Saltbushes *Atriplex confertifolia*, *A. nuttallii*, *A. canescens*, and *A. torreyi* had the lowest measured cell osmotic potential. Although pickleweed *Allenrolfea occidentalis* grows in the saltiest soil measured, it did not have the lowest cell osmotic potential. This apparent inconsistency may be explained by the succulent characteristics of pickleweed.

INTRODUCTION

The variation of species of plants from one habitat to another has intrigued mankind for centuries. Ecological inquiry is mostly directed towards explaining distribution patterns of organisms (Ritchie and Hinckley, 1975). Many environmental factors affect the capacity of plants to grow in certain habitats, but most important are those factors associated with availability of water (Kozlowski, 1964). Water is not only the driving variable of most importance for almost all contemporary desert community interactions, but is probably the basis of community evolution in the past (McMahon and Schimpf, 1981).

Water is being pumped from aquifers in closed basins in the Western United States for various uses. This pumping is likely to cause a reduction in the amount of ground water available for existing vegetation. Responses of vegetation to a reduction in water is now and will continue to be of considerable interest to the residents of these areas. Questions that concern managers of these lands include, which species will survive if water availability is greatly reduced and which species are likely to replace those present before pumping? By compiling published and unpublished data on the drought tolerances of plants in the Western United States (fig. 1), it is possible to determine which plants will be most affected by the water-level declines caused by ground-water withdrawals.

Purpose and Scope

The purpose of this report is to present data on xylem pressure potential, cell osmotic potential, and soil salinity that may be used to estimate the relative drought and salinity tolerances of plants in the Western United States.

Published data of xylem pressure potential, cell osmotic potential, and soil salinity, along with extensive unpublished data collected by the authors, were reviewed and summarized. Xylem pressure potential, cell osmotic potential, and soil salinity were calculated for each species for which there were data. Relative drought tolerances were estimated by listing the plant species according to the minimum xylem pressure potentials reported. A similar index of drought tolerance was determined from the data on cell osmotic potential. Data on soil salinity associated with different species of plants were compiled to estimate an index of tolerance to soil salinity.

Concepts

Water moves through a plant in a continuous, cohesive hydraulic system that extends from the roots to the leaves. Water enters the system through the roots and is transpired from the system primarily through evaporation from the leaves. Movement of water throughout this "soil-plant-atmosphere continuum" (Philip, 1957) is caused by differences in chemical potential from one part of the continuum to the next (Dileanis and Groeneveld, 1988).

Total water potential within a plant is represented by the equation (Kramer, 1983):

$$\psi_\omega = \psi_\pi + \psi_p + \psi_m + \psi_g ,$$

where

ψ_ω = total water potential,

ψ_π = osmotic potential,

ψ_p = pressure potential,

ψ_m = matric potential, and

ψ_g = gravitational potential.

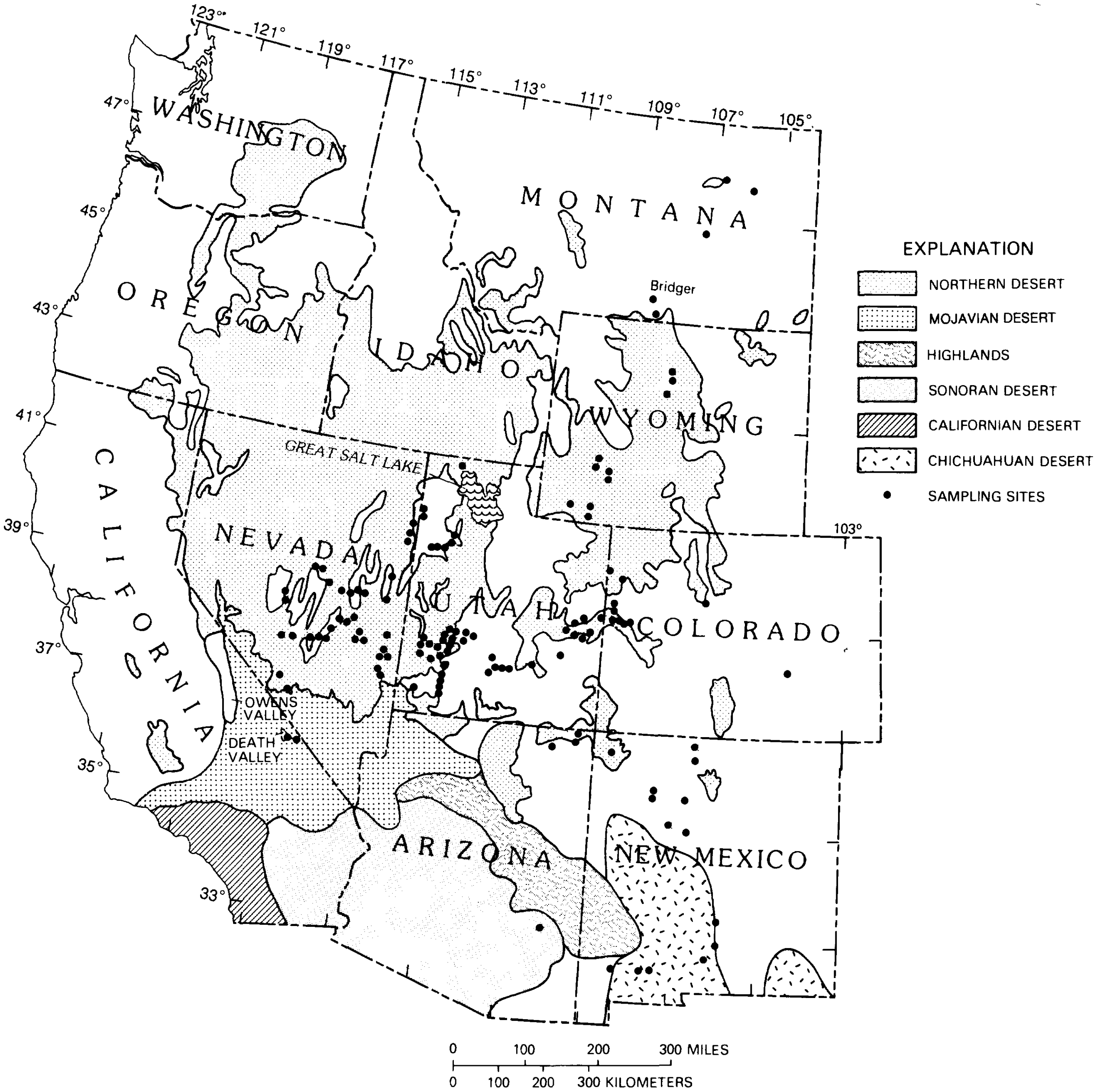

FIGURE 1.—Major desert classifications in the Western United States. Dots on the map represent sites studied by F.A. Branson and R.F. Miller. Study areas of other authors cited in this report are not shown.

Gravitational water potential is not considered in shrubs because it represents only 0.01 MPa per meter of plant height. In tall trees, gravity effects are measurable and important (Scholander and others, 1965). For instance a 100-meter-tall Sequoia would require 1 MPa of gravitational potential to transport water from the roots to the top. Matric potential within the plant is also considered to be small in proportion to pressure potential and osmotic potential.

Differences in pressure potential (usually measured as xylem pressure potential) is primarily induced by atmospheric potential, which is often less than -200 MPa in desert environments. This low potential results in evaporation of water from substomatal chambers of leaves by transpiration. The loss of this water through transpiration results in a negative potential within the substomatal chambers, which in turn draw water from areas of higher potentials in the xylem tissues. Water then moves into the root tissues in response to the potential gradient to replace that transpired through the leaves. The graph in figure 2 illustrates the soil-plant-atmosphere continuum. The large differences in potentials from one end of the continuum to the other only occur during the day when large negative potential differences develop between the atmosphere and the surface of the leaves. Transpiration is primarily a function of atmospheric potential (Van Bavel and others, 1963). During the night when atmospheric potential is high, there is little movement of water, thus very little gradient within the continuum. During the day, atmospheric potential continues to control transpiration as long as soil water does not become limiting. If transpiration rates exceed the capacity of the plant to move water from the soil through the plant tissues, the plant must decrease transpiration by responses such as closing stomatal openings.

Total water potential must be less than matric and osmotic forces that retain water in the soil. Plants adapted to growing in desert environments have developed morphological and physiological mechanisms to aid in extracting more water from the soil or to reduce transpiration. Morphological adaptations, such as sunken stomata, abundant leaf hairs, and thick cuticular layers reduce transpiration. Adjustment of stomatal openings is the most important regulator of transpiration (Hsiao, 1973). The primary mechanism used by plants to enable extraction of water from soils, as lower soil matric potentials develop, is osmotic regulation (Dileanis and Groeneveld, 1988). This mechanism, particularly well developed in desert plants, concentrates solutes in root cells where water is absorbed selectively through semipermeable membranes even when soil matric potentials are less than -2 to -3 MPa.

TOLERANCES OF PLANTS TO DROUGHT AND SALINITY

In reviewing the available literature for drought and salinity tolerances of plants, it is apparent that different authors have used many different methods to evaluate the capacity of plants. In this section of the report the most often used techniques to determine plant tolerances are briefly summarized and compared.

Measurement of Xylem Pressure Potentials

The most common method of measuring xylem pressure potential is the use of the pressure chamber, developed by Scholander and others (1965). The pressure chamber is used by sealing a small leafy stem into the chamber with a gas-tight rubber stopper. Pressurized air or nitrogen is introduced into the chamber until fluid appears at the surface of the cut stem. Xylem pressure potential is calculated as the negative equivalent of the positive pressure required to force xylem fluid from the stem.

Although the pressure chamber measures xylem pressure potential, in most plants it also gives an adequate estimate of total water potential. This is because osmotic potential within the xylem is

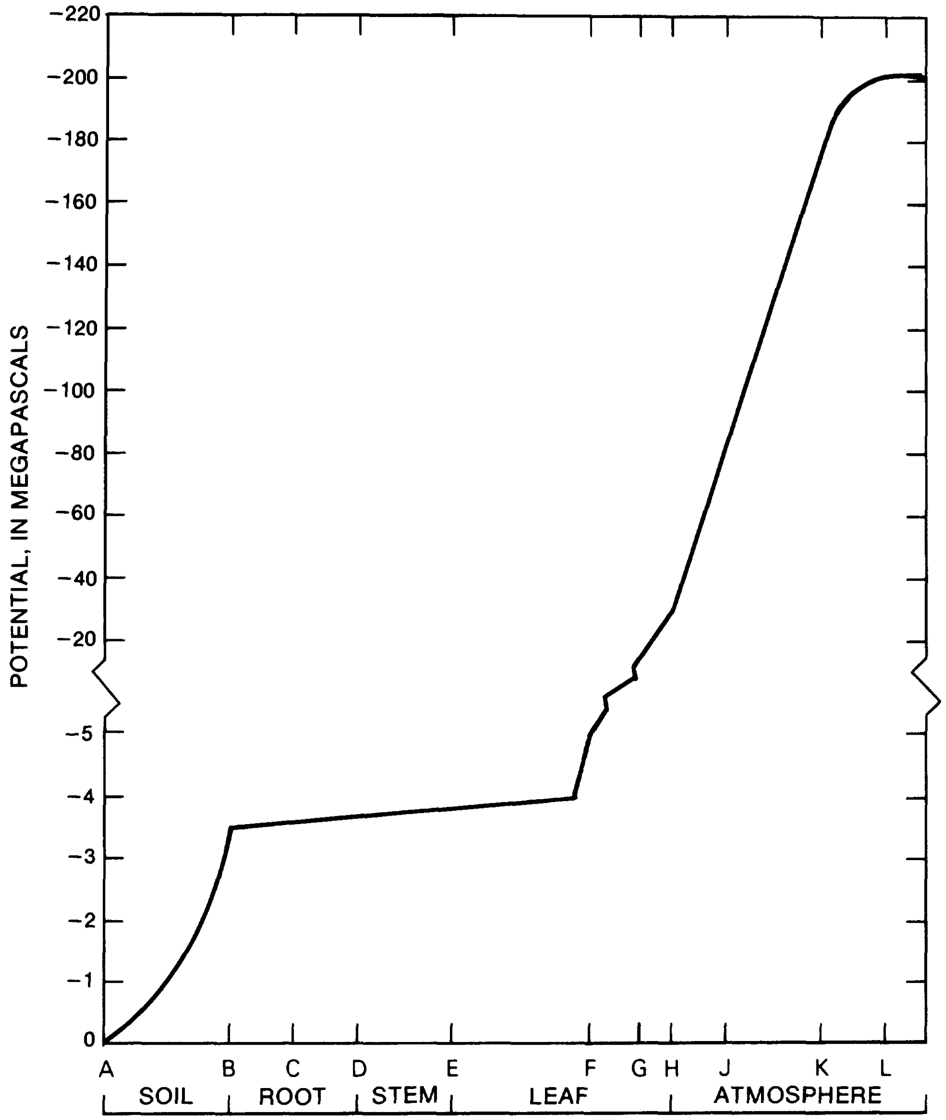

FIGURE 2.—Hypothetical energy profile for the soil-plant-atmosphere continuum for a habitat that has shallow ground water in a hot arid climate. As illustrated, the continuum consists of: (A-B) soil; (B) surface of root hairs; (C) cortex; (D) endodermis; (D-E) xylem vessels and tracheids leaf veins; (F) mesophyll cells; (F-G) intercellular space and substomatal chamber; (G-H) stomatal pore; (H-J) laminar boundary layer at leaf surface; (J-K) turbulent boundary layer; (K-L) free atmosphere. (Adapted from Philip, 1957.)

usually high when few dissolved substances are present and is therefore generally considered negligible (Richie and Hinckley, 1975; McMahon and Schimpf, 1981).

Measurement of Cell Osmotic Potentials

Maintainance and regulation of low cell osmotic potentials are adaptations of plants to saline and arid environments. Osmotic adjustments permit cell enlargement and growth to continue at total water potential levels that would otherwise be limiting (Kramer, 1983). The capacity of species to maintain low cell osmotic potentials also allows access to a greater volume of soil water (Monson and Smith, 1982).

Methods used to measure cell osmotic potential include pressure-volume curves (Scholander and others, 1965), refractive index (Barrs, 1968), freezing-point depression (cryoscopy), and by the use of various osmometers. All methods that use expressed sap to obtain freezing-point depression are subject to dilution error caused by mixing cell wall or apoplastic water with protoplasmic (symplastic) water. Xylem water has been found to be relatively free of salts; thus, the dilution error is avoided when using the pressure-volume curve method. A concentration error is induced when sap is expressed from certain halophytes. In halophytes, such as species of *Atriplex*, salt accumulates in trichomes (vesiculated hairs) on leaf surfaces; osmotic potentials in trichomes may reach -50 to -70 MPa (Mozafar and Goodin, 1970). When trichomes burst, salts are deposited on leaf surfaces causing possible error when expressed sap is used to estimate cell osmotic potentials. Separating epidermal tissue containing trichomes from leaves is extremely difficult, sometimes impossible, but if not done, questionable results are obtained. Washing leaf surfaces to remove salts is unsatisfactory because of possible dilution of leaf-tissue solutions. Most methods, including the psychometric technique, may yield erroneous results if leaf-surface salts are not removed. Although suspect, data derived from cell sap expressed from leaves by pressure are used in this report because they represent the only available data for many species.

Sholander and others (1965) were the first to demonstrate field use of pressure-volume curves to determine cell osmotic potentials of cell sap for species of moist and dry habitats. The method was refined and is now extensively used (Tyree and Hammel, 1972; Tyree and others, 1973; and Cheung and others, 1975). Tyree and Hammel (1972) found that when enough liquid was expressed to approach the linear part of the pressure-volume curve, the balancing pressure closely matched the cell osmotic potential of intracellular sap determined by the freezing-point depression method.

Measurement of Soil Salinity and Osmotic Potentials

Soil osmotic potentials were measured in the upper 10 cm of soil by using electrical conductivity of saturated paste of soil and water (a method proposed by Richards, 1954). It is assumed that soil-surface salt contents determine species of plants that can become established in an area. Soil osmotic potentials at field capacity (amount of water held in soil after drainage) are shown because at this water content most of the salts are in solution.

OSMOTIC POTENTIALS OF PLANTS

Range of Xylem Pressure Potentials

No single factor determines the distribution of species, but differences in soil water availability and plant responses to these differences must be important. Adaptations to high water stress or low potentials is substantially responsible for determining plant adaptation and distribution in nature (Ritchie and Hinckley, 1975). Pressure-chamber measurements have also been used to evaluate drought tolerances of shrub species considered useful for reclamation of disturbed lands (Wilkins and Klopatek, 1984). A number of studies show a direct response of lowered xylem pressure potential to lowered soil water potential (Slatyer, 1961; Ellison, 1969; Moore and others, 1972; Sucoff, 1972; Bamberg and others, 1975; Branson and Shown, 1975; Easter and Sosebee, 1975; Syvertsen and others, 1975; Branson and others, 1976; Redmann, 1976; Campbell and Harris, 1977; Clark and others, 1980; Kleinkopf and others, 1980; Nilsen and others, 1983; and Wilkins and Klopatek, 1984).

Minimum, mean, and maximum total xylem pressure potentials for 71 western plants are shown in figure 3. As appears to be

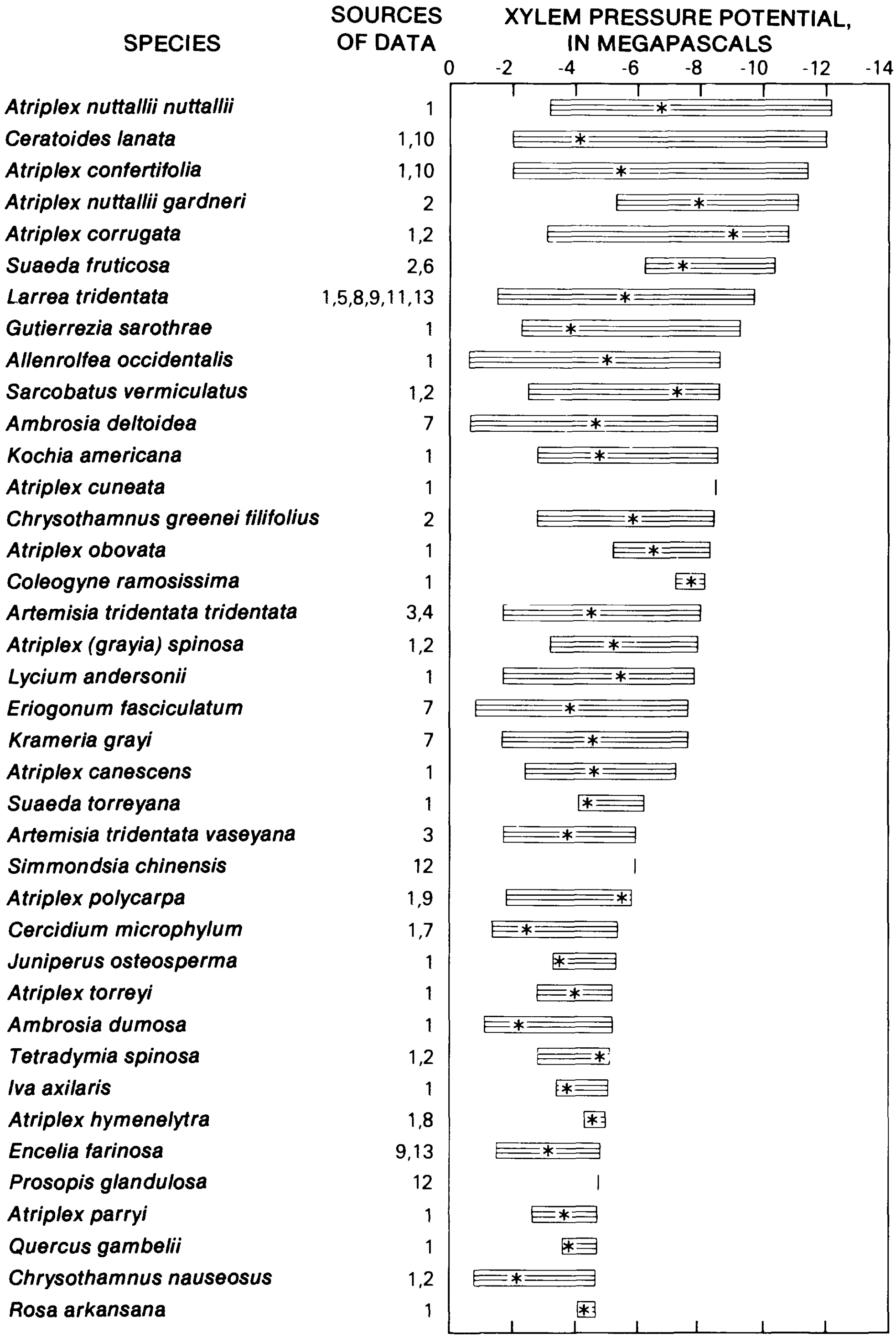

FIGURE 3.—Minimum, mean (*), and maximum total xylem pressure potentials for 71 plant species. Where only one measurement is available it is represented by a single vertical line. Species that tolerate the lowest potential are the most drought tolerant. Sources of data are: (1) F.A. Branson, U.S. Geological Survey, written commun., 1987; (2) Branson and others, 1976; (3) Branson and Shown, 1975; (4) Campbell and Harris, 1977; (5) Cunningham and Burk, 1973; (6) Detling and Klikoff, 1973; (7) Halvorson and Pattern, 1974; (8) Pearcy and others, 1974; (9) Monson and Smith, 1982; (10) Moore and others, 1972; (11) Syvertsen and others, 1975; (12) Nilsen and others, 1984; (13) Odening and others, 1974; (14) Wambolt, 1973; and (15) White and Carrie, 1984.

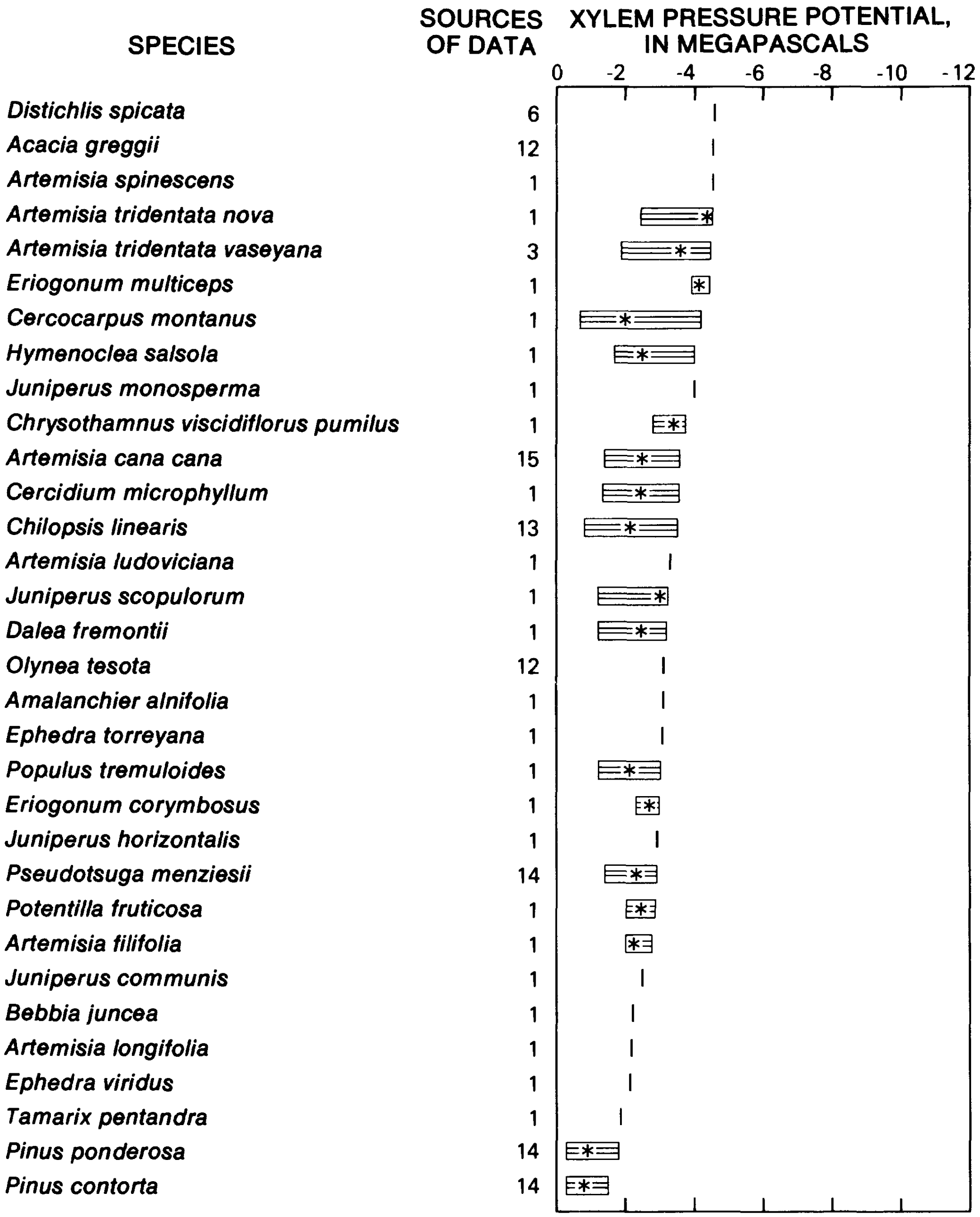

FIGURE 3.—Minimum, mean (*), and maximum total xylem pressure potentials for 71 plant species—Continued.

true of salinity tolerances (Daubenmire, 1948), most negative potentials are more indicative of drought tolerances than are the mean highest potentials. Maximum xylem pressure potentials, achieved when soil water is readily available, are similar for most species. Species shown in figure 3 include xerophytes, halophytes, and some mesophytes, but no drought-avoiding annuals, hydrophytes, or succulent species such as cacti. The order of species shown in figure 3 is from lowest to highest measured xylem pressure potentials. Published references are included in the figure caption, but most of the data shown are from unpublished material collected by the authors.

Nuttall saltbush (*Atriplex nuttallii nuttallii*), had the lowest xylem pressure potential of hundreds of plants that were measured. This low potential exceeds that of plants growing in the lower part of Death Valley (see *Atriplex hymenelytra* and *Hymenoclea salsola*, fig. 3) and many other desert areas. An area near Bridger, Montana, where these measurements were made could be designated an "edaphic desert" because of the high runoff characteristics of the clayey soil. The second lowest measurements of xylem pressure potential was made on winterfat (*Ceratoides lanata*) by Moore and others (1972) in Utah. Even at this low potential (-12 MPa), the plants were actively photosynthesizing. The results of Moore and others (1972) differ from those of Branson and others (1976), who found seasonal minimum potential of winterfat to be higher than those of Nuttall saltbush (*Atriplex nuttallii*), mat saltbush (*A. corrugata*), and shadscale (*A. confertifolia*).

Many of the Northern Desert shrubs (fig. 3) attain lower xylem pressure potentials than do species of the hotter Mojave Desert, such as creosote bush (*Larrea tridentata*), bur-sage (*Ambrosia deltiodea*), and Anderson wolfberry (*Lycium andersonii*). Latitude and altitude do not seem to be significant factors affecting these results. In extremely dry habitats in Death Valley, Mojave Desert species are usually restricted to areas where water accumulates in shallow depressions or minor channels. Some desert shrub species survive without being restricted to such moisture collection sites.

Phreatophytes, which require readily available ground water, such as Nevada saltbush (*Atriplex torreyi*), mesquite (*Prosopis glandulosa*), rubber rabbitbrush (*Chrysothamnus nauseosus*), and saltgrass (*Distichlis spicata*), are characterized by intermediate xylem pressure potentials.

All the tree species in this study had high xylem pressure potentials. Lodgepole pine (*Pinus contorta*) has the highest potential and various species of juniper (*Juniperus osteosperma*, *J. monosperma*, *J. scopulorum*, and *J. horizontalis*), have the lowest for tree species. Species that have intermediate values are quaking aspen (*Populus tremuloides*) and Douglas fir (*Pseudotsuga menziesii*). Plants characteristic of wet habitats are not shown, but many of them have negative xylem pressure potentials that do not exceed -1 MPa (Scholander and others, 1965).

It is probable that the order of the species shown in figure 3 from most negative (top) to least negative (bottom) xylem pressure potentials also represents most-to-least drought tolerance for the species shown. The graph would be more useful if all species had been measured the same number of times. For some species, several hundred measurements were made and sampling extended over a wide geographic range for one or more seasons. For some species the data are for only one location at one time. Nevertheless, the assumption of relative drought tolerance may be valid for most species shown.

Range of Cell Osmotic Potentials

The term "osmoregulation" has been applied to seasonal and diurnal changes in cell osmotic potential in response to decreasing soil matric and atmospheric potentials. The capacity of plants to maintain low cell osmotic potential and to regulate it in response to soil matric and atmospheric potentials are elements of a species tolerance to drought. Regulation of osmotic potential was present in four of seven Arizona Sonoran Desert species (Monson and Smith, 1982) and ranged from 0.3 to 0.8 MPa. For chaparral species of southern California (Bowman and Roberts, 1985), the seasonal trend was toward increasingly negative cell osmotic potentials with little or no recovery at the end of the summer drought period, however, turgor-loss point varied both seasonally and diurnally. Monson and Smith (1982), whose measurements were for an entire year for Sonoran Desert plants of Arizona, found both seasonal adjustments and recovery of cell osmotic potentials in midwinter.

Species are listed in order of minimum cell osmotic potentials to maximum potentials (fig. 4). It is not possible to estimate the errors that may be present in the freezing-point depression measurements for some of the halophytes, but perhaps the order would be the same had other methods been used. As one example of the possible magnitude of the discrepancy between methods, Bennert and Mooney (1979) measured cell osmotic potentials as low as -13 MPa for desert holly (*Atriplex hymenelytra*) in Death Valley by the cryoscopic method, but -4.26 MPa was the lowest value determined by pressure-volume curves.

The halophytes listed in this study have the lowest cell osmotic potentials. Shadscale (*Atriplex confertifolia*), although often found growing in nonsaline sites (Billings, 1949; Branson and others, 1976) has the lowest cell osmotic potential. Nuttall saltbush *Atriplex nuttallii* has very low cell osmotic potential, as is true of xylem pressure potential (fig. 3). It is surprising that big sagebrush (*Artemisia tridentata*) has such low cell osmotic potential, exceeding that of many halophytes. Harris (1934) gave the locations for each of the 208 sites where this species was studied so it might be possible to reevaluate some of the more anomalous values. One possibility for the low values is that windblown salts may have accumulated on the leaves. Another upland, nonhalophytic species that attains relatively low cell osmotic potential is creosote bush (*Larrea tridentata*). Bennert and Mooney (1979) classified this species as drought tolerant with the ability to adjust osmotic components to changes in the hydrologic environment.

Some phreatophytes, such as Nevada saltbush (*Atriplex torreyi*) and saltgrass (*Distichlis spicata*, fig. 4) have low cell osmotic potentials, but some, such as greasewood (*Sarcobatus vermiculatus*) and mesquite (*Prosopis velutina* and *P. glandulosa*) have relatively high potentials.

Range of Soil Osmotic Potentials

Figure 5 shows the range of soil osmotic potentials associated with 40 different western plant species. One would expect pickleweed (*Allenrolfea occidentalis*), which grows in very salty environments such as the salt pan in Death Valley and salt marshes adjacent to the Great Salt Lake, to have lower cell osmotic potentials than those shown. Perhaps the succulent characteristics of the pickleweed permits the retention of enough water to dilute cell-sap salts. Pickleweed grows in the saltiest habitats, but is also found in a wide range of sites including some that are nonsaline. It is by far the most salt-tolerant species studied.

Species which grow in relatively moist habitats, such as big bluestem (*Andropogon gerardi*) (Hake and others, 1984) and giant reed (*Pharagmites communis*) (Harris, 1934), have high cell osmotic potentials.

A number of the saltbushes (*Atriplex sp.*) are extremely salt tolerant. Mat saltbush (*Atriplex corrugata*), Parry saltbush (*A. parryi*), and fourwing saltbush (*A. canescens*) are commonly found where water tables are at shallow depths that permit the migration of

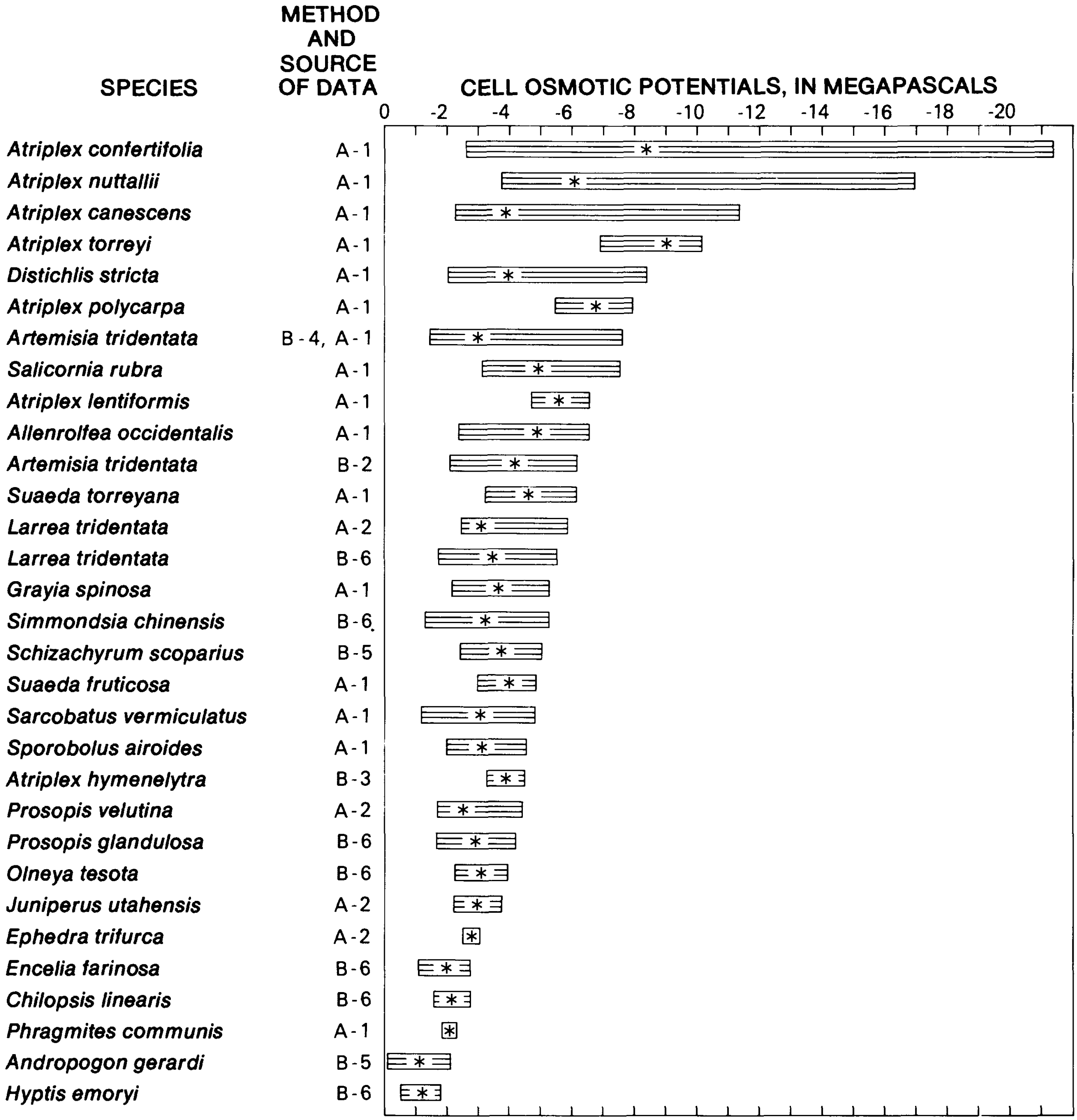

FIGURE 4.—Minimum, mean (*), and maximum cell osmotic potentials in 31 plant species measured by freezing-point depression method (A) or by pressure-volume curve method (B). Sources of data are: (1) Harris, 1934; (2) Walter and Stadelmann, 1974; (3) Bennert and Mooney, 1979; (4) Campbell and Harris, 1977; (5) Hake and others, 1984; and (6) Nilsen and others, 1984.

salts to the soil surface. Other phreatophytic species, such as rubber rabbitbrush (*Chrysothamnus nauseosus*) and greasewood (*Sarcobatus vermiculatus*) show intermediate tolerances. Not all saltbushes were found growing in saline soils (for example, *Atriplex polycarpa* and *A. hymenelytra*).

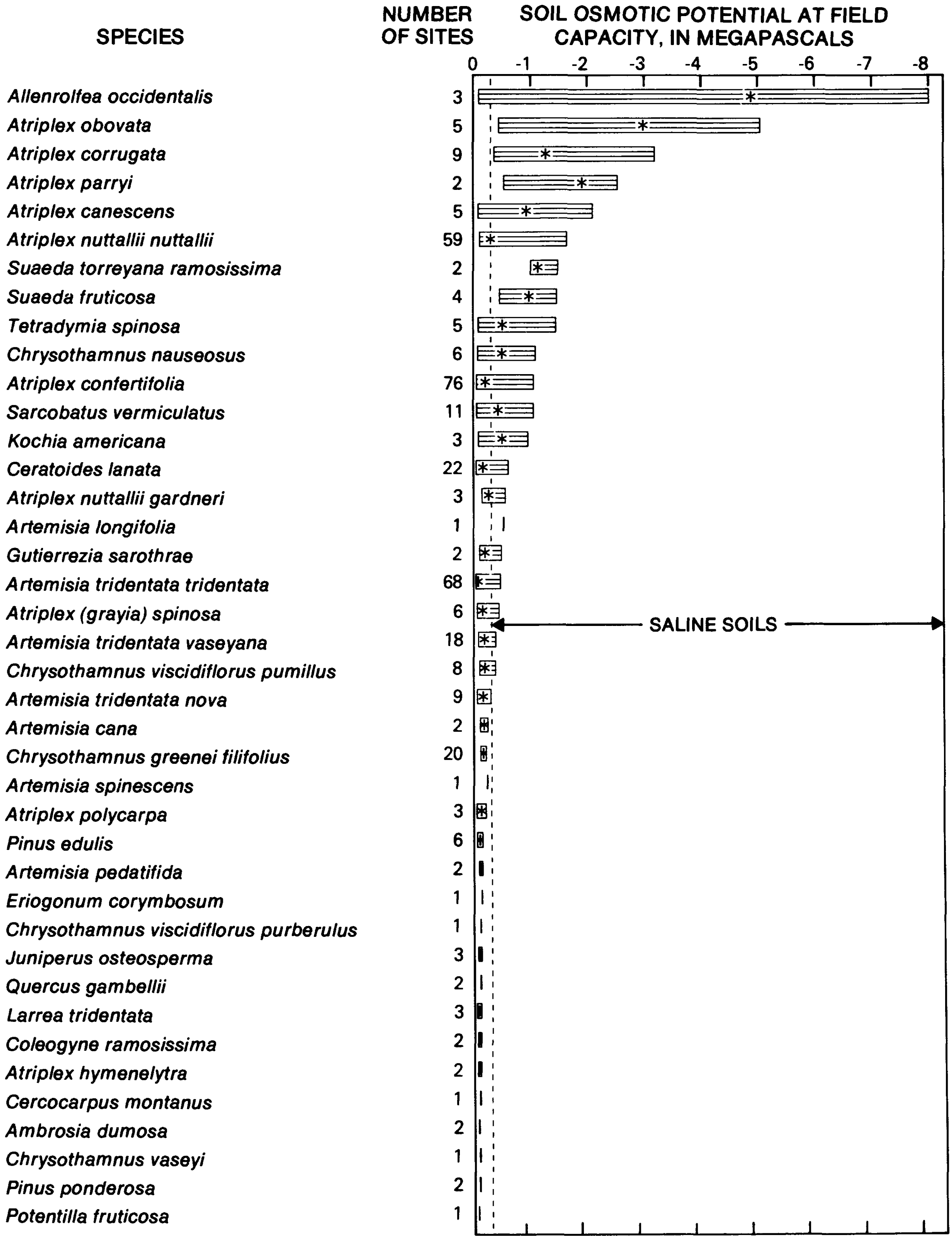

FIGURE 5.—Minimum, mean (*), and maximum soil osmotic potentials at field capacity for the upper 10 centimeters of soils in 40 plant habitats. Where only one measurement is available it is represented by a single vertical line. Sources of data are: F.A. Branson and R.F. Miller, U.S. Geological Survey, written commnn., 1987; Branson and others, 1976; and Miller and others, 1982. All soils to the right of the vertical dashed line are saline.

SUMMARY

The distribution of plant species in the Western United States is caused by variations in the capacities of different species to tolerate dry conditions and different amounts of soil salinity. It is proposed that minimum xylem pressure potentials, which were measured over a large part of the Western United States, are indicative of drought tolerance, and that minimum cell osmotic potentials are indicative of salt tolerances of plant species.

Of the species measured, Nuttall saltbush (*Atriplex nuttallii nuttallii*) was found to be the most drought tolerant. Although pickleweed (*Allenrolfea occidentalis*) grows in the saltiest soil measured, it did not have the lowest cell osmotic potential. This apparent anomaly may be explained by the succulent characteristics of pickleweed. Saltbushes (*Atriplex confertifolia*, *A. nuttallii*, *A. canescens*, and *A. torreyi*) had the lowest cell osmotic potentials measured.

Sites that have vegetation with high cell osmotic potentials can be very dry (such as areas where bur-sage [*Ambrosia dumosa*] grows) or wet (where shrubby cinquefoil [*Potentilla fruticosa*] grows) or can have soils with an intermediate moisture content (where little bluestem [*Schizachyrun scoparius*] grows). Generally, only low soil osmotic potentials in salty to moderately salty soils, markedly influence plant distribution. In areas with low salinity soils, soil water availability is a more selective influence.

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GLOSSARY

Apoplastic water.--Water that in cell walls and xylem elements is water outside the protoplast.

Atmospheric potential.--The force exerted by the atmosphere to remove water from plants, soils, and water surfaces. Stress values are positive and potential values are negative.

Cell sap.--The watery solution of various substances, including salts, alkaloids, and sugars that occurs within cells.

Cortex.--The tissue between the epidermis (outer layer of cells) and the stele (inner tissues of stems and roots).

Edaphic desert.--Desert conditions in a non-desert climate caused by high runoff from clayey soils.

Euryhydric.--Refers to the capacity of certain species to withstand large water deficits.

Field capacity.--Amount of water held in soil after drainage by gravity.

Halophyte.--Plants that tolerate high concentrations of soil salts.

Hydrolabile.--Species that adjust osmotic components to changes in the hydrologic environment.

Hydrolabile behavior.--Adjustments that are made by certain species of their osmotic components in response to changes in the hydrologic environment.

Hydrophytes.--Plants that grow partly or wholly immersed in water.

Mesophytes.--Plants that grow under conditions of intermediate environmental wetness.

Osmotic potential.--That part of total potential that is caused by dissolved salts.

Phreatophyte.--A plant which derives at least part of its water supply from ground water and is more or less independent of rainfall.

Pressure-volume curve.--Obtained by placing a turgid twig or stem in a pressure chamber and subjecting it to stepwise increases in pressure, while the volume of sap expressed at each pressure is measured and the data used to construct a curve.

Soil osmotic potential.--That part of total soil water potential attributable to dissolved salts.

Symplastic water.--That water occurring in vacuoles and cytoplasm.

Total water potential.--The difference between free energy of water in a particular system and that of pure water. Water potential is decreased by factors that decrease vapor pressure.

Transpiration.--The loss of water from plants to the atmosphere.

Turgor-loss point.--Synonymous with permanent wilting percentage and is the point in the drying curve at which positive turgor pressure in plant cells cannot be regained.

Xerophyte.--A plant which can subsist with a small amount of moisture (such as a desert plant).

Xylem potential.--Refers to the water potential of water in the xylem portion of the transpiration stream.