SOME SPECIAL VEGETATION TYPES COMMON TO ALL DESERTS

Some habitat types are highly localized within the general desert landscape, frequently because the plants that they support require specific soils. The vegetation structure and even the species composition within these specialized habitats may be virtually the same anywhere these conditions occur. Thus habitats such as playas, sand dunes, sites containing gypsum soils, and riparian situations may be quite similar anywhere they occur in the four North American deserts. Because of this similarity, these habitats are dealt with separately here.

Riparian Vegetation

The term riparian has quite different meanings to different people. The concept used here is that riparian vegetation is made up of those plants that occur along drainageways and associated floodplains that differ from the species in the

surrounding desert.

This definition specifically considers as riparian habitats a wide spectrum of drainage-channels. Even small rills in desert landscapes may alter vegetation composition and form. In a particular spot, for example, a quick look might suggest that the area is dominated by Burrobush and Creosote Bush, and perhaps supports a few other species. Closer scrutiny reveals that in fact the majority of the Burrobushes are arrayed in lines that follow tiny drainages that are less than two inches deep. This situation, of course, is more subtle than are riparian systems along a major watercourse, where a stream channel and usually two well-developed terraces parallel the river (plate 3). The first terrace is the area encompassing the normal flood excursions of the river. One to eight feet above this is the second terrace, which marks the area covered only by extreme floods.

On the first terrace, trees such as willows and cottonwoods grow close to the water. Farther back on the terrace, where the soil is saturated, is a band of Arrow Weed. Even farther back is a zone containing Screwbean and Quail Bush, as well as a

variety of plants from other genera.

The second terrace is the zone most often occupied by the mesquites. These trees may form veritable forests, which are generally referred to as bosques, a word of Spanish origin. Bosques were a common sight along desert rivers at the turn of the century. They stabilized banks and encouraged the accumulation of silt that was rich in organic matter. The extent of such areas varied according to the flooding pattern of each river. However, these natural patterns were altered by the appearance of dams and irrigation channels.

In addition, the introduction of Tamarisk and other members of the Old World genus *Tamarix* severely affected bosques composed of native species. Tamarisk was introduced into the United States in the early 1800s as a decorative species, and it is still planted for this purpose in many arid areas of the world. This species is a rapid spreader: A single plant may produce 600,000 seeds per year. Furthermore, its leaves secrete salt, an adaptation to reduce the tree's salt content. As

Desert Willow Chilopsis linearis 306

Seep Willow Baccharis glutinosa

Desert Broom
Baccharis sarathroides

Apache Plume Fallugia paradoxa 96

California Washingtonia Washingtonia filifera 327

Smoke Tree Dalea spinosa 305, 313, 334

Vermilion Flycatcher Pyrocephalus rubinus 572 a result, surface soils under the tree accumulate salts, which inhibit the germination and establishment of non-salt-tolerant natives. Finally, the large quantities of litter produced by Tamarisk encourage fire. Tamarisk can resprout from its roots following fire, while many native species cannot. All these factors aid the spread of Tamarisk and reduce the numbers (and influence) of such native species as mesquite.

Other second-terrace or minor-channel species include Desert Willow, a relative of the Catalpa, whose linear leaves and lavender flowers catch the eye; Seep Willows and Desert Broom, species whose brilliant green colors set them off, even during dry periods; and Apache Plume, which has beautiful white flowers, and fruits that are characterized by light pink featherlike plumes. At least two species of acacias are also abundant in this area.

The predominance of acacias and mesquites in riparian situations has been attributed to their semitropical origins. In the areas where these genera probably evolved, warm, moist conditions prevail. Their presence in a warm desert along a moist watercourse should therefore be of no great surprise. A few quite unusual plants are bound to riparian situations. The most spectacular is probably the California Washingtonia, an attractive palm that occurs in California and in a very few scattered locations in western Arizona.

Another species, one that follows very closely the middle of drainage channels without permanent water, is Smoke Tree. At a distance, this plant resembles a puff of smoke. Permanent water is, of course, required by many fishes and some amphibian species. However, it should be equally obvious that animals requiring vertical structure in their environment, and not necessarily a stream *per se.* can find a haven among riparian plants. It has been documented that fifty to eighty percent of all species known to occupy broad geographic ranges within American deserts are influenced by the presence of a riparian environment.

Of some 308 bird species in the Sonoran Desert, about twenty percent are confined to riparian settings; another sixty percent or so can live in, and are frequently found in, riparian environments. Certainly the hordes of White-winged Doves that nest in these areas—they are intimately related to the presence of mesquites—attest to the importance of the riparian zone for some bird species. Some, such as the Vermilion Flycatcher, are seen almost exclusively in riparian situations or near spring-fed ponds.

In deserts, bats are most often associated with free-standing water. Most species can be observed as they swoop to obtain a drink or to feed on insects hovering above the water. Large mammals find refuge in riparian bosques. Although they may occur in other habitats or throughout the desert, the population densities of medium-size and large mammals are greatest in riparian systems. Certain species—for example, Muskrats and Beavers—are virtually confined to riparian habitats

The management of riparian areas is of considerable

Burrobush Hymenoclea salsola 365

Creosote Bush Larrea tridentata 342

Arrow Weed Pluchea sericea 344

Screwbean Prosopis pubescens 302, 311, 320

Quail Bush Atriplex lentiformis

Tamarisk Tamarix chinensis 304, 324

importance to humans. Flood control, hunting, fishing, boating, swimming, picnicking, irrigation, and erosion control are all important uses of riparian systems. These actions are not only related to the health of the systems, but they also influence man. You need only watch the thousands of people who sit in innertubes and float down desert rivers (such as the Verde and Salt rivers in Arizona), and who follow their ride with a picnic and "a cool one" under the mesquites, to realize the recreational value of riparian systems, to say nothing of their economic importance—both direct and indirect. Historically, riparian zones were of utmost importance to native Americans, who often positioned their villages in relation to riparian habitats. Although we sometimes try to ignore their importance to the contemporary citizens of the desert, these ecological systems will not let us forget their importance. In many desert areas, including some farmlands and towns, floods would not have taken place-or at least would have been less severe—if the protective nature of riparian vegetation had been left unaltered.

Sand Dunes

Sand dunes occur in all North American deserts, where they cover approximately six percent of the land surface (plates 4 and 5). For the most part, the dunes are composed of particles ranging between 0.13 mm and 0.5 mm in diameter. These grains are generally silicon dioxide but they may also derive from gypsum, a calcium sulfate compound (plate 6). Sand dunes are principally formed by the action of wind, specifically—because of the tiny size of sand particles—by a process termed eolian saltation (a wind-induced bouncing of the grains along the surface). Such movement results in the formation of a variety of dune types. These can be classified into three general categories based on the relative strength of the wind, the supply of sand, and the amount of vegetation cover (which is not independent of the other two factors). Longitudinal dunes are long in comparison to their width, and they are symmetrical in cross section. They form where there are strong winds and little sand. Transverse dunes are shorter and somewhat asymmetrical in cross section. They lie close to one another and are of variable length. Transverse dunes usually support little vegetation and develop under low to moderate winds in areas of moderate to enormous supplies of sand. U-shaped dunes, as their name implies, are shaped like a gigantic letter U. Their arms trail behind the advancing dune. (This situation differs from another dune with a horseshoelike shape, the barchan, a type of transverse dune whose arms precede the dune in its forward movement.) U-shaped dunes develop where there is moderate wind, moderate vegetation coverage, and moderate supplies of sand. Active, or moving, dunes of any type can create problems for

Active, or moving, dunes of any type can create problems for plants. Established plants may be covered by moving sand, or, conversely, the movement of sand away from plant roots may expose them. In addition, active dunes contain few plants to enrich the sandy "soil," and the sand grains themselves do not

Sand Dune Buckwheat Eriogonum deserticola

Croton Croton wigginsii

contain many of the nutrients essential to plant growth. These disadvantages are somewhat balanced by an advantage: the relatively high availability of water in sand dunes. With soils that are composed of particles that are finer than sand—especially clays—water is bound tightly to soil particles and may not be very available to plants' root hairs. However, because of the larger size of sand particles, all of the rainfall occurring on a dune is essentially sopped up, sponge-fashion, by the dune sands. Little runoff or erosion occurs; the water is loosely held to the sand grains and is thus available to plants. Thus, a dune—seemingly dry on the surface—is one of the more mesic sites in a desert.

Plants overcome the negative aspects of dune existence by employing a number of mechanisms. The rapid growth of stems and branches can prevent a plant from being buried, while the production of long, horizontally directed roots helps to keep part of the root anchored in the soil. In the Algodones Dunes (on the southern portion of the Arizona-California border), you can see large numbers of these exposed root systems. Follow one of them for several yards to the "shrub" portion of the plant, and you will find sand dune specialists such as Sand Dune Buckwheat and Croton. The rapid growth rates necessary for the plant to keep ahead of the sand occur in over fifteen families of North American plants. These high rates also require that the dune plants have very high rates of photosynthesis and that these high rates occur throughout the year—not just during short growing seasons—for sand may move any time there is wind, regardless of season. The nutrient problems facing dune plants are solved by at least two mechanisms. Some dune plants survive simply by being tolerant of low nutrient conditions. Other species may form symbiotic relationships, either with vesicular-arbuscular mycorrhyzal fungi that aid in the uptake of water and phosphorus, or with nitrogen-fixing bacteria, or with both. Dunes may contain numerous plant species. One can find sixty species on the gypsum dunes of White Sands National Monument in New Mexico; ninety-seven species on the Algodones Dunes in California; and fifty-three species on the Coral Pink Sand Dunes in Utah. This plethora of plants includes species that are endemic to the particular dune systems; dune specialists with wider distributions; and, in dunes that have become more stabilized, an assortment of desert plants from nearby areas. The latter may include Creosote Bush, any one of several saltbushes or even mesquites.

Gypsic Soils

Gypsum, a form of hydrous calcium sulfate, occurs around the world in many climates. Most commonly, however, gypsum soils—which range from gypsic rock outcrops to moving dunes, ninety-six percent of which are composed of gypsum "sands"—occur in semiarid or arid areas.

Plants that occur on gypsic soils may be highly selected, depauperate (undersized) samples of the flora growing on the

Fremont Cottonwood Populus fremontii var. wislezenii

Soaptree Yucca elata 328

Squaw Berry Rhus aromatica surrounding nongypsic soils. In most cases, however, there is also a group of obligate gypsophiles (species that live only on gypsum soils).

In the United States, gypsum soils occur in both deserts and other areas, but they are especially common in the West. Perhaps the best-known of such sites is the 225-square-mile area in New Mexico that includes the White Sands National Monument, whose "white sands" are actually gypsum particles. This area contains about sixty species of plants. Of this number, roughly ten percent are obligate gypsophiles. These include a perennial grass, Boutelona breviseta, which occurs in a number of gypsic areas of the Chihuahuan Desert; some perennial herbs (Nerisyrenia linearifolia, Nama carnosum, and Tequila [Coldenia] bispidissima); and some dwarf shrubs (Frankenia jamesii and Pseudoclappia arenaria). In general, this array of grasses, perennial herbs, and dwarf shrubs typifies the gypsophiles found in all gypsum soils.

Few true gypsophiles occur as tree forms. Although a number of relatively large plants—from shrub-size species to small treelike plants—occur on gypsic soil, all of them occur on other soils as well. These include a variety of Fremont Cottonwood (*Populus fremontii* var. *wislezenii*), as well as Soaptree and Squaw Berry, all of which show contorted stem and root forms on gypsic dunes

It is not at all clear why plants find gypsum soil to be such a harsh environment. While some scientists have suggested that gypsum soils are saline as well, and that salinity is the limiting factor, this often does not seem to be the case. It may be that a high amount of calcium or sulfur is the culprit. The question of whether sulfur is a toxic component for plants in general is actively being researched, and answers concerning the possibility of sulfur acting as a plant poison in gypsum soils may be forthcoming in the near future.

Nonetheless, some genera of plants are tied to gypsum soils. Where gypsic and nongypsic soils abut one another in a clearly demarcated way, the gypsophilic and nongypsophilic plants undergo an equally abrupt transition. In places where gypsum soils are covered by as little as an inch of nongypsic materials, the flora contains no gypsophiles. The species with such sharp responses belong to a number of families and genera. Three of the more prevalent ones in the United States are Tequilia, a genus in the forget-me-not family, which contains seven gypsophiles within one group of nine closely related species; Sartwellia, a genus in the sunflower family, whose four species are all gypsophiles; and Nerisyrenia, an herbaceous genus in the mustard family that is composed of nine species, all but one of which are gypsophiles. This is but a small portion of the North American genera that contain gypsophiles; they occur in some fourteen plant families.

The best representation of gypsophiles occurs in the Chihuahuan Desert. This is in line with the general geographic pattern, which is that gypsum areas in the North have fewer gypsophiles than do apparently equivalent areas in the South.

Some Special Vegetation Types

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The flora occurring on gypsic soils consists of an unusual, albeit geographically limited, assemblage of plants. A number of species may be rare enough to qualify as threatened or endangered. Indeed, certain species that have existed since before 1950 in White Sands National Monument have not been conspicuous in more recent times.

Animals do not seem to differentiate as readily between gypsic and nongypsic soils as do the plants. The most obvious adaptation in a place like the White Sands National Monument is that the animals that live in the white-colored gypsum areas are lighter in color than the same species in the immediately adjacent, nongypsic areas. The visitor is most likely to notice this in one of two light-colored lizards, or perhaps a light-colored weevil or tiger beetle. This concession to the environment is not intrinsically related to gypsum; the same adaptation would occur in response to any light substrate.

Playas and Saline Soils

In arid zones, standing water usually contributes to an increase in the salinity of the soils beneath it. Ordinarily this is merely a result of the accumulated water evaporating; as it does, salt is concentrated in the remaining water until all the water is evaporated, whereupon salts are left in the lowest ground areas. The salinization of the surface soil can also occur when salts move upward within the soil profile as water evaporates. Saline soils and playas, or ephemeral lakes, are closely linked. During dry periods, playas are merely expanses of saline soil. Playas are, in essence, temporary lakes that are dry for much longer periods than they are wet. Ordinarily they are formed by the runoff from entire watersheds, but some have more localized origins. Playas lose very little of their water through percolation into the soil; as a result, water flowing into a playa translates directly into variations in the lake volume.

There are nearly 50,000 playas in the deserts of the world. Most are small, seldom exceeding thirty-six square miles. Playas are not uniform in physical, chemical, or biological properties from one place to another. The lowest areas—those that are wet for the longest time—usually contain very fine soil particles, such as silts and clays. Toward the edges, coarser particles, such as sands, occur. Salinity follows a similar gradient; it is highest in the middle and decreases toward the outside edges. The depth of the water table with respect to the surface also varies from playa to playa. The combination of these three factors—the salinity, the soil characteristics, and the proximity of the water table—to a large extent determines the distribution of plants around various playas. Many secondary features develop in playas. If springs are involved, the sediments they deposit may be cemented into mounds. In some places in the world (for example, Lake Eyre in Australia) these mounds may be over thirty feet tall. Mound structures may also develop from wind-borne sediments that are trapped by the bases of plants. The size of a mound is determined by the plants' ability to get their roots to water.

Greasewood
Sarcobatus vermiculatus
345

Iodinebush

Sea Purslane

Pickleweed

Saltgrass

Salicornia rubra

Distichlis spicata

Allenrolfea occidentalis

Sesuvium verrucosum

Thus if the water table is too deep, significant mounding does not occur. A good example of a plant-mediated mound formation can be seen on the salt flats at the northern end of Utah's Great Salt Lake, where large areas are covered with mounds that are a foot or two high; these have formed in nearly pure stands of Greasewood. In other places in the Southwest, such mounds may reach almost ten feet in height. Salt crusts of varying shapes and patterns can develop. Often the crusts are formed as polygonal plates of fine-grained soil, which are separated from each other by cracks. Together they look like the scales on a giant turtle's back. Pits, which are formed when gases from decomposing organic matter escape, are another example of secondary saline-soil structures. Most plants have a relatively low tolerance for salinity. In crop plants, salinities above one tenth of a percent can cause physiological reactions. On the other hand, salt-tolerant desert species and plants occuring in salt marshes along the edges of oceans may tolerate up to six percent salinity. Plants in saline areas face unique difficulties. First, they must be tolerant of the specific chemicals forming the salts on a given site. Salt types vary but usually involve compounds that have been formed from calcium, magnesium, or sodium, and that have reacted with chloride, sulfate, or carbonates. Second, because the soil is saline, water moves toward the area of highest salt concentration, not toward the plant—a situation that can make it difficult for a plant to take up water. Some plants may take up particular salts; this gives their cells high salt concentrations while allowing them to retain water, or, in technical terms, to maintain their turgor (a plant that has not kept its turgor is wilted). But there is a limit to how much salt can be accumulated without ill effect. Plants deal with this constraint in several ways. Some develop a tolerance to high salt concentrations. Others become succulent. A succulent plant stores water in its tissues; this gives its leaves or stems a watery, distended appearance. The stored water enables the plant to dilute the salts it takes up. Finally, some plants actively excrete salts through hairs or pores on their leaves. This is the case with certain species of saltbushes (Atriplex). The variation in the capacity of different plants to manage salts and the differences in salt content in the soils around playas together cause zones of vegetation to develop. The most highly saline areas characteristically contain the succulents Iodinebush, Sea Purslane, seepweeds (Suaeda), and Pickleweed, as well as a species of grass, Saltgrass. Pickleweed, one of the most salt-tolerant species in the United States, can endure up to six percent salinity. It is often the only species on open, flat salt pans. Interestingly, it is not very drought-tolerant; thus it is often excluded from certain saline areas because they are too dry, not because they are too salty. The seepweeds are very salt-tolerant; there are some fourteen species in North America, and several of these are locally common in the deserts. Certain species, such as the widespread Suaeda depressa, are very plastic: They can alter

Horned Pondweed Zannichellia palustris

Widgeongrass Ruppia maritima

Fennelleaf Pondweed Potamogeton pectinatus

Tiger Salamander Ambystoma tigrinum 289, 290, 291

Four-wing Saltbush Atriplex canescens 352 their form to suit the environment. In saline soils, this species adopts a dwarfed, prostrate growth form or, alternatively, exists as a single-stemmed, upright plant. In soils with lower salinities, the plant is much more robust and may have several upright stems. (Such variation in the very form of a plant is a taxonomist's nightmare.)

Iodinebush, though often occurring with Pickleweed, has a lower salt tolerance. It frequently forms low hummocks by trapping wind-borne soil particles, and such areas can dominate large areas around playas or swales (depressions). Saltgrass has shallow roots and forms rhizomes in areas that are less saline than those tolerated by the other species mentioned. In somewhat less saline areas of the playa, we begin to see a moderate number of shrubs, representing roughly two to six species. These are frequently saltbushes (Atriplex) or greasewoods (Sarcobatus). Numerous grasses or grasslike plants also occur in such areas, and they may be quite dense. Where there is some standing water, as in saline springs or seeps, several submerged aquatic plants, all extremely salttolerant, may occur. Perhaps the three most common species from the Great Basin to the Chihuahuan Desert are Horned Pondweed, Widgeongrass, and Fennelleaf Pondweed. All three have virtually worldwide distributions. These species often provide food for ducks and other migratory birds. When playas fill with water, numerous invertebrates may occur in great numbers. These include ostracods and cladocerans (both are groups of tiny crustaceans); the larvae of a variety of insects, especially including hardy species like the brine flies of the family Ephydriadae; and certain mosquitoes. All of these species usually have broad environmental tolerances and are able to occupy fresh to saline water. Vertebrates capable of responding to ephemeral sources of water are generally amphibians. As if from nowhere, spadefoot toads (Scaphiopus) come out following rains to form deafening choruses. They are often accompanied by true toads (Bufo) and occasionally by a few other frogs as well. When flooded, playas may harbor the Tiger Salamander or even an occasional mud turtle (Kinosternon), as long as the salinity is not too great. Human beings have more than a passing interest in saline soils and the plants that grow in them. Expansion of agricultural productivity into the desert areas of the world will require either the creation of salt-tolerant varieties of current agricultural crops or the selection of new species with the potential for human use. Four-wing Saltbush has promise as a forage crop. Eighteen to twenty percent of its content is protein, a level comparable to that in alfalfa. It is easily digested by cattle and sheep. This species and others such as Russian thistles (Salsola) and mollies (Kochia), which can be burned as fuel, may allow us to put arid "wastelands" into agricultural production. While work is going forward at a rapid rate with regard to using native, salt-tolerant plant species for agriculture, much remains to be done. We have barely tapped the potential of our desert areas to provide resources for human beings.