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Source: *Ecology*, Vol. 57, No. 6 (Nov., 1976), pp. 1104-1124

Published by: [Ecological Society of America](#)

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MOISTURE RELATIONSHIPS IN TWELVE NORTHERN DESERT SHRUB COMMUNITIES NEAR GRAND JUNCTION, COLORADO¹

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Abstract. Twelve northern desert shrub communities having the same macroclimate but differing habitats were studied. Arranged in order of decreasing production of live stems plus current growth, the communities were: (1) *Sarcobatus vermiculatus* (9,172 kg/ha), (2) *Grayia spinosa* (7,412 kg/ha), (3) *Artemisia tridentata* (5,474 kg/ha), (4) *Chrysothamnus nauseosus* (4,836 kg/ha), (5) *Atriplex confertifolia* (3,194 kg/ha), (6) *Eurotia lanata* (2,026 kg/ha), (7) *Hilaria jamesii-Atriplex confertifolia* (1,995 kg/ha), (8) *Atriplex corrugata* (1,949 kg/ha), (9) *Chrysothamnus greenii filifolius* (1,866 kg/ha), (10) *Atriplex nuttallii* (1,309 kg/ha), (11) *Elymus salinus* (865 kg/ha), and (12) *Tetradymia spinosa* (564 kg/ha). The communities were relatively simple in terms of plant composition; the dominants in many of them contribute > 90% of the plant cover. Seasonal patterns of both internal-plant stresses and soil-moisture stresses were measured. Both sets of values increased from late May until early September when increases in rainfall caused both to decrease. Minimum internal-plant stresses were similar for all species but maximum values differed greatly. Maximum plant-stress value ranged from 103 bars for *A. nuttallii* to only 40 bars for *C. nauseosus*. Internal-plant stresses were closely related to minimum soil-moisture stresses found within soil profiles at the time of sampling. The relationship was good for upland species but poor for species in moist habitats. Similar close relationships were found for internal-plant stress and quantities of moisture stored in soils. Correlation coefficients for internal-plant stress vs. wind and atmospheric stress were low and nonsignificant, but air temperature was significantly correlated with plant stress in several species. Evapotranspiration from the 12 communities ranged from 60 mm for the *C. greenii filifolius* habitat to > 130 mm for the *G. spinosa* habitat. Evapotranspiration was significantly related to percent live cover ($r = +.84^{**}$). Soil salinity at field-capacity values ranged from > 16 bars to < 1 bar; only 5 of the 12 habitats had saline soils. The highest root mass (2,547 kg/ha) was in the *C. nauseosus* soil—the lowest (569 kg/ha) in the *A. corrugata* soil. Efficiency of water use (plant growth per unit of water used) was lower for species occupying dry habitats than for those in moist habitats. Phenological observations showed that most species occupying moist habitats continued active growth for longer periods. A study of persistence of leaves showed 10% annual loss of leaves in *A. corrugata*. Ninety percent of leaves of this species were retained throughout the season whereas < 20% of marked leaves were retained by *A. tridentata* and *A. nuttallii*.

Key words: Colorado; evapotranspiration; internal-plant stress; leaf persistence; phenology; soil-moisture stress; soil salinity.

INTRODUCTION

A primary objective of this paper is to provide some answers to the question, "Why do plants grow where they do?" In a desert environment, factors that control the availability of water probably exert primary control on distribution of species and plant communities. It is undoubtedly impossible to account for all the factors that interact and influence plant distribution (Billings 1952). Progress can, however, be made towards understanding such natural phenomena by the "method of successive approximation" (Poore 1962), that is, successive measurements of the environment and evaluation of biotic responses. As knowledge accumulates from successive studies, more reliable answers to ecological questions should be available.

Our approach to the problem of causative factors for plant-community distribution differs from that often used by plant geographers, bioclimatologists, and others who often emphasize macroclimate differences and changes as causes. We selected a small area where plant communities differ but macroclimate is virtually the same for all the communities. Billings (1949) would probably consider these to be edaphic communities within the climatic climax *A. confertifolia* zone, which is macroclimatically dryer and hotter than the adjacent *A. tridentata* zone which extends to much higher altitudes.

One means of reducing the number of measurements of complex variables required for meaningful answers is to limit measurements to factors that integrate the effects of several variables. Two such integrative factors were measured in this study: (1) moisture stress in plants, which integrates the energy gradient between atmosphere, vegetation, and soils,

¹ Manuscript received 11 September 1975; accepted 12 May 1976.

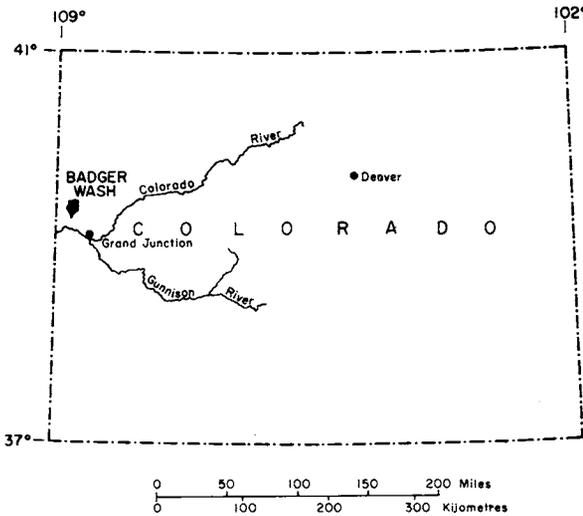


FIG. 1. Index map of Colorado showing the location of Badger Wash Basin where plant communities were studied.

and (2) soil moisture and its retentive force, which integrates the combined influences of precipitation, solar radiation, surface characteristics, exposure, and slope, as well as soil texture, structure, depth, and amount and kind of retentive surfaces.

Study area

These integrative factors were measured to study moisture relationships of 12 northern desert shrub communities typical of the area south of the Book Cliffs in western Colorado and eastern Utah. The study sites are ≈ 40 km west of Grand Junction, Colorado near the boundary with Utah (Fig. 1). Soils associated with the plant communities have developed on various members of the Mancos Shale and alluvium derived from it (Lusby et al. 1963). This geological parent material is a massive (2,440 m in places) marine deposit of Cretaceous age. It is composed of shale with interbedded sandstone. These, when alternatively exposed, provide contrasting habitats for plant communities.

The soils in most cases are poorly developed. They consist mainly of a shallow weathered mantle overlying the bedrock. Alluvial deposits result in deeper soils that can vary in character from fine to coarse, depending on the source. The soils are also the product of an arid climate. On the average, < 230 mm of moisture falls on the area per year. Much less precipitation occurred during the study period. Pan evaporation is 2,340 mm or $\approx 10\times$ annual precipitation.

Plant communities occurring in the various environments resulting from interaction of geological material and climate are representative of the extensive vegetation type mapped by Küchler (1964)



FIG. 2. A nearly pure stand of *Atriplex corrugata* occupies the left foreground and middleground to the right. *Artemisia tridentata tridentata* occurs as a narrow strip adjacent to the channel and *Chrysothamnus nauseosus nauseosus* occupies the central portion of the channel. *Atriplex nuttallii nuttallii* covers the dryer uplands in the background.

as saltbush-greasewood (*Atriplex-Sarcobatus*). Mancos Shale is present under grossly similar climatic conditions over a large area of eastern Utah, western Colorado, and northwestern New Mexico. Similar plant communities cover much of this area and also form extensive stands in Nevada and western Utah.

Several of the species included in these communities range from Canada to Mexico and are dominants on some 73×10^6 ha (Branson et al. 1967). The 12 communities investigated, named according to the dominant species in each, were: (1) *A. nuttallii nuttallii*, (Although the nomenclature of Harrington [1954] is followed in this report and meaningful subdivisions of species are made in his manual, recent taxonomic studies by Hanson [1962] and Nelson [1969] indicate that *A. gardneri* may be the valid name for this species.) (J. R. Nelson [personal communication 1976] classifies the subspecies of the study area as *A. g. cuneata*.) (2) *A. confertifolia*, (3) *A. corrugata*, (4) *S. vermiculatus*, (5) *T. spinosa*, (6) *G. spinosa*, (7) *C. nauseosus nauseosus*, (8) *C. greenei filifolius*, (9) *E. lanata*, (listed as *Ceratoides lanata* Nevski by Fernandez and Caldwell 1975), (10) *A. tridentata tridentata*, (11) *H. jamesii-A. confertifolia*, and (12) *E. salinus*. Some of the communities studied are shown in Fig. 2.

METHODS

Six pairs of study sites were selected in October 1971. Each of the paired sites were adjacent and across fences separating grazed and ungrazed pastures in the Badger Wash study basins (Lusby et al. 1963, 1971). Grazing had been excluded from one member of each pair since 1953. Because only

minor and inconsistent differences were found between grazed and ungrazed plants, the populations were considered similar, and where appropriate, the data were pooled for analyses. At the end of 13 yr (1953–66) Lusby et al. (1971) found ground cover to be essentially unchanged on ungrazed watersheds and only minor changes on grazed watersheds. The entire region was heavily grazed prior to the passage of the Taylor Grazing Act in 1934 but grazing intensities have decreased considerably in the past 20 yr, and grazing intensities are now considered moderate to light. In the spring of 1972, six additional sites were established to obtain information about plant communities for which paired sites could not be obtained. A plot 10 m long and 1 m wide was marked with metal stakes at each study site and all plant sampling was accomplished within these plots by working from outside the marked area. This was done to prevent compaction by other than grazing animals. Photographs were taken of each plot to record differences in aspect.

Differences in species and quantities of plant cover, as well as soil-surface characteristics were measured by the first-contact point-quadrat method of Levy and Madden (1933). This method was selected because Branson and Owen (1970) determined that it resulted in better relationships between bare soil and runoff than several other methods tested. It was hoped that the method would also provide good relationships between cover and water use. More data characterizing aboveground portions of each plot were obtained in July 1973 when the study was completed. Aboveground biomass determinations were made on four 1- × 2-m plots for each of the 12 plant types. Current growth, standing live, and standing dead material for each species was clipped, bagged separately, oven dried, and weighed.

Periodic measurements were made at each study site to determine moisture stress in the plants, as well as moisture content and the force with which it was retained in various horizons of the soil. Sampling was initiated following fall rains in 1971. It was continued at 3-wk intervals from April through October in 1972. Little or no precipitation fell on the area until October 1972, and all growth during 1972 was sustained from this single increment of moisture stored in the soil. During 1973 measurements were obtained following snowmelt and again in late July.

Plant growth was measured on selected plants in six of the plant communities by wrapping insulated wires around the stems of shrubs near the growing tips and measuring the lengths of all branches above each wire. Persistence of leaves on the various shrubs was measured by marking 10 leaves on each of four shrubs per species with dots of red finger-



FIG. 3. An elutriative flotation device used to remove roots from soil samples. Water is forced into the bottom of the funnel and roots collected on the wire-mesh screen to the left of the elutriator. Roots are then washed from the screen onto the filter paper shown to the right of the elutriator.

nail polish paint. The number of marked leaves remaining was counted on each sampling date.

The force exerted to remove moisture from the soil by the dominant shrub at each site was measured on five separate twigs on each sampling date. Force intensities were measured by means of a compression chamber described by Waring and Cleary (1967). The maximum stress measured by the compression chamber we used is 138 bars. The chamber measures the pressure necessary to force water back to the cut end of a twig thereby recording the original tension on the uncut water column. This tension is a measure of the force generated in a plant to insure movement of water from the soil into the plant. Measurements of relative humidity and wind speed were also obtained to compare with measurements of moisture-retention forces. Wet- and dry-bulb temperatures used to compute relative humidity and atmospheric stress were obtained with a battery-powered psychrometer. A hand-held anemometer was used to determine peak wind speeds.

Live plus dead root masses under each of the 12 plant communities were determined by an elutriative flotation device (Fig. 3). Water applied to the base of a funnel created decreasing forces towards the surface which caused coarse particles to remain near the funnel bottom and fine particles and roots to move over the lip of the funnel onto a 2.4-mesh/mm screen. The water force could be regulated so that only roots and particles fine enough to pass through the screen moved over the funnel lip. Some agitation of the material towards the base of the funnel to release small root fragments was accomplished by using a small wire rake. After roots are on the screen there is an additional opportunity to wash fine particles from them. Roots were washed from the screen onto a 300-mm filter paper which was

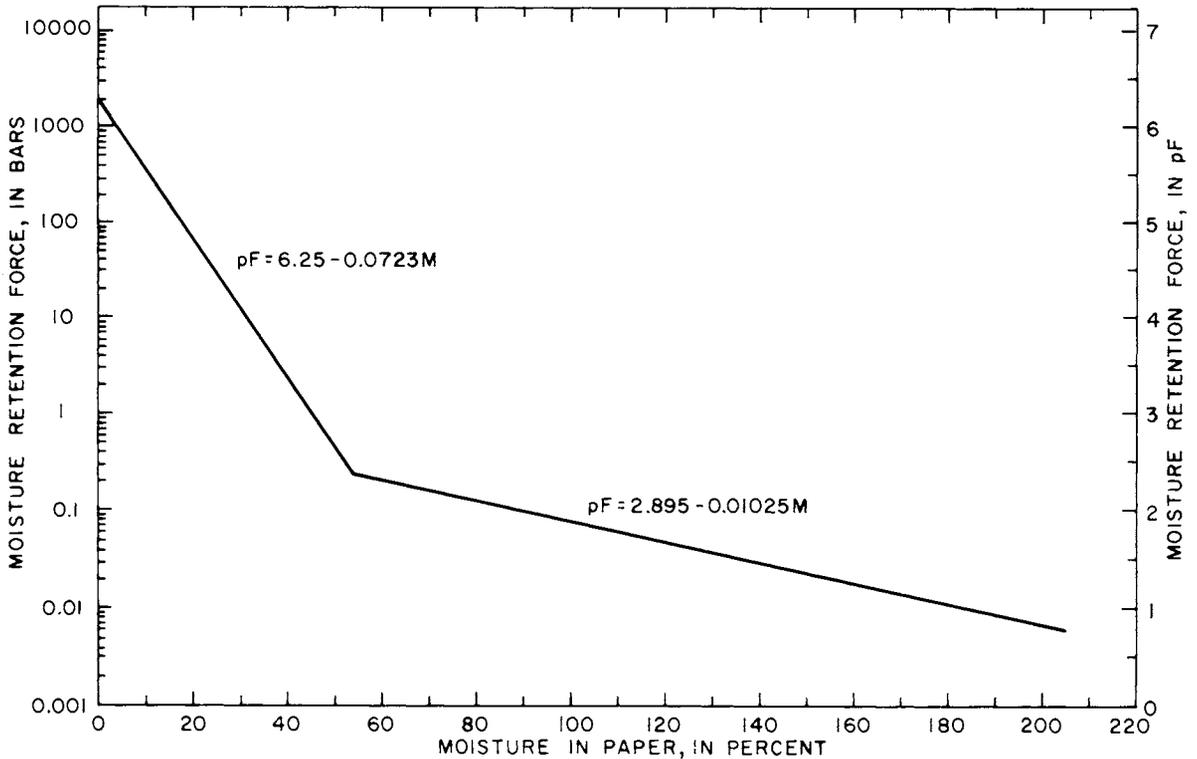


FIG. 4. Calibration curve for standard filter paper used to determine moisture-retention force (stress or tension) of soil samples.

then oven-dried. After drying, the filter papers plus roots were weighed while filter papers were warm (atmospheric moisture absorption can cause significant errors if this procedure is not followed). Roots were then brushed from the papers and the papers were reweighed. Root masses were determined for four soil profiles in each of the 12 communities. Sample increments in each profile were 100 mm deep by 50 mm in diameter.

Soils were sampled at each site at the same time plant measurements were made. Sampling positions were selected at random within each of the 10-m² plots. To minimize soil disturbance, previously sampled sites within the plot were avoided. Sampling was accomplished without stepping in the marked plots. Samples were obtained with a tubular auger 50 mm in diameter. All the soil obtained from each consecutive 100-mm depth increment was retained for analysis. Each profile was sampled to the underlying parent rock, to depths where the size of stones prevented augering or, when possible, to the water table. Each sample was emptied directly into a sealable polyethylene bag of 1.37-liter capacity. A disk of standard filter paper (McQueen and Miller 1968) previously treated to prevent decomposition by soil organisms was inserted with each sample. If a wet spot became evident when the paper contacted the

soil, three papers rather than one were inserted. This was done in such a manner that the outside papers prevented wet soil from adhering to the paper in the center. Wet samples were not disturbed, but granular samples were tumbled in the closed bag to mix them in order to minimize moisture gradients within each sample. Each bag was then inserted into a metal container and the lid sealed with plastic tape to prevent the escape of moisture. After transport to the laboratory, samples were stored together in cabinets in a room kept at approximately 20°C. The temperature of the samples thus varied less than the temperature of the room. A more satisfactory moisture equilibrium is achieved between the soil and the standard papers if temperature fluctuations are minimized (Al-Khafaf and Hanks 1974). After storage for more than a week to achieve moisture equilibrium, the moisture content of both the soil and the included standard paper was determined gravimetrically. Both were dried in a forced-draft oven at 110°C. The moisture content of both the soil and the paper was computed as grams of moisture per gram of oven-dry material. The force with which moisture was retained by the soil at the time of sampling was determined from the moisture content of the standard papers. The calibration relationship of McQueen and Miller (1968) used for this purpose is illustrated in Fig. 4.

The sorption force can be interpreted either as bars or pF. Bars are convenient to use when the magnitude of the increase in force as moisture is desired. Sorption force is conveniently illustrated as pF when a measure of degree of wetness is needed, because the pF increases linearly as the degree of wetness decreases.

The moisture-sorption force expressed as pF is the logarithm of the height of a column of water capable of producing a force, at its base, equivalent to the force with which water is retained by the soil. The relationship between bars and pF is also evident in Fig. 4. At 1 cm pF is 0 and there is .001 bar of force. At 10 cm the pF is 1 and there is .01 bar of force. At 100 cm, pF is 2 and there is 0.1 bar of force, a force often used as a measure of field capacity in sandy soils. The calibration lines for the filter paper intersect at 0.21 bar or at pF 2.35. This is within the accepted field-capacity stress range of values of 0.1 to 0.3 bar. Others have reported a break in moisture conductivity and retention curves at this level. In discussing capillary conductivity, Gardner (1956) said that conductivity of soil reaches a limit at 0.15 to 0.2 bar. Michurin and Lytaye (1967) presented evidence that, "the maximum thickness of water film subjected chiefly to the action of sorption forces is 9 or 10 molecular layers (25Å). Beyond this critical thickness, the effect of sorption forces is much less than that of gravity and the excess water drains off." The change in energy level when 10 molecular layers of water are absorbed coincides with the intersection of the two calibration lines for the standard paper in Fig. 4. Michurin and Lytaye (1967) also determined that five molecular layers of moisture are adsorbed to surfaces at 15 bars (pF 4.20). At pF 5.00 three molecular layers of water remain adsorbed to surfaces. Expressed as bars, the sorption force is 100, the equivalent of approximately a 100,000-cm column of water. Branson et al. (1970) presented evidence that this is about the maximum level of moisture-retention force at which desert shrubs are capable of desorbing moisture. The next step in the pF scale is 6.00. This pF is achieved at the surface of soil profiles, apparently as the result of evaporation resulting from solar radiation (Miller and McQueen 1972). The same sorption force expressed as bars is 1,000. The equivalent expressed as a column of water is $\approx 10^6$ cm, or 10 km. The soil must be heated to temperatures exceeding 100°C to achieve a pF of 7.00. A sorption force of 10,000 bars or 10^7 cm is the equivalent of pF 7.00. This sorption force would not be achieved under natural field conditions.

After samples of soil were oven-dried to determine their moisture content, they were saturated with dis-

tilled H₂O. Wetted samples were allowed to stand overnight before the final saturation end point was determined (Richards 1954). The moisture content at saturation was determined from the change in weight after water was added to the oven-dry soil. The moisture content was computed as grams of H₂O per gram of soil. The electrical conductivity of the saturated soil and its pH were determined (Richards 1954).

RESULTS AND DISCUSSION

Plant communities

Each of the plant communities studied is relatively simple in terms of plant composition (Table 1). For many of the communities, the dominant species constitutes 90% or more of the plant cover and most communities could be referred to as monospecific. In the area studied some of the community dominants, such as *A. tridentata*, *E. lanata*, and *G. spinosa* were not found outside of the communities where they were the dominants even though adjacent communities were sampled. Except for the *H. jamesii*-*A. confertifolia* and *E. salinus* types, grasses and forbs are of minor importance in the area. Most of the upland communities have > 50% bare soil.

Yields of live stems plus current growth (standing crop) for the 12 plant communities is shown in Fig. 5. Standing dead stems were added to detached plant material and considered mulch. The range of values from < 600 kg/ha to > 9,000 kg/ha is indicative of the variety of habitats that can occur within a single macroclimate. Most of the high-yield sites receive supplemental run-in moisture or send roots to the saturated zone (water table); the low-yield sites generally have fine-textured soils, minimal soil moisture, high runoff, and some have saline soils.

Work on northern desert shrubs as indicators of soil salinity dates from Hilgard (1911) and earlier. More recent summary papers include Gates et al. (1956), and Branson et al. (1967). In an intensive study of edaphic factors influencing plant distribution for five species at each of 10 sites, Gates et al. (1956) found numerous significant differences between soil characteristics, but there were overlapping ranges of tolerances for all of the species. In a discussion of northern desert-shrub communities, Branson et al. (1967) proposed a classification based on maximum measured soil osmotic stress. More recently, it has been pointed out that quantity of soil moisture available to each plant community and the maximum soil-moisture stress achieved by each plant community may be important determinants of plant community distribution (Branson et al. 1970).

TABLE 1. Percent cover of species, rock, bare soil, and mulch in 12 plant communities as measured by the first-contact point-quadrat method. T = present but < 1% cover

	Hilaria jamesii-			Chrysothamnus			Eurotia			Tetradymia			Sarcobatus		
	<i>nuttallii</i>	<i>confertifolia</i>	<i>folia</i>	<i>confertifolia</i>	<i>folia</i>	<i>denata</i>	<i>nauseosus</i>	<i>filifolius</i>	<i>lanata</i>	<i>spinosa</i>	<i>spinosa</i>	<i>spinosa</i>	<i>vermiculatus</i>	<i>latus</i>	<i>salinus</i>
Shrubs															
<i>Artemisia spinescens</i> D. C. Eaton	T		1												
<i>Artemisia tridentata</i> (Nutt.) <i>tridentata</i>				29											
<i>Atriplex confertifolia</i> (Torr. & Frem.) Wats.		7	11	2			1	T							
<i>Atriplex corrugata</i> Wats.					25		1			4					
<i>Atriplex n. nuttallii</i> S. Wats.	17							1		T					6
<i>Chrysothamnus greenii filifolius</i> (Rydb.) H. & C.	T		1					12							
<i>Chrysothamnus nauseosus</i> (Pall.) Britton <i>nauseosus</i>							36								
<i>Eurotia lanata</i> (Pursh.)									24						
<i>Grayia spinosa</i> (Hook.) Moq.										40					
<i>Gutierrezia sarothrae</i> (Pursh.) Britt. & Rusby			1				1				2				
<i>Sarcobatus vermiculatus</i> (Hook.) Torr.													22		
<i>Suaeda fruticosa</i> (L.) Forsk.			1										18		
<i>Tetradymia spinosa</i> Hook. & Arn.											9				
Grasses															
<i>Bromus tectorum</i> L.			2				4		T						
<i>Elymus salinus</i> Jones															24
<i>Hilaria jamesii</i> (Torr.) Benth.		13				2			5						
<i>Oryzopsis hymenoides</i> (R. & S.) Ricker		1					2		T						
<i>Sitanion hystrix</i> (Nutt.) J. G. Smith	T	T					T		2						
Forbs															
<i>Aster venustus</i> M. E. Jones															
<i>Eriogonum pumilus concinnoides</i> Cronquist	1														
<i>Eriogonum bicolor</i> Jones		3						3							1
<i>Opuntia</i> sp.		T													
<i>Sphaeralcea coccinea</i> (Pursh.) Rydb.		T	1							1					
Cryptogams															
Algal crust															
Moss		7	1												
Rock		T					1	2					T		6
Bare	74	46	65	39	60	39	36	74	51	32	77	29	29	31	50
Mulch	6	20	16	8	8	23	17	8	17	26	8	8	8	31	12

PLANT COMMUNITY

SARCOBATUS VERMICULATUS
 GRAYIA SPINOSA
 ARTEMISIA TRIDENTATA
 CHRYSOTHAMNUS NAUSEOSUS
 ATRIPLEX CONFERTIFOLIA
 EUROTIA LANATA
 HILARIA JAMESII
 ATRIPLEX CONFERTIFOLIA
 ATRIPLEX CORRUGATA
 CHRYSOTHAMNUS GREENEI
 ATRIPLEX NUTTALLII
 ELYMUS SALINUS
 TETRADMIA SPINOSA

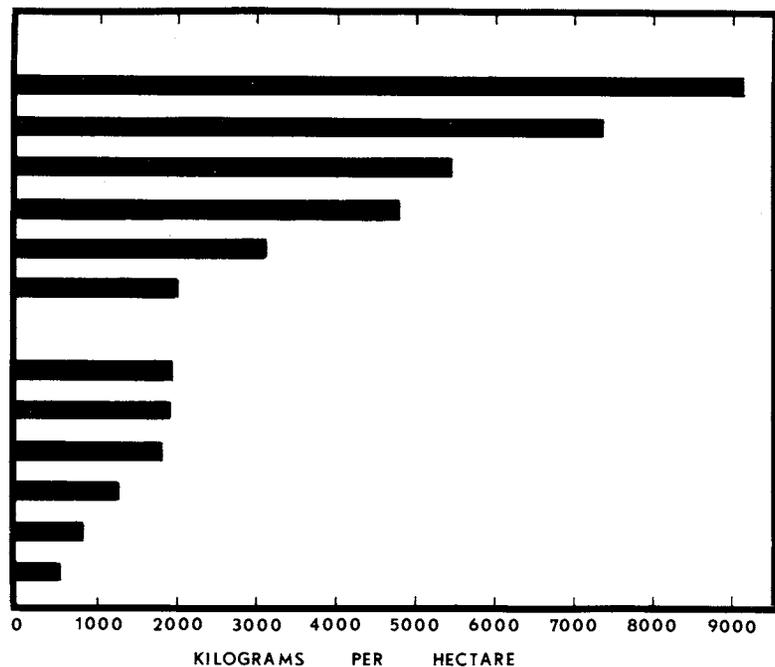


FIG. 5. Yield of live stems plus current growth (standing crop) for 12 plant communities arranged in order of decreasing productivity.

Internal-plant stress as related to soil-moisture stress and soil-water storage

In a study of *A. tridentata vaseyana* near Wolcott, Colorado, Branson and Shown (1975) found internal-plant stress to be more closely related to the lowest soil-moisture stress measured in the soil profile than to any of 11 additional variables tested. A similar close relationship exists for most species of the present study. The seasonal pattern of the relationship for *A. nuttallii nuttallii* is shown in Fig. 6. Only seasonal patterns and differences between species are presented in this report. Although plant-moisture stress is known to vary diurnally, Love and West (1972) found only small variations in diurnal stresses for *E. lanata* and *A. confertifolia* between 0900 and 1700 h. When measuring seasonal patterns of stresses for these species, they considered it satisfactory to disregard diurnal variations as we have done in this report. Diurnal variations are greater when soils are moist than during dry periods (Poole and Miller 1975). Our objectives included determinations of differences between species and maximum seasonal values within species; for these objectives diurnal fluctuations were considered to be of minor importance.

From late May through early September both internal-plant stress and soil-moisture stress increase, followed by a decline in stress as quantity and frequency of precipitation increase in the fall. The slightly inverse relationship for March, April, and

early May is puzzling. It is possible that atmospheric variables have a greater effect on plant stress than does soil-moisture stress when soil moisture is readily available to the plant during the cool spring months.

Shown in Fig. 6 are mean values for two *A. nuttallii nuttallii* sites. Maximum internal-plant stress for one of the sites was 103 bars, which is the average of five measurements; one of the five values was 117 bars, slightly higher than the 112 bars reported as the maximum stress measured for *Acacia aneura* in Australia (Slatyer 1961). This value (117 bars) is nearly 8× the 15 bars sorption force often considered to be the "wilting point." A previously reported high value of 130 bars for *Atriplex obovata* (Branson et al. 1969) was the result of an unfortunate arithmetic error (the recomputed value was 70 bars) and should not be considered a maximal value.

Seasonal patterns of internal-plant stress and soil-moisture stress for species other than *A. nuttallii* are similar and are, therefore, not presented in this report. Differences in the patterns are mainly in peak values attained late in the growing season when soil-moisture quantities were lowest. In general, the more moist the habitat the lower the peak values attained. A general view of the *A. nuttallii* community is shown in Fig. 7.

Maximum, minimum, and mean internal-plant stresses for the 10 shrub species studied are shown in Fig. 8. As appears to be true for salinity tolerance

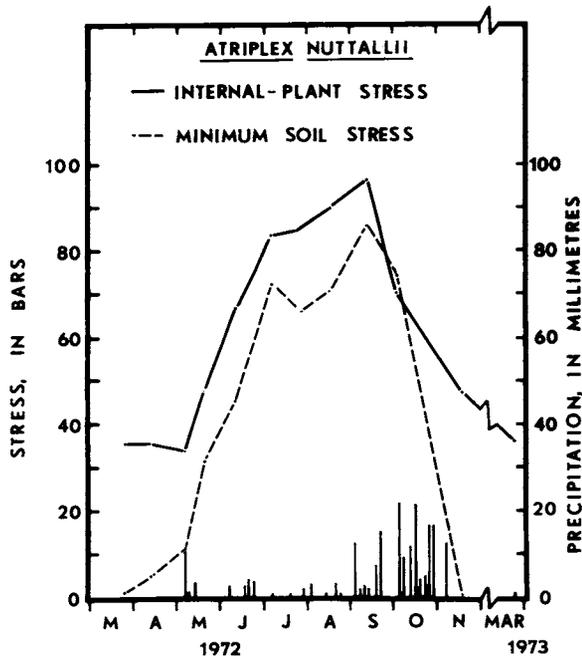


FIG. 6. Seasonal patterns of internal-plant stress, minimum soil-moisture stress, and precipitation for the *Atriplex nuttallii nuttallii* site.

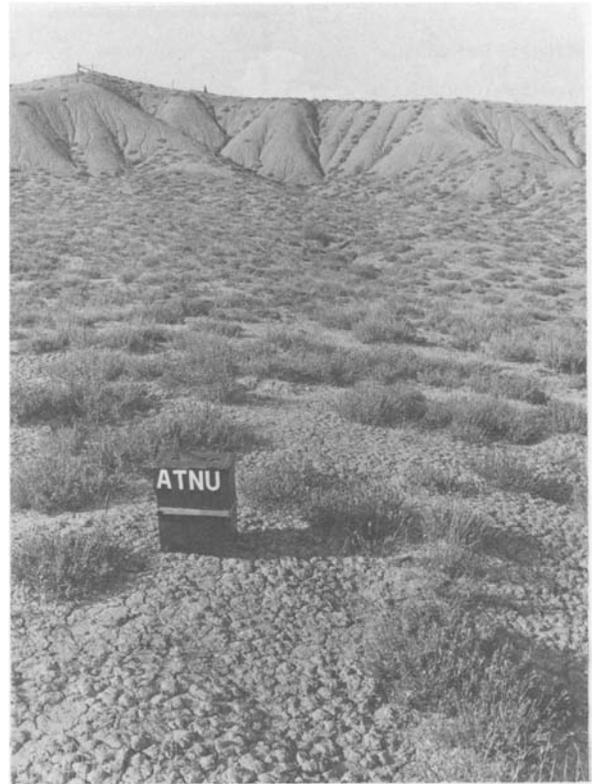


FIG. 7. A general view of the *Atriplex nuttallii nuttallii* community. The stand is almost pure and extends to the top of the hills in the background. One can observe on slopes in the background that plants become more widely spaced as slope angles increase.

(Daubenmire 1948), maximal stresses attained by species may be a more reliable index of drought tolerance than mean or minimum values. Some of the species that show high maximal stresses (i.e., *A. nuttallii*, *A. confertifolia*, and *E. lanata*) sometimes grow with species having much higher moisture requirements, but where they occur in relatively pure stands, as in communities reported here, they should indicate different degrees of tolerance to dryness of habitats. An unknown that must be considered when comparing differences between species and different results obtained for the same species from different geographic areas is ecotypic variation. Extensive testing under uniform conditions will be required to define the ecotypes of the species and subspecies that may be present in the Badger Wash area. Perhaps laboratory tests would be required to determine maximum drought tolerances for these 11 species, but seasonal measurements in habitats where they normally occur, and comparisons with nearby habitats may be more meaningful in understanding why species occur where they do. The year of measurements being somewhat dryer than normal may have been a fortunate circumstance for these measurements because conditions of extreme stress may determine the kinds of plants that survive in many habitats.

Correlation for 8 to 22 pairs of plant stress and minimum soil-moisture stress for 11 communities having shrub species is shown in Fig. 9. The method used was found unsuitable for measurement of

stresses in the grass-dominated community, *E. salinus*. The highly significant correlation coefficients account for as much as 86% of the variability and indicate that by means of regression lines, internal-plant stress for most of these species could be used to obtain estimates of minimum soil stress.

Internal-plant stress for upland communities is more closely related to soil-water stress than is true for communities receiving run-in water or communities supplied with ground water (Fig. 6). Soils of the *A. corrugata* community were always somewhat moist (the highest of the minimum soil stresses was < 10 bars), the *C. nauseosus* communities received supplemental run-in water and probably ground water, and the *S. vermiculatus* community had a continuous supply of ground water at 3.7 m. The zero soil stress at 3.7 m, which is within the rooting zone of greasewood, makes the relationships of plant stress to minimum soil stress almost meaningless. For the moist sites, plant stress may be more directly related to atmospheric variables than to soil-moisture stress.

A close relationship between internal-plant stress and quantity of water stored in the soil profile would

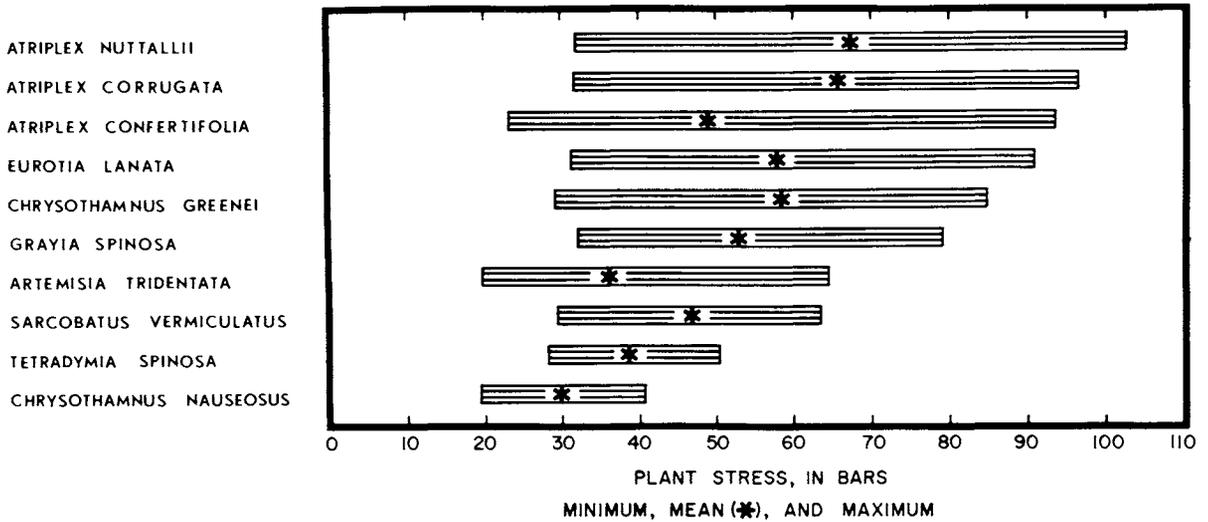


FIG. 8. Minimum, mean, and maximum internal-plant stresses measured for the 10 shrub species.

be of more utilitarian value than the relationship between plant stress and lowest soil stress. If plant-stress measurements provide a reliable estimate of soil-water storage, they could be used as a rapid, convenient, and inexpensive means of assessing quantities of water evapotranspired and possibly, by

early spring measurements, of predicting seasonal forage production potential. The correlation coefficient for plant stress and soil water stored in *A. nuttallii* (Fig. 10) is highly significant and slightly higher than the coefficient for plant stress versus minimum soil stress. These results differ from those

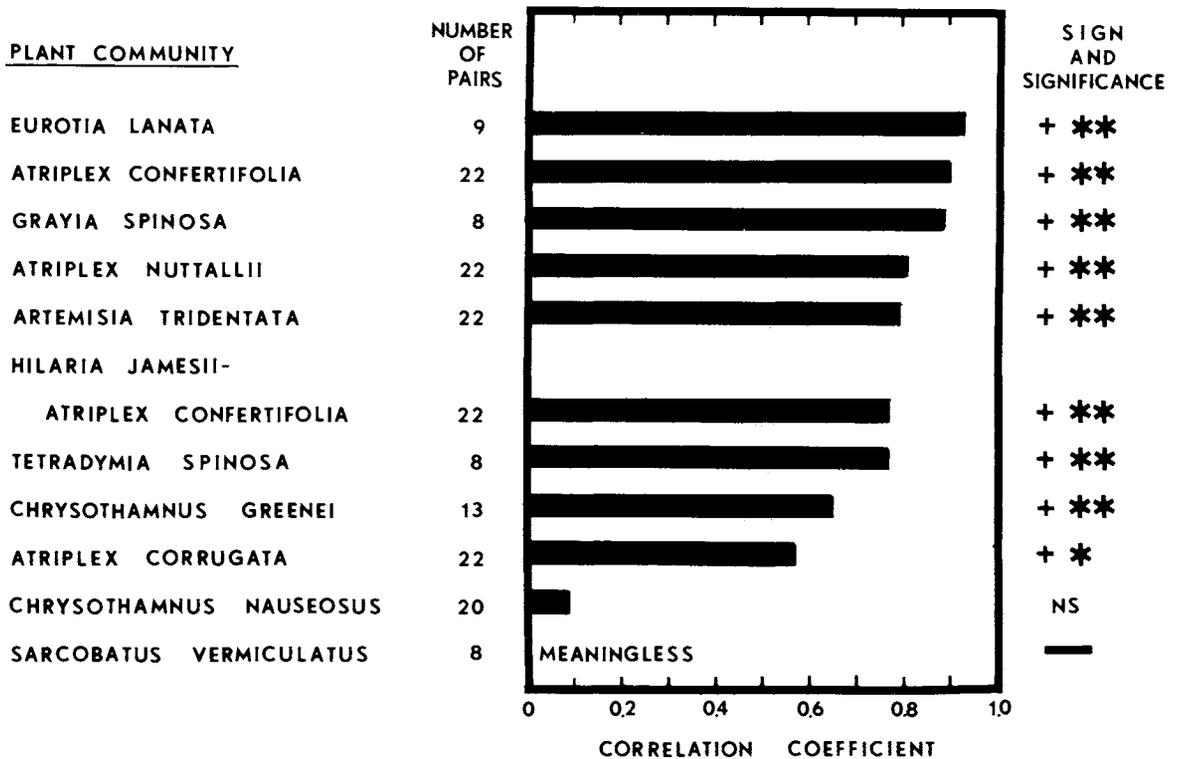


FIG. 9. Linear correlation coefficients for the relationship between internal-plant stress and minimum soil-moisture stress measured in 11 plant communities. Double asterisks (**) indicate significance at the .01 level, single asterisks at the .05 level, and NS indicates not significant at the .05 level.

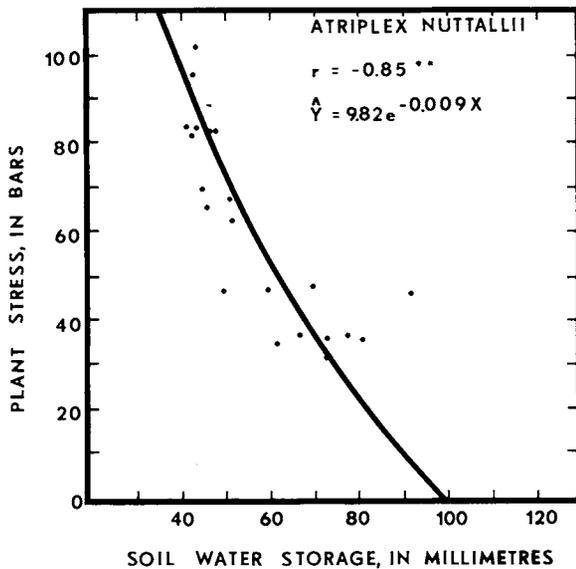


FIG. 10. Curvilinear correlation coefficient and regression line for the relationship between soil water stored and internal-plant stress in *Atriplex nuttallii*.

reported earlier by Branson and Shown (1975), who found plant stress to be more closely related to minimum soil stress than to 11 additional variables. To make both sets of values exponential, a curvilinear regression line (log of soil-water storage) was computed (Fig. 10).

The scatter of data points (Fig. 10) indicates that the relationship between plant stress and soil-moisture storage is closer when quantities of water stored are low. These results agree with other data (Figs. 9 and 6) which indicate that when soil-moisture stress is low, environmental factors other than soil moisture may exert some control on internal-plant stress.

Correlation coefficients (curvilinear) for the 11 plant communities (no stress measurements were made on *E. salinus*) can be compared in Fig. 11. In general, the coefficients are slightly lower than the relationships for plant stress and minimum-soil stress but many are highly significant. A similar relationship between soil-water content and internal-plant stress has been reported for red pine (*Pinus resinosa*) in Minnesota (Sucoff 1972). For *S. vermiculatus*, moisture stored in the top 1.5 m was correlated with internal-plant stress. At depths > 1.5 m, soil water was near or above field capacity throughout the year. The data also indicate that, although ground water is available to the community, meaningful seasonal fluctuations occur in the top 1.5 m of the soil profile. The fact that the water table at 3.7 m showed little fluctuation during the growing season probably indicates that *Sarcobatus* utilized little ground water. Our work elsewhere

(R. F. Miller, *personal communication*) shows considerable fluctuations in water tables near the surface but decreasing fluctuations where water tables are 4 m or more below the soil surface. These fluctuations we attribute to evapotranspiration.

Virtually no relationship was found between soil-water storage and internal-plant stress in the two *C. nauseosus* communities. Shallow ground water at < 2 m was found in one site but rock fragments prevented hand augering to depths adequate to fully characterize the soil of the other. The results of Robinson (1958) indicate that ground water may have been present at a depth of < 4.5 m in both sites.

A close but inverse relationship was expected between minimum soil-moisture stress and quantity of water stored in the soil profile; our data show a highly significant correlation coefficient of -0.96 for this relationship (Fig. 12). Since soil-moisture stress increases at an exponential rate and values for water stored in the soil are linear, the latter were transformed to logarithms for the regression and correlation analyses. The highly significant correlation coefficients shown in Fig. 7, 8, and 9 indicate that regression lines could be used to estimate any of the three variables (soil water stored, minimum soil-moisture stress, and internal-plant stress). Of the three, internal-plant stress is most easily and rapidly measured and could be used to estimate either of the other two values. Regression lines for each species are different and further tests of the reliability of estimated values would be desirable.

Shown in Fig. 13 is the seasonal pattern of soil-water storage for the site occupied by *A. nuttallii*. The water stored in 1971–72 was slightly below normal and in 1972–73 above normal, but a similar trend is indicated for both years. Water stored in fall, winter, and spring is the source for plant growth during the growing season. Few rains add significant quantities to soil water stored during the growing season. Results by Love and West (1972) in Utah, under climatic conditions similar to that of our study area, show that rains of 8 mm or less had little effect on plant moisture stress. As shown in Fig. 6, no summer rains exceeding 8 mm occurred until September, when plant and soil stresses began to decline.

Internal-plant stress and atmospheric variables

Correlation coefficients for internal-plant stress and atmospheric stress (+.14 NS) and wind (−.36 NS) for the *A. nuttallii* community are very low and nonsignificant (Fig. 14). Similar results were found for all the 11 species tested. As shown in Fig. 14, wind velocities and atmospheric stress have quite different seasonal trends than does internal-plant stress (Fig. 6). Atmospheric stress and wind

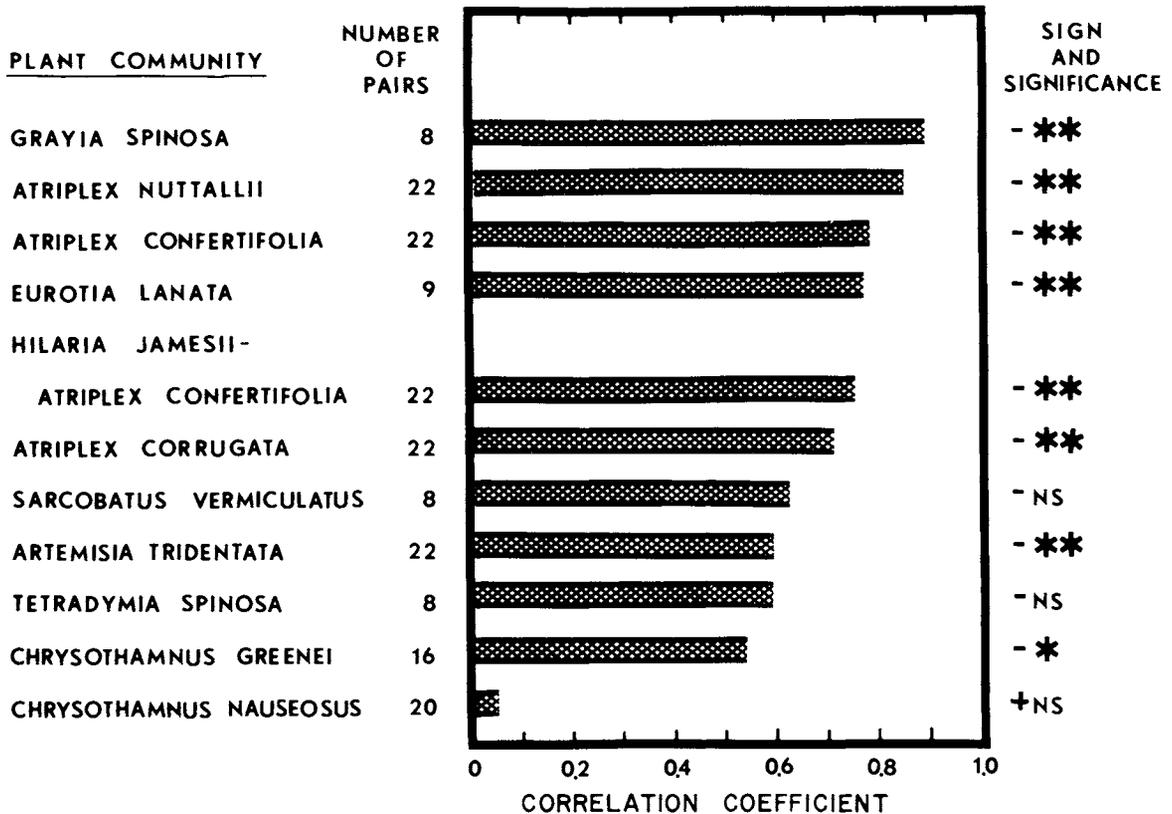


FIG. 11. Curvilinear correlation coefficients for the relationship between soil-water storage and internal-plant stress in 11 plant communities.

velocities are also somewhat more variable between sampling dates. These results indicate that factors such as soil-moisture conditions are far more important determinants of internal-plant stress for the species studied. Similar results were recorded for mountain shrubs in Utah (Dina et al. 1973) and for *A. tridentata* in Colorado (Branson and Shown 1975).

Our findings almost totally disagree with results reported for mesquite in Texas (Haas and Dodd 1972), irrigated sudangrass in Arizona (Van Bavel et al. 1963), and red pine in Minnesota (Sucoff 1972). Van Bavel et al. (1963) reported that under well-watered conditions, transpiration by sudangrass was totally related to atmospheric demand. Arid habitats, associated limited soil-moisture supply in our study area, and probably plant characteristics may account for these conflicting results. It is known that desert species have various morphological and physiological features that reduce water loss. For species in this study some of these features include early leaf fall and long dormant periods (*T. spinosa* and *G. spinosa*, see Fig. 21), plants with whitish lanate hairs on stems and leaves (*E. lanata* and *T. spinosa*) that increase reflectance, and reduce water-

vapor transport from stomata by obstructing air movement near them. Several of the species are considered to be halophytes (*S. vermiculatus*, *A. confertifolia*, *A. nuttallii*, and *A. corrugata*) which usually infers high concentrations of salts in cell sap which tends to reduce water loss by evaporation. Harris (1934) reported an osmotic pressure of 205 bars and several values of more than 150 bars for *A. confertifolia*. It is probable that accumulation of salts on leaf surfaces and in vesiculated leaf hairs (trichomes) caused some error in osmotic pressure measurements by Harris. It is now known that high concentrations of salts occur in vesiculated leaf hairs of *Atriplex* species and as these rupture, salts are deposited on leaf surfaces (Mozafar and Goodin 1970).

The correlation between air temperature and internal-plant stress (Fig. 15) is $+0.55^{**}$ and indicates that temperature or factors associated with it may cause plant stresses to be high or low. Plant stresses reach a peak later in the season than do air temperatures, probably because of the overriding influence of soil-moisture depletion on plant stresses.

As shown in Fig. 16, the relationship between air temperature and plant stress is highly significant for

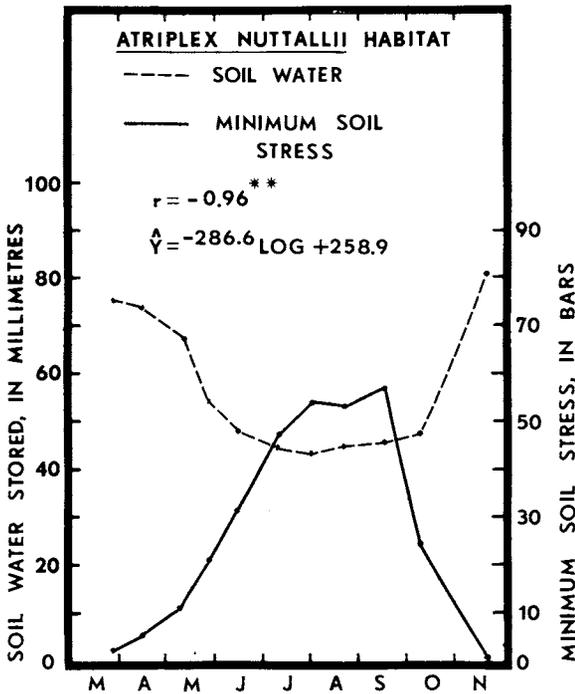


FIG. 12. Linear correlation coefficient, seasonal patterns of soil-water storage, and minimum soil-moisture stress in the *Atriplex nuttallii* plant community.

fewer than half of the 11 species. In general, the relationship is closer for species having more readily available soil water. An exception is *C. nauseosus* for which plant stress was not closely related to any of the environmental variables measured. Fragments of rock prevented augering deeper than 2 m in one of the two sites occupied by this species and the significant quantity of roots that extended beyond our sampling depths may partially explain these poor relationships.

Soil-water storage and evapotranspiration

Shown in Fig. 17 are estimated relative quantities of water evapotranspired by the 12 plant communities studied. These values were obtained by subtracting minimum soil-water storage (August 1973) from maximum storage (March 1973). Values for 1973 instead of 1972 were used because comparable values for maximum spring moisture storage were not obtained from all habitats in 1972. The largest quantity was measured in the highly permeable (soil saturation percentage of ≈ 30) *G. spinosa* soil. Low runoff and probably snow entrapment resulted in high moisture storage in this soil. In the Mojave Desert of southern Nevada, soils of *G. spinosa* associated with *Lycium andersonii* also had more available soil moisture than six additional plant communities studied (Rickard and Murdock 1963). Values shown for the next three sites (*C. nauseosus*,

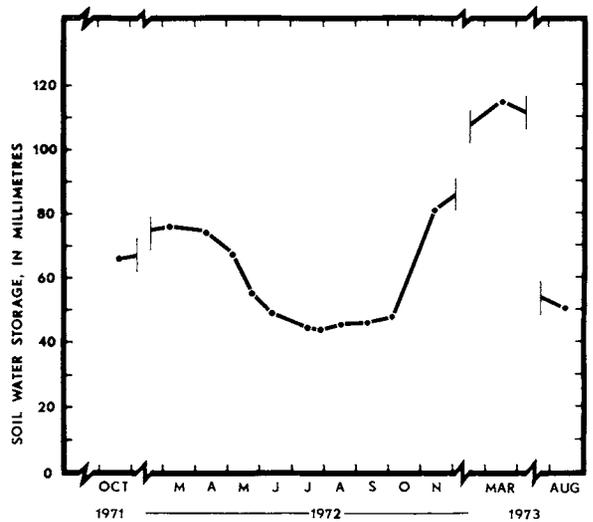


FIG. 13. Seasonal patterns of soil-water storage for the habitat occupied by *Atriplex nuttallii*.

A. tridentata, and *S. vermiculatus*) may be underestimates. All three sites receive run-in moisture and all but the *Artemisia* site had ground water available to the plant roots at least part of the growing season. The method does not measure ground water use. The probability that ground water was available to greasewood may explain the difference between our results and those of Rickard (1967), who found that nearly twice as much water was used by greasewood as by big sagebrush. For the upland communities the method should provide a reliable estimate of water use.

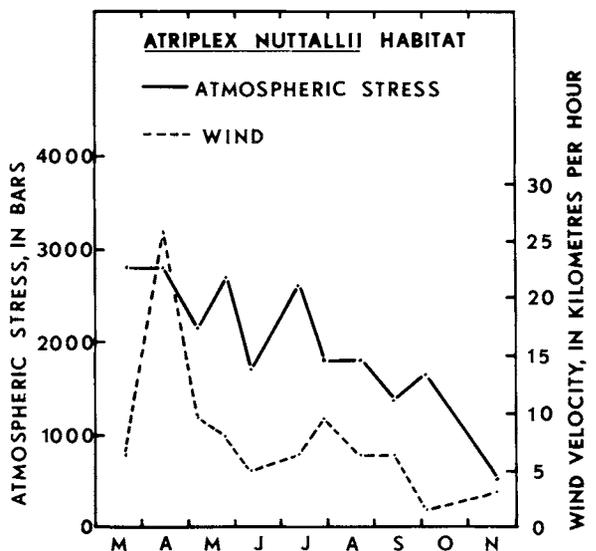


FIG. 14. Seasonal patterns of wind velocities and atmospheric stress in the *Atriplex nuttallii* habitat.

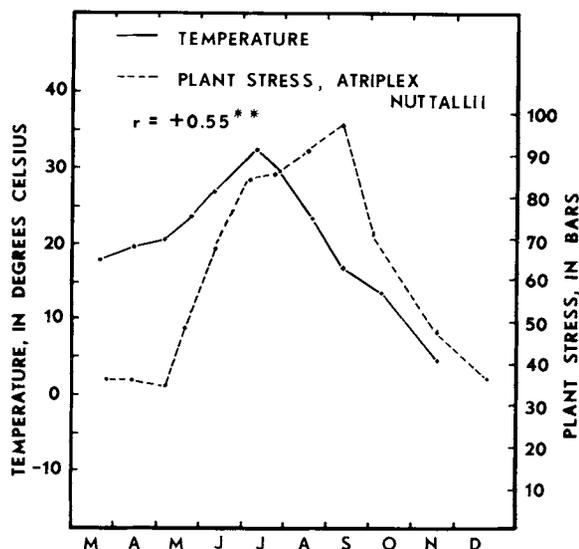


FIG. 15. Linear correlation coefficient and seasonal patterns for air temperature and internal-plant stress in *Atriplex nuttallii*.

There is a general inverse relationship between amounts of bare soil and quantities of water evaporated. A major deviation from the general trend is found in the *T. spinosa* community. The soil in this community was moist (minimum soil stress did not exceed 15.8 bars) and salty (electrical conductivity ≈ 7) and we suspect that much of the soil water was evaporated instead of transpired. The same general situation also exists in the *A. corrugata* community. This diminutive, succulent, evergreen shrub produces an almost immeasurably small annual growth and must transpire very little water, but exhibits greater aerial cover than might be expected for the water evaporated. Also, more than half of the cover measured was algal crust and mulch (Table 1), both of which would probably have less effect on water use than live shrub cover. Although salty, the high moisture content of this soil contributed to the presence of algal crusts thereon. In evaluating plant distribution in Death Valley, Hunt (1966) states, "In general, algae were obtained beyond the limit of the flowering plants (6% brine line) as far as the 8% brine line."

The correlation coefficient for percent bare soil and soil-water storage for the 12 plant communities is -0.78^{**} . These results are in agreement with those by Branson and Owen (1970) who found a highly significant relationship ($r = +0.86^{**}$) between annual runoff and percent bare soil for the same watersheds studied in this paper. For percent live cover, the relationship with soil-water use is somewhat higher ($r = +0.84^{**}$) than for bare soil.

The correlation coefficient for standing crop (Fig. 5) and soil-water use is $+0.67^*$. Considering all of

the variables and some of the difficulties encountered in measurement of soil-water use, this coefficient is higher than might be expected.

The range of values shown in Fig. 17 are somewhat comparable to those of Hillel and Tadmor (1962) who used a similar method to compute evapotranspiration in the Negev Highlands of Israel. Their estimates of water available for plant growth were: 50 mm for rocky slopes, 35 mm for loessial plains, 160 mm for wadi beds, and about 90 mm for sands. If their estimates are correct ours may be conservative, because although the soil conditions are not identical, precipitation for the report area is about double that for the Negev study.

Soil salinity

Degree of salinity exerts control over kinds of plants that occupy some land surfaces. By definition, plants that occupy saline soils (soils having $EC \times 10^3$ of > 4 or > 4 mmho/cm) are termed halophytes, but because of limited soil-salinity data, confusion exists about salinity tolerances of many species. Shown in Fig. 18 are electrical conductivity and osmotic stress values for soils of the 12 plant communities studied. These are averages of measurements to the active rooting depth (defined below in the section on roots) of four soil profiles from each community. Measurements of saturation paste conductivity were converted to more commonly reported saturation extract conductivities by the formula presented by Richards (1954):

$$EC_e = [5.4 - .007 (SP)] EC_s$$

where

EC_e = Saturation extract conductivity

SP = % water in saturated soil

EC_s = Saturation paste conductivity.

To compute osmotic stress at field capacity, an additional formula (Richards 1954) was used:

$$OP \text{ (osmotic pressure)} = 0.36 EC_e \times 2.$$

Most of the species shown (Fig. 18) have been considered to be halophytes or salt desert shrubs. Sites selected within a single area cannot represent maximum salt tolerances for all species present. However, our data show only the five soils occupied by *A. corrugata*, *S. vermiculatus*, *A. nuttallii*, *C. nauseosus*, and *T. spinosa* would be considered saline. In agreement with these data, Wallace and Romney (1972) found *A. tridentata* to be moderately salt sensitive and *G. spinosa* highly salt sensitive. These findings conflict with statements by Van Dersal (1938) that *G. spinosa* "may occur on alkaline soil" and Dayton (1931) that "It is common in alkaline situations. . . ." Our data for four additional widely separated sites (one in Wyoming and three in Utah) show osmotic stresses at field capacity had the low

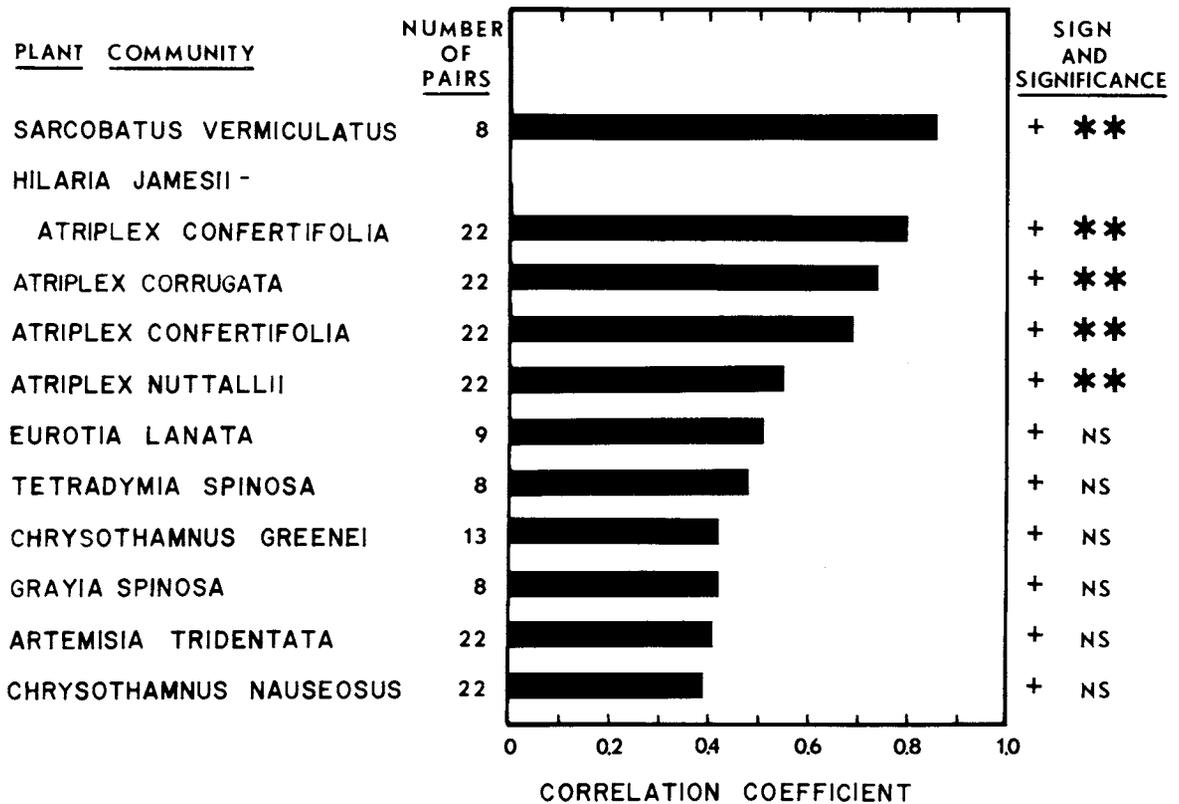


FIG. 16. Linear correlation coefficients for air temperature and internal plant stress in shrubs of 11 plant communities.

range of 1.0–0.5 bar and a mean value of 0.7 bar. However, supporting the views that *G. spinosa* may be salt tolerant, data of Rickard and Keough (1968) show an average EC_e of 9.6 mmho/cm for the 150 cm soil profile in Washington where *G. spinosa* (7.5% of ground cover) grew in association with *S. vermiculatus* (14.2% of ground cover).

Soils of the *A. corrugata* communities have osmotic stresses of about 12 bars or atmospheres at field capacity (EC_e of 16.6 mmho/cm). Although high, this value is somewhat lower than the EC_e of 25.8 mmho/cm reported for soils of this community in eastern Utah (Ibrahim 1963). These values would also become higher as the soils become dryer than field capacity but the relationship would not be linear because salts, especially gypsum, common in soils derived from Mancos Shale, would form precipitates with an increase in soil dryness.

Artemisia tridentata occurs on saltier soil than might be expected. Other authors (Kearney et al. 1914, Shantz and Piemeisel 1924) found this species to occupy soils low in salts. Where soils had significant amounts of salts, Kearney et al. (1914) found sagebrush plants to be stunted and shallow-rooted. Of five species (*A. tridentata*, *E. lanata*, *A. confertifolia*, *S. vermiculatus*, and *A. nuttallii*)

studied in northwest Utah by Gates et al. (1956), soils occupied by *A. tridentata* had mean EC_e (about 7 mmho/cm) and maximum EC_e (about 17 mmho/cm) values which exceed the one we show in Fig. 16. Apparently, factors other than soil salts determine the distribution of species occupying the soils low in salts.

Soils of both communities in which *A. confertifolia* was a dominant were low in salts. These results provide quantitative support for the views of Fautin (1946) and Billings (1949) that shadscale may occur on nonsalty soils and contradict the often verified statement (Kearney et al. 1914, Stewart et al. 1940, Shantz and Piemeisel 1924) that shadscale occupies soils that are saline in the lower part of the rooting zone. These apparent habitat differences may be attributable to different ecotypes or possibly mean that this species occupies relatively dry sites that may or may not be salty.

Root distribution and root biomass

Root profiles in Fig. 19 are arranged left to right according to decreasing root mass to the depth of effective rooting. Effective rooting depth is defined as the depth at which root weights became less than 3 g/sample (sample size was 100 mm deep by 50 mm

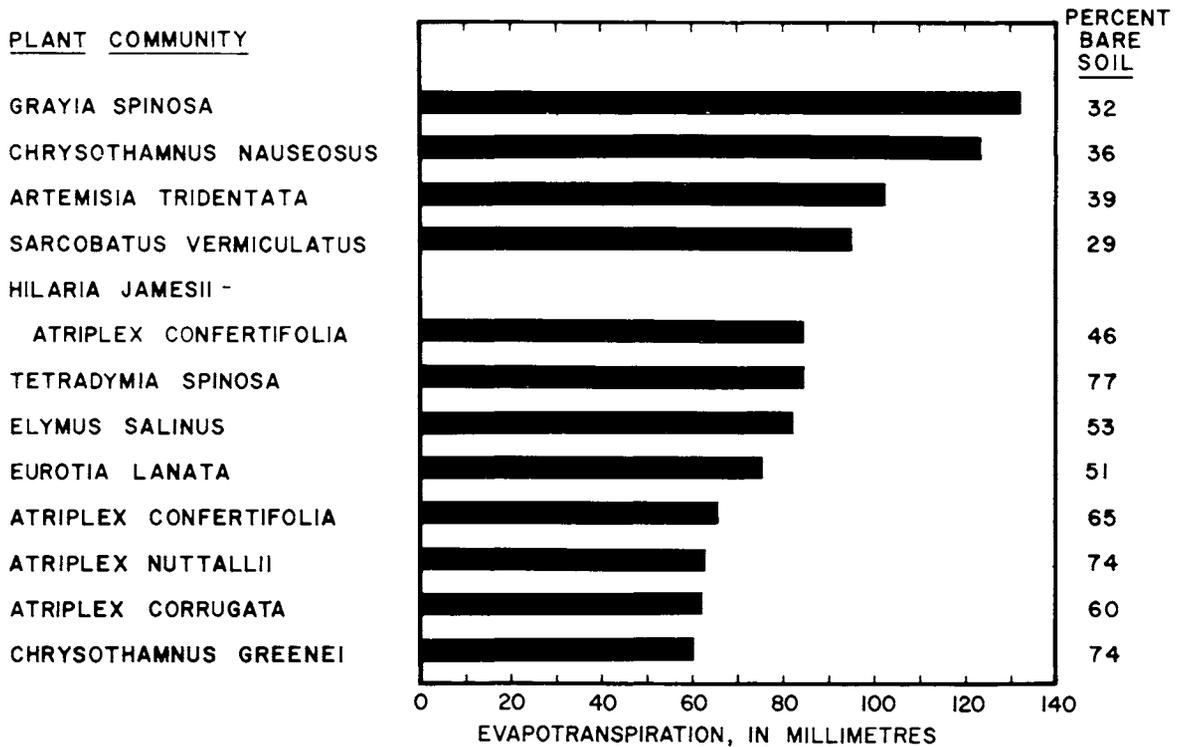


FIG. 17. Relative quantities of water evapotranspired and percent bare soil for 12 plant communities. Note the general inverse relationship between bare soil and water use.

in diameter) or less than 15 g/dm^3 . It is assumed that the small mass of roots at greater depth is relatively unimportant. Two exceptions to this assumption would probably be found in the *C. nauseosus* and *S. vermiculatus* communities where some roots probably extend to readily available ground water. Nevertheless, for comparative purposes the assumption should be valid.

The one grass community, *E. salinus*, shows a root distribution pattern different from most of the shrub communities. The main root mass in the grass community is in the upper part of the soil profile whereas in most of the shrub communities, especially *A. confertifolia* and *C. greenei*, there is a quite gradual decrease in root weights with an increase in soil depth. The grass-shrub community, *H. jamesii*-*A. confertifolia*, shows an intermediate pattern of root distribution.

Although one might expect root mass to be related to soil-water storage and use (Fig. 17), there are notable exceptions (compare *E. salinus* and *G. spinosa* in Fig. 17 and 19). Differential rates of root decomposition and differing ratios of shoot to root production between species may cause these differences.

Most of the curves in Fig. 19 appear rational, although infrequently encountered large shrub roots cause some variation. Least variable was the grass

community, *E. salinus*. Somewhat erratic results were obtained for the relatively coarse rooted *C. nauseosus nauseosus*.

Plant growth and water use

In Fig. 20 measured seasonal water use and plant growth are compared. For all communities except *C. nauseosus* the curves for plant growth and cumulative water use are similar. Moisture use in the *C. nauseosus* soil started before the shrubs produced new leaves (apparently by evaporation but possibly by transpiring green twigs) and less water use per increment of growth was measured than would be expected when viewing the plant growth and water-use curves for the other shrubs. The possibility of transpiration of unmeasured ground water and the difficulty of obtaining soil samples from adequate depths may explain this apparently atypical curve.

In general, the curves show a wider disparity between growth and water use as growth by a species becomes less. Stated differently, "water-use efficiency" (actually, in these results it is water lost from the habitat per unit of growth) becomes lower as total growth by the different species becomes lower. The drought-tolerant species are not necessarily efficient users of soil moisture, at least in terms of growth per unit of water evapotranspired. Admittedly, results for these species would probably

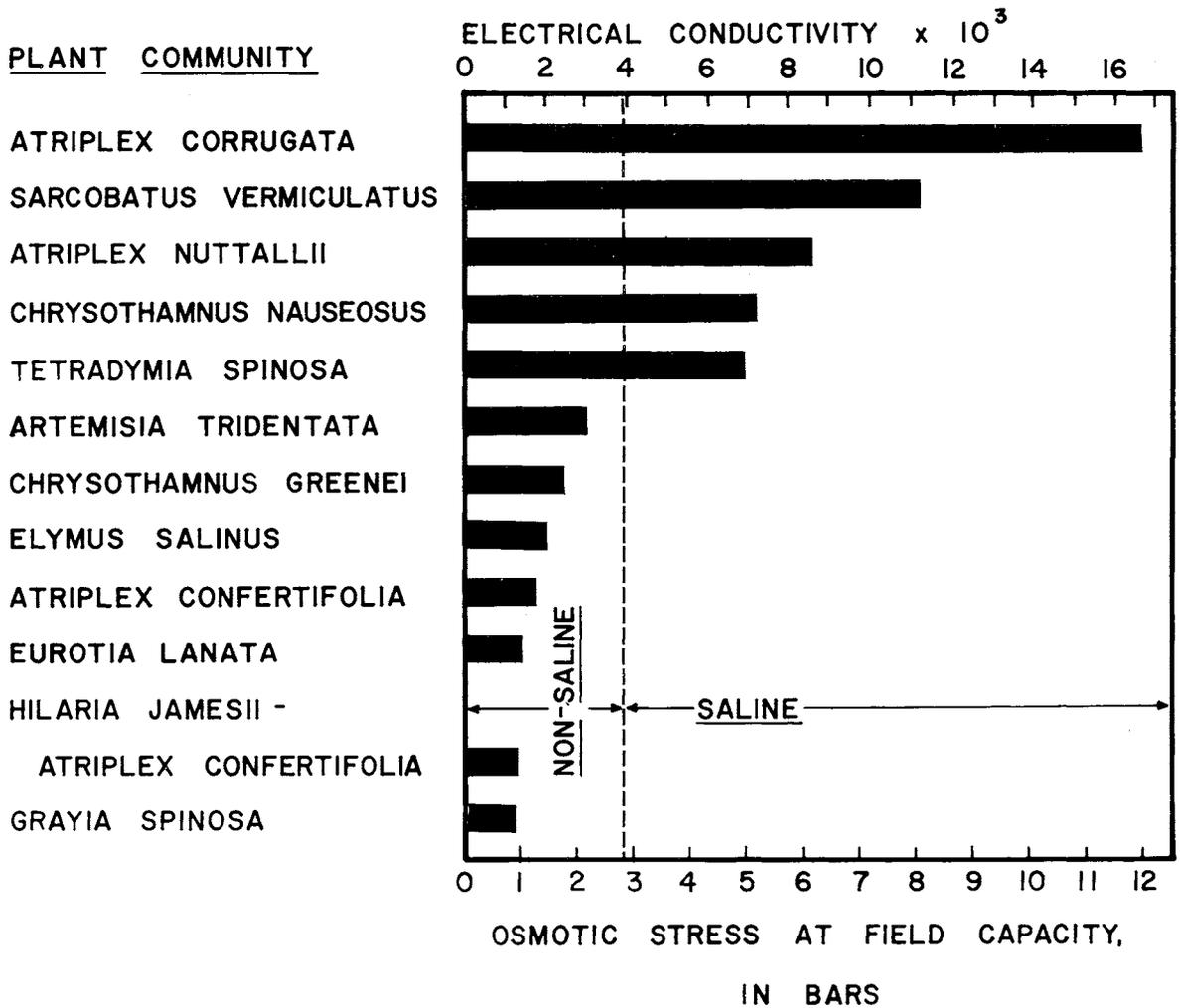


Fig. 18. Average electrical conductivity and osmotic stress at field capacity for soils of 12 plant communities.

be different if the plants were grown under uniform conditions in growth chambers or greenhouses, and many of the species studied may be highly efficient in terms of carbon fixation per unit of water transpired. However, growth of these species under uniform conditions would not duplicate conditions of the habitats in which they are found. Under artificial conditions, with the evaporation component removed, the reverse of the results shown might be found, but such results would shed little light on the question of why plant species occur where they do. These decreases in plant growth and water use by species are accompanied by increases in bare soil which probably causes the evaporation component of evapotranspiration to be larger. If these limited results permit extrapolation one could conclude that as plant cover approaches zero, nearly all of the water stored in soils would be lost by evaporation instead of transpiration.

Atriplex corrugata is a most unusual species. Although it produces an almost immeasurably small annual increment of growth, it completely dominates the two sites studied. Salt tolerance and capacity to remove soil water at high osmotic stresses (Fig. 18) must explain its dominance on certain sites. Maximum internal-plant stresses (Fig. 8) of *A. nuttallii* slightly exceed those of *A. corrugata* but soils occupied by the former are considerably less salty (Fig. 18).

Phenological stages of shrubs

The most striking phenological difference shown for the 11 shrub species (Fig. 21) is the duration of the dormant period. Both *G. spinosa* and *T. spinosa* are in the dormant stage for much of the year and resume growth later in the spring than most species observed. Although the calendar date on which dormancy was recorded varied from one year to another,

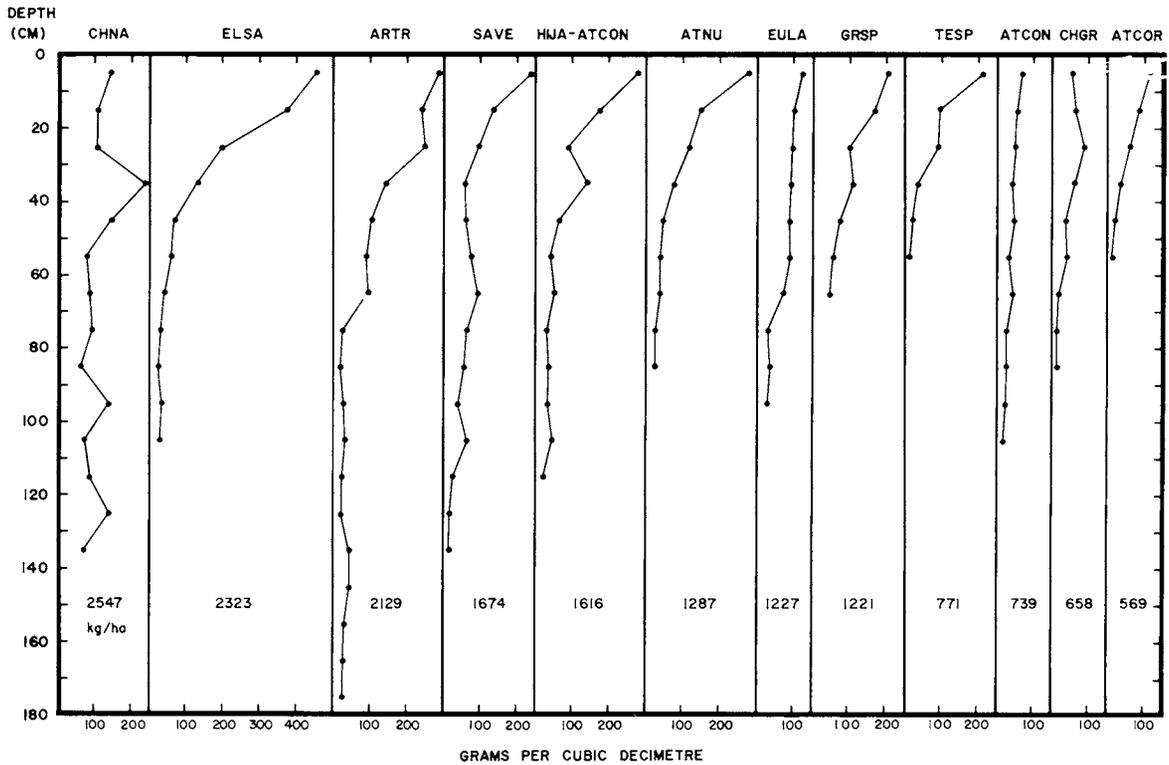


FIG. 19. Profiles of root weights as related to soil depth in 12 plant communities. Symbols at the top of the graph refer to community dominants as follows: CHNA = *Chrysothamnus nauseosus*, ELSA = *Elymus salinus*, ARTR = *Artemisia tridentata*, SAVE = *Sarcobatus vermiculatus*, HJA-ATCON = *Hilaria jamesii-Atriplex confertifolia*, ATNU = *Atriplex nuttallii*, EULA = *Eurotia lanata*, GRSP = *Grayia spinosa*, TESP = *Tetradymia spinosa*, ATCON = *Atriplex confertifolia*, CHGR = *Chrysothamnus greenei*, and ATCOR = *Atriplex corrugata*. Calculated kg per ha for each profile is shown and each data point on the curves represents g/dm³ per sample depth.

G. spinosa was consistently one of the earliest to reach the dormant stage at the Nevada Test Site (Wallace and Romney 1972). Their data show that most species become dormant at a later date during years of high precipitation. Although 1972, the year observations were made, was dryer than average, the results for the different species should be comparable. Even the "evergreen" species, (*A. corrugata*, *A. nuttallii*, *A. confertifolia*, *E. lanata*, and *Artemisia tridentata*) appeared dormant by mid or late summer. Dormancy is difficult to determine for "evergreen" species and visual assessment of dormancy in species that retain green leaves must be considered arbitrary. Measurements of carbon fixation or transpiration rates would provide more reliable information. Caldwell et al. (1972) found that positive net photosynthesis occurred in *E. lanata* and *A. confertifolia* at leaf temperatures of -5°C , and there was both net photosynthesis and transpiration in *A. confertifolia* at plant-moisture stress of 65 bars in early August. Dormancy can be determined visually with some degree of certainty only for the deciduous species (*Grayia*, *Tetradymia*, *Sarcobatus*, *Suaeda*, and *Chrysothamnus greenei*), but green

stems and twigs in these species may be physiologically active during the summer. Although *A. tridentata* exhibited considerable loss of leaves it apparently was not dormant during the period of observation. The two Compositae species, *A. tridentata* and *C. nauseosus* flowered later in the year and used water for a longer time than other species observed.

Although precipitation for the year was lower than average, all species completed the life cycle of leaf growth, flowering, and seed production. Active growth continued later in some of the species (*S. vermiculatus*, *A. tridentata*, and *C. nauseosus*) having a more abundant soil water supply. An exception to this generalization is found in *G. spinosa* which became dormant early but was found on a moist habitat. Possibly in *Grayia*, dormancy is related to both day length and water availability.

Persistence of leaves on evergreen shrubs

For salt-desert species, the distinction between evergreen and deciduous is sometimes difficult. One means of determining relative degrees of "evergreenness" is to observe the time interval that in-

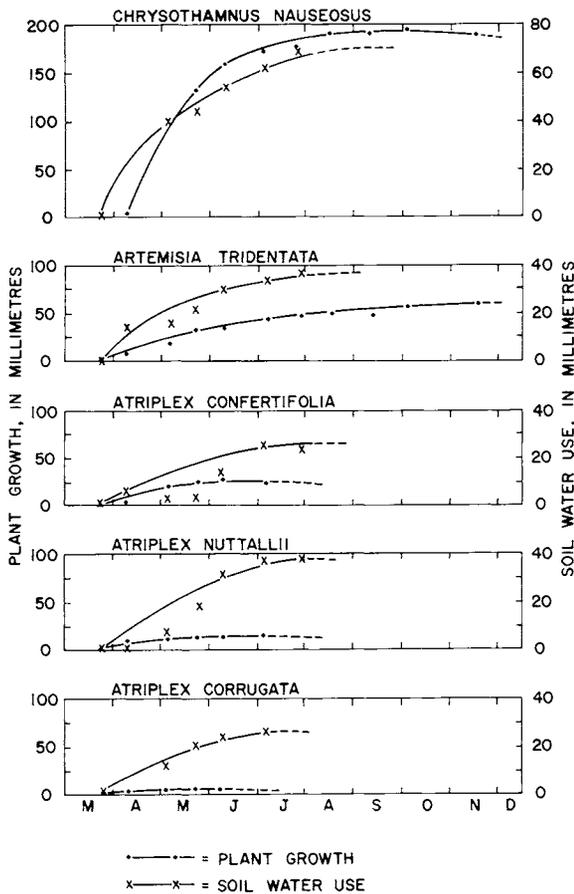


FIG. 20. Seasonal plant growth and associated water use for five shrub species.

dividual leaves remain attached to plants. The method does not account for leaves that are replaced during the growing season, and thus is only a partial measure of evergreenness. Results from the use of this technique for three species (*A. corrugata*, *A. nuttallii*, and *Artemisia tridentata*) are shown in Fig. 22.

Of the three species, the method used indicated only *A. corrugata* to be truly evergreen. The marking material used (red fingernail polish was found to be more durable than India ink) did not permit observations of the same leaves for more than 1 yr, but it is probable that individual leaves of *A. corrugata* remain attached for several years. The other two species lost leaves far more rapidly and rate of leaf replacement must account for degree of evergreenness in these species.

Persistence of leaves affects nutritional qualities of plants. Those retaining leaves longer maintain higher levels of protein, phosphorus, and carotene for longer periods.

These results for *A. tridentata* agree with those of Diettert (1938), who found that although the plants

are "evergreen," the leaves do not function for a very long period; mature leaves that persist over winter are shed in the spring as new leaves develop. New leaves developed in early spring are often shed before the end of the growing season and leaf fall increases during critical periods of reduced water supply.

Monk (1967) found that in north-central Florida abundance of evergreen species increases as soil fertility and pH decreased. He also proposed that "evergreenness" may be an adaptation to drought. All of our sites had nearly neutral pH of ≈ 7.4 except the slightly gypsiferous winterfat soil which had an average pH of ≈ 6.8 . However, our most evergreen species, *A. corrugata*, occupied one of the driest sites and the soils contained the most salts; the least salty and most moist site was occupied by a deciduous species, *G. spinosa*.

CONCLUSIONS

The question posed at the beginning of this paper "Why do plant communities occur where they do?" is not completely answered by the information presented. Puzzling differences exist in ordinations or rankings of plant communities according to standing crop (live stems plus current growth) (Fig. 5), maximum seasonal plant stress (Fig. 8), quantities of water evapotranspired (Fig. 17), and soil salinity (Fig. 18). We conclude that plant species respond differently to single factors and that a probable reason for the differing ordinations is that plants respond to the total environment, not single factors. If rational weighing could be given to each of the factors and a single value derived for each plant community, the ultimate in plant community ordination might be achieved. However, with our present limited knowledge of the relative importance of different environmental variables, assigning such importance values would be arbitrary. Although the ordinations of plant communities are not in complete agreement, maximal values for variables such as internal-plant stress, soil salinity, and amounts of water available for plant growth within plant communities must be of major importance in determining the distribution of plant species. If true, this statement would agree with the statements of Ungar et al. (1969), who, from their study of plant communities on saline soils near Lincoln, Nebraska, conclude: "Vascular plants growing at the extreme end of ecological gradients are often capable of growing under intermediate conditions, but are limited to extreme environments by their inability to compete with other species at moderate sites. They occupy extreme sites not because of some need, but because they can tolerate the local environmental extremes while others cannot."

Throughout their extensive geographic range, many

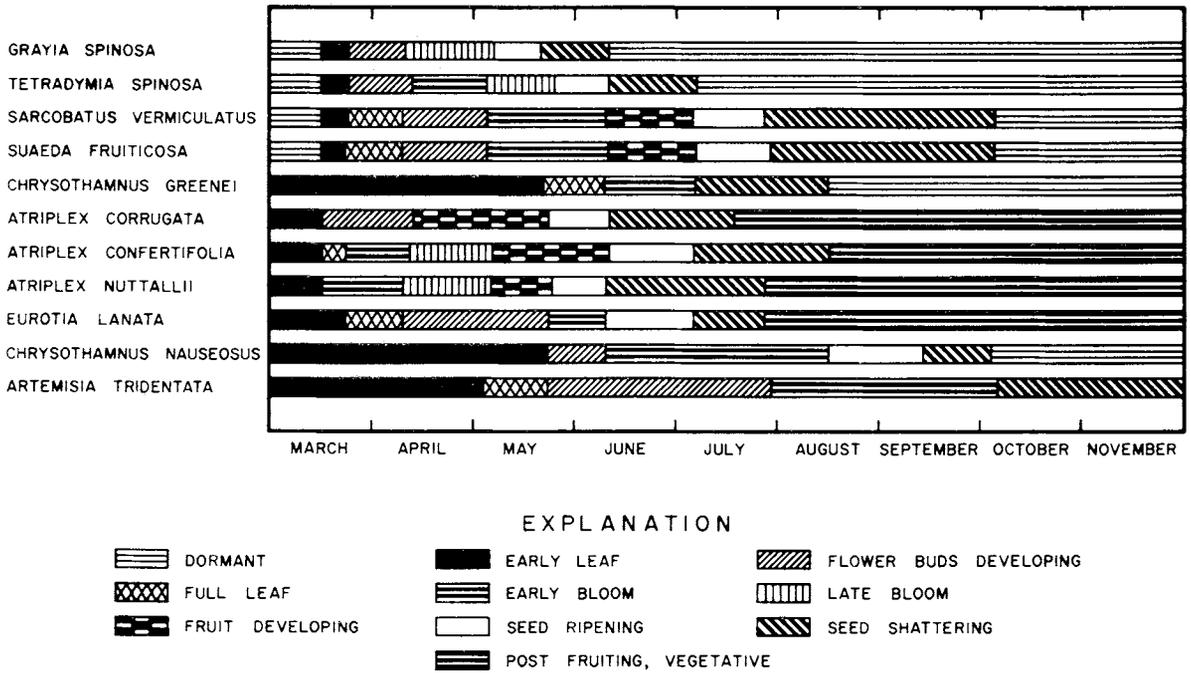


Fig. 21. Phenological stages for 11 shrub species.

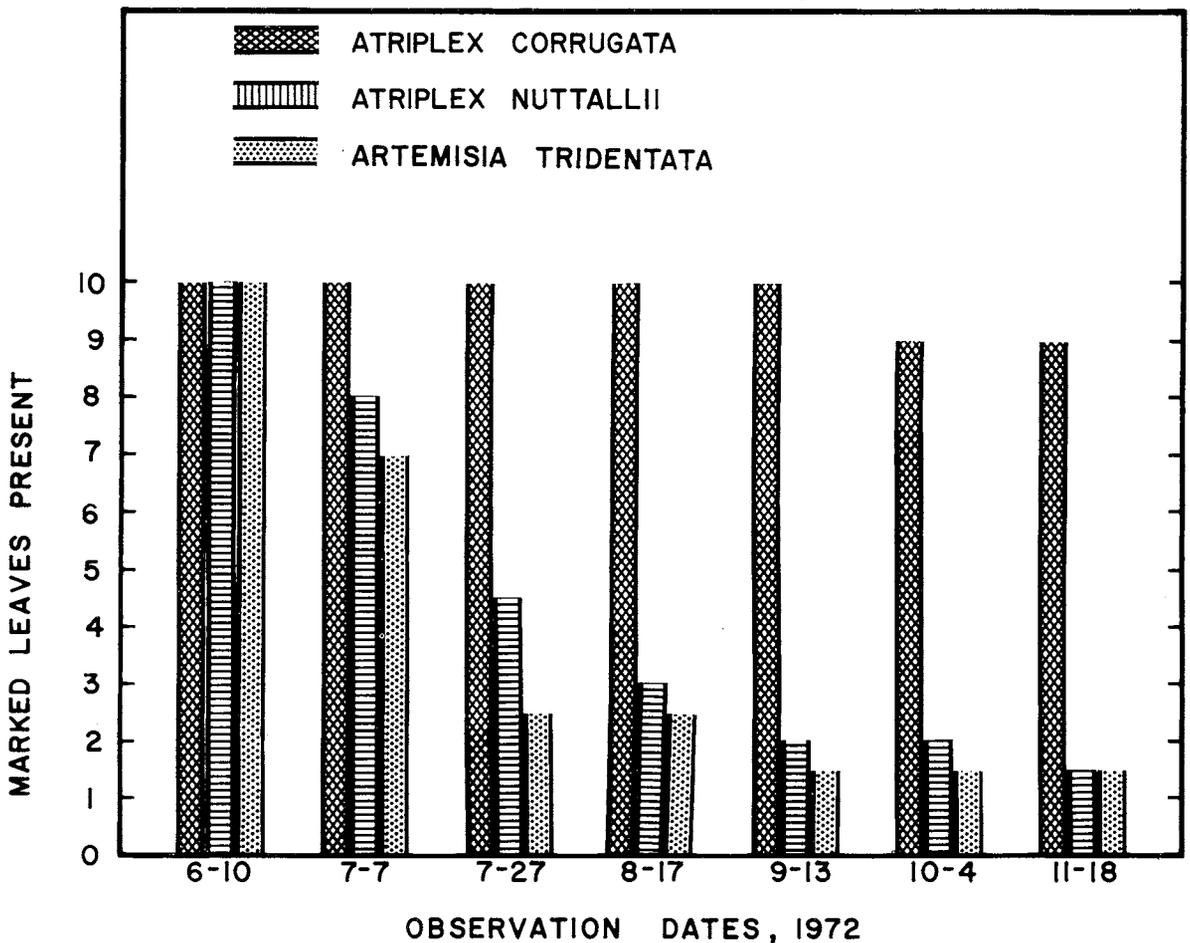


Fig. 22. Persistence of leaves on three northern desert shrub species.

of the species of this study are found in habitats that appear similar to those found in the Badger Wash study basin. However, because of some unknowns such as ecotypic variations within species, the presence of species can probably be used only to predict a range of environmental conditions. Nevertheless, knowing these tolerance ranges can be extremely valuable in evaluating landscapes for various purposes. Our present knowledge of these plant communities permits rapid approximations of soil water stored and evapotranspired, soil texture, soil salinity, runoff, sediment yields, and rehabilitation potentials of species and habitats.

We can offer some generalizations about habitat relationships of the species studied. *Chrysothamnus nauseosus* was found in or near minor ephemeral stream channels where there was a shallow (≈ 2 -m) water table. *Sarcobatus vermiculatus* also grew near major ephemeral stream channels where salty ground water occurred at a depth of 3.7 m. *Artemisia tridentata*, in this dry climate (230 mm precipitation) is restricted to areas near upland ephemeral channels with nonsaline soils. The most salt-tolerant species in the area was *A. corrugata*. *Tetradymia spinosa* occupied a similarly moist but less salty site. Highest internal-plant stresses, a measure of drought tolerance, were measured in *A. nuttallii*, a species on upland soils that were both salty and dry. *Chrysothamnus greenei* was on intermediate but nonsaline dry slopes. *Elymus salinus* was most abundant on steep, north-facing slopes. There was considerable soil creep on these slopes; grass may have been dominant here because fibrous roots added greater stability to slopes than top-rooted shrubs. The *A. confertifolia* habitat was sandy, dry, and nonsaline. The soil occupied by both *A. confertifolia* and *Hilaria jamesii* was a sandy paleosol with very well-defined soil horizons. A sandy upland site with snow accumulation and the highest computed evapotranspiration was occupied by *G. spinosa*. This was also a paleosol characterized by caliche in the B-horizon. *Eurotia lanata* was dominant on a loessial, dry, nonsaline, silty, and slightly gypsiferous upland soil.

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