

152.1 Great Basin Desertscrub

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The most northerly of the four North American deserts, the Great Basin Desert, evolved from both cold-temperate and warm-temperate vegetation. Its affinities with cold-temperate progenitors sets it apart from the other three deserts, which have almost exclusive ties with warm-temperate and tropical-subtropical archetypes. Major plant dominants having cold-temperate affinities are sagebrushes (*Artemisia*), saltbushes (*Atriplex*), and Winterfat (*Ceratoides lanata*). These distinctly cold-temperate dominants are joined in varying degrees by species having evolutionary ties with warmer climates. Included here are species of rabbitbrush (*Chrysothamnus*) blackbrush (*Coleogyne*), hopsage (*Grayia*), and horsebrush (*Tetradymia*) (Axelrod, 1950).

Rzedowski (1973) and MacMahon (1979) show by using coefficients of generic similarity that the affinities between the cold Great Basin desertscrub biome and the warm Sonoran and Chihuahuan desertscrub biomes are weaker than the ties between the last two deserts and the Argentine "Monte." That the intercontinental floristic links are stronger than the intracontinental ones illustrates that there is strong resistance for the evolutionary process at the generic level to transcend temperature boundaries.

The major series within this biome, both in the Southwest and farther north, are those dominated by various species of sagebrush (*Artemisia*) or by Shadscale (*Atriplex confertifolia*). In this region these two series may be joined by several of lesser extent including Blackbrush (*Coleogyne ramosissima*), Winterfat (*Ceratoides lanata*), Greasewood (*Sarcobatus vermiculatus*), or rabbitbrush (*Chrysothamnus*).

These principal scrub species are much-branched, non-sprouting, aromatic, semishrubs with soft wood and evergreen leaves. These shrubs are mostly without spines. There are few cacti—either in numbers of individuals or species. Those present tend to be of short stature or prostrate and include a few chollas (*Opuntia whipplei*, *O. pulchella*), prickly pears (*Opuntia polyacantha*, *O. gracilis*, *O. erinacea*), and hedgehog cacti (*Echinocereus triglochidiatus* var. *melanacanthus*, *E. fendleri* var. *fendleri*). Small cacti (*Pediocactus*, *Sclerocactus*) and *Echinocactus polycephalus* var. *xeranthemoides* occur in the more southern locales.

Species diversity is characteristically low in all major communities of this biome with a dominant shrub occurring to the virtual exclusion of other woody species. Another feature setting this desert apart from others of the region is the absence of characteristic desert plants in minor waterways; nor is there a fringe of more closely spaced upland plants along these habitats of slightly more favorable moisture conditions (Shreve, 1942). There are, however, both cosmopolitan and characteristic plants along flood plains of the larger waterways: included here are Greasewood (*Sarcobatus vermiculatus*), Four-wing Saltbush (*Atriplex canescens*), and New Mexican Forestiera (*Forestiera neomexicana*). The introduced Russian Olive (*Elaeagnus angustifolia*), and in the warmer regions Saltcedar (*Tamarix chinensis*), may be present along wetland stream channels.

As with the other deserts of North America, there is evidence that the Great Basin Desert evolved comparatively recently, perhaps only 5,000 to 12,000 years ago (Butler, 1976; Stutz, 1978). The evidence for this comes from a variety of sources. Of particular significance to the present discussion is the observation that two major genera of Great Basin desertscrub, *Artemisia* (section *Tridentatae*) and *Atriplex*, are

Table 18. Precipitation data from 14 stations in the Southwest within and directly adjacent to Great Basin Desertscrub.

Station Lat./Long.	Elevation (m)	Mean monthly precipitation in mm												Total
		J	F	M	A	M	J	J	A	S	O	N	D	
Bluff, UT 37°17' 109°33'	1,315	15	13	14	13	9	7	17	25	19	25	13	19	192
Cortez, CO 37°21' 108°34'	1,883	26	21	26	27	24	14	29	6	29	39	21	31	293
Alamosa, CO 37°27' 105°52'	2,297	6	7	9	16	16	13	30	29	18	18	6	9	176
Taos, NM 36°23' 105°36'	2,124	20	17	23	24	25	23	44	52	27	28	18	19	321
Aztec, NM 36°50' 108°00'	1,719	19	16	18	18	15	12	22	33	23	30	14	23	242
Farmington, NM 36°45' 108°10'	1,644	14	12	13	15	12	12	20	30	22	30	12	17	205
Fredonia, AZ 36°57' 112°32'	1,425	26	22	24	17	11	7	17	31	17	21	20	25	238
Page, AZ 36°56' 111°27'	1,302	7	11	17	8	11	5	9	18	17	17	11	15	146
Kayenta, AZ 36°44' 110°16'	1,725	14	13	13	10	9	8	28	34	15	26	11	13	194
Tuba City, AZ 36°08' 111°15'	1,504	11	9	15	9	9	6	17	25	16	17	10	14	157
Winslow, AZ 35°01' 110°44'	1,492	11	10	12	8	7	9	31	38	19	16	10	15	187
Ganado, AZ 35°43' 109°34'	1,932	17	16	20	17	10	11	40	46	28	32	16	23	277
Sanders, AZ 35°13' 109°20'	1,779	19	19	23	14	4	12	41	47	21	19	18	26	263
Saint Johns, AZ 34°30' 109°22'	1,747	15	14	20	11	9	11	52	53	31	26	10	18	270

extremely plastic groups, and there is strong evidence of a continuing fast tempo of evolution in both (Beetle, 1960; Stutz, 1978). Recent work on *Atriplex* suggests that the genus is "awesomely genetically rich" (Stutz, 1978). Perennial members of this genus are all possessors of the "Kranz" type of leaf anatomy, an anatomical "flag" denoting the C_4 photosynthetic pathway, a physiological condition adapting plants to hot, bright desert conditions. Much evidence points to northeastern Mexico as a likely evolutionary center from which most perennial North American *Atriplex* species have arisen (Stutz, 1978). That a species with a physiological adaptation for existence under hot, arid conditions does so well in the winter-cold Great Basin desertscrub, may be explained by the preadaptive tolerance to low temperatures that arose incidentally as the new taxa in Mexico evolved mechanisms to withstand the special conditions imposed by the gypsiferous soils so prominent in the area. The ability to accumulate salts as a means of surviving on highly saline soils may have provided the preadaptive ability to withstand low temperatures. The accumulated salts could act both as an osmotic adjustment for accommodating physiologic and climatologic drought and as an "antifreeze" in colder climates.

Great Basin desertscrub is located mostly north of the 36th parallel although the biome is represented south of that line along the Little Colorado River drainage in Arizona and New Mexico, where, in some places, it is referred to as the Painted Desert (e.g. Benson, 1969). It occupies roughly 59,570 km² at elevations mostly between 1,200 m and 2,200 m (sometimes even higher to 2,600 m). Most of the desert receives less than

250 mm of precipitation per year. Mean monthly precipitation shows a strong winter dominated pattern on the west, with a gradual shift eastward toward a stronger summer influence with wet and dry seasons less distinct than in the other deserts (Table 18).

Part of the area of summer rainfall dominance has approximately the same amount of winter precipitation as the drier parts of the Sonoran Desert (Tables 18 and 23). Northeastern Arizona, for example, receives monthly amounts for December, January, and February in excess of 50 mm only 1 year out of 25 (Sellers and Hill, 1974). These monthly amounts, based on values averaged for the entire area regardless of elevation, would be even less were only low-lying desert localities considered.

The low winter season precipitation is compensated for by relatively low temperatures. Maximum daily values may remain below freezing during many days of the three coldest months—December, January, and February. Minimum daily temperatures probably reach freezing or lower most nights during December and January, although nighttime freezing can occur in all but the warmest months of summer. Summer temperatures are moderately high. For much of the area, the spring season of increasing air temperatures is also a period of gradual decrease in available moisture supplies.

Sagebrush Series

The total area of the West now dominated by sagebrush has been estimated at 1,093,690 km² (Beetle, 1960). This estimate includes all biotic communities in which *Artemisia* species in



Figure 83. Big Sagebrush (*Artemisia tridentata* var. *tridentata*) community on Fishtail Mesa, Grand Canyon National Park, Coconino County, Arizona, ca. 1,860 m elevation. This remote, inaccessible site has never been grazed by livestock (Jameson et al. 1962). The open growth of essentially one woody dominant and the lack of significant amounts of perennial grass is typical of much of this community in our area even in the absence of livestock grazing. The grasses present include such "cold season" species as Desert Needlegrass (*Stipa speciosa*), Indian Ricegrass (*Oryzopsis hymenoides*) and Longtongue Mutton Bluegrass (*Poa longiligula*).

section Tridentatae are important members, and thus includes considerably more than Great Basin desertscrub. This large area is occupied by 18 closely related taxa of *Artemisia*, "each defining in its own way a different ecological area" (Beetle, 1960).

Sagebrush-dominated communities within the Southwest have as dominants mainly three species of the 18 taxa noted above: Big Sagebrush (*Artemisia tridentata* var. *tridentata*), Bigelow Sagebrush (*A. bigelovii*), and Black Sagebrush (*A. arbuscula* ssp. *nova*), although at least three other species occur here to a limited extent (Beetle, 1960). *Artemisia arbuscula* ssp. *nova* is much more restricted in occurrence in our area than are the other two species. *A. bigelovii* has a range that is generally more southerly and easterly than that of *A. tridentata* and within our region is the most widespread of the three species, occurring along the valleys and canyons of the Colorado, Little Colorado, and the San Juan rivers, and in the upper reaches of the Rio Grande. The range of *A. tridentata* frequently overlaps that of *A. bigelovii* but the former is missing from virtually all of the Little Colorado River drainage (Beetle, 1960).

Studies specifically outlining the ecologic roles of the different sagebrush types are lacking for our area but in general *A. tridentata* var. *tridentata* is found from 1,500 to 2,150 m on a variety of deep soil sites. *Artemisia arbuscula* ssp. *nova* is found on shallow soils from 1,500 m to 2,500 m elevation. *A. bigelovii* is found in canyons, gravelly draws and on dry flats at 1,800 m or lower (Beetle, 1960; Munz, 1974). In all cases these species extend beyond the limits of Great Basin desertscrub, occurring as subdominants in other communities such as Great Basin conifer woodland and Great Basin grassland.

Sagebrush communities are regarded by many as steppe or shrub steppe because of the usual importance of grasses (Young et al., 1976; Daubenmire, 1970). In the Columbia River area and elsewhere, grasses, if not eliminated by grazing, are important understory elements in distinctly shrub-steppe communities. Increasingly to the south, however, sagebrush may grow to the virtual exclusion of grasses even in areas that have never been grazed by domestic livestock (Vale, 1975; Jameson et al., 1962, Fig. 83) and, unlike



Figure 84. Bigelow Sagebrush (*Artemisia bigelovii*) community on Boysag Point, Grand Canyon National Park, Coconino County, Arizona, ca. 1,675 m elevation. Boysag is a small promontory accessible only across a narrow, broken approach. The area received light sheep grazing intermittently between 1920 and 1943 but has not been grazed by livestock since. The introduced *Bromus rubens* (midground) was probably carried here during the grazing period and continues to reproduce locally even though the area has been free of grazing for 36 years (date of photograph, June 1979). Grass cover is roughly 8% (Schmutz et al., 1967) and is provided by such species as Black Grama (*Bouteloua eriopoda*), needlegrasses (*Stipa*), muttongrasses (*Poa*), and Hairy *Tridens* (*Tridens pilosus*). *Opuntia erinacea* and *Agave utahensis* are prominent succulent members of this desertscrub community. Photograph by R.M. Turner.

related vegetation to the north, sagebrush communities lacking a significant graminoid component are not necessarily in a grazing disclimax (Young et al., 1976). The near absence of grasses has been attributed to strictly climatic controls—i.e., the timing and amount of precipitation—the paucity of grasses being correlated with low annual precipitation, falling predominantly in the winter (Christensen, 1959; Cronquist et al., 1972). Therefore, sagebrush is recognized as occurring in both a Great Basin grassland and in a Great Basin desertscrub.

Plant species found on two sagebrush sites with little or no livestock grazing are shown in Table 19. One of the sites, Fishtail Mesa (Jameson et al., 1962), is an ungrazed island

Table 19. Percentage of plant cover (by line-intercept method) for Fishtail Mesa (from Jameson et al. 1962) and Boysag Point (from Schmutz et al. 1967).

	Fishtail Mesa (altitude 1,860 m)	Boysag Point (altitude 1,675 m)
Shrubs		
<i>Artemisia tridentata</i> var. <i>tridentata</i> and <i>A. bigelovii</i>	24.4	8.8
<i>Opuntia</i> (prickly-pear) species	0.6	1.1
<i>Opuntia</i> (cholla) species	—	0.0
<i>Ephedra viridis</i>	0.7	0.8
<i>Gutierrezia sarothrae</i>	1.1	0.3
<i>Ceratoides lanata</i>	0.4	0.3
<i>Yucca baccata</i>	0.0	0.1
<i>Atriplex canescens</i>	0.1	0.1
<i>Mammillaria</i> species	—	0.2
<i>Fallugia paradoxa</i>	0.0	0.1
<i>Coleogyne ramosissima</i>	0.8	0.0
<i>Eriogonum</i> species	—	0.7
<i>Polygala rusbyi</i>	—	0.0
<i>Chrysothamnus greenei</i>	0.0	1.0
<i>Agave utahensis</i>	0.0	0.3
Grasses		
<i>Bouteloua eriopoda</i>	0.0	2.3
<i>Bouteloua gracilis</i>	—	0.2
<i>Hilaria jamesii</i>	0.0	1.8
<i>Poa</i> species	—	1.2
<i>Stipa</i> species	—	2.6
<i>Sporobolus cryptandrus</i>	0.0	0.5
<i>Oryzopsis hymenoides</i>	—	—
<i>Erioneuron pilosum</i>	0.0	—
<i>Sitanion hystrix</i>	0.0	—
<i>Poa secunda</i>	—	0.0
Forbs	—	0.3

— = less than 0.1 percent.

plateau in northwestern Arizona (Fig. 83) and the other site, Boysag Point (Schmutz et al., 1967; Fig. 84), is a relatively ungrazed promontory of the Kaibab Plateau, 12 miles to the southwest. The presence of such grasses as grammas (*Bouteloua*), Galleta (*Hilaria jamesii*), and Desert Needlegrass (*Stipa speciosa*) mark these stands as a southern fasciation of the Great Basin desertscrub (Young et al., 1977). These communities provide valuable references against which to judge grazing effects. It is noteworthy that the stands differ greatly in both the amount of sagebrush and the amount of perennial grasses present. At Boysag Point, the total cover of perennial grasses (8.6%) was as great as the sagebrush cover (8.8%); at Fishtail Mesa the perennial grass coverage was only 0.12%, that of the sagebrush, 24.39%.

Seral communities within the sagebrush series are heavily influenced by one or two forces,—grazing and fire. Sagebrush foliage is not readily eaten by domestic or native ruminants and contains oils that inhibit microbial activity in rumens (Nagy et al., 1964). Avoidance of sagebrush results in reduction of the more palatable grasses and forbs and an increase in sagebrush. Since approximately 1900, introduced annuals have become increasingly conspicuous throughout this biome and must be considered prime forces in arresting succession in many areas. These annuals, largely from Eurasia, filled a near void when introduced, beginning about 1900. Before



Figure 85. Shadscale (*Atriplex confertifolia*) community in the basin of the Little Colorado River on the Navajo Indian Reservation near Cameron, Arizona, ca. 1,280 m elevation. This is another example of shrub dominance by a single low shrub species in this cold-arid biotic community.

that time, domestic livestock had greatly reduced the herbaceous component of this community. Under conditions of heavy grazing, native annuals were unable to exist and alien species, once introduced, quickly occupied the abandoned niche [Young et al., 1972, 1976]. These new species include Cheatgrass Brome (*Bromus tectorum*), Russian thistles (*Salsola paulsenii* and *S. iberica*), Filaree (*Erodium cicutarium*), and Tumble Mustard (*Sisymbrium altissimum*). All originated in Eurasia and have accompanied domestic livestock herds here and throughout semi-arid parts of the world. Once these aliens have taken their place in the disclimax community, they relinquish this position to native species slowly or not at all, even if grazing pressures are eliminated (Fig. 84). Cheatgrass Brome has spread to become a common codominant of seral stands of sagebrush and other communities in this biome and, indeed, in many stands it may be considered a disclimax dominant.

Although the history of fire in the Great Basin Desert has not been specifically studied in this area, it has been much studied to the north, and findings there should be applicable elsewhere. Fire has been considered a minor force in presettlement Great Basin Desert areas [Galbraith and Anderson,

1971], yet during the last 50 years it has become a potent force in shaping communities in this biome. Where Cheatgrass Brome has become a significant constituent of sagebrush stands, the incidence of fire is greatly increased. Because sagebrush does not sprout after burning, it is slow to reoccupy a site after fire. The highly flammable Cheatgrass thus plays a double role in altering the stands of sagebrush it has come to occupy: under grazing pressure it increases in density, effectively closing the ecosystem to native perennial grasses; the increased fuel it creates when dry promotes more frequent fires not withstood by sagebrush. The two-phase system of disturbances has placed much of the sagebrush zone in a stage of arrested succession [=Cheatgrass Brome fire disclimax].

After fire, the role of the nonsprouting sagebrush may eventually be taken by sprouting species of such genera as *Chrysothamnus*, *Tetradymia*, and *Gutierrezia*. These more fire adapted plants arose from neotropical ancestors in the Madro-Tertiary geoflora; the sagebrush they replace is from the Arcto-Tertiary geoflora. The seral sequence, progressing from plants in the fire disclimax with tropical or warm temperate affinities to cold temperate climax species, is often

Table 20. Presence of woody and succulent plants at 9 widely distributed shadscale stands in southern Nevada and southern California (from Billings, 1949).

Species	Number of Stands
<i>Atriplex confertifolia</i>	9
<i>Artemisia spinescens</i>	7
<i>Ephedra nevadensis</i>	5
<i>Forsellesia spinescens</i>	5
<i>Grayia spinosa</i>	3
<i>Lycium andersonii</i>	3
<i>Yucca brevifolia</i>	3
<i>Ceratoides lanata</i>	2
<i>Tetradymia glabrata</i>	2
<i>Ambrosia dumosa</i>	2
<i>Ephreda funerea</i>	2
<i>Lycium sp.</i>	2
<i>Sarcobatus baileyi</i>	1
<i>Lycium cooperi</i>	1
<i>Dalea polyadenia</i>	1
<i>Hymenoclea fasciculata</i>	1
<i>Tetradymia spinosa</i>	1
<i>Kochia americana</i>	1
<i>Opuntia bigelovii</i>	1
<i>Echinocactus polycephalus</i>	1
<i>Eriogonum umbellatum</i>	1
<i>Lepidium fremontii</i>	1
<i>Yucca schidigera</i>	1

repeated in Great Basin communities (Young et al., 1976). A similar example of seral shifts in composition from warm to cold adapted species was noted by Schmutz et al. (1967): "cool season" versus "warm season" grass cover occurred at a ratio of 44 to 56 in a relatively ungrazed sagebrush community (Boysag Point) compared with a ratio of 20 to 80 in a nearby heavily grazed sagebrush stand. "This strange union of contrasting evolutionary lines in one seral sequence... leaves open to question the evolutionary equilibrium of the pristine flora" (Young et al., 1976; see also Fig. 88).

Shadscale Series

Shadscale (*Atriplex confertifolia*) is a wide ranging saltbush found from Chihuahua and the panhandle of Texas (Correll and Johnston, 1970) northward to northeastern Montana and eastern North Dakota (Branson et al., 1967) and from southern California to northeastern Oregon. Except for its absence in Washington, it occurs in all states in which extensive stands of sagebrush occur, and it is only in and adjacent to the Great Basin Desert that it is found as a wide ranging dominant.

The largest continuous area of Shadscale dominance is in southeastern California and Nevada, extending from west-central Nevada (north of our area) to west of Death Valley, California (Billings, 1949; Cronquist et al., 1972). Billings (1949) considered Shadscale vegetation in this part of its range to be transitional between sagebrush and the Creosotebush series of the Mohave desertscrub biome. He noted that on some mountain ranges these same zones appear on a smaller scale with Shadscale occupying a belt intermediate between Creosotebush below and sagebrush above. Eastward, extensive areas of Shadscale occur within Great Basin desertscrub along drainages of Colorado River tributaries such as the Little Colorado, San Juan, and Green Rivers in Arizona, Utah, New Mexico, and Colorado (Fig. 85, 86). In the last two

states it also occurs in the upper Rio Grande basin.

In southern Nevada and southeastern California, the Shadscale series is found from 990 m to 1,775 m (Billings, 1949). Eastward and northward this vegetation is found mainly between 1,220 m and 1,525 m.

The general appearance of this community is one of open starkness with the dominant woody plants attaining heights of only 0.3 m to 0.6 m (Figs. 85, 86). Stands of this plant in Tooele Valley, Utah, were aptly described by Kearney et al. (1914): "No other vegetation in this valley gives the impression of being so nearly conquered by the environment. Even the few species which grow on the salt flats have the appearance of finding their habitat more congenial."

Few quantitative studies of Shadscale communities have been made in the Southwest. In one such study, Billings (1949) tallied all woody and succulent plants found at nine widely distributed stations in the western transition to Mohave Desert. These are listed in Table 20.

In two quantitative studies in the Great Basin Desert north of this area in Colorado (Branson et al., 1967) and in Utah (West and Ibrahim, 1968), the only shrub besides Shadscale found on plots examined by Billings (1949) was Bud Sagebrush (*Artemisia spinescens*). In addition to the above species, other important shrubs found throughout the Shadscale series in Great Basin desertscrub include:

- Shadscale (*Atriplex confertifolia*)
- Gardner Saltbush (*Atriplex gardneri*)
- Nuttall Saltbush (*Atriplex nuttallii*)
- Greene Rabbitbrush (*Chrysothamnus greenei*)
- Rubber Rabbitbrush (*Chrysothamnus nauseosus*)
- Broom Snakeweed (*Gutierrezia sarothrae*)
- Black Greasewood (*Sarcobatus vermiculatus*)
- Seep Weed (*Suaeda fruticosa*)

Although widely scattered, perennial grasses are commonly found in the Shadscale community; few species are represented and include mainly Galleta (*Hilaria jamesii*), Indian Rice Grass (*Oryzopsis hymenoides*), Bottlebrush Squirreltail (*Sitanion hystrix*), Desert Needlegrass (*Stipa speciosa*), and Alkali Sacaton (*Sporobolus airoides*),—again showing the Great Basin affinity of this biome.

Much of the early work on this community was done in habitats where subsoil accumulations of salts were common (Clements, 1920; Kearney et al., 1914; Shantz and Piemeisel, 1940). As a result, an early consensus developed that Shadscale usually indicated a saline soil,—a belief that has been shown to be incorrect by more recent studies (Billings, 1949; West and Ibrahim, 1968; Branson et al., 1976). Although often occurring in valleys, the plant is frequently also found on upland sites; for example, on pediment remnants in southeastern Utah (West and Ibrahim, 1968), on rolling hills in northern Arizona, and on rocky slopes in southeastern California (Vasek and Barbour, 1977).

Soils within the Shadscale series are often covered with desert erosion pavement. The rocks of this covering are commonly dark in color and contrast sharply with the lighter soil beneath (Billings, 1951).

Shadscale grows where the precipitation may be considerably lower than that of adjacent sagebrush. In Nevada and eastern California, annual precipitation ranges from 78.2 mm to 144.3 mm for the series (Billings, 1949). At six stations in the adjacent sagebrush vegetation, precipitation ranged from 196.3 mm to 240.3 mm with an average for the series of 223.3



Figure 86. Mixed shrub community of Great Basin Desertscrub, Valley of the Gods, San Juan County, Utah, ca. 1,400 m elevation. Blackbrush (*Coleogyne ramosissima*), the dominant foreground plant, gives way downslope to Shadscale (*Atriplex confertifolia*). The dark narrow column of plants along the watercourse is composed of Greasewood (*Sarcobatus vermiculatus*). Additional plant species here include *Ephedra torreyana*, *Gutierrezia sp.*, *Hilaria jamesii*, and *Bromus tectorum*. Photograph by R.M. Turner.

mm. As an example of rainfall conditions farther to the east, Ibrahim et al. (1972) reported an average annual rainfall of 156.2 mm for a large Shadscale area in southeastern Utah.

That Shadscale is characteristic of the driest Great Basin desertscrub region is shown by Figure 85. A large low rainfall (150-200 mm) "sink" (including Greenriver, Utah; Shiprock, New Mexico; Lees Ferry and Winslow, Arizona) circumscribes much of the Shadscale land in the north-central part of the North American Southwest. Farther west, the vast rainshadow in the lee of the Sierra Nevada is an area of low precipitation also largely dominated by Shadscale. On a broad scale, because low precipitation is correlated with low altitude, Shadscale generally occurs below sagebrush.

Where the Shadscale community occurs in a Mohave desertscrub-Great Basin desertscrub transition zone, as for example at the Nevada Test Site (Beatley, 1975), Shadscale occupies the floors of enclosed basins and Creosotebush occurs next above at the higher positions in the basin, in a reversal of the usual zonation sequence. The lower tempera-

tures of the bottom lands were inferred to have excluded Creosotebush from these sites.

Like the Sagebrush series, the Shadscale series has been widely used for grazing livestock. Certain associated shrubs such as *Artemisia spinescens* and *Ceratoides lanata* are palatable as are most of the perennial grasses. It is used mostly as a winter range for sheep, but cattle are grazed year-long where water is available. Cheatgrass *Brome* is found in those parts of this series with highest rainfall, but this exotic species apparently requires more moisture than is available throughout the drier sections (Billings, 1949).

Blackbrush Series

In addition to sagebrush- and Shadscale-dominated areas, some southern parts of the Great Basin desertscrub biome are dominated by Blackbrush (Fig. 86). Very little has been written about this community, which occurs primarily in southern Nevada, southeastern California, northcentral Arizona, and southeastern Utah. Beatley (1976) considered it as



Figure 87. Blackbrush (*Coleogyne ramosissima*) community near Indian Gardens, Grand Canyon National Park, Coconino County, Arizona, growing on soil derived from Cambrian Bright Angel Shale, ca. 1,125 m elevation. Beginnings of the Tonto Platform can be seen on the right. This broad flat shelf is a prominent feature of the Grand Canyon landscape and is formed because the Bright Angel Shale is highly susceptible to erosion. The Tonto Platform, straddling the Mohave Desert-Great Basin Desert "tension line" is almost uniformly dominated by Blackbrush. The foreground area is watered by a spring and supports a riparian scrubland of Common Reed (*Phragmites communis*) and Coyote Willow (*Salix exigua*). Photograph by D.T. MacDougal, 1905.

belonging to the Mohave desertscrub biome but recognized it as ecotonal to Great Basin and Mohave desertscrub communities. Cronquist et al. (1972), however, noted that this community is best developed along the valleys of the Colorado and lower Green Rivers in southeastern Utah, an area clearly within Great Basin desertscrub. It is found in extensive stands on the Tonto Platform in the Grand Canyon (Fig. 87). Hackman (1973), Hunt et al. (1953), and Everitt (1970) showed this vegetation covering extensive areas in the San Rafael, Fremont, and Dirty Devil River drainages in southeastern Utah. Its presence in both Mohave desertscrub and Great Basin desertscrub mosaics is a condition similar to that of other communities (e.g., Creosotebush-White Bursage and Mesquite) which transcend biome boundaries but whose associates differ when passing from one biome to another.

Bowns and West (1976) have provided the most compre-

hensive discussion of ecological and morphological information about Blackbrush. They note that fire effectively destroys this species and the plant does not aggressively reoccupy these sites. The post-burn communities are variable, although *Bromus rubens* and *B. tectorum* are common pioneer species (Beatley 1966, 1976). The replacement shrubs are usually undesirable as forage for domestic livestock (Bowns and West, 1976). Perennial grasses are commonly prevalent in unburned stands and Bradley (1964) considered this series an important vegetation type in the Mohave Desert for Desert Bighorn Sheep (*Ovis canadensis nelsoni*) because of the occurrence of these grasses (e.g., *Oryzopsis*, *Hilaria*).

Beatley (1976) concluded that temperature conditions alone do not separate this vegetation from adjacent Creosotebush communities. Rainfall, however, did seem to be an important controlling factor with Blackbrush occupying sites



Figure 88. Sand Sagebrush (*Artemisia filifolia*) stand in contact with Mohave Desertscrub species such as Creosotebush (*Larrea tridentata*, large plant at left), 2 miles east of Washington, Utah, ca. 900 m elevation. In 1914 (upper photo), Sand Sagebrush was the clear dominant. By 1979 (lower photo), Creosotebush was the dominant, raising the question of what environmental conditions had changed to cause the transfer of dominance from a plant with cold-temperate affinities to one with sub-tropical affinities. Upper photograph by H.L. Shantz; lower by R.M. Turner.



Figure 89. Saltbush series of Greasewood (*Sarcobatus vermiculatus*), on Monte Vista National Wildlife Refuge in San Luis Valley, Colorado, ca. 2,320 m elevation. Low precipitation, saline soils, and cold nighttime temperatures extend Great Basin desertscrub eastward to the high, rain-shadowed basin of the upper Rio Grande. Greasewood is one of the few dark green shrubs among the mostly gray shrubs of this desert biome. It and other salt tolerant plants, such as *Allenrolfea*, *Atriplex*, and *Suaeda*, range over a wide amplitude of environments from cold-temperate to subtropic, their occurrence primarily dependent upon soil salinity and occasional flooding.

where rainfall exceeds the needs of many Mohave desertscrub species. In cold drainage basins, Blackbrush is found only on upper bajadas and is excluded from the basin floors under the influence of cold air accumulation. Low temperatures probably control its upper limits on bajadas and northward where it abuts Shadscale or sagebrush communities.

In southern Nevada, crown coverage reaches values of 45-51% in nearly pure stands of Blackbrush, the highest coverage values of any desertscrub communities of the region, and is probably indicative of the relatively high rainfall of the sites it dominates (Beatley, 1976). The physiognomy of this community is uniform as is typical of many Great Basin desertscrub series. Widely scattered individuals of the following species may be present (Cronquist et al., 1972):

- Sand Sagebrush (*Artemisia filifolia*)
- Parry Sagebrush (*Artemisia parryi*)
- Big Sagebrush (*Artemisia tridentata* var. *tridentata*)
- Shadscale (*Atriplex confertifolia*)

- Rough Joint-fir (*Ephedra nevadensis*)
- Torrey Joint-fir (*Ephedra torreyana*)
- Bush Buckwheat (*Eriogonum fasciculatum*)
- Three-leaved Snakeweed (*Gutierrezia microcephala*)
- Diamond Cholla (*Opuntia ramosissima*)
- Stenopsis (*Stenopsis linearifolius*)

Other Series

Within Great Basin desertscrub are several additional plant communities imbedded within the matrix of the more widespread Sagebrush, Shadscale, and Blackbrush series. The occurrence of these minor communities appears largely dependent upon edaphic conditions rather than being the result of particular climatic conditions. The dominant species of these minor communities are all members of two key Great Basin desertscrub plant families — Compositae and Chenopodiaceae.

Sand Sagebrush (*Artemisia filifolia*) is a widespread species

occurring from Nevada to Chihuahua and north as far as Wyoming and Nebraska. It is a plant of sandy soils, often occupying dunes or areas of deep, loose sand. It is found and is locally dominant in regions representative of Great Basin desertscrub, Mohave desertscrub (Fig. 88), Plains grassland, and semidesert grassland.

Common occupants of valley bottoms and playa margins are stands representing a saltbush series. The dominant species of this series is often Greasewood (*Sarcobatus vermiculatus*) (Fig. 89), a plant able to tolerate high salt content (Branson et al., 1976) but it is not an infallible indicator of high salinity; its occurrence may be dependent solely upon associated high soil moisture content (Fautin, 1946; Branson et al., 1976).

Plants that locally grow with Greasewood or are themselves dominants are species of *Atriplex*, particularly Fourwing Saltbush (*Atriplex canescens*), Fivehook Bassia (*Bassia hyssopifolia*), Inland Saltgrass (*Distichlis spicata* var. *stricta*), Common Russian Thistle (*Salsola kali*), and seepweeds (*Suaeda* spp).

Winterfat (*Ceratoides lanata*) is another species that has broad ecological amplitude, occurring mainly in the Shadscale region but extending into the arid limits of sagebrush and even the mesic limits of the Creosotebush series (Mohave desertscrub) (Cronquist et al., 1972). Germination of its seeds has been shown to have broad genetically defined responses to temperature and salinity, helping to explain the broad ecologic amplitude of the plant (Workman and West, 1967).

A distinct fauna is centered in Great Basin desertscrub. Several distinctive mammalian representatives follow the sagebrush communities of this biome into the boundaries for the Southwest: Townsend's Ground Squirrel (*Spermophilus townsendi*), Dark Kangaroo Mouse (*Microdipodops megacephalus*), and Sagebrush Vole (*Lagurus curtatus*). Others as the Pallid Kangaroo Mouse (*Microdipodops pallidus*) and Chisel-toothed Kangaroo Rat (*Dipodomys microps*) appear to favor the *Atriplex* and other desertscrub series. Still others such as the Townsend Pocket Gopher (*Thomomys townsendi*), Belding Ground Squirrel (*Citellus beldingi*), and Pygmy Rabbit (*Sylvilagus idahoensis*) do not reach the area. The Merriam's Shrew (*Sorex merriami*), Great Basin Pocket Mouse (*Perognathus parvus*), Ord's Kangaroo Rat (*Dipodomys ordii*), and the Montane Vole (*Microtus montanus*) are centered in, but not restricted to, this biome and are best represented at the desert's higher altitudes. A number of mammals, e.g., the Coyote (*Canis latrans*) and Black-tailed Jackrabbit (*Lepus*

californicus), are more or less influent and found throughout this and other western biomes.

Unlike the cold temperate deserts of Eurasia with its onagers, camel, and gazelles, large ungulates are generally poorly represented in the Great Basin Desert. The Pronghorn (*Antilocapra americana*) occurs largely as an incursionary species from adjacent or former grassland. The Desert Bighorn (*Ovis canadensis nelsoni*) is now generally lacking in this biome—probably because the cold winters encouraged a history of domestic sheep grazing in these habitats with their attendant introduction of diseases transmittable to the resistance-poor native sheep.

As some of their names imply, several birds are characteristic of sagebrush communities—Sage Thrasher (*Oreoscoptes montanus*), Sage Sparrow (*Amphispiza belli*), and Sage Grouse (*Centrocercus urophasianus*). This last species, while well adapted and restricted to Big Sagebrush communities, also requires insect-rich wet meadows or interspersions of grassland for nesting and rearing young. The widely introduced Chukar Partridge (*Alectoris chukar*) has been successfully established largely in rocky precipitous habitats within Great Basin desertscrub. There it feeds almost entirely on the invading winter-spring growing annuals of its Eurasian homelands—*Salsola*, *Erodium*, and *Bromus tectorum*.

Because of its long, cold winters, reptiles are not as well represented in the Great Basin Desert as in the warmer biomes. Some of the more common representative species such as the Sagebrush Lizard (*Sceloporus graciosus*) and the Great Basin Spadefoot Toad (*Scaphiopus intermontanus*) occur throughout other Great Basin biomes whereas others present, as the Leopard Lizard (*Crotaphytus wislizenii*), Collared Lizard (*C. collaris*), and Northern Side-blotched Lizard (*Uta stansburiana*), are found in several other biomes as well. A number of subspecies are indicative of Great Basin desertscrub and a recent history of evolutionary separation. These include the Northern Desert Horned Lizard (*Phrynosoma platyrhinos platyrhinos*), Great Basin and Northern Whiptails (*Cnemidophorus tigris tigris* and *C. tigris septentrionalis*), Great Basin and Northern Plateau Fence Lizards (*Sceloporus occidentalis biseriatus* and *S. undulatus elongatus*), Great Basin Gopher Snake (*Pituophis melanoleucus deserticola*), Wandering Garter Snake (*Thamnophis elegans vagrans*), and the Great Basin and Hopi Rattlesnakes (*Crotalus viridis luteosus*, *C. viridis nuntius*).