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THE DESERT GRASSLAND
A HISTORY OF VEGETATIONAL CHANGE AND AN ANALYSIS OF CAUSES[1]

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INTRODUCTION

The desert grassland concept used here corresponds essentially with that of Shantz' desert grassland and desert savanna (Shantz and Zon, 1924). Shreve's desert grassland transition (Shreve, 1917) is identical in part but also includes rather extensive areas, largely in eastern New Mexico and western Texas in the Staked Plains area classified as short grass or tall grass by Shantz. Clements' desert plains (Clements, 1920) appears to include much the same area as Shantz' desert grassland.

As both Shreve and Clements point out, the desert grassland is ecologically similar to the short or mixed-grass plains. There is a wide overlapping of many genera and species, and a few of the grasses dominant in extensive portions of one also occur as widespread dominants in the other. The difficulty encountered in attempting to separate the two is indicated by the differences of opinion of Shreve, Shantz and Clements as to geographical area of the desert grassland. A logical solution would seem to be to

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class the various so-called "desert grassland" associations as associations or associes of the mixed grass plains.

The desert grassland lies primarily in southeastern Arizona, southcentral and southwestern New Mexico and southwestern Texas. The area does not include the entire portions of the states mentioned but occurs as local grasslands rather widely interspersed with other types. Although to a considerable extent occupying extensive plains areas, it also typically lies as broad belts around the bases of the many southwestern mountain ranges, principally at elevations of from 3,000 to 3,500 feet. South of the border it extends far into Mexico, and, as Clements (ibid.) points out, the center of the desert grassland probably lies in Mexico.

The bulk of the desert grassland consists of broad basins or slightly sloping, very nearly flat drainages. Extensive areas, particularly on the slopes of the Guadalupe, Davis and Santiago Mountains in southwest Texas and along the lower slopes of the mountain ranges of southern Arizona and New Mexico, are hilly. Drainages, usually as dry washes, but occasionally as running streams, cross the region at frequent intervals. Even some of the larger so-called "rivers" may be intermittent or dry most of the year.

The desert grassland is the most arid of all North American grassland regions. Mean annual precipitation is low, ranging from about 12 to 18 inches in the west (Shantz' desert grassland) to from 20 to 30 inches in the east (Shantz' desert savanna) (U. S. Department of Agriculture, 1941). Most of the precipitation occurs as rain, not as snow, and falls largely during two seasons, summer and winter. The summer rains occur primarily during July and August; winter rains from December to February, inclusive. Summer rains are largely in the form of thunderstorms with heavy precipitation for short periods; winter storms are largely equinoctial and are characterized by relatively gentle precipitation that may fall intermittently for several days. Over the eastern third of the region at least 70 per cent of the annual precipitation falls during the period April 1 to September 30. Farther west this percentage decreases until on the western edge in south-central Arizona about 45 per cent falls during this period (Dorroh, 1946).

Temperatures and wind velocities are high and evaporation is rapid. Water loss by evaporation from an open tank frequently

amounts to as much as 80 inches (Smith, 1956). A 14-year record at 4,000 feet on the Santa Rita Experimental Range in southern Arizona showed an average of 109 inches. High temperatures, low humidities and high wind velocities account for the extremely high evaporation rate.

Because the rainy seasons are short and somewhat uncertain, both grasses and forbs tend to grow and set seed rapidly. Most of the growth takes place during August, but, since temperature is not a limiting factor at this time of year, the growth period is determined solely by the amount and distribution of precipitation and by the time the rains occur. By October most of the grasses are dry and usually remain so until the next rainy season. Because of the less favorable temperatures during the winter growing season and the not-infrequently desiccated condition of the soil by spring, most of the grass growth occurs in the summer rainy period.

Although the region is called desert grassland, it is far from being an essentially unbroken expanse of grasses, as are the tall and mixed-grass prairies. In some places essentially pure stands of grass prevail; in others there is an open savanna with grasses beneath oaks or mesquites. In still others the grasses are interspersed with a wide variety of low-growing trees or shrubs. Both perennial and annual grasses are common. Most of the annuals germinate and grow only during the heat of the summer rainy period; annual forbs, which may also be abundant in some years, grow largely during the cool winter and spring months. There are some exceptions to these general growth patterns. The annual fescues, for example, are primarily winter grasses; mexican poppy (*Kallstroemia grandiflora*)[3] is a summer-flowering forb.

Three genera, *Bouteloua*, *Hilaria* and *Aristida*, provide most of the grass species in the type. Although *Bouteloua* is represented by many perennial species, *B. eriopoda*, *B. gracilis* and *B. curtipendula* are probably the most abundant. In the genus *Hilaria*, three species, *H. mutica*, *H. belangeri* and *H. jamesii* are most common. Although several species of *Aristida* are prevalent, four of the most common are *A. divaricata*, *A. hamulosa*, *A. glabrata* and *A. longiseta*. Other grass genera characteristic of at least part of the area are *Andropogon*, *Eragrostis*, *Heteropogon*, *Leptochloa* and *Trichachne*.

[3] Scientific names, unless otherwise indicated, correspond with those in Kearny and Peebles (1951).

The woody plant growth is extremely diversified, being derived in part from the southern desert shrub below, in part from the chaparral and pinyon-juniper above. Although shrubs, low-growing trees and cacti were always present to some extent in the grassland, they were originally largely restricted to drainages that supported little grass or to rocky or shallow-soil areas.

In spite of the large number of woody genera and species, only a few comprise the bulk of the trees and shrubs; varieties of *Prosopis juliflora* are outstanding. Three varieties are encountered most commonly. As classified by Benson (1941), these are varieties *velutina, torreyana* and *glandulosa.* Other shrubs that are locally or generally abundant include *Larrea tridentata, Acacia, Opuntia, Yucca, Flourensia cernua, Haplopappus* and *Gutierrezia.* For the most part these provide little or no feed for livestock, so that as they have replaced the grasses, the value of the country for grazing has decreased.

No figures are available that give the area of the desert grassland originally or currently dominated by woody plants. It is, however, a matter of abundant record that these woody species today occupy several million acres in the Southwest that were formerly either grassland or supported only an open stand of shrubs. Recent estimates, for example, place the acreage of mesquite at more than 70,000,000 (Bell and Dyksterhuis, 1943; Parker and Martin, 1952); cacti of the genus *Opuntia* at 60,000,000 in Texas alone, and an additional 1,000,000 in Arizona (Dameron, 1939); snakeweed in Arizona at 4,500,000 and burroweed in Arizona at 5,500,000 (Upson, Cribbs and Stanley, 1937). Acreages given for these species overlap in part; with the exception of mesquite, they do not include New Mexico. Were this state included, additional millions of acres would be added.

Although stands of woody plants in the desert grassland area antedate historical records, the beginning of an extensive invasion by these species coincided essentially with settlement of the area by white men and has continued to the present. In this study an attempt is made to give a picture of previous and present vegetation, and to examine and evaluate each of the various factors that may have been instrumental in effecting the brush invasion that has been noted.

Observations and investigations of travellers, surveyors and

scientists, extending back through a long period of years, provide extensive data useful in determining not only the changes that have occurred but also the reasons for these changes. One of the main values of a study of this sort lies in the assembling and quoting verbatim from a variety of original sources. Quotations are of particular value when taken from old accounts or when discussing controversial topics. The vegetational changes that have taken place in the desert grassland and the factors underlying these changes are controversial. Scientific conclusions must be based on supporting data. Many of the supporting data in this paper are in the form of recorded observations. If the conclusions do not seem valid, the basic data are there for the reader to re-analyze and use as a basis for his own conclusions. In order to preserve the integrity of the original text, no changes have knowingly been made in wording, punctuation or spelling.

GRAZING HISTORY

Livestock raising in the Southwest dates back to about 1500. Columbus, on his second voyage to the West Indies, stocked Hispaniola with sheep, cattle and horses. Some of these were later transported to Mexico and served as a nucleus for the Mexican herds. Cortez also brought rather large numbers of stock, principally horses and sheep, directly to Mexico from Spain. These herds were the progenitors of the large numbers that later spread over much of California, Arizona, New Mexico and Texas (Thompson, 1942).

Francisco Vasquez de Coronado, in an attempt to find the seven fabled cities of Cibola, journeyed in 1540-1542 from Mexico through what is now southeastern Arizona, across New Mexico, northwestern Texas and Oklahoma, and as far east as the present site of Dodge City, Kansas. He took with him on this expedition 1000 horses, 500 cows and 5000 sheep (Castañeda, 1907). Numbers of these strayed or were lost from time to time and formed the nucleus of the herds encountered by later plains travellers (Thompson, 1942).

Before the time of Coronado's journey, stock raising was already well established in Mexico on a number of well-known large ranches. North of the Rio Grande, however, Indian hostility for many years was an effective deterrent to widespread colonization.

Not until 1598, when Juan de Oñate crossed the Rio Grande at El Paso and travelled across New Mexico and Arizona to the head of the Gulf of California, was the number of livestock increased perceptibly in the area later to be known as the United States. Oñate took with him on this expedition 7,000 cattle in addition to horses and sheep. From this time on, cattle, horses and sheep increased in numbers. Indian raids were a constant hazard, and livestock tended to be concentrated in the vicinity of the principal towns of Santa Fe, Taos, El Paso and Tucson. Smaller herds grew up around individual rancherias in the larger valleys, such as the Rio Grande and Santa Cruz. In some instances the larger of these ranches grew to be small villages as a protection against the Indians (Gregg, 1844).

Because of the necessity for concentrating the herds around the villages, the forage for miles around the population centers was depleted and game was scarce. In the unpopulated areas, on the other hand, forage was usually plentiful in most years. Although game was sometimes hard to obtain, it was abundant when judged by modern conditions.

EARLY VEGETATION

Sources of Data

Changes in the vegetation of the desert grassland region have been of two principal sorts, invasion by woody species and changes in composition and density of non-woody species. There is an abundant record of the first of these, primarily because the early travelers were almost completely dependent on grasses as feed for their animals and on trees and shrubs as fuel for fires. Although few of the pioneers were botanists or were able to distinguish many of the species they encountered, most of them did recognize mesquite and many were able to separate the gramas from other grasses. It is possible consequently, to reconstruct, to a considerable extent, a picture of the vegetation as it appeared in the time of the first settlers.

The early Spanish conquistadores left little or nothing in the way of a plant record of value. They were occupied with matters other than making a record of the vegetation of the country through which they passed. Neither were their expeditions staffed with naturalists.

The first reliable accounts of the vegetation of the West occur in a number of sources dated about the middle of the 19th century. These accounts were written by men who were drawn into the Southwest largely for one of three general motives. One of these was an increasing appreciation on the part of a few individuals of the potential value of the Southwest and California. This stimulated wagon-road, railroad and International Boundary surveys. The second was the discovery of gold in California and the '49 gold rush that brought thousands of people into and through the Southwest. The third was the desire or necessity to subjugate Mexican forces in New Mexico, Arizona and California that resulted in detailing military forces to the far West.

Both the survey crews and the army forces were staffed in part with qualified naturalists who were interested in recording the plants, animals and physical features of the country they passed through. The accounts of these naturalists, supplemented by diaries of prospectors or other early settlers, forty-niners or casual passers-through constitute the chief early sources of information.

Late in the century these sources began to be supplemented by U. S. Department of Agriculture and experiment station research reports that have continued to the present. Excerpts from the various records of all sorts not only indicate the early character of the vegetation; they also provide valuable data on the forces operating on this vegetation to maintain or change it. The basic changes in vegetation that have taken place in the desert grassland are essentially similar to those that have occurred over extensive grassland areas to the east and north.

Early Mesquite-Grassland Relationships

It appears to be impossible to estimate accurately the areal extent of shrub invasion in the desert grassland. Increases in density or area at specific locations are not difficult to determine, but the early records are not sufficiently complete to permit construction of more than an approximation of the extent of woody plant domination, say, 100 years ago. Parker and Martin (1952) summarize the evidence with reference to mesquite as follows: "Overwhelming evidence exists of extensive mesquite invasions of grasslands throughout the present range of the plant in the Southwest . . . . The extent of the spread of the plant from its original habitat is

not known precisely. But the invasion must involve many millions of acres. Prior to its encroachment on grassland ranges the plant was confined mostly to the valley bottom lands and drainage courses and to a few scattered trees in the uplands. In fact, most of the upland country in the Southwest, excluding the mountains and higher foothills, was open grassland . . . . The area where mesquite forms the main aspect of the vegetation involves more than 70 million acres of range lands in the Southwest . . . . By conservative estimate at least half the total area, or about 35 million acres, represents mesquite invasions which have taken place during the past century".

Although these statements refer specifically to mesquite, this species serves as a reliable index to the general invasion picture. There is, however, some question as to the accuracy of the statement that mesquite was originally "confined mostly to the bottom lands and drainage courses and to a few scattered trees in the uplands"; also that "most of the upland country . . . excluding the mountains and higher foothills, was open grassland". This is a rather common misconception, the fallacy of which has been pointed out by Bogusch (1951, 1952) and Malin (1953). Malin treats the subject as a historical geographer rather than an ecologist but, perhaps inadvertently, proves the value of this approach in certain types of ecological studies. He reviews some of the early literature and cites a number of quotations indicating that mesquite has not increased its geographical range since about 1800: "In a floristic sense, the geographical range of distribution of mesquite (*Prosopis* spp.) is about the same in 1952 as at the opening of the nineteenth century, or 150 years ago". This conclusion is attested by the historical accounts cited by Malin and by others (Cooke, 1846; Marcy, 1866; Bartlett, 1854a, 1854b). Although the largest trees and densest stands were usually encountered in the drainages, there were occasional thickets on the uplands (Cooke, 1846).

Marcy (1866) commented at frequent intervals on the mesquite his party encountered while traveling through upland areas that were essentially grassland: "On the 15th of July we left Fort Belknap [in northcentral Texas], and travelled back . . . for fourteen miles . . . upon the large prairie east of that post. Here we encamped, and at an early hour the following morning left the

road, striking out into the prairie . . . toward the Little Witchita River, passing over a rolling country covered with groves of mesquit trees . . . . Our course the next day was northwest for six miles, crossing several small tributaries of the Trinity, all of which were wooded with mesquit . . . . Toward the east from this elevation [a small mountain in the lower Texas Panhandle] nothing could be seen but one continuous mesquit flat, dotted here and there with small patches of open prairie . . . .

"In the journeys I had made before upon the Plains I had observed the mesquit-tree extending over vast tracts of country . . . . It covered a great portion of the country over which we traveled . . . . Between the twenty-sixth and thirty-sixth parallel of north latitude, within the ninety-seventh and one hundred-third meridians of longitude, it is found abundantly, often constituting vast tracts of woodland, and is, indeed, almost the only silva of the section. It is also found in very many places between the Rocky Mountain range and the Pacific Ocean, but appears to flourish better and to attain greater dimensions in the vicinity of the Gila River than in any other locality I have heard of west of the Rio del Norte [Rio Grande]. In going north from the parallel of thirty-three degrees . . . the trees gradually become smaller and smaller, until at last they are mere bushes; and finally, on arriving near the latitude of thirty-six degrees they entirely disappear". It is evident from these and other similar observations by Marcy that mesquite occurred rather abundantly over extensive areas in the headwaters of the Red River, both on the uplands and along the river bottoms.

Bartlett (1854a), in travelling through the Llano River country of south-central Texas, commented on the presence of mesquite on the upland: "Our route today had been over a level prairie country deficient in wood, save a few scattering mezquit trees of diminutive size". And, commenting in a more general way: "The mezquit (*Algarobia glandulosa*) is an important tree in this region, and is mentioned by various travelers as mezkeet, musquit, muckeet etc . . . . Where the prairies are frequently burned over, the tree is reduced to a shrubby state, a great number of small branches proceeding from one root, which goes on developing and attains a great size, though the portion above the ground may not be more than four or five feet high". And again in the vicinity of

the Pecos River: "Unlike all the other streams we had passed, the Pecos has not a single tree or shrub along its banks to mark its course . . . . On both sides is a vast open prairie, entirely destitute of trees, though scantily covered with mezquit chapporal, and other plants of the desert".

Much of the mesquite invasion that has been so widely observed seems to have been in the nature of thickening of open savannas. Cook (1908), one of the early Department of Agriculture research workers in Texas, commented on this: "Many localities are only now being invaded by the woody vegetation. Very often the old mesquite pioneers, the scattered trees which made the 'open mesquite country' of other decades, are still conspicuous among their much smaller progeny and the crowds of other camp-following species which now occupy the land to the almost complete exclusion of the grasses upon which the herds of former days were pastured".

Although groves of mesquite were fairly common on upland sites, the densest stands and largest trees were usually found in the so-called bottom lands of the drainages. Bartlett (1854b), in his travels through Arizona, made frequent references to mesquite in the river bottoms. Although the Casa Grande ruins near Coolidge, Arizona, are today largely surrounded by irrigated land, the immediate vicinity supports a stand of creosote bush and numerous dead mesquites intermixed with a few that still show signs of life. Contrast this with the picture given by Bartlett: "After following this trail in an easterly direction about eight miles across the plateau, which was covered with small mezquit trees, we turned off to the southeast. Another mile brought us to the building of which we are in search rising above a forest of mezquit . . . . This bottom . . . is thickly covered with mezquit-trees from twelve to twenty feet in height . . . .".

Mesquite was abundant in the Santa Cruz River bottoms south of Tucson (ibid.): "We were off this morning before the sun had risen, and soon entered a thickly wooded valley of mezquit. A ride of nine miles brought us to the mission at San Xavier del Bac . . . . Leaving the village, we rode on a mile further, and stopped in a fine grove of large mezquit trees near the river, where there was plenty of grass. We . . . resumed our journey along the valley as before, through a forest of mezquit trees". And, continu-

ing south up the Santa Cruz, "The valley continued about half a mile wide, thickly covered with mezquit trees of a large size. The bottom-lands resembled meadows, being covered with luxuriant grass, and but few trees. The immediate banks of the river . . . are lined with cottonwood trees of a gigantic size . . . . During our journey today, some five or six miles back, I noticed the ruins of Tumacacori. Its beautiful and picturesque church showed finely among the thick grove of trees by which it is inclosed". Although most of the Santa Cruz flood plain is now cleared and planted to irrigated crops, the bulk of it was still wooded when the author first saw the area in 1930. Local groves of trees remain, primarily where excessive arroyo cutting has prevented cultivation.

Reid (1858), journeying south up the Santa Cruz toward the present Mexican boundary, was impressed by the extensive grasslands both on the uplands and in the flat lands bordering the stream: "Leaving San Xavier we moved up the Santa Cruz . . . forty miles to Tubac . . . The bottoms in places, are several miles wide and highly fertile. Cotton-wood and musquite, of good size, are abundant in them. The valley, tableland and mountain sides here, as elsewhere in the [Gadsden] Purchase, are covered with a luxuriant coating of grama grass . . . . We left Tubac . . . and drove fifteen miles to the Rancho do los Calabasas . . . . If you will portray in your imagination a bottom covered with tall, golden colored grass . . . divided by a meandering stream a dozen yards wide and as many inches deep, this shaded by cotton-woods, willows and musquites . . . you will have a view of Calabasas".

Vegetation of Major Drainages

Froebel (1859) gives an interesting description of the Santa Cruz near Tucson: "We encamped a few miles above the town, in a pleasant part of the valley. A rapid brook, clear as crystal, and full of aquatic plants, fish and tortoises of various kinds, flowed through a small meadow covered with shrubs".

Browne (1950) described the valley of the Santa Cruz as he saw it in 1864: "The valley of the Santa Cruz is one of the richest and most beautiful grazing and agricultural regions I have ever seen. Occasionally the river sinks, but even at these points the grass is abundant and luxuriant. We traveled, league after league, through waving fields of grass, from two to four feet

high . . . . This day's journey through the valley of Nogales, or the 'Walnut trees', was one of the most pleasant of our trip . . . . Grass up to our horses' shoulders covered the valley . . . . Abundance of mesquit, cottonwood, willow and walnut is found in the river-bottoms and the grass is so luxuriant that in many places it is difficult to travel out of the beaten tract".

Near the mouth of the San Pedro in southeastern Arizona the valley was apparently rather densely wooded (U. S. Congress, 1848): "The valley of this river is quite wide, and is covered with a dense growth of mezquite, (*Acacia prosopis*) cotton wood, and willow, through which it is hard to move without being unhorsed . . . . About two miles from our camp the San Pedro joins the Gila . . . . The place of meeting is a bottom three miles wide, seeming a continuation of that of the Gila. It is principally of deep dust and sand, overgrown with cotton wood, mezquite, chamiza, willow, and the black willow."

Much of the flood-plain area in the main drainages of the desert grassland supported dense stands of sacaton grass four to six feet tall. Thornber (1910), an early botanist at the University of Arizona, saw and described many of these bottoms before they had been changed appreciably from their original condition: "In moist valleys, cienegas, and occasionally canyons, tall sacaton grasses were the predominant plants. These valleys, examples of which are the Santa Cruz, San Pedro, San Simon, and Little Colorado were veritable cienegas or flood plains over which the excess of storm water spread from time to time in broad sheets, retarded by the accumulated vegetation of past years, and occasionally by groups of beaver's dams . . . . Such sacaton meadows or cienegas were commonly fringed with thickets of cat's-claw, screw beans, and mesquite, while cottonwoods and willow grew in their moister parts".

The extent of at least one of these cienegas is indicated by Bartlett (1854a) in his description of what is now known as Black Draw in extreme southeastern Arizona: "Here was stretched out before us a level patch of green, resembling a luxuriant meadow, some eight or ten miles long, by one broad; and beyond, on a little spur of the plateau, lay the ruins of the hacienda of San Bernardino . . . ." Today this area, except where cultivated, is a dense mesquite woodland.

Even though the main valley of the San Pedro appears to have supported a stand of sacaton grass for the most part, its confluent drainages and portions of its lower reaches were at least in part mesquite covered (Cooke 1846): [We found] "good grass and mesquite brush in the little valley of a dry branch . . . . As we approached the broken ground with a long black streak of mesquite, etc., where we imagined we should find the San Pedro, we . . . fell into the smooth valley of the dry branch of the night's camp . . ."

There apparently were local stands of mesquite interspersed with the coarse-growing sacaton (ibid.): "The road today was quite crooked and rather difficult to open, the bottoms having very high grass and being lumpy . . . . The bottom grass is very tall and sometimes difficult to pass through. The mesquite here becomes a small tree, and with others this afternoon gave quite a wooded appearance to much of the bottom . . . . [The river bottom] is a mile or two wide and a plain on either side, inclined both to the river and down stream, the mesquite in places taking the exact resemblance of orchards". Clarke (1852) also described the San Pedro valley in somewhat similar terms: "The road is pretty good down this splendid valley, although in some places rather rough, from thick tufts of grass, that have grown up in it since it has been used".

Bryan (1925), writing about the San Pedro, noted that "The floor of the valley was originally covered by sacaton grass with groves of cottonwood, ash and willow. Since the arroyo was cut . . . between the years 1883, when the arroyo was first formed at the mouth of the river, and 1892, when the head water fall cut through the boundaries of the Boquillas Grant 125 miles upstream . . . a great forest of mesquite has sprung up". It would appear that this last statement is not entirely correct, since early explorers (Bartlett, 1854a; Cooke, 1846) commented on groves of mesquite in both the Santa Cruz and San Pedro River bottoms.

When Cooke passed through the Southwest with the Mormon Battalion in 1846-47 he commented a number of times on the mesquite but usually with reference to the "rising ground". His description of the area surrounding the San Bernardino Ranch indicates an abundance of mesquite even at that time (Cooke, 1846): "Generally descending, we then passed over a good firm ground toward the west and saw, miles off, the ruins of the ranch

of San Bernardino. We descended into the broad flat bottom to the east of it, crossed and encamped near the old houses and a remarkably fine spring fifteen paces in diameter . . . . The soil of this great bottom is pronounced very good, but the grass is now very poor, and the rising ground is a 'chaparral' of mesquite wood . . . .

"I have marched eight miles to the west into a pass of a low range of mountains . . . . Apparently hundreds of cattle water here daily. The road which we cut is much uphill and generally through thickets of mesquite, generally stony, and producing little else than thorns or thorny bushes". And, as the party pursued their way westward: "We followed, as I think, a wagon road . . . . It crossed some hilly ground, . . . the mesquite being the greatest obstacle . . . . Then ascending five or six miles somewhat north of west, it was necessary to cut our way through mesquite".

As Cooke's party approached Tucson they encountered more mesquite, perhaps in the Pantano Wash area (Cooke, 1846): "The road lay over a plain of hard white gravel and sand covered with mesquite and prickly pears of every variety; it seemed interminable. I had been led to believe the distance [to San Xavier] eight or ten miles; it proved sixteen . . . ." As the group worked down the Santa Cruz they encountered the dense mesquite bosque of that area: "The thicket [near San Xavier] soon became a dense forest of mesquite trees two feet in diameter".

Farther down the Santa Cruz northwest of Tucson additional mesquite was encountered, though primarily adjacent to the river. Grass became increasingly scarce as the party progressed westward: "The next three miles down our dry creek of Tucson were excessively difficult . . . our beautiful prairie road was much obstructed by mesquite . . . . From 5:45 to 8:45 (o'clock), I marched on rapidly . . . over baked clay ground obstructed occasionally by mesquite thickets and encamped on similar ground with very little grass in spots . . . . The mules had come forty-seven miles without water . . . , and no grass—nothing but artemisia and a few mesquites".

Upland Vegetation

"Of this road which I have made from Tucson I will say more when the river is reached, but thus far I will pronounce it the

most extensive desert I have seen; clay, sand, gravel, artemisias, mesquites, and a few other bushes. Far away to the west, as far as the eye could follow, it was the same. And I am told for a hundred miles south of the Gila there is still no water; and there is no wood no animals . . .but every two or three miles was seen a little grass (a sort I had never seen) of a silky, light, straw color, with a head like a plume; also a very little grama".

Hinton's description of various portions of southeastern Arizona 19 years after Froebel's travels in the 1850's indicates no apparent change in the interim. Hinton's accounts are of particular value, since they describe the vegetation in considerable detail and relate it to specific geographical or other landmarks. For example, we have his description of the area between the San Pedro and the Santa Cruz Rivers south of Tucson (Hinton ibid.): "Coming from the direction of the San Pedro and south through the cienaga, a wide, beautiful view opens before the traveler. For miles south, east and west, the magnificent rolling plain is outspread. Every foot of the surface is covered with grass. Clumps of Emory's oak are found growing among the foothills. They are just dense enough to afford shade, and yet do not interfere with the growth of the grass. There is no understory of bushes, so that the scene fairly bears comparison with a park. Streams with water, warm but pure, from the mountain, flow down almost every ravine. Springs are abundant, and furnish a large volume of water".

Most of the area thus glowingly described in 1878 today supports a stand of mesquite, some with an understory of grass but much of it with little or none. Limited areas, principally on the north slopes of the Whetstone Mountains, are still largely grass-covered. In general, however, the original grassland aspect has changed to one dominated by shrubs. Hinton (ibid.) gives perhaps the best description available of the region from Tubac west to the Baboquivari Mountains. The road west from Tubac "runs through a broad, open valley, abounding in groves of walnut, oak, ash, and mesquite, fringing the bed of a creek, which is usually dry at this season . . . . The valley extends nearly all the way up from the Sopori to the foot-hills of the Cerro Colorado. It is covered with a luxuriant growth of grass, and is one of the finest grazing regions for cattle and sheep to be seen in the territory . . . . On the north side [of the creek] there is a rise of several hundred

feet to the level of a mesa, which extends, as far as the eye can reach, toward San Xavier del Bac. This plateau is dry and rocky, but produces fine grama grass, and furnishes an inexhaustible range for sheep. To the southward lie the rolling hills that join the Atacosa Mountains. These are also covered with grass, and dotted with Palo-verde, mesquite, and cactus. Wild game of all kinds is abundant in this region".

Although this area still produces an abundance of grass, most of the landscape today is dominated by mesquite and catclaw. The valleys support the oldest and largest trees and the least grass. Where Hinton referred to several species of broadleaf trees along the edge of a dry creek, the few that are found in that particular habitat today are lost in the general stand of mesquite that fills the valley. The plateau to the north that impressed him with its grama grass is covered today by a mixture of shrubs with a variable grass understory.

Hinton (ibid.) described the country for a distance of about 38 miles west of the Baboquivari Mountains as "fine grazing land" and as "a country of fine grass". Except on the mountain slopes this region today produces little but mesquite, creosote bush and other shrubs. Further to the west there was apparently little grass: "Passing directly west . . . the country everywhere grows wilder and the trails are dangerous to man and beast, owing to the arid desert over which . . . they pass. Grass is poor and water often very insufficient, with long stretches without any being found". The low precipitation and general lack of stockwater has discouraged settlement and utilization of this area. As a consequence it has changed little in the years that have intervened since Hinton described it.

As one progresses to the east, Hinton's (ibid.) early descriptions are still about the best that were written at that time. Excerpts from some of his paragraphs pertaining to the desert grassland follow: "Passing across a high rolling plain, between the northern wing of the Santa Ritas and the broken formation to the eastward, known as the Whetstone Mountains, the prospector will find it covered with nutritious grasses not so brown and sere looking as the black grama and other indigenous grasses, but showing evidences of a heavier rainfall than elsewhere.

". . . the Babacomori Ranch . . . embraces the western branch of the Rio San Pedro, the Rio Babacomori, a beautiful valley not

over a half mile wide . . . in the midst of a broad rolling plain or mesa abundantly covered by nutritious and luxuriant grasses. The stream is clear, about twenty feet wide and two feet deep and contains an abundance of water the year round for all purposes—so at least, declare the stockmen". Babacomori Creek, although containing a little water as an interrupted flow today, would not be recognized from Hinton's description. Much of the area it drains is still grassland but, to a large extent, grassland that is being invaded by mesquite.

Hinton quotes from an unnamed explorer in describing the area around Fort Grant located in the lower foothills on the southwest slope of the Graham Mountains: "The Caliuro mountains to the west, the Graham mountain range with Camp Grant to the north, the Chiricahua mountains to the east and the Mexican boundary to the south inclose an extensive plain of at least 800 square miles . . . . This vast area is without either running streams or timber, but covered to a great extent with fine grass. The soapweed, the cactus, the sage-brush, and the grease-wood are but little found here . . . . Approaching Sulphur Springs from the east, the road lies for miles through a dense growth of saccatone grass, of far less value than the shorter grama that fairly covers the ground at the springs . . .". This region, though still basically grassland, has been invaded in many places by mesquite and to some extent by other shrubs such as Acacia, burroweed and rabbitbrush. Extensive areas support a dense stand of mesquite; others are more open but the large number of small bushes indicates that the encroachment is continuing.

The San Simon valley apparently supported little mesquite in 1877 (Hinton ibid.): "Looking down the cañon from Camp Bowie a beautiful view may be had of a portion of the San Simeon plains, literally strewn with flowers. The Valley of the San Simeon is about 25 miles in width, and contains much fine grazing and some agricultural land. It is covered with grama—a grass rivalled in nutritious quality only by the mesquite grass of Texas. Southward from Camp Bowie, at the base of the Chiracahua mountains the grass becomes abundant . . . . Mesquite is most conspicuous and abundant from the base of the mountain [Graham] to a certain altitude, and sparse on the mesa . . . . The sacaton and three varieties of grama grass cover the plain . . . . The country abounds

in game, such as deer, antelope, wolf, wild turkey, duck and quail".

Although mesquite grew sparingly in many places where it is abundant today, the numerous references made to it indicate that extensive stands were by no means uncommon. Hinton's (ibid.) comments confirm the observations of others: "Besides the pine, oak, cottonwood, sycamore, ash and other trees, there grows in Arizona the so-called mesquite invariably on good soil. Forests of it are found in the southern portions of the Territory."

Parry gives a good general description of the vegetation of southeastern Arizona. Parry was a botanist and his objective appraisal is of more value than those of some of the early explorers who were trying to induce other settlers to come into the country (Parry 1859). "VEGETATION OF THE UPPER VALLEY OF SAN BERNARDINO, SAN PEDRO, AND SANTA CRUZ WITH THAT OF THE ADJOINING MOUNTAINS RANGES. The country embraced in the above limits . . . is diversified with high wooded mountains and upland plains, well watered valleys and dry and barren tracts . . . . Live oaks, the nut pine, cedar, ash, walnut and cotton wood are produced either upon the mountains or in the upland valleys. Its plains are covered with a uniform growth of upland grama grass, or in the more arid localities by mezquit and its thorny associates". This account still applies rather aptly to this portion of southeastern Arizona. The most marked change that might be noted is a growth of mesquite and other shrubs in some areas that were formerly free of woody plants. A minor change has been a partial breakdown under mesquite invasion and grazing of the "uniform" stand of upland grama grass. When an area such as this is fenced, grazed and covered with stock water developments, little of the original uniformity of cover may remain.

There is no evidence to indicate that the so-called salt flats of the Wilcox Playa have differed appreciably within historic times from their general appearance today. Around the margin, on the other hand, extensive stands of mesquite have become established. In many places these extend back for considerable distances from the edge of the playa. Parke (1857) described the area as it appeared about 100 years ago: "The Playa de los Pimas, the largest encountered during our examinations, is immediately to the west

of the Dos Cabezas or northern end of the Chiricahui mountains, and covers an area of about fifty square miles. Its surface was, when crossed February 28, 1854, and also July 30, 1855, hard and smooth, and apparently as level as a frozen lake. In fact, the effect in crossing, excepting in point of temperature, was very analogous to that experienced in crossing a broad, smooth field of ice. Not a particle of vegetation is found upon its surface, which is entirely free from dirt, and so hard that our mules and heavily laden wagons scarcely made an impression upon it. It is bounded by smooth and grassy plains, sloping back to the bases of the mountains".

Early travelers and settlers in the Southwest commented frequently on the vast stretches of open grassland they encountered. Extensive areas were apparently dominated by grasses that today support shrubs or low-growing trees. Bartlett (1854b) described the area now know as the San Rafael Valley in southeastern Arizona as "a smooth gravelly plain, without a tree or a bush". Most of this same area could be described similarly today. Mesquite has become dominant, however, in some of the drainages, and juniper has extended its range considerably on the western bajada of the Huachuca Mountains. For the most part, though, this is still open, rolling grassland.

Bartlett's party, traveling east after leaving the San Rafael Valley, dropped south a short distance into Mexico around the south end of the Huachuca Mountains. For several miles they traveled down an easterly flowing tributary of the San Pedro (ibid.): "The valley was covered with grass but not a tree or shrub was visible". After a few miles but before reaching the main valley of the San Pedro, "we ascended the plateau, and then pursued a course due east, over a plain as level as a floor, and without a tree or a shrub, covered with a short grass that had sprung up since the rains". This open grassland gave way to mesquite as the party approached the San Pedro about seven miles south of the present International Boundary line: "Keeping the same direction, slightly descending for nine miles, through a level plain covered with mezquit chapporal, we reached Agua Prieta . . . ." This is apparently Black Draw, approximately 15 miles east of Douglas, Arizona.

The area described by Bartlett as "covered with mezquit chap-

poral" probably still supports essentially the same species as it did at that time over 100 years ago. Darrow (1944) showed most of this region as desert shrub grassland with creosote bush and acacia the predominating shrubs. When examined by the author in the spring of 1956 the same plants were dominant, intermixed with scattered small mesquites that appeared to be old but slow growing. Bartlett, like many of the early explorers, probably did not distinguish between true mesquite and the closely related and similar appearing acacia. His designation of the vegetation as chaparral would correctly designate it even today, since Webster (1954) defines chaparral as "any dense, impenetrable thicket of stiff or thorny shrubs or dwarf trees". Photographs taken in 1892-96 (International Boundary Commission, 1899) and repeated in 1956, 60 years later, also show little change in the dominant brushy vegetation.

A good general description of the vegetation of southeastern Arizona as it looked 100 years ago is given by Bartlett (ibid.) as he viewed the country from a promontory in the Guadalupe Mountains: "A magnificent view of the country in every direction is obtained from this spot. On looking back the way we had come, the whole pass with its defiles and mountains, its forests of oaks and pines, its deep gorges and grassy valleys, lay before us; . . . some of the hills were covered with grass, and others were dotted with clumps of cedars, while small live and post oaks predominated".

Having crossed the Guadalupe Mountains, the party swung slightly south of east and crossed the Animas Valley a short distance below the present International Boundary. This area was described as (ibid.) "a very broad and level plain from twenty-five to thirty miles across, on which not a tree or a bush was to be seen. Low gravelly hills of a conical form rose from the plain on our left from fifty to two hundred feet in height, covered with grass, but destitute of trees". The Animas Valley today is still an open plain destitute of trees or shrubs. On the west, however, it upgrades into the San Luis Mountains, a low range of mountains extending into Mexico and covered with a somewhat open stand of Mexican-blue (*Quercus oblongifolia*) or Emory oak (*Q. emoryi*) and juniper with a grass understory. It is doubtful that these were the low, conical hills referred to by Bartlett, since

they are hardly conical, and much of the oak and juniper growing in the area today appears to antedate Bartlett's expedition.

In an earlier expedition Bartlett (1854a) described the country between Horsehead Crossing on the Pecos River of Southwest Texas and the Rio Grande near El Paso. Horsehead Crossing was approximately 30 miles northeast of the present town of Fort Stockton in Pecos County. Bartlett's description follows: "Unlike all the other streams we had passed, the Pecos has not a single tree or shrub along its banks to mark its course . . . . On both sides is a vast open prairie, entirely destitute of trees, though scantily covered with Mezquit, chapporal, and other plants of the desert . . . . [We followed] a northwesterly direction, keeping near the Pecos, the course of which we could occasionally trace by the rushes which grew on its banks. The country continues exceedingly barren and destitute of trees or shrubs, except the thorny chapporal which generally grows on desert spots. A short grass appears here and there, but is now completely dried up".

And, four days later, "still journeying along the river, barren plains continue, with fewer mezquit than before. Dried grass and weeds prevail . . . . Leaving the Pecos we took a direction a little north of west over a range of hills composed of gravel and marl . . . . The country since leaving the river was well covered with grass, but entirely destitute of trees or shrubs . . . . The Hueco or Waco Mountains, our next landmark, lay before us here at twenty-five miles distance".

The portion of the Pecos River that Bartlett describes as not having "a single tree or shrub along its banks", today is densely vegetated adjacent to the stream with a thick stand of salt cedar (*Tamarix gallica*), mesquite and other shrubs, interrupted here and there by the remains of tobosa flats. These species are restricted largely or entirely to the stream bed; on the adjacent upland a scrubby stand of low-growing shrubs, largely creosote bush, whitethorn (*Acacia constricta*) and tarbush prevails, much as it did in Bartlett's time. As one travels westward toward the Hueco Mountains and the Rio Grande, the shrubs are replaced more and more by grassland until finally the bushes remain largely as invading outposts on low hills and other upland areas, or as mesquite thickets in some of the bottoms. It is probably significant that Bartlett described the region extending for many miles east of the

Hueco Mountains as "entirely destitute of trees or shrubs" but "well covered with grass". Most of the woody plants present in the area today, therefore, have apparently become established since 1854.

Different individuals can pass through the same country and receive, in part at least, different impressions. Note, for example, the account of Francis T. Bryan as given in Senate Executive Document 64 (1850): "Marched today nineteen miles to the Waco mountain. The road was over rolling prairie, having high mountains on the right and left some distance from us . . . the grazing along the road was also good; but there was no wood at all to be had. July 29 . . . today we arrived at the Rio Grande, opposite Isleta, after a march of twenty-two miles . . . . The country through which we passed was extremely barren; scarcely any vegetation, except a very little brushwood". Although this description essentially bears out Bartlett's impressions as to the open nature of the area, it does call attention to a little brush that Bartlett may have felt was of too little importance to mention.

Bray's analysis of "Trans-Pecos" Texas at a time intermediate between first settlement of the area and the present indicates the changes that were taking place about 50 years ago. His description of the ecology and vegetation of the region is of particular value, since it represents an early ecological viewpoint (Bray, 1901): "The consideration of plant formations in western Texas may begin appropriately with the grass formations, for, excepting only the highest mountain summits of Trans-Pecos Texas, the climate is a 'grass plains climate' and the grasses may be said to form the matrix of the vegetation of the region . . . . In discussing the grass formations as they now exist we are dealing with a vegetation which, though still the dominant type, has not only a more restricted distribution than formerly, but is undergoing perceptible changes, not only in restriction of its area as the dominant formation, but in the association of species within the formation.

"With respect to the relation of grass formations to woody formations in the Rio Grande Plain, the encroachment of the latter has been so vigorous as practically to destroy continuous areas of open grass formation . . . . The energy and rate of encroachment of woody vegetation during the past half century lead one to believe that there is scarcely an area of consequence in the state

that woody vegetation of some type will not occupy and cover more or less completely, granting of course that no artificial means are employed to check it".

Six years later, after continued observation and study, Bray (1906) wrote: "The woodland is rapidly gaining almost everywhere; the chaparral of the Rio Grande plain, the Edwards Plateau timber, the east Texas forest species, the live oak of the coast prairie, even the desert shrub, all are invading the domain of grassland and introducing shade-loving grasses and other plants where the nutritious sun-loving grasses have long been in complete possession of the ground".

The changes that Bray noted have, of course, continued to this day and may logically further continue until his prediction of a more or less complete woody cover becomes fact.

The "Jornada del Muerto" was a portion of the Santa Fe Trail that stretched for about 90 miles and roughly paralleled the Rio Grande from a point a few miles north of the present town of Hatch, New Mexico, northward to near Old Fort Craig. There are several discriptions of the "Jornada" as it appeared approximately 100 years ago. The accounts differ as to the amount of grass; they are also inconsistent in describing the shrubby growth on the 90 mile stretch. When Beale made the journey he was apparently in an optimistic mood and saw little except grasses and wild flowers (Beale, 1858): "The whole extent, as far as vision reached ahead, was a level plain, covered thickly with the most luxurious grass, and filled with beautiful wild flowers . . . . Hundreds and hundreds of thousands of acres, containing the greatest abundance of the finest grass in the world . . . . are here lying vacant . . . . We have passed the terrible 'journey of death' . . . . The grass, as I have before remarked, everywhere excellent and abundant, and nothing but water required to make it in every way desirable . . . ."

Froebel (1859) also described the Jornada as containing "excellent grass the whole way".

Kendall (1856), in a more pessimistic mood, described the Jornada as "a level, sterile and desolate plain—a desert with no vegetation save here and there a few stunted thorns, different species of the cactus of dwarf-like proportions, and clumps of one of the smaller kinds of palm, growing to the height of some six or seven feet, with long, coarse leaves branching up from roots

and forming a very mat from the closeness with which they grow together. These clumps were called bear grass by our men . . . ." Although Kendall mentioned no grass, most accounts do comment on it as being abundant. The "bear grass" that he describes appears to be *Nolina microcarpa*, still commonly known as bear grass and common in much of the desert grassland.

Marcy's description of the Jornada in 1852 indicated that the area was not entirely destitute of woody vegetation, although he recorded nothing larger than small shrubs (Foreman, 1939): "We found the grass good, and a small growth of scrubby brush, which answered very well to cook with; but there were no trees or other vegetation except several varieties of the cactus and palmetto".

Wislizenus' (1848) account contrasts strongly with Marcy's in that Wislizenus observed an abundance of mesquite trees: "The general direction through the Jornada is nearly due south. To the right, or west of our road, in a distance of about five miles, runs a chain of mountains extending to the river; towards the east the Sierra Blanca, a long, high and steep mountain range, distant about 30 miles, is always in sight of us. The wide country between those two mountains, through which we have to travel, is a high plain . . . with dry, hard soil, tolerable grass, and an abundance of mezquite and palmillas. The latter grow here already to the height of from 10 to 12 feet, and give to the scenery some peculiar impression, reminding one of African landscapes. No other tree grows in the Jornada. The Palmilla and mezquite furnish the only fuel".

Although there is still much grass along the route of the old "Jornada del Muerto", most of the area today is dominated by shrubs of various sorts (Gardner, 1951). Mesquite forms a long black streak several miles in length near the southern end of the route. The horses, cattle and mules of the early caravans apparently ate their fill of mesquite beans in the Rio Grande bottoms and voided the viable seed as they worked their way northward. Other shrubs that are locally or generally abundant in the area today are creosotebush, Mormon tea (*Ephedra*), rabbitbrush (*Chrysothamnus*), snakeweed and tarbush.

Although Cooke (1846) with his Mormon Battalion followed a route along the river west of the Jornada trail, much of the way he made a number of references to the vegetation. In the northern part of the Jornada, he mentions camping "on a high plain covered

with grama grass". The following day he refers to the mesquite, a small bush "common on the Missouri and Platte prairies". He also says the expedition "passed cactus plants ten feet high, and saw a specimen of an extraordinary variety, a bush of many small stems bearing long thorns . . . covered with a full allowance of the minute prickers". The following day he mentions camping in "a small prairie of grama grass". From the next day's camp, he describes the hills west of the Rio Grande as being "covered with the dry yellow grama grass and . . . dotted with cedars". And, the day following, "the hills passed today are well clothed with grama grass". Although the notes for the next day do not refer to grass, they do mention that there was "plenty of cedar for fuel, also the mesquite bush". At the next camp, however, again "there was plenty of grama grass".

And so it went until the party swung off to the West about ten miles above the present town of Hatch. Cooke's notes indicate a general dominance and abundance of grass on the upland prairie and on the hills though with some cacti and other woody plants, particularly in the hills and in the river bottom. Although no further reference is made to the Guadalupe Mountains of this area, they were probably covered in part with oak, juniper and other woody species.

Early Photographs

There are few good photographs of the desert grassland that date back more than 50 years. With a few exceptions, those that do were not referenced by specific landmarks. One exceptionally valuable set of photographs taken from 1892-1896 shows each of the United States-Mexican boundary monuments from El Paso to San Diego (International Boundary Commission, 1899). As these were usually spaced at intervals of from one to three miles and are easily located, they constitute an excellent source of material for showing graphically the changes that have taken place during the last 60 years. In order to make this comparison, many of the monuments from Nogales to El Paso were rephotographed during the spring of 1956.

Although some changes in composition or condition of the vegetation are evident, these are minor for the most part. Areas that were largely brush-covered in 1896 still are today; those that

were in grass are still largely grass. There has, however, been a noticeable tendency for brushy species to become thicker and to replace in part the grasses. Mesquite has become more abundant, and, where specific individuals photographed in 1896 are still present, they cover a larger area and have become taller. Where chamise (*Atriplex canescens*) was formerly moderately abundant, it now occurs sparingly and usually shows signs of overuse. Creosote bush has increased in abundance and has invaded some areas that were formerly primarily grassland.

From Hermanas, New Mexico, east to El Paso the soil becomes increasingly sandy and subject to severe wind erosion. Soil movement at the time the monuments were first photographed, however, was much less than when rephotographed in 1956. Much of this area supports less vegetation today, and wind erosion and dune formation are much more active.

Utilization of palatable vegetation by grazing animals appears quite generally to have been heavier 60 years ago than it is today. This use undoubtedly resulted, at least in part, however, from the horses and mules used by the engineering crews constructing and photographing the monuments. Motor-driven equipment in 1892 was still a thing of the future. On the other hand, growing conditions in the Southwest had been poor and grazing pressures heavy in 1892 and 1893 when many of these early photographs were taken. A good account of conditions at that time is given by Haskett (1935): "The overstocked ranges were being depleted annually of their grasses, none being left over for the lean years. All ranges were fully utilized, none being held in reserve. In the spring of 1891 the bubble burst; droughty conditions, the first of any consequence, brought on a state of affairs that increased in intensity throughout the next two years. By June, 1892, the grass had practically all disappeared from the ranges, many of the waterholes had failed and cattle losses had been heavy . . . . The drought ended in July, 1893. Conservative estimates place the loss of cattle at fifty per cent, and some ranchmen say that it ran as high as seventy-five per cent".

Cattle numbers in Arizona in 1891 when the drought struck were probably at an all-time high. Although the tax rolls showed 720,940 animals, there were probably actually in the neighborhood of 1,500,000 head on the range (ibid.).

SUCCESSIONAL STATUS

The desert grassland has long been considered as a climatically determined climax (Clements, 1920; Campbell, 1929; Whitfield and Anderson 1938; Whitfield and Beutner, 1938; Clements and Shelford, 1939; Gardner, 1951). Shreve (1917) regarded this area as transitional between a true grassland and the shrub deserts to the west and south. He presumably would not have considered this desert-grassland transition as a climatic climax in view of a statement contained in his monograph on the Sonoran Desert (Shreve, 1951): "It is not possible to use the term 'climax' with reference to desert vegetation. Each habitat in each subdivision of a desert area has its own climax, which must be given an elastic definition and must not be interpreted as having a genetic relation to any other climax. It is merely the particular group of species which, in somewhat definite proportions and with a fairly definite communal arrangement, is able to occupy a particular location under its present environmental conditions".

Whitfield and Anderson (1938) and Whitfield and Beutner (1938) assume that short grasses are climax in the desert grassland. If these writers were using Tansley's concept of a polyclimax, this assumption would be valid insofar as grasses (though not necessarily short grasses as they stipulate) constitute a fire climax. However, inasmuch as they are employing Clement's climatic climax concept, grasses do not seem to fulfill the requirements of a true climax. They do, on the other hand, fit the requirement of a subclimax or, more specifically, of a proclimax (Clements, 1934).

Many workers regard the desert grassland, or, indeed, almost all grasslands, as subclimax to a true climatic climax of woody plants. Schmieder (1927) discusses at some length the possibility of the Argentine Pampa being a climatically induced climax. He concludes that neither climate nor soil accounts for the grassland, since trees grow not only "wherever they are planted in the Pampa" but even more abundantly in the more arid regions adjoining the grassland. He reasons that aridity can hardly be a factor in preventing tree growth in the Pampa, since it is not even in the adjacent areas of greater aridity. His statement on this is definite: "The grassland is then not a climax formation but represents a secondary invasion into the xerophytic forest".

A South African study by Staples (1930) led to an essentially similar conclusion, namely, that "Themeda triandra [a grass] is only a stage in the succession. The climatic and soil climax vegetation is undoubtedly forest . . . ." Phillips (1935) questions whether more than local areas of grassland in the Union of South Africa are a true climatic climax. West (1951) reaches a similar conclusion regarding the grasslands of Weenen County, Natal: "All of this grassland is subjected to periodical fires and must be regarded as a sub-climax caused and maintained by fire . . . . Periodic burning maintains the typical 'Undisturbed Veld' while protection induces considerable changes in composition and structure leading to the eventual suppression of the grass and its replacement by forbs and woody shrubs seral to bush and forest". West (ibid.) cites the following studies as substantiating the effect of fire in retarding development of vegetation toward a woody-plant climax: Busse (1908), Jaeger (1911), Bews (1912), Obst (1923), Galpin (1926), Henkel (1928), Bayer (1938), Phillips (1926, 1930, 1931, 1935a, 1935b) and Clements (1934).

Brown (1950) studied the effect of grazing intensity on shrub invasion of a southern Arizona desert grassland range. Although he noted a few more mesquites on heavily grazed range than where all grazing animals and rabbits were excluded, these differences were slight. Brown concluded from this analysis that grazing pressure was not a controlling factor affecting shrub invasion on ranges of this sort and that grassland was sub-climax to a shrub climax in southern Arizona.

Humphrey (1953) discussed the changes that have taken place in the North American desert grassland area in historical time and analyzed some of the underlying causes. His summary is pertinent here: "A study of historical and vegetational data points to the conclusion that the desert grassland of southwestern United States and northern Mexico is not a true climax. Rather, it is a subclimax maintained by fire. Today, with fires largely a thing of the past, the true climax of low trees, brush and cacti, with an understory of grasses and low-growing shrubs is developing extensively on areas that were once grassed".

The validity of a grassland climatic climax, not only in the Southwest but in grassland areas generally, has been questioned by a geographer (Sauer, 1950). Sauer concludes his analysis as

follows: "The more we learn of climatic data the less success is there in identifying climate with grassland . . . . I know of no basis for a climatic grassland climax, but only of a fire grass 'climax' for soils permitting deep rooting".

In conclusion, there seems to be no valid ecological basis for classifying the desert grassland as climax. My previous study (Humphrey, 1953), in which this conclusion was reached, was made without knowledge of the South African studies. These investigations substantiate my earlier decision that the desert grassland could not be classified as a climatically induced climax; it is, instead, a fire-caused subclimax.

FACTORS UNDERLYING VEGETATIONAL CHANGES

One or more of five factors have been held by most workers to be largely responsible for the principal long-time vegetational change with which we are here concerned, namely, woody plant invasion. These five factors are (*a*) grazing by domestic livestock, (*b*) competition or the lack of it, (*c*) effects of rodents, (*d*) changes in climate and (*c*) suppression of grassland fires. Each of these possibilities will be discussed in turn. Space does not permit an exhaustive analysis of the literature pertaining to each. An attempt has been made, however, to review objectively representative studies dealing with each topic. Some citations that may be considered important by various readers will, without doubt, be missing. These omissions will in some instances represent differences of opinion as to what should have been included; at other times they may be items that have been overlooked.

Grazing by Domestic Livestock

Domestic livestock grazing has long been discussed and studied as a factor affecting shrub invasion into grassland areas. Much of the earlier work in the Southwest was based largely on speculation; more recent studies have tended ever increasingly to be objective analyses. The possibility of grazing as a factor affecting rate of shrub invasion in southern Arizona was largely discounted by Griffiths (1910: "The probability is that neither protection nor heavy grazing has much to do with the increase of shrubs here, but that it is primarily the result of the prevention of fires". Thornber (1910), then botanist at the University of Arizona, also noted this

increase in mesquite but attributed it at least partly to grazing pressure: "It is a fact worthy of note that young mesquite plants are coming in quite thickly over considerable areas of the grassy portions of this tract. There is reason to believe that stock grazing on these ranges previous to their being fenced is in part responsible for this growth of mesquite, since the young plants that were formerly held in check by close grazing and occasional fires, grow undisturbed now . . . . It is well known that grazing animals have had much to do with the spread of mesquite, both in this and other countries, particularly Texas".

In a study by Glendening (1952) of mesquite increase under different grazing treatments, no correlation was observable between rate of increase and grazing treatment. Plots were fenced and subjected to three treatments from 1932 to 1949: "(1) cattle and rabbits excluded, grazed by small rodents, (2) cattle excluded, grazed by rabbits and small rodents, (3) grazed yearlong by cattle, rabbits and small rodents". During this 17-year period it might be expected that these different treatments would have given rise to differences in amount and composition of grasses within the three study areas. The only consistent change, however, was an extreme reduction in density of all grasses, regardless of treatment. This high grass mortality and the failure of new plants to become established were believed to be due in part to drought and in part to competition from already established mesquites. During the study period "mesquite more than doubled in numbers on all plots and the increase was greater, both numerically and percentagewise, on the protected than on the unfencd plots".

In the same study it was noted that both the arborescent and prickly pear types of *Opuntia* cactus, unlike mesquite, increased as a result of grazing pressure from cattle and rodents. This increase resulted both from seed germination and from propagation of joints broken off and distributed by grazing animals.

The conclusions drawn from this study are given below and appear to be highly pertinent not only for much of southern Arizona but for extensive areas from central Texas westward. "Mesquite, once seed trees are present, may rapidly increase in abundance regardless of grazing treatment. At the same time, where moderate stands of mesquites (50-80 per acre) are left to increase on grazed areas, the perennial grass cover will become less dense, less pro-

ductive, and under some conditions, may go out almost completely.

"It is improbable that moderation in livestock grazing will prevent the loss of grass within mesquite stands where the trees have gained sufficient size and density to completely utilize or materially reduce the moisture supply, and where the population of seed planting rodents is high".

Degree of utilization failed to effect any control of snakeweed (*Gutierrezia sarothrae*) in New Mexico. Campbell and Bomberger (1934), in a study of snakeweed invasion on the Jornada Experimental Range in southern New Mexico, found that, although light forage utilization resulted in a marked increase in density and number of tufts of black grama, there was no corresponding decrease in either density or number of snakeweed plants. Instead, snakeweed density increased while number of plants remained essentially unchanged. Although there was some mortality of established snakeweed plants due to drought or insects, this loss tended to be offset by the establishment of new seedlings. The authors concluded that, although drought and biotic factors affect snakeweed numbers, there is no apparent control of the weed by competition from grasses.

Although grazing is considered by many to be the principal factor responsible for the invasion of woody plants, the immediate cause is frequently explained as secondary to grazing. Bray (1901, 1904a, 1904b), for example, although recognizing the importance of grazing in furthering the spread of mesquite in Texas, attributed this spread primarily to the removal of grass by grazing and the consequent check on the spread of grass fires that formerly had kept the shrubs under control. Jardine and Forsling (1922) made an analysis of successional stages in the desert grassland of southern New Mexico; their study indicated that under long-continued overgrazing the stand of perennial grasses was replaced by forbs and half-shrubs and these, in turn, by mesquite. These conclusions were apparently based on theory, and were not supported by quantitative data.

In a later study in the same area, Campbell (1929) concurred in these observations, using as evidence "the occurrence of mesquite plants on the overgrazed and trampled areas near wells." At the same time he recognized the possibility that these plants might have resulted from seed brought in by animals concentrated around

the water, and dropped on bare trampled soil. Campbell's conclusions, like those of Jardine and Forsling, are not supported quantitatively. Areas supporting different plant communities were observed and the assumption apparently made that different successional stages were represented. The paper does not indicate that any of these communities were studied over a series of years and actual vegetational changes recorded. While, therefore, it is possible that there may be a succession in the area studied, as postulated by these authors, they have failed to provide the necessary data to substantiate the thesis.

Although Foster, Krausz and Leidigh (1917) consider reduction of fires to be the principal factor responsible for the increase and invasion of brush in Texas, they attribute the change to a minor extent to close grazing. Their conclusions, like those of most of the early workers, are qualitative and not subject to verification. They appear, however, to be based on extensive experience. With reference to mesquite, their summary statement is of interest: "The rapidity and extent of its spread are due to the abundance of its seed, the vigor of the young trees, lack of competition between the seedlings and native grasses, because of overpasturing and burning, and the fact that livestock are the primary agents in transporting the seed".

Compare this statement with one made 35 years later by Glendening (1952) for a desert grassland range in southern Arizona: "Observations made during the past four years indicate that several factors may influence the rate of increase of mesquite on grassland ranges. Important among these are: (1) abundance of seed as affected by the number of seed-bearing trees present and its dispersal by livestock, rodents and water; and (2) conditions affecting germination of seeds and survival of seedlings, including density of the competing grass cover and seedling damage by livestock, rabbits, rodents and insects". The fact that these workers, though widely separated by time, geography and methodology, reached essentially similar conclusions is significant and would appear to lend validity to their conclusions.

Bogusch (1952), also, although recognizing that cattle grazing has been a factor in the invasion of brush, holds other factors in part responsible. He points out the inter-related complexity of these factors. Fences constructed to control cattle movements are be-

lieved by Bogusch to be one of the more important causes of mesquite invasion. These fences force cattle to remain on ranges already overgrazed and thus to distribute the seeds on ground where they will have a maximum chance to grow and become established. Even when mesquite invasion does not take place immediately, this livestock restriction results in over-grazing and eventual destruction of grasses on certain areas which are thus made ready for later invasion.

Whitfield and Beutner (1938) recognize that changes in plant cover have taken place in the desert grassland. They do not, however, look further than overgrazing and drought as possible causes for this change. They assume that, because grass cover was observed to increase under protection from grazing, grazing pressure had been responsible for the invasion of shrubs and that reduction of grass cover under overuse is necessarily correlated with shrub increase.

Whitfield and Anderson (1938) attribute the change from grasses to shrubs to the removal of competing grasses by grazing, thus allowing the shrubs to compete successfully. This conclusion is not supported by quantitative data and appears to be based on unproved assumptions. The possibility of other factors, such as climate, fire and rodent activity, is apparently not considered.

Stewart (1951, 1955a) states that grazing is an important factor in the increase and spread of woody plants but assigns it a secondary role. As others have done, Stewart believes that fires were formerly the chief controlling factor and that grazing has removed much of the vegetation, making it difficult for fires to run or to become sufficiently hot to kill shrubs as they once did.

Tharp (1952) notes that shrubs, largely mesquite and *Acacia*, have invaded extensive areas in southwestern Texas. He apparently ascribes this change entirely to overgrazing and does not appear to recognize the part that other factors may have played. Referring essentially to that portion of the State south of the 29th parallel of latitude and west of the 98th parallel of longitude, he says: "Although this region is largely overrun with mesquite and species of *Acacia*, there is considerable evidence, much of it in the testimony of men still living or having died during the past quarter century, that the region was largely grassland under virgin conditions and that it became infested with 'brush' or 'chaparral' sub-

sequent to overgrazing by herds of domestic cattle. It would seem that 'brush' dominated the rougher, rocky areas from the beginning and that from these centers it rapidly covered grasslands as they became overgrazed".

Mehrhoff (1955) analyzed vegetational changes in the desert grassland of a southern Arizona range. He concluded: "Introduction of grazing animals has had an adverse effect on the grassland vegetation, not only because of the large herd numbers, but also because of the effects on soil and the reduction of litter and dry grasses which formerly carried range fires . . . . Cattle and rodents are important factors affecting the rate of shrub invasion in that they act as a medium for the dissemination of seeds and vegetative joints of some invading species".

Branscomb (1956) evaluated shrub invasion on the Jornada Experimental Range in southern New Mexico and analyzed the causes of this invasion. After correlating degree of forage utilization with rate and amount of shrub invasion he concluded that grazing pressure may have been one factor affecting shrub encroachment in that area, and that grazing pressure had contributed to the encroachment of shrubby species upon semi-arid grassland ranges in the Southwest.

There is no doubt that mesquite invasion has been aided by domestic livestock spreading the seed in their droppings. It is a matter of common knowledge in mesquite-infested areas that large numbers of mesquite seeds pass uninjured through the digestive tracts of cattle and are deposited in a medium highly suited to their germination (Smith, 1899; Griffiths, 1910). This was noted for both honey mesquite (*Prosopis juliflora* var. *glandulosa*) and velvet mesquite (*P. juliflora* var. *velutina*) with calves, mules and lambs by Fisher (1947), with sheep by Glendening and Paulsen (1950) and with cattle and horses by Reynolds and Glendening (1949). This ability of the seeds to withstand digestion has been a factor of considerable importance in spreading the species.

Although brush invasion in the desert grassland can be attributed only in part to domestic livestock, grazing has affected the vegetation in several ways. One of these is the selective effect that results from livestock preference for certain forages. This obviously gives an advantage to species, such as many of the shrubs, that are

grazed lightly or not at all, and permits them to replace those that are more palatable. This might be called the selectivity factor.

The effect of competition is closely allied to that of selectivity. As the more palatable plants are removed by continued close grazing, competition between these species and the less palatable shrubs and other weedy species is reduced. Species that were formerly kept out by competition alone are able to invade. The importance of this factor has caused some observers to over-rate it as an explanation for the spread of all kinds of brush in the Southwest. As has been pointed out, however, neither protection from grazing nor competition by grasses has been able to prevent the increase of shrubs.

In summarizing grazing by domestic livestock as a factor affecting invasion of the desert grassland by woody plants, certain facts appear valid. Domestic livestock have increased the rate of spread of mesquite and other woody species to areas that were formerly open grassland. This spread has been due in part to more effective seed dissemination in animal droppings, in part to grazing selectivity and reduced competition from grasses and in part to removal of fuel by grazing the grasses that formerly served to carry range fires. The effects of competition and fire are covered in more detail later.

Change of Climate

Climate has long been assumed to be one of the chief factors, sometimes the only one, responsible for the presence of a grassland type of vegetation. Dana (1865) was an early exponent of this idea, and proposed the theory that "the degree of moisture is the most influential of all causes that tend to determine either the presence of forests or absence of prairies". He presented no objective data to support his theory but based his conclusions on a sort of deductive reasoning.

Cox (1936) ascribed the presence of our western prairies to the recurrence of periodic protracted and severe droughts. He recognized a possible limited effect of fires and storms but did not enlarge on these factors. Using as supporting evidence the death of old oaks "more than a hundred years old, . . . more or less reliable weather records extending back fifty to one hundred years" and "the rings of growth of old trees at the edge of the prairies", together with a "study of the long time fluctuations in the water

level in land-locked lakes", Cox concluded as follows: "As an explanation of the prairies, I, therefore, suggest that the most adverse weather cycle or most severe drought occurring over a long period of time in any region determines the character of vegetation in that region".

Mehroff (1955), after analyzing tree ring chronologies, the longest available climatic records and vegetational changes, concluded that "there is no evidence to indicate that climatic change has been a major factor in effecting the change from brush to grass", and that "neither wet nor dry periods have apparently affected the rate of invasion of noxious plants".

Branscomb (1956), in his southern New Mexico study, concluded: "An analysis of climatic data covering the past 90 years in the area indicates a cyclic climatic pattern that favors the encroachment of shrubs upon grasslands in the area when other biotic factors have been adversely affecting the grass species and shrub growth has not been retarded by physiological or mechanical damage".

Bogusch (1952) discusses this same point, concluding: "It is our studied opinion that the effect of climatic oscillations and cycles has far less effect upon initiating brush invasion than it does in perpetuating it. During the early ecesic development of the seedlings, those of the woody plants require favorable moisture conditions. These seedlings are no less vulnerable to drought than are those of grasses. Once the woody plants are established, however, their roots possess phenomenal penetrating powers and can reach sources of water which are often unavailable to other plants".

Price and Gunter (1942), in a discussion of the extension of ranges of both animals and woody plants in southern Texas, ascribe these changes to two factors, overgrazing and a progressive increase in aridity. The statement is made that it is difficult to determine the degree to which each of these factors was operative in bringing about the changes noted. In general, however, the investigators feel that destruction of the former grass cover by grazing and drought laid the soil bare and provided a habitat suited to the establishment of shrubs. Taylor (1934) is cited as pointing out the importance of abnormal years in effecting changes in plant and animal life. Taylor calls attention to the fact that in desert areas the hottest, driest years are likely to exert the greatest influence.

Schulman (1956) has made the most thorough analysis of long-time climatic changes, based on tree-ring chronologies, that has been attempted to date. His conclusions, although including a more extensive area than the desert grassland, apply there also: "The entire upper basin of the Colorado . . . appears to have experienced 'unusual' weather for almost the entire past century, as has its lower basin tributary, the Gila River system. Three long surges in tree growth and the related variable, rainfall, characterize the climate since 1869: deficient beginning in 1870, excessive beginning in 1905, and deficient again beginning in 1931. These intervals were, of course, not unbroken by years of opposite character . . . . In southern Arizona the rainfall chronology parallels, on the whole, that in the main catchment areas of the Colorado River in Colorado and Utah . . . . A major difference in recent decades is the relatively more pronounced nature of the current drought . . . . It appears highly likely . . . that this is the most severe drought since the late 1200's. If this is correct we have, then, a direct climatic explanation for the high mortality which has been observed in recent years in *Carnegia gigantea* (sahuaro) and in the low-level, woodland pines *Pinus leiophylla* var. *chihuahuana* and *P. engelmanni* (*P. apacheca*)".

Schulman's analysis, which shows deficient precipitation from 1870 to 1904, excessive from 1905 to 1930 and deficient from 1931 to 1955, appears to be particularly significant when viewed in the light of vegetational changes in the desert grassland during this same period. Woody plants have increased their range and density in this area during all three of these periods (Smith, 1899; Bray, 1901, 1904a, 1904b, 1906; Cook, 1908; Wooton, 1916; Foster, 1917; Foster, Krausz and Ledigh, 1917; Shantz and Zon, 1924; Johnson, 1931; Whitfield and Anderson, 1938; Buechner, 1944; Bogusch, 1950, 1952; Gardner, 1951; Stewart, 1951; Glendening, 1952).

Periods of drought, if beneficial to shrubs, would seemingly have to benefit them by reducing competition from competing grasses or other vegetation. A drought protracted or severe enough to kill a large part of the competing vegetation would leave much of the ground bare for establishment of woody species. Subsequent precipitation sufficient to germinate seed of these plants and to permit them to become well rooted might result in an ultimate change

from a grassland type of vegetation to one dominated by shrubs or trees.

A period of better-than-average precipitation, on the other hand, could conceivably so reduce competition for moisture that shrubs might become established in a dense stand of grasses. It seems highly probable that, where seed sources were available, both of these alternatives may have occurred—either locally or periodically. There is, however, no evidence that would seem to link the consistent and widespread increase of woody species that has been taking place during the last hundred or so years in the Southwest to a change in climate.

Plant Competition

Competition for moisture or light has long been believed by many ecologists to be one of the prime factors restricting the invasion of shrubs into grassland areas. In those localities where a true grassland climax exists, competition may be important; where shrubs are the climatic climax, on the other hand, its value as a controlling factor would appear doubtful. Many writers, however, ascribed importance to competition as formerly effective in restricting or preventing shrub invasion in the desert grassland.

Wooton (1915) apparently had noticed that snakeweed could be controlled through competition from grasses. Although he recommended use of fire, "one method economically possible [is to] give the grama grass a chance and it will crowd out the snakeweed". He cites instances of where this had happened in eastern New Mexico and along railroad rights of way.

Bray (1904b) and Buechner (1944), although recognizing the cessation of fires as a prime factor in brush invasion, attributed much of this invasion to reduction of competition through breaking down of the sod under continued overstocking. Whitfield and Beutner (1938) also assume that because of heavier grazing on the grasses, shrubs have been less subjected to competition than before the introduction of large cattle numbers. As a consequence, shrubs have tended to increase at the expense of the grasses.

Parker and Martin (1952) evaluated the various factors they felt might have been responsible for the spread of mesquite. Although they were able to find "little specific information regarding the effects of different grazing systems on the rates of mesquite

reproduction", they assumed that "any system which will improve the vigor of the perennial grasses should discourage the establishment of mesquite".

Glendening and Paulsen (1955) conducted an intensive study of the factors affecting establishment of velvet mesquite in southern Arizona. Although some of the earlier workers based their conclusions on the effect of competition in other more humid regions, Glendening and Paulsen's analysis is the result of extensive observations and measurements on a desert grassland site. Their statements, therefore, appear to be particularly pertinent: "Data from this study indicate that establishment of velvet mesquite seedlings is markedly curtailed by the perennial grasses . . . . Germination, emergence and growth of mesquite seedlings to the first true leaf stage is markedly reduced by grass. Survival through the first spring drought is rare on well-grassed sites".

The studies on plant competition as a factor affecting invasion of woody plants in the desert grassland are in essential agreement that competition, aided by selective grazing, has been a factor in this change. In general, ranges with a poor grass cover are invaded by woody plants more rapidly than those with a good stand of grasses. The fact should not be overlooked, however, that during the hundreds of thousands of years during which shrubs have had an opportunity to invade, they did not. Competition might have slowed down the rate of invasion; it would hardly seem to have been able to slow it down to the point of exclusion.

Rodents and Rabbits

Rodents and rabbits as a factor affecting the increase of woody plants in the desert grassland have been speculated upon by many, investigated by relatively few. The studies that have been made do indicate, however, that these animals may exert a very appreciable influence, not only on shrubs but on grasses and forbs as well. Norris (1950) concluded that in the mesquite—snakeweed types of southern New Mexico, grazing pressure by rodents and rabbits was sufficient largely to prevent improvement of the range. Improvement, as he used the term, implied an increase in forage-producing grasses. Although there was a marked increased in forage production on ranges protected from rodent and rabbit grazing, there was no significant effect apparent on the amount of snake-

weed. Mesquite, the only other important shrub, was not measured because of an unavoidable large experimental error.

Although Norris (ibid.) noted no increase in snakeweed under rabbit and rodent grazing, he cites a study by Parker (1938) that indicated an increase in snakeweed on ranges where the grass cover had been markedly thinned by these animals. Parker is cited as stating that rodents can keep grassland in a deteriorated condition with snakeweed the principal cover. This appears logical, as snakeweed is grazed little or not at all by rabbits or rodents, while associated grasses may be largely eradicated.

Vorhies and Taylor (1933) noted that mesquite in southern Arizona constituted 36 per cent of all food consumed by the antelope jackrabbit and 56 per cent of all food of the Arizona jackrabbit. The observations of these investigators, however, did not indicate that the growth of mesquite in the area studied had been handicapped. They concluded, on the other hand, that jackrabbits had favored the growth of mesquite through the removal of competing grasses.

Vorhies and Taylor (ibid.) quote from Aldous (no reference) to the effect that rabbits on the Jornada Experimental Range in southern New Mexico may favor range restoration. This is effected by browsing of young mesquite which invades after the grasses have been killed by overgrazing. As a result of rabbit browsing, the plants develop new shoots from buds below ground level, thus forming a low-growing, bushy shrub that is effective in checking wind erosion and in permitting establishment of snakeweed and reestablishment of the original climax grasses. The validity of this assumption appears doubtful in view of the extensive root system of mesquite and its effectiveness as a competitor for moisture. Mesquite infestation tends to drive out grasses instead of favoring them. Vorhies and Taylor (ibid.) conclude that jackrabbits probably favor not only mesquite but most of the other browse species. This is effected by the damage they do grasses and other species that normally compete with the shrubs.

Hill (1928) comments on the encroachment of grassland areas in southern Arizona by woody "desert" species. He attributes this change primarily to heavy grazing by domestic livestock, "supplemented during recent years very noticeably by rodents such as the

kangaroo rat and the jackrabbit". He assumes, as Taylor and Vorhies (1933) did later, that this change was taking place as a result of lessened competition as the more palatable species were driven out. Although Hill's conclusion appears to be primarily an assumption, it was based on considerable field experience and observation.

More recent studies in southern Arizona have indicated definite positive effects of rodents in increasing woody plants, mesquite in particular. Reynolds (1950) observed that seed of large-seeded grasses, forbs and shrubs occurred in the cheek pouches of Merriam kangaroo rats (*Dipodomys merriami merriami* Mearns) much more commonly than small-seeded species. The observation is made that more seed is collected and stored during good harvest years than is needed, and seed from some of these caches presumably germinates. In this way these rodents may inadvertently plant not only grasses and forbs but shrubs also. Both mesquite and cholla cactus seeds were observed in cheek pouches rather commonly, and rodent-grazed plots ultimately showed more of these species than plots closed to rodents.

Reynolds' study was pursued further by Reynolds and Glendening (1949). This investigation showed that mesquite beans are a preferred food item of kangaroo rats and that large numbers of these beans are stored in shallow underground caches, many of which are forgotten. These seeds later germinate, thus facilitating spread of the trees. As the trees increase, the competition they provide decreases the stand of grasses and thus improves the habitat for kangaroo rats. The number of potential "seed planters" is thus increased and the rate of spread of mesquite is further augmented.

The possibility of other rodents as agents in the spread of mesquite is indicated by Arnold (1942). In a southern Arizona study, a major portion of the diet of the sand pocket mouse (*Perognathus penicillatus pricei* Allen) was found to be mesquite seeds and other parts of the plant. No record was made of the ultimate disposition of these seeds, but if they are buried as with the kangaroo rat, it is probable that not all are recovered.

An interesting theory for the recent spread of mesquite in West Texas is advanced by Horne (1941). He suggests that one factor may be the killing of millions of prairie dogs that formerly ate the

young mesquite plants. The theory does not appear tenable, since most of the mesquite spread took place prior to any extensive control of these rodents.

Studies on the effect of rodents or rabbits on cactus dissemination are rather limited. Glendening (1952), in a southern Arizona study, noted that rabbits were apparently instrumental in facilitating the spread of jumping cholla (*Opuntia fulgida*). Prickly pear (*O. engelmannii*) showed no response, while barrel cactus (*Enchinocactus wislizeni*) decreased on plots open to rabbits.

Kangaroo rats may be an effective agent in the dissemination of cactus seeds. As noted above (Reynolds, 1950), seeds of cholla cacti were found frequently in the cheek pouches of kangaroo rats, and after a period of time young cholla plants were more abundant on rodent-grazed than on rodent-protected areas.

Timmons concluded that jackrabbits "are important agents in the dissemination of viable prickly pear seed and presumably in the spread of prickly pear plants through western Kansas pastures". He observed 2.5 prickly pear seeds per pellet in a prickly pear-infested pasture. Germination of these seeds was 50 per cent greater than from seed taken from dried pods.

The prevalence of jackrabbits in the desert grassland and the observance of cacti of both the prickly pear and cholla types in much of the area indicate rather strongly that rabbits have been in part responsible for the spread of these plants. They have also undoubtedly been spread by other animals, such as coyotes, birds, deer and javelinas, that eat the fruit. Conditions that cause the increase of these seed-eating animals or that diminish other food supplies normally used by them must further the spread of woody plants with seed-bearing edible fruits.

Fire

Next to overgrazing, fire has long been considered by many to be the prime factor responsible for the invasion of woody plants in the desert grassland. Because of a paucity of data obtained from controlled experiments, much of the evidence is qualitative and subjective. Its partial lack of objectivity, on the other hand, is compensated for to a considerable extent by the large number of observations and the fact that a rather considerable body of men

representing many years experience and judgment reached many of the same conclusions.

The prevalence of fires in grassland areas prior to white settlement and in the early years of that settlement is often questioned. There is no doubt that grassland fires, caused either by man or lightning, have been a characteristic feature of this landscape for an indeterminate period (Sauer, 1950; Stewart, 1954, 1955b). The most spectacular, and probably the most frequent, fires occurred in the tall-grass prairie. As a consequence, the literature contains abundant references to fires in this area (e.g., Michaux, 1805; Shantz, 1911; Shantz and Zon, 1924; Shimek, 1911; Bowman, 1914; Sampson, 1921; Gleason, 1922; Schaffner, 1926; Catlin, 1926; Johnson, 1931; Buechner, 1944; Sauer, 1950; Stewart, 1951, 1953, 1954, 1955b; Bogusch, 1952). The majority of these fires were probably man-caused (Hanson, 1939; Stewart, 1951, 1955a).

Records of grassland fires in the Southwest date back about as far as the historical record. Cabeza de Vaca, recording his travels of 1528 in southeastern Texas, wrote (Nunez, 1905): "[The Indians] go about with a firebrand, setting fire to the plains and timber so as to drive off the mosquitoes, and also to get lizards and similar things which they eat, to come out of the soil. In the same manner they kill deer, encircling them with fires, and they do it also to deprive the animals of pasture, compelling them to go for food where the Indians want".

Phillips (1930) cites early instances of distructive fires. These include Vasco de Gama's account of such dense clouds of smoke visible from the sea at Cape of Good Hope in 1497 that he christened the cape "Terra de Fume"; and the statement that the Europeans learned burning from the Hottentots, citing Kolbe (1727) as authority for this statement: "The various Placaats . . . of Nov. 9, 1658 . . . Dec. 16, 1661 . . . [and] Feb. 19, 1687 of the Dutch East India Company at the Cape, threatened punishment to those who fired grass".

There is available a rather extensive body of literature pertaining to burning in the grasslands of the West and Southwest. Many of these accounts are simply descriptions of fires witnessed by early travellers; others attempt to relate the frequent fires and their ultimate suppression to the plant succession, particularly the rather

rapid invasion of woody species that began about the time the fires ceased. Since much of the value of these early accounts is lost by rewording, excerpts from several are quoted verbatim. An early observation is by Bracht (1848): "It is sometimes asserted a considerable part of West Texas is not available for cultivation because of a lack of timber . . . . He who knows these regions will have observed that, as soon as the needless prairie fires cease, small brush and young forests appear within a space of few years without the assistance of man".

Wells (1819), in an article on the origin of prairies, was of the opinion "that the vast prairies and barrens, extending over the greater part of the western states . . . were primitively occasioned, and have been since continued, by the *combustion of vegetables*. . . . Woodland is not commonly changed to prairie by one burning, but by several successive conflagrations; the first will kill the undergrowth, which causing a greater opening, and admitting the sun and air more freely, increases the quantity of grass the ensuing season: the conflagration consequently increases, and is now sufficiently powerful to destroy the smaller timber; and on the third year you behold an open prairie". This same idea, that fires and grassland are correlated, pervades the literature through the years to the present (Bourne, 1820; Gregg, 1844; Bracht, 1849; Gray, 1856; Froebel, 1859; Christy, 1892; Bentley, 1898; Smith, 1899; Bray, 1901, 1904a, 1904b, 1906; Cook, 1908; Griffiths, 1910; Jepson, 1910; Thornber, 1910; Bowman, 1914; Wooton, 1915, 1916; Foster, 1917; Foster, Krausz and Leidigh, 1917; Cooper, 1922; Shantz and Zon, 1924; Schmieder, 1927; Weaver and Clements, 1929; Johnson, 1931; Bayer, 1938; Buechner, 1944; Young, Anderwald and McCully, 1948; Sauer, 1950; Stewart, 1951, 1953, 1954, 1955b; West, 1951; Humphrey, 1953; many others.

Observations made by a few of the early investigators who were active in Texas, New Mexico and Arizona are particularly valuable, since these workers were active at a time when the change from grass to brush was in its early stages and, consequently, presumably before the factors effecting this change had been too long operative. One of these, a U. S. Dept. of Agriculture worker (Bray, 1901), who was particularly active in the late 1800's and

early 1900's, wrote: "Regarding the establishment of woody vegetation it is the unanimous testimony of men of long observation that most of the chaparral—and mesquite-covered country was formerly open grass prairie . . . . Apparently under the open prairie regime the equilibrium was maintained by more or less regular recurrence of prairie fires. This, of course, is by no means a new idea, but the strength of it lies in the fact that the grass vegetation was tolerant of fires and the woody vegetation was not. It was only after weakening the grass floor by heavy pasturing and ceasing to ward off the encroaching species by fire that the latter invaded the grass lands". The same theme prevades most of Bray's publications on Texas ranges. Although he attributes some of the change from grass to brush to over-grazing or other destruction of the sod by humans, he assigns the primary role to the checking or cessation of fires. Note, for example, his discussion of the Edwards Plateau of Texas (Bray, 1904a): ". . . if the Edwards Plateau were an uneroded highland, its vegetation would, under natural conditions, be open grass prairie. As a matter of fact . . . it is in process of transformation from a grass prairie to timberland. This transformation is being hastened by the interference of man. Both agriculture and grazing have operated to prevent the recurrence of prairie fires, which, so long as they were periodic, kept the field swept clean of woody vegetation. The grass throve under this burning; seedlings of trees were killed". And, in another publication of the same year (Bray, 1904b): "This struggle of the timberlands to capture the grasslands is an old warfare. For years the grass, unweakened by overgrazing of stock, and with the fire for an ally, held victorious possession. Now the timber has the advantage. It spreads like infection. From the edge of the brush each year new sprouts or seedlings are pushed out a few feet farther, or, under the protection of some isolated live oak or briar or shrub, a seedling gets its start, and presently offers shelter for others. This has been going on all along, but in former days these members of the vanguard and the scattered skirmishers were killed by the prairie fires, and the timber front was held in check or driven back into the hills".

Bowman (1914) briefly discusses the role of fire in restricting tree growth. He cites the Edwards Plateau as typifying the effects

of fire, stating that settlement of the area has stopped the periodic burning of the grasses, which were harmed by fire much less than the woody species.

Foster (1917) also attributes invasion of woody plants in the Edwards Plateau largely to control of fires, observing that before the white men settled the country it was repeatedly burned by the Indians and that these fires prevented establishment of forests. He concludes: "Almost unquestionably the spread of timbered areas received its impetus with the gradual disappearance of grassland fires and has been hastened by the reduction of the grass cover itself . . . ."

Foster, Krausz and Leidigh (1917) reiterate this conclusion, but related it to land-use practices: "The reduction of fires, brought about by fencing and the division of large areas into smaller farms and ranches, together with overpasturing have been followed by an invasion of woody growth, thickets, and wide areas of timber . . . ." These authors attribute the spread of trees in other portions of the State also to cessation of fires. Buechner (1944) concludes in a similar vein that fires set by Indians were the primary factor that originally maintained the Edwards Plateau as a treeless prairie.

Another U. S. Dept. of Agriculture research worker, active in the Southwest at about the same time, corroborated Bray's observations (Cook, 1908): "Before the prairies were grazed by cattle the luxuriant growths of grass could accumulate for several years until conditions were favorable for accidental fires to spread. With these large supplies of fuel, the fires that swept over these prairies were very besoms of destruction not only for man and animals, but for all shrubs and trees which might have ventured out among the grass, and even for any trees or forests against which the burning wind might blow. That such fires were evidently the cause of the former treeless condition of the southwestern prairies is also shown by the fact that trees are also found in all situations which afford protection against fires . . . . Nor is there any reason in the nature of the climate or the soil why trees should not thrive over the vast areas of open prairie land". And, writing of the early white settlers; "Settlers in south Texas early adopted the practice of burning over the prairies every year; partly to protect their homes against the fires, partly to give their cattle readier access to the fresh growth of grass. The fires were often set near the coast, the

strong breeze which blows in from the Gulf spreading the flames over many square miles. While the grass was still abundant these annual burnings were able to keep the woody vegetation well in check . . . ."

Griffiths (1910), also working for the Dept. of Agriculture, and writing about the same time of a southern Arizona range that was rapidly being converted from grass to brush, concluded: "The probability is that neither protection nor heavy grazing has much to do with the increase of shrubs here, but that it is primarily the direct result of the prevention of fires . . . . Previously, before the country was stocked, it probably produced more grass than it does now, and was frequently burned over, the fire extending down as far as vegetation would permit. Such burning did comparatively little injury to the grasses, but was very destructive to all small shrubs; consequently, these were able to exist only along the sandy washes, where the grasses were least productive, and upon the lower areas, where fires did not molest them . . . . The main factor, though, in the opinion of the writer has been that of fire. It is firmly believed that were it not for the influence of this factor the grassy mesas would to-day be covered with brush and trees . . . . In short, the same laws apply here that govern in our great prairie states . . . where the treeless plains were kept so by frequent fires".

Thornber, a contemporary of Griffiths and botanist at the Arizona Agricultural Experiment Station, was carrying on studies on the same area where Griffiths' observations were made. Thornber (1907) noted that burroweed, catclaw, creosote bush, Mormon tea, velvet mesquite and graythorn (*Condalia lycioides*) were all killed by range fires. Three years later, referring to the same area, he wrote (Thornber, 1910): "Twice since the small range enclosure has been under close observation, fires have burned over parts of it as a result of the continued accumulation of dead vegetation, and heavier plant growth induced by favorable seasons, viz., the winter spring of 1904-1905, and the summer seasons of 1907 and 1908. In the first instance, the fire burned for the greater part of two days . . . . Not only was the dried annual growth burned on the open range, but such shrubs and trees as creosote bush or greasewood, rayless goldenrod, Mormon tea, bush hackberry or garanbullo (*Celtis pallida*), mesquite, and palo verde were killed. That such fires burning over the mesas and foot hills have not

been uncommon in times past may be judged by the fact that in many placed abundant remains of charred stumps of at least 10 years duration are frequently met with . . . . Useless shrubs, like creosote bush or greasewood, Mormon tea, bush hackberry or garanbullo and rayless golden-rod, the latter of which has spread rapidly within recent years over much of the better class of range country, may be killed outright at a very small expense by burning over during the annual dry fore-summer . . . ."

Wooton (1915), in discussing factors affecting range management in New Mexico, observed that snakeweed was readily killed by burning, but that accompanying grasses were harmed very little. As snakeweed is one of the principal woody plants that has invaded New Mexico ranges in recent years, its sensitivity to fire appears to be of considerable importance.

Wooton also worked for a period on the same southern Arizona ranges as Griffiths and Thornber. He commented (Wooton, 1916) on the increase in cacti, both prickly pears and the arborescent or cholla-type opuntia, but observed that heavy grass tended to kill them out, "probably because of occasional fires which sweep the grassed area." He also noted that mesquites and other shrubs were slowly increasing even under protection from grazing: "The only retardation they [have] received was from the occasional fires, some of which have been severe enough to completely kill plants 10 to 12 feet high, though usually only the smaller bushes are killed back to the ground". Additional discussion in the same publication indicates that fires occurred rather frequently and were sometimes extensive and severely damaging to mesquite.

Johnson (1931), Buechner (1944) and Bogusch (1952) concur in and individually elaborate on the conclusion reached by Bray, Cook and others that cessation of fires is chiefly responsible for woody plant invasion.

Young, Anderwald and McCully (1948) recognize that fires at one time played an important part in keeping Texas ranges grassland instead of brush. They feel, however, that these fires probably weakened much of the sod and thus provided conditions suitable for shrub invasion. Although grass fires do weaken some grass plants and may completely kill others, it appears questionable that this would have much effect in facilitating invasion of shrubs. It has been generally observed that minerals released by burning have a

fertilizing effect that stimulates grass growth, thus providing additional fuel for subsequent fires. Most shrubs require several years to become established, a period of years that must be fire-free. It should be kept in mind that the rankest growing grass encountered by the pioneers was in the tall-grass prairie and that much of this was apparently burned over almost every year. Yet, even under the extreme heat thus generated year after year and in an area much of which was not far removed from abundant woody plant seed sources, the trees were unable to invade.

Humphrey (1949) reported on data collected in southern Arizona in 1935 from two areas that had been burned two years before. The study indicated that fires in June immediately preceding the summer rains were almost 100 per cent effective in killing burroweed and were moderately effective in the control of velvet mesquite. Both perennial and annual grasses were more abundant on the burned areas, even after being subjected to two years of heavier grazing by rabbits and cattle.

Grassland fires usually leave no record in the form of fire-scarred trees. Evidence of this sort is not unknown, however, and additional research might indicate a frequence greater than is commonly assumed. Humphrey (1953) examined mesquite trees bordering several dry desert washes on a grassland-mesquite range in southern Arizona. Thirty-two trees with a basal diameter of 12 inches or more were studied. Of these, only one out of 17 with a diameter 12 inches or less bore signs of charcoal. Sixty-nine per cent of those 14 inches or larger, on the other hand, showed unmistakable signs of charring from previous fires. Wooton (1916), in the last known written record of fires in the same area, wrote: "The complete protection of the reserve for a number of years has resulted in a rather heavy crop of dry grass, which burns readily, especially in the dry, hot weather of May or June, just before the summer rains begin. Several such fires have occurred, due to lightning, carelessness of passers, or incendiarism . . . . In June, 1914, occurred one of the largest and hottest fires, which burned over about four sections of the heaviest grass". Records of this sort, supplemented by fire-scarred mesquites and early photographs showing dense stands of grass with little or no mesquite, all point to the former prevalence of fires in the area.

Reynolds and Bohning (1956) experimentally burned a portion

of this same range in June, 1950. They recorded percentage kills on various species as follows: burroweed, 88; barrel cactus, 67; jumping cholla, 44; cane cholla, 42; prickly pear, 28; and velvet mesquite, 9. A valuable forage-producing shrub, guajilla (*Calliandra eriophylla*), was damaged but none of the plants was killed. Four years later this species had a greater crown density than on the unburned area.

It might seem, offand, that the kills reported in this study might not be sufficient to maintain a range essentially free of woody plants. The authors point out, however, that difficulty was experienced in obtaining a uniform burn due to inadequate fuel in the vicinity of mesquite trees. Previously, when fires occurred frequently, there were apparently no mature mesquites on this and similar areas. As a consequence, grass grew unhampered by competition from trees, and the fires must have been sufficiently hot to be much more destructive than they now are. An additional feature of importance was the relative frequence of occurrence of fires that prevented most of the woody plants growing larger than seedling or near-seedling size. These would have been more readily killed than larger, more mature plants. In addition, only occasionally would they have matured sufficiently to produce seed. This would have further reduced the potential number of new plants.

It is perhaps too much to expect that a reviewer of any controversial subject should not reach certain conclusions of his own after considering the evidence pro and con. The effect of fire on vegetation is certainly controversial and there is great difference of opinion as to its effect on the floristic composition of grassland areas, We have seen that this difference extends from one school of thought that would attribute essentially all grassland areas to the effects of fire, to the opposite view that these effects were negligible or lacking. Perhaps no conclusion could be considered incontrovertible; certainly it could not be expected to be agreed to by all. However, the combined evidence appears conclusive to the writer that grassland fires in the desert grassland, as perhaps in grassland areas the world over, have been instrumental in preventing the establishment of woody species. This control has operated in many ways, not the least of which is the difference in length of time required for grasses as contrasted with most desert grassland woody plants to mature sufficiently to produce seed. Some half-shrubs,

such as burroweed and snakeweed, that are exceptions to this, may mature in one or two years. The dominant invading shrubs, on the other hand, of which mesquite is outstanding, will normally not produce seed for several years. Fires occurring at intervals more frequent than this and killing the plants or burning them to the ground would continue to keep them suppressed. Although ground fires may leave the majority of mesquites alive, periodically recurring burns will kill the young plants and even mature trees back to the ground. Plants that are not killed tend to stump sprout, sending up several shoots where there may have been only one before. As a consequence, no single stem develops to the extent that one might expect. This delays the age at which flowering and seed setting may be expected. This phenomenon was observed by Lutz (1934) on shrubs in the New Jersey Pine Barrens.

Recurrent fires, merely by their effect in repeatedly burning back to the ground those shrubs that are not killed outright, may maintain woody species in a juvenile nonfruiting stage. This reaction may be almost as effective in control of the shrubs as killing them outright. It requires merely that a range be burned frequently enough to prevent fruiting and subsequent re-establishment of the sprouting shrubs. Perennial grasses, many of which set seed the year they germinate, recover rapidly, forming new and even mature plants in a relatively short period. A related point of importance here is the fact that when a woody plant is either top-killed or completely killed, the result of many years' growth is destroyed. Unless grass plants are completely killed, on the other hand, only a single-years growth, which has probably already died, is removed.

Grasses are morphologically better adapted than shrubs to withstand the effects of fire, since the growing points in dormant grasses are close to the ground level where they escape the severest heat. Shrubs, by contrast, have their growing tissues exposed on the ends of branches and in the cambial layer just beneath the bark. Killing the cambium, even though only at the base of the bush or tree, will result in death of the entire plant above the killed zone.

Extensive areas within the desert grassland region are still essentially brush-free. Others that support a dense stand of mesquite and other shrubs supported these same species in essentially the same density about 100 years ago. Because of soil or topographic differences, all areas within a given precipitation zone are not equally

capable of producing grass. A series of low-rainfall years also, particularly on shallow-soil areas, would not have produced enough grass to carry fires on many range areas and would have permitted growth of rather large mesquites. Fires were, in a sense, accidental or unplanned, even when set by primitive man or early white settlers. Consequently, some areas would have been burned more often than strictly necessary to suppress brush; others undoubtedly were fire-free many years, even though fuel was adequate.

Seed of adapted species must be distributed in a plant community if this community is to be replaced by another. Where conditions are favorable for such a floristic change, the rapidity with which it may be effected is to a considerable degree dependent on the number of seeds or other propagules introduced. The slowness with which many desert grassland ranges have been invaded by woody plants seems to be due in considerable part to this factor. Or, perhaps the 100 odd years during which the area has been subjected to more or less heavy grazing has been too short a period for extensive invasion to have occurred. Only during the last 30 to 50 years have these ranges been essentially fire-free. In terms of woody-plant migration and establishment, this is very little time.

DISCUSSION

Radical changes in plant community floristics are dependent on (*a*) developmental changes in endemic or nearby exotic vegetation, (*b*) introduction of new species or varieties, or (*c*) marked changes in the environment. A brief analysis should indicate which one or more of these applies to the desert grassland.

DEVELOPMENTAL CHANGES IN ENDEMIC OR EXOTIC VEGETATION. Developmental or evolutionary changes do not normally happen within the space of a few years. Even over periods of thousands of years, such changes are usually so slight as to be non-detectable or non-existent. During the approximate 100 years in which most of the desert-grassland woody plant invasion has taken place, the possibility of evolutionary modification having taken place is so remote as to merit no consideration. Such a thesis becomes even more untenable when one considers that not one but many woody species have been advancing into areas that were formerly dominated by grasses. The only conclusion possible,

therefore, is that developmental change of the plant species involved does not explain the floristic changes that have occurred.

INTRODUCTION OF NEW SPECIES OR VARIETIES. Were the invading species new introductions or in any sense exotics, the possibility would exist that the new species were better able than their predecessors to compete with the grasses and replace them. Apparently without exception, however, the woody grassland invaders are all native to the Southwest and have always been lurking around the edges, now advancing a little, now retreating, but always basically held in a kind of static state of check by some force or forces. The introduction of new species, therefore, must also be written off.

CHANGES IN THE ENVIRONMENT. By process of elimination there remains only the possibility that one or more factors of the environment have changed sufficiently to have affected the vegetation to a marked degree. The principal environmental factors that may have been modified are change of climate, grazing by domestic livestock, plant competition, rodents and rabbits, and fire. Each of these appears to have aided in the spread of shrubs. The effect of some, as for example, climate, appears slight; that of others, such as grazing and fire, is of considerable importance. Research shows that even after many years of grazing protection and subsequent development of a high perennial grass density, mesquite and other shrubs continue to invade. Evidence of this sort indicates that the absence of domestic livestock was not enough, in itself, to prevent shrub invasion. Rodents and rabbits, although facilitating shrub invasion in some instances, do not appear to have been sufficiently effective to have been a major factor in an extensive shrub invasion.

We are left, therefore, with fire as the apparent controlling factor, which, with or without the others, originally kept the shrubs from invading. It seems probable that had fires not periodically swept the desert grassland, most, or perhaps all, of the area would have supported a woody overstory long before the first white man set foot on North America.

SUMMARY

Extensive portions of the desert grassland of southern Arizona, New Mexico and southwestern Texas have been invaded by woody species. Mesquite, creosote bush, cacti of the genus *Opuntia*, bur-

roweed and snakeweed are among the principal invaders. The prime factors commonly believed to have caused this change are reviewed and evaluated. These are (1) change of climate, (2) grazing by domestic livestock, (3) plant competition, (4) rodents, (5) fire. Of these various factors, change of climate seems to have had the least effect. Fires that were formerly frequent and widespread were the chief agency restricting shrub invasion. Since fires have been controlled, the introduction of domestic livestock, plant competition and rodents have been effective agents that have favored woody plants at the expense of grasses. Had fires continued to sweep the grasslands down through the years to the present with their original frequency, the desert grassland would probably occupy about the same area today as it did prior to the white settlement of the Southwest.

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