Geographic Distribution and Factors Affecting the Distribution of Salt Desert Shrubs in the United States[1]

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Highlight

Four previously published classifications of intermountain shrub vegetation and a new classification based on maximum salt tolerances and water relationships are presented. Maps show that the geographic range of salt desert shrub species far exceeds the distribution of mappable communities in which these shrubs are dominants. Species differ in their capacity to tolerate soil osmotic stress, but variable results from measurements of osmotic stress in 20 different plant communities indicate that additional factors must be important in determining species present in different habitats. Data obtained by the use of a new method of measuring total soil moisture stress in field samples show that the capacity of different species to remove soil moisture to different maximum stresses appears to determine the kinds of plants that occupy different habitats. Total soil moisture stresses for 14 plant communities sampled ranged from 19 to more than 90 bars.

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The phrase "salt desert shrub" has been interpreted in a variety of ways by different authors. The vegetation commonly found below 5,500 ft. in the Great Basin and eastern Utah with extensions into many other States has been referred to as a "formation", a "desert", a "biome", a "zone", a "type", an "area", a "province", and possibly by other names. For the most part, these names represent different points of view rather than confusion. Admittedly, most classification systems are artificial but they are helpful to anyone who tries to understand complex natural phenomena. Before reviewing the classification systems that have been applied to salt desert shrub vegetation, a brief evaluation of the meager information available on the origin of Great Basin desert species may be informative.

Origin of Salt Desert Shrub Vegetation

In terms of geologic time, the deserts east of the Sierra and Cascade Mountains are of relatively recent origin. During epochs as recent as Pliocene (less than 10 million years before present), Axelrod and Ting (1960) propose that Sierran forests, requiring 20 to 25 inches more precipitation than now occurs, occupied lowlands of the western Great Basin. The Sierra-Nevada Mountains rose 3,000 ft. in early Pleistocene, another 3,000 ft. by mid-Pleistocene and still another 1,000 to 1,500 ft. by the end of Sangamonian time (ca 70,000 years before present). The increased aridity inland caused by the rise of Pacific Coast mountain ranges resulted in the change from mesophytic forests to drought tolerant shrubs.

Early Pleistocene (ca 1,000,000 years before present) was moist and cool in the Great Basin. From the fossils of herbivores such as bison, camel, elephant, and horse it is inferred that grasslands were widespread in the Great Basin in early Pleistocene (Axelrod, 1950). Conifers and woodlands were found at lower altitudes than today and deserts were much restricted. The present vegetation developed from Tertiary floras which Axelrod (1950) groups as Arcto-Tertiary and Madro-Tertiary. The genera *Chrysopsis, Chrysothamnus, Eriogonum, Grayia, Salvia, Sphaeralcea, Stenopteris,* and *Tetradymia* are thought to have originated in the neo-tropics because their relatives now extend into the tropics. Some of the many genera that are thought to have northern origins because they occur both in Eurasia and North America include: *Artemisia, Atriplex, Eurotia, Suaeda, Koeleria, Agropyron, Salicornia, Elymus, Hordeum,* and *Festuca.*

Table 1. Classification system for vegetation of the Great Basin proposed by H. L. Shantz (1925).

Northern Desert Shrub Formation
Sagebrush association *(Artemisia tridentata)*
Small sagebrush association *(Artemisia nova)*
Little rabbitbrush associes *(Chrysothamnus puberulus)*
Shadscale association *(Atriplex confertifolia)*
Winterfat associes *(Eurotia lanata)*
Hop-sage and Coleogyne association *(Grayia spinosa* and *Coleogyne ramosissima)*
Bud sagebrush association *(Artemisia spinescens)*
Mat saltbush association *(Atriplex corrugata)*
Gray molly association *(Kochia vestita)*
Salt Desert Shrub (Greasewood) Formation
Greasewood association *(Sarcobatus vermiculatus)*
Greasewood shadscale association *(S. vermiculatus* and *Atriplex confertifolia)*
Seepweed association *(Dondia torreyana)*
Pickleweed association *(Allenrolfea occidentalis)*
Samphire association *(Salicornia utahensis* and *S. rubra)*
Saltgrass associes *(Distichlis stricta)*
Alkali sacaton associes *(Sporobolus airoides)*
Rabbitbrush associes *(Chrysothamnus graveolens)*

Table 2. Shreve's (1942) classification of Great Basin Desert vegetation.

Juniperus utahensis (6,000 to 7,000 ft)
Artemisia tridentata (upper belt)
Atriplex confertifolia (lower belt)
Kochia vestita
Sarcobatus vermiculatus
Distichlis stricta-Sporobolus airoides
Salicornia rubra, S. utahensis, Allenrolfea occidentalis
Coleogyne ramosissima

Classifications of Salt Desert Shrub Communities

One of the earliest and most complete classifications is that of H. L. Shantz (1924, 1925; Table 1). His groupings of Northern Desert Shrub Formation and Salt Desert Shrub (Greasewood) Formation affect our thinking today, but the variety of concepts applied in more recent community classifications indicates that there is still a search for the ideal system or concept. The criterion used by Shantz for the two major communities appears to have been upland sites versus those sites receiving "run in" moisture. More recent publications have shifted many of the communities from one grouping to the other, resulting in a regrouping of all salt-tolerant species into the Salt Desert Shrub (Greasewood) Formation and ignoring the runoff-runin moisture criterion of Shantz. Hutchings and Stewart (1953) list only big and black sagebrushes in their "Sagebrush-grass Formation" and most of the other common shrubs are assigned to the Salt Desert Shrub Formation. The Clemensian terminology of Shantz is of interest. He felt that winterfat was a successional or seral community because it sometimes replaced shadscale. This is one of Shantz's views that now seems erroneous. For example, winterfat communities are now being invaded by *Halogeton glomeratus* (Eckert, 1954); and Fautin (1964) proposed that much of the type had been replaced by little rabbitbrush *(Chrysothamnus stenophyllus)*. The Clemensian terminology (Weaver and Clements, 1938) occurs infrequently in recent papers.

Shreve (1942), in his Botanical Review article on North American deserts, used both the zonation concept and edaphic factors in his ordination of plant communities (Table 2). However, Shreve questioned the view that there are "fundamental units" of vegetation and recognized that even when multiple criteria are used it is difficult to classify vegetation types. Shreve cites the work by Kearney and collaborators (1914) and lists their values for salt tolerances of the species present near the Great Salt Lake. Shreve's presentation is a general description, but the classification in Table 2 may be derived from it.

Table 3. Bio-ecologic classification of Great Basin vegetation by Fautin (1946).

Pinon-Juniper Biome
Northern Desert Shrub Biome
Shadscale Community
Tetradymia Community
Greasewood Community
Winterfat Community
Black Sage Community
Pickleweed Community
Little Rabbitbrush Associes
Sagebrush Community
Southern Desert Shrub Biome

Fautin (1946) proposed a bio-ecological classification with the "biome" (Table 3) being the equivalent of a "biotic formation." The author objected to the "Sagebrush Climax" of Clements (Weaver and Clements, 1938) because other climax communities in southwestern Utah seemed of

Table 4. The zonation concept applied to Great Basin vegetation by Billings (1949).

Sagebrush zone
Shadscale zone
Edaphic climaxes in zone:
Greasewood
Greasewood-shadscale
Pickleweed
Winterfat
On dune sands:
Dalea polyadenia-Tetradynia glabrata
Chrysothamnus stenophyllus

Table 5. A new classification proposed for the Intermountain shrub region, with maximum tolerances to osmotic stress and water relationships as criteria.

OSMOTIC STRESS AT FIELD CAPACITY ATMOSPHERES	
	Juniper-pinyon Zone
	Sagebrush Zone
0.01	Little rabbitbrush community *(Chrysothamnus viscidiflorus)*
0.1	Big sagebrush community *(Artemisia tridentata)*
0.2	Black sagebrush community *(Artemisia nova)*
	Salt Desert Shrub Zone
	Bud sagebrush community *(Artemisia spinescens)*
0.6	Winterfat community *(Eurotia lanata)*
2.2	Shadscale community *(Atriplex confertifolia)*
3.2	Desert molly community *(Kochia americana)*
5.0	Greasewood community *(Sarcobatus vermiculatus)*
5.0	Nuttall saltbush community *(Atriplex nuttallii)*
	Mat saltbush community *(Atriplex corrugata)*
OSMOTIC STRESS AT SATURATION ATMOSPHERES	Salt Marsh Zone
1.5	Rabbitbrush community *(Chrysothamnus nauseosus)*
2.8	Alkali sacaton community *(Sporobolus airoides)*
16	Saltgrass community *(Distichlis stricta)*
23	Seepweed community *(Suaeda torreyana)*
35	Glasswort community *(Salicornia utahensis* and *S. rubra)*
35	Pickleweed community *(Allenrolfea occidentalis)*
50	Algae
75	Fungi

importance equal to that of sagebrush. In fairness to Clements, it should be noted that Clements referred to the type as the Sagebrush Formation *(Atriplex-Artemisia)* which indicates some recognition of the importance of species of the two most widespread genera. The classification of Fautin also shows disagreement with Shantz in the rank of winterfat as a climax community.

A classification adopted by many recent authors is that by Billings (1949; Table 4). Billings, in contrast to systems used previously, applied to the Great Basin flora the zonation concept as used by Daubenmire (1943) for flora of the Rocky Mountains. An interpretation of Billings' article shows the listing of two major zones: (1) Sagebrush is the upper, wetter one, and (2) Shadscale is the lower, dryer one. He views all the communities within the shadscale zone as minor edaphic climaxes forming a mosaic. The quantitative data in the paper by Billings is on Nevada vegetation with references to the work by Fautin (1946) for information on Utah Great Basin vegetation.

Proposed in Table 5 is a new vegetation classification based on maximum salt tolerances of communities and on the capacity of one group, the Salt Marsh Zone, to exist partially submerged in water during all or part of the year. The data are presented in atmospheres osmotic stress at field capacity because of the ease of interpreting these values in terms of plant physiology. Maximum values for each community were obtained from published reports and from unpublished data obtained by the authors. The osmotic stress at 15 atm soil-moisture stress, the suction force sometimes considered to be the permanent wilting point, can be obtained by multiplying the values shown by two except for the Salt Marsh Zone. Osmotic stress at saturation is shown for Salt Marsh Zone communities because these habitats usually have moist soils. To obtain total soil moisture stress for communities other than those of the Salt Marsh Zone, the stress associated with soil-particle size (physical or matric stress) would be added to values for osmotic stress.

For all the communities in the Salt Marsh Zone except rabbitbrush and alkali sacation, the osmotic stress alone exceeded the 15 atm sometimes used to represent the permanent wilting stress. Under conditions that are too salty for vascular plants in salt marshes of Death Valley, Hunt (1966) found algae surviving osmotic stresses of 50 atm and fungi on areas with as much as 75 atm.

The zonation concept seems suitable for the kinds of vegetation described for two reasons. There is altitudinal zonation of vegetation in the areas that results from increasing precipitation and decreasing temperatures with an increase in altitude. There are also zones of vegetation that represent responses to increasing concentrations of soil salts as one proceeds from higher to lower altitudes. These two factors, altitudinal effects and salinity effects, generally parallel each other as one descends into each of the many closed basins within the Great Basin. In addition to increased aridity and salinity with descent into each basin, soil-particle sizes tend to become smaller as one approaches the playas, resulting in higher soil moisture stresses. Local areas, such as those occupied by wind-blown sand and certain geologic materials, provide exceptions to this generalization.

The salt marshes that occupy some playa bottoms are presented in Table 5 as a separate zone and it should be noted further that these are not true desert plant communities in the sense that they are limited to deserts. Salt marshes are also common in moist climates (Weaver and Clements, 1938, p. 227) and are even more abundant along seacoasts (Chapman, 1960). Many of the genera and some of the species are the same over much of the world.

Although the maximum osmotic stress values shown in Table 5 appear to provide a rational ordination of plant communities, caution must be applied when using plants as precise indicators of salinity. Gates et al. (1956) found that although mean values differed significantly between communities, there were overlapping salt tolerances for the five salt desert shrub communities studied. However, classification of plant communities on the basis of maximum tolerances is in agreement with the statement by Daubenmire (1948): "In general, the greater the salt tolerance of a species, the wider the range of salinity of the soils on which it grows, i.e., the degree of maximal salt tolerance is more definite than the minimal."

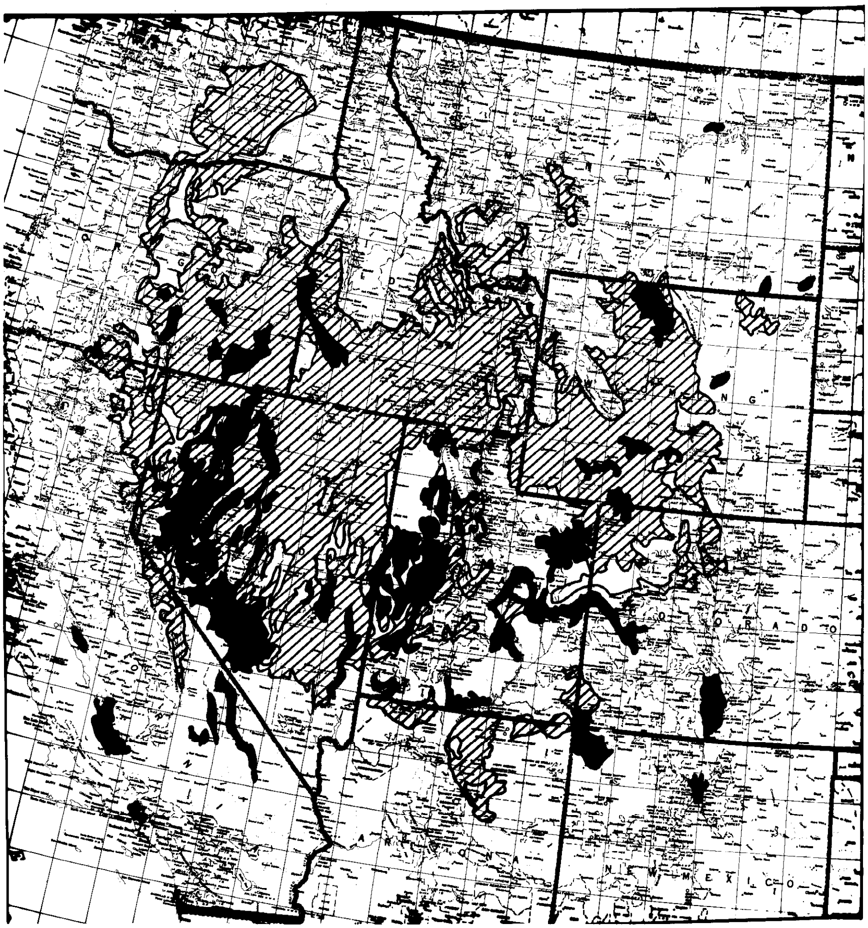

Fig. 1. Distribution of the saltbush-greasewood type (in solid black) and the sagebrush type (cross-hatched). (Revised from Kuchler, 1964).

Distribution of Salt Desert Shrub Communities

The Great Basin Desert as mapped by Shreve (1942) extends far beyond the Great Basin physiographic province into the Columbia Plateau and the upper Colorado River basin. More information now exists than was available to Shreve, and the boundaries could be extended to include a larger portion of Wyoming, parts of Montana and a larger portion of New Mexico and still comply with Shreve's criteria which emphasized life forms, structure, and floristics. Shreve's map indicates the extent of plant communities listed in Table 5. Shreve characterizes the Great Basin Desert as being ". . . largely above 4,000 ft. and has frequent periods of freezing temperatures of a week or more in duration." This contrasts with the Mojave Desert to the south which is largely below 4,500 ft. and is warmer and dryer. A major criterion used by Shreve to separate the two deserts is the presence of creosote bush (*Larrea tridentata*) in the Mojave Desert.

Undoubtedly the best vegetation map of the United States available at present is the one by Küchler (1964). Shown in Fig. 1 are tracings from Küchler's map with the addition of some salt desert shrub areas in Montana and Wyoming. The cross-hatched area represents the types where big sagebrush is dominant and has a planimetered area of 143 million acres, a larger area than some of the estimates that are in print (U.S. Dept. Agr., 1936). The extent of sagebrush types is shown because salt desert shrubs, at least in minor amounts, occur throughout most of the area occupied by big sagebrush.

The solid black area representing the extent of areas dominated by salt desert shrubs has a planimetered area of 38 million acres which is somewhat less than

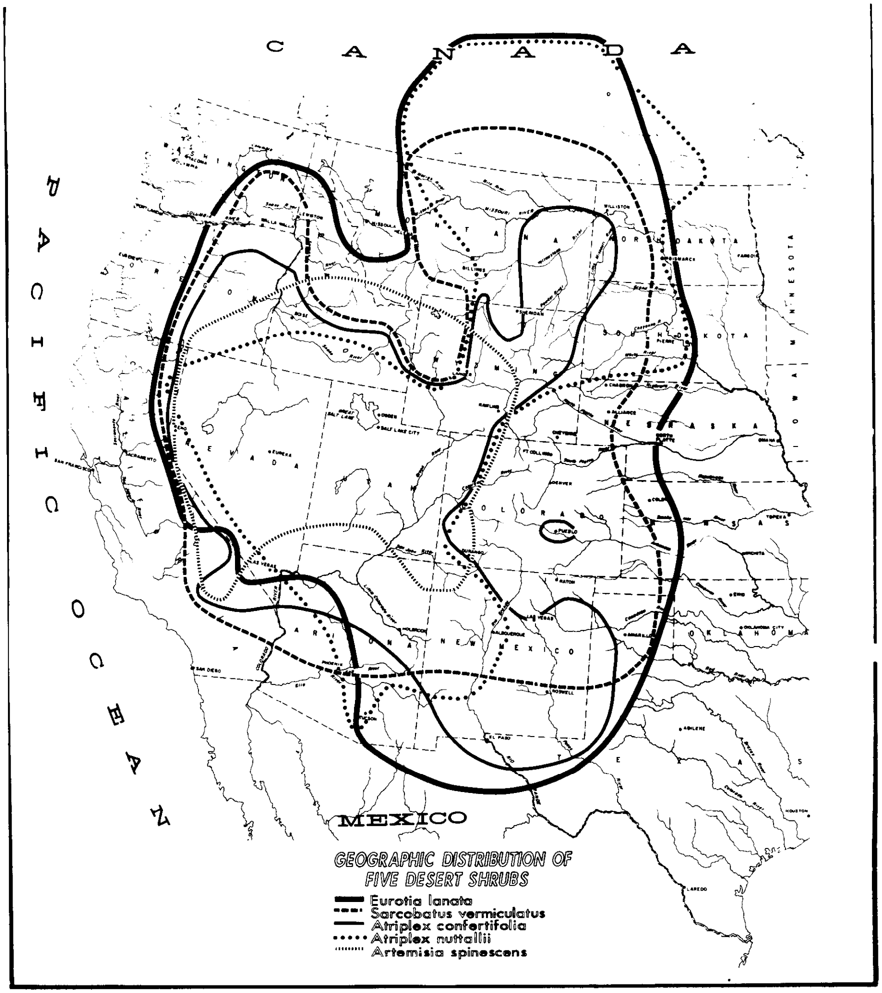

Fig. 2. Approximate geographic distribution of winterfat *(Eurotia lanata)*, greasewood *(Sarcobatus vermiculatus)*, shadscale *(Atriplex confertifolia)*, nuttall saltbush *(A. nuttallii)*, and bud sagebrush *(Artemisia spinescens)*.

many of the estimates in the literature (Hutchings and Stewart, 1953). The three small areas in Montana and one in northeastern Wyoming are not shown on Küchler's map. Although small, these areas are important because the sparse plant cover and fine-textured soils give rise to high sediment yields and, in some areas, spectacular erosion. An example of the latter is the Willow Creek valley in northeastern Montana which has an eroded trench about 20 ft. deep and 30 miles long. Much of the trenching has occurred during the life of residents of the area. The basin has been thoroughly treated by the U.S. Bureau of Land Management to control erosion.

Geographic Distribution of Salt Desert Shrub Species

The distribution of salt desert shrub species is far greater than the areas dominated by these plants (compare Fig. 1 with Fig. 2). The wide latitudinal and longitudinal ranges of these species indicate that some factor or factors other than climate determine areas in which salt desert shrubs are dominants. Edaphic factors seem to determine the presence of pure stands of salt desert shrubs but, as pointed out earlier, many species have overlapping tolerances for soil characteristics that have been measured. This view of climatic effects is not in full agreement with that of Billings (1949) who states that "The shadscale zone is characterized by a much dryer climate than the sagebrush zone and lies between the sagebrush and creosotebush zones." The complexity of the problem "Why do plants grow where they do?" has been thoroughly explored by Billings (1953). It is hazardous and possibly erroneous to attempt to over-simplify the cause and effect relationships responsible for plant species distribution.

Throughout the distributions shown, salt desert shrubs exert dominance locally, but usually on areas too small to appear even on large scale vegetation maps. However, extensive and nearly pure stands are largely restricted to the states of Nevada and Utah. The most widely distributed of the salt desert shrubs is winterfat. The wide ecologic amplitude of winterfat is demonstrated by both the extensive geographic area in which it occurs and the variety of species with which it is associated. Altitudinal range of winterfat is from 2,000 to 10,000 ft.

Greasewood, nuttall saltbush, and shadscale are almost as widely distributed as winterfat. There is no apparent reason for the disjunct distribution of shadscale in western Colorado, where it is common, and the isolated area of shadscale in southeastern Colorado.

There are a number of salt tolerant shrubs in the Mojave, Sonoran, and Chihuahuan Deserts, but these have not been included in the Salt Desert Shrub Zone of the Great Basin desert. Although absent or rare in the Great Basin desert, they merit a brief mention here. Cattle spinach *(Atriplex polycarpa)* is one of the most important saltbushes in the Sonoran and Mojave deserts. Soils occupied by it are usually coarse to medium textured, not high in salts, and are generally considered irrigable. Desert holly *(Atriplex hymenalytra)* is one of the most drought tolerant plants of the southwest deserts. In Death Valley (Hunt, 1966) it occupies ". . . the lowest, smoothest, saltiest, and hottest parts of the gravel fans."

One of the most widely distributed saltbushes is four-wing saltbush *(Atriplex canescens)*. Although its latitudinal range is from Montana to Mexico it is seldom found in pure stands. Four-winged saltbush ususally occurs on sandy soils.

Some causative factors for the presence of salt desert shrub communities

Shown on Fig. 3 are plant communities as found on different strata of Bearpaw Shale exposed on a hill in Montana. The data shown are hits per 100 pins as measured by the all contacts point-quadrat method at 2-inch intervals over a distance of 1,080 ft from the top to the bottom of the hill. The Curtiss (1956) continuum concept or the Whittaker (1953) population pattern concept could be applied to the data, but the classical concept (Hanson and Churchill, 1961) which recognizes dominance and names communities seems preferable. Nuttall saltbush communities are present on the dry, exposed hilltop and again on fine-textured alluvium at the base of the hill. Big sagebrush types occur adjacent to the two nuttall saltbush types. Centrally located on the hill in a highly gypsiferous soil is a buckwheat *(Eriogonum multiceps)* community. Two species showing wide ecologic amplitude are western wheatgrass *(Agropyron smithii)* and knotweed *(Polygonum aviculare)*. It is probable that propagules from species of each plant community have reached all the habitats on the hill almost annually, but the communities remain distinct. This statement leads to the very difficult question, "Why are these adjacent plant communities different?"

This report seems to us to require some brevity, thus only

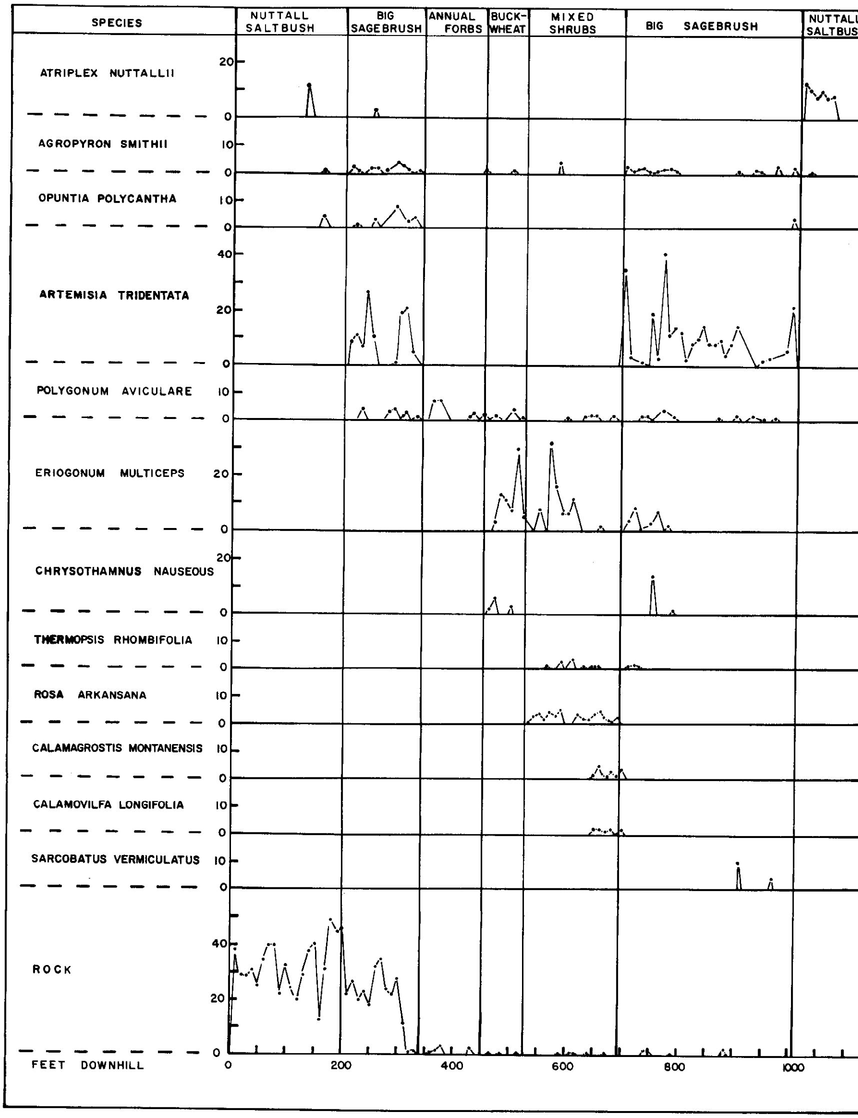

Fig. 3. Plant communities on a hill with different strata of Bearpaw Shale exposed. The data are hits per 100 pins, as determined by the all contacts point-quadrat method with pins at two-inch intervals.

the highlights of Fig. 4 will be discussed. The moisture use index (differences between maximum and minimum storage calculated in cc) is low for the two nuttall saltbush communities, and maximum total soil-moisture stress reached near the depth to which roots penetrated was greatest in these two communities. These data show that nuttall saltbush is the most drought tolerant of the species present on the sampling sites. Centrifuge moisture equivalents, representing moisture storage possible at field capacity to the depth of rooting, are similar to, but exceed, the moisture-use index. These are expected results because field capacity percentages were seldom reached in the soils studied. pH has no apparent effect on the plant community differences. The high pH at the top of the hill is caused by an outcrop of limestone, indicated as rock at the bottom of Fig. 3. Total soluble cations are highest in soils of the two nuttall saltbush communities indicating that this species is salt tolerant as well as drought tolerant. As has been found in many other studies (Gates et al, 1956; Fireman and Hayward, 1952), big sagebrush

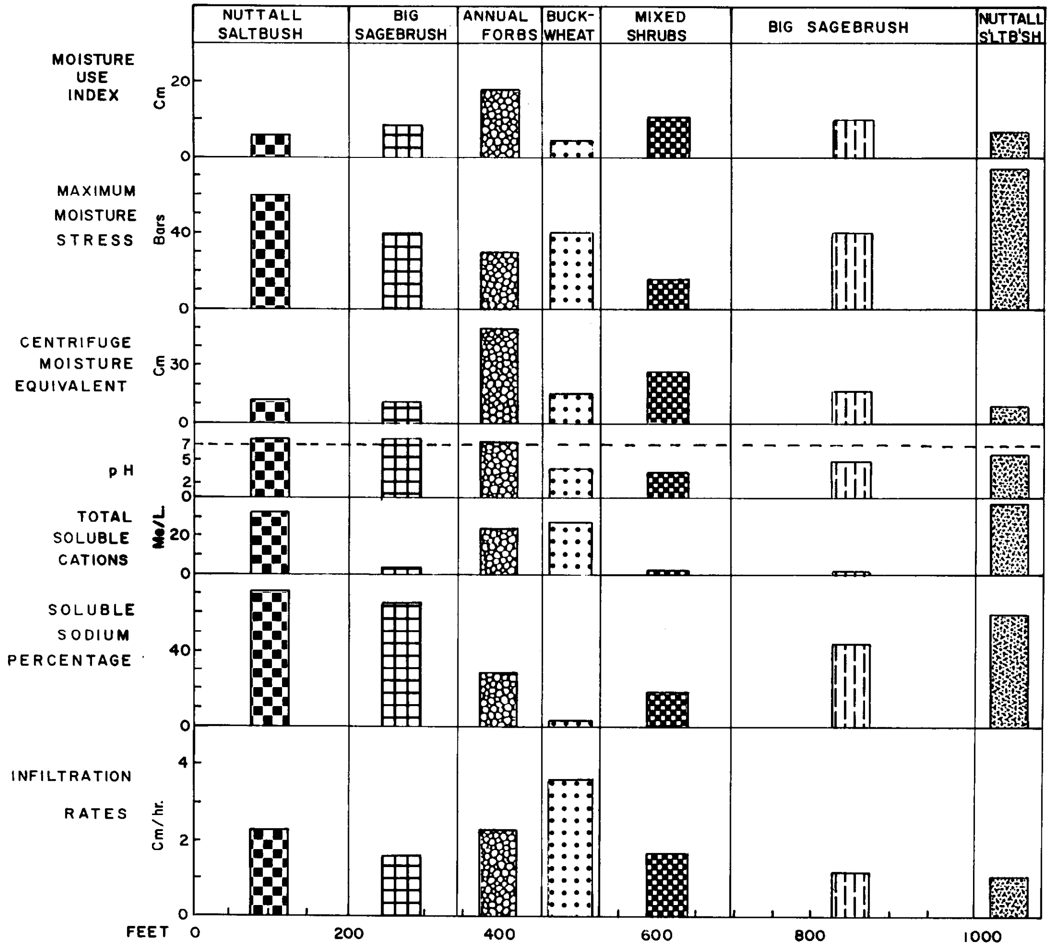

FIG. 4. Physical and chemical characteristics of soils for the seven plant communities shown in Fig. 3.

occupied sites that contained low quantities of salts.

The soils of the nuttall saltbush communities were sodic and, surprisingly, the two big sagebrush communities were also present on soils containing high soluble sodium percentages. Gates et al. (1951) found big sagebrush on soils with low sodium values. Soils of the buckwheat type had low sodium contents, but relatively high quantities of salts. This provides evidence that the primary cation in the soils occupied by buckwheat is calcium and additional evidence is provided by the presence of gypsum crystals, selenite, on the soil surface.

Infiltration rates as measured by a portable infiltrometer (McQueen, 1963) gave variable results that do not appear directly related to soil moisture measurements. All rates were low and only one, the buckwheat, had a rate exceeding one inch (2.54 cm)/hr. The infiltrometer has measured rates of up to nearly 14 inches/hr. on sandy soils in California (Branson et al., 1961).

From these data it is concluded that soil-moisture relationships are the primary cause of the different plant communities. Quantities of soil salts also appear to be important as a cause of community differences, but it may be that the major effects of salts is their osmotic stress contribution to total soil-moisture stress. The only community of the seven that may be present as a result of kinds of soil chemicals is the buckwheat type which occurred on gypsiferous soil.

Minimum and maximum total soil-moisture stress for seven plant communities in the Willow Creek basin in Montana are shown in Fig. 5. Total soil moisture stress was measured by a method which permits measurement of stresses of 0 to 1,500 bars (one bar = .99 atmosphere) in field gravimetric samples (Branson et al., 1962). Total stresses reached nearly 800 bars in nuttall saltbush soil in the fall. The vertical dashed lines shown for each community represent the average (six sampling periods during the year) total soil-moisture stress at the depth where plant roots become few in number. The fact that the curves for all soil moisture measurements made tend to come together at this characteristic depth in the communities must have meaning

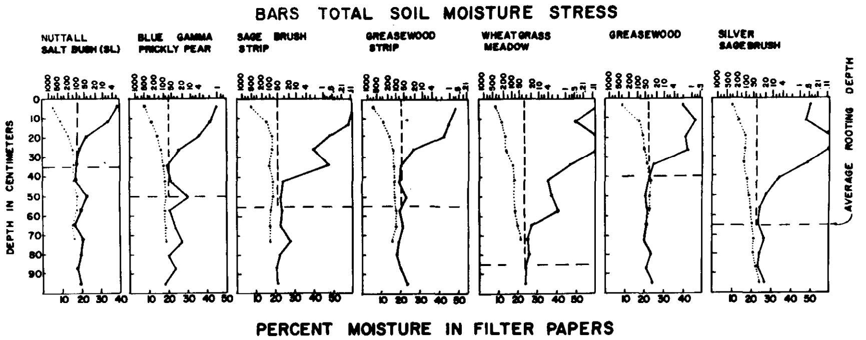

FIG. 5. Minimum total soil moisture stress for the season is represented by the solid line, maximum stress by the dotted line, and average maximum stress attained by each community is shown by the vertical dashed line. The data are for 7 plant communities in the Willow Creek basin in northeastern Montana.

when related to the kinds of plants growing on the different soils. One interpretation is that the average total soil-moisture stress at this depth represents the maximum stress to which the plants present on each site can remove moisture from the soil. Stresses greater than this average are attributable to water removed from the soils by solar energy. Of the communities shown, nuttall saltbush had the smallest quantity of plant material to intercept solar radiation and the highest moisture stress near the soil surface, whereas the quantity of plant material was greatest in the silver sagebrush community which had the lowest total soil-moisture stress at the average rooting depth. Average total soil-moisture stress was more than 90 bars for the nuttall saltbush soil and 35 bars for the silver sagebrush soil. These data were derived from a new calibration of filter paper moisture as a measure of total soil moisture stress and differ somewhat from the values shown in Fig. 4. Analysis of variance for these data shows that differences between the seven communities are highly significant.

The data on average total soil moisture stress can be more easily compared in Fig. 6 than in Fig. 5. The range of values for the 14 plant communities is from more than 90 bars for nuttall saltbush to only 19 bars for the mixed shrub community. To one familiar with the habitat requirements of the species shown, the grouping appears logical. One possible exception is the low drought tolerance indicated for the greasewood-western wheatgrass type. A possible explanation of this seeming discrepancy is that soil moisture sampling was to a depth of three ft, but greasewood is known to have roots extending to more than 19 ft in the area studied.

Measurements of osmotic stress do not show that halophytes occupy only soils high in salts (Fig. 7). Data shown in Fig. 7 were obtained as a part of a study of mechanical treatment effects (Branson et al., 1966) in Montana, Wyoming, Utah, Colorado, Arizona, and New Mexico. Although the criterion for site selection was the presence of mechanically treated land, a variety of vegetation types were included in the 58 areas sampled. Barren ground and nuttall saltbush occupied the sites highest in salts, but other halophytic types such as nuttall saltbush-blue grama, shadscale, spiny horsebrush, and winterfat, were

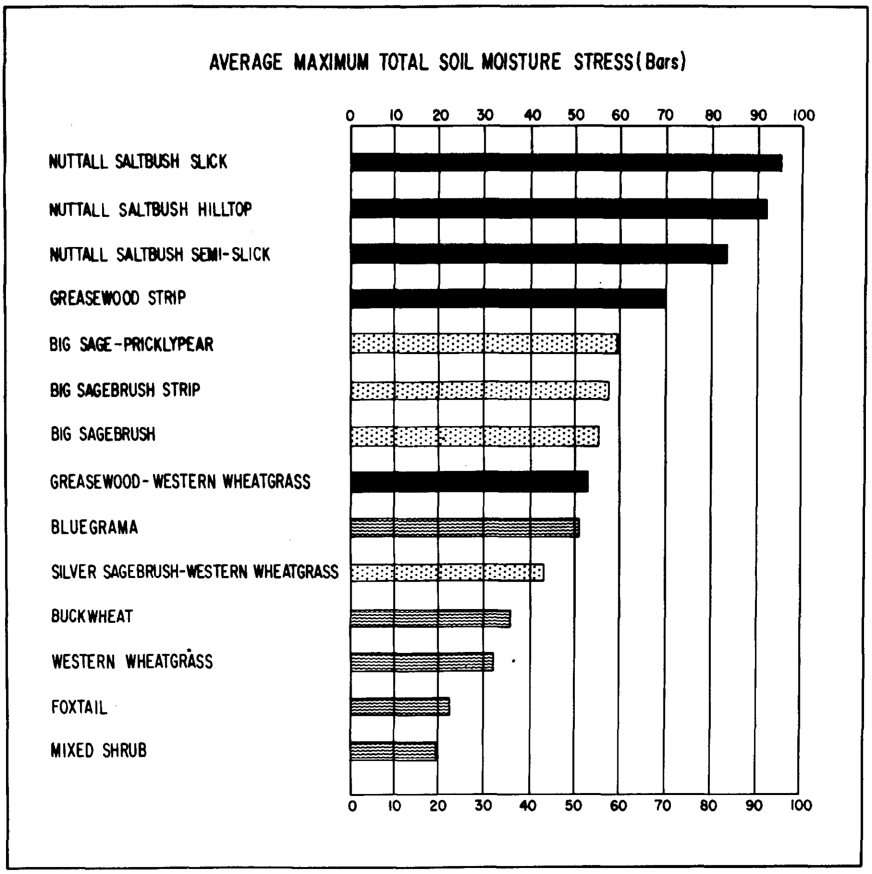

FIG. 6. Average total soil moisture stress at average rooting depth in 14 plant communities in the Willow Creek area, Montana. Black bars indicate salt desert shrubs, stippled bars nonhalophytic northern desert shrubs, and wavy lines indicate types not considered to be northern desert shrub communities.

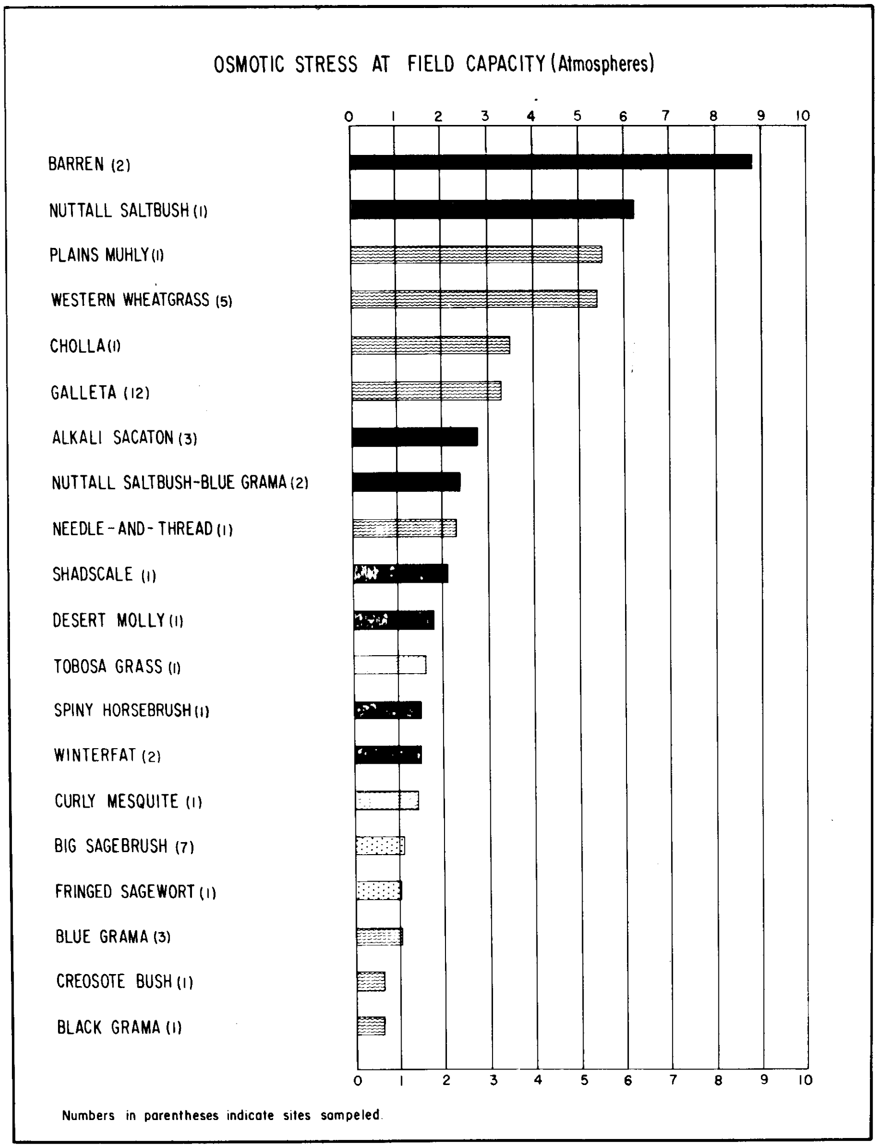

FIG. 7. Osmotic stress caused by soil salts in 20 vegetation types in six western states. Sites sampled varied from 12 to one per type with a total of 58 sites sampled. Black bars indicate salt desert shrubs.

the dominants on soils relatively low in salts. Although the results are not conclusive, the data in Fig. 6 and 7 indicate that total soil-moisture stress provides a more precise measure of drought tolerance than does osmotic stress alone. The data also indicate that the capacity of halophytes to tolerate high total soil-moisture stress may be more informative in attempts to explain dominance by these plants than soil-salt content alone. If ecological literature were not already too cluttered with terminology, the term "xerohalophytes" could be proposed for most salt desert shrub species to indicate that either or both xeric or halic soils may determine their presence on a site.

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