

Structure and Function of Chihuahuan Desert Ecosystem
The Jornada Basin Long-Term Ecological Research Site
Edited by: Kris Havstad, Laura F. Huenneke, William H. Schlesinger
Chapter 10. Debra P.C. Peters, Robert P. Gibbens 2006



Submitted to Oxford University Press for publication
ISBN 13 978-0-19-511776-9

10

Plant Communities in the Jornada Basin: The Dynamic Landscape

Debra P. C. Peters and Robert P. Gibbens

Plant communities of the Jornada Basin are characteristic of the northern Chihuahuan Desert both in structure and dynamics. Although a number of plant communities can be differentiated, five major vegetation types are often distinguished that differ in plant species cover and composition, as well as other factors, such as animal populations, soil properties, and elevation. These five types are black grama (*Bouteloua eriopoda* [Torrey] Torrey) grasslands, plays grasslands, tarbush (*Flourensia cernua* DC.) shrublands, creosotebush (*Larrea tridentate* [Sess & Moc. Ex DC) shrublands, and mesquite (*Prosopis grandulosa*) shrublands. Similar to many other parts of the Chihuahuan Desert, these plant communities have experienced major shifts in vegetation composition over the past 50–150 years (York and Dick-Peddie 1969). The most dramatic changes in vegetation and associated ecosystem processes have occurred as a result of a shift in life form due to woody plant encroachment into perennial grasslands (Grover and Musick 1990; Bahre and Shelton 1993).

This encroachment of shrubs has occurred in many arid and semiarid regions of the world, including the Western United States, northern Mexico, southern Africa, South America, New Zealand, and Australia (McPherson 1997; Scholes and Archer 1997). A number of drivers have been implicated in these grass–shrub dynamics, including various combinations of livestock grazing, small animal activity, drought, changes in fire regime, and changes in climate (Humphrey 1958; Archer 1989; Allred 1996; Reynolds et al.

1997; Van Auken 2000). The causes of shrub invasion are quite variable and often poorly understood, although the consequences consistently lead to the process of desertification (Schlesinger et al. 1990). This chapter describes the characteristics of each vegetation type and the documented changes in each type at the Jornada. We then discuss the key drivers influencing these dynamics.

Vegetation Characteristics

Vegetation in the Chihuahuan Desert region has been classified as desert-grassland transition (Shreve 1917), desert savanna (Shantz and Zon 1924), desert plains grasslands (Clements 1920), desert shrub grassland (Darrow 1944), and shrub-steppe (Kuchler 1964). Desert grassland is often used as a general descriptive name for the area (McClaran 1995), although landscapes at the Jornada and throughout the northern Chihuahuan Desert often consist of a mosaic of desert grasslands, Chihuahuan Desert shrublands, and plains-mesa sand scrub (Dick-Peddie 1993). Because of this combination of vegetation types, the flora is diverse (Brown 1994). A total of 77 families, 285 genera, and 490 species have been identified from the region (Allred 2003). Predominant families include the Asteraceae (59 genera, 93 species), Poaceae (35 genera, 78 species), and Fabaceae (18 genera, 36 species). A complete species list for the Jornada Basin can be found online at <http://jornada-www.nmsu.edu>.

Five major vegetation types can be distinguished at the Jornada based on the dominant species and the associated species composition. Each vegetation type is often associated with a particular soil type and geomorphic position; ecotones between vegetation types in time and space can also be found (Wondzell et al. 1996). A variety of

winter and summer annuals are seasonally abundant in all communities (nomenclature follows Allred 2003).

Black Grama Grasslands

The dominant grass species on sandy or gravelly upland sites is black grama. Black grama dominance is highest on deep, loamy soils (Paulsen and Ares 1962). A weak calcium carbonate layer is often present below the surface. On sandier soils, dropseeds (*Sporobolus* spp.) and threeawns (*Aristida* spp.) as well as forbs are more abundant. In wet years, black grama cover can reach up to 75% of total vegetative cover, whereas in dry years, black grama can average 44% of the total (Paulsen and Ares 1962). Black grama is an important forage species year round (Wright and Streetment 1958; Paulsen and Ares 1962). This long-lived (35–40 years) C₄ grass grows in open stands of individual ramets or sets (Canfield 1939; Wright and Van Dyne 1976). Recruitment by seed occurs infrequently as a result of low and infrequent production of viable seeds, few seeds stored in the soil, and a restrictive set of microenvironmental constraints on seedling establishment (Minnick and Coffin 1999; Peters 2000, 2002b). Vegetative spread occurs through the production of stolons (Nelson 1934).

Associated species in black grama grasslands include mesa dropseed (*Sporobolus flexuosus* [Thurb. Ex Vasey] Rydb.), purple threeawn (*Aristida purpurea* Nutt.), and spike dropseed (*S. contractus* A. S. Hitchc.). These species often dominate where black grama has been eliminated. A number of perennial and annual grasses and forbs, as well as perennial shrubs, occur in these communities (Schmutz et al. 1992; Dick-Peddie 1993). Associated shrubs include soaptree yucca (*Yucca elata* Engelm.), broom

snakeweed (*Gutierrezia sarothrae* [Pursh] Britt & Rusby), ephedra (*Ephedra trifurca* Torrey), and scattered mesquite.

Playa Grasslands

Communities found in low-lying areas with heavy, clayey soils and run-in water are typically dominated by tobosa (*Pleuraphis mutica* Buckley), side oats grama (*Bouteloua curtipendula* [Michx.] Torrey), and alkali sacaton (*Sporobolus airoides* [Torrey] Torrey). Soils are often impervious to deep water infiltration with slow infiltration rates and show little change in texture or structure with depth. A cemented calcium carbonate layer is rarely present. Up to 80% of total cover in wet years and 62% in dry years can be attributed to tobosa on these sites (Paulsen and Ares 1962). Tobosa is a highly productive, drought-tolerant C₄ grass that is palatable only during the growing season (Paulsen and Ares 1962). This short-lived species (7 years) maintains its dominance through time by expanding vegetatively through the production of rhizomes (Neuenschwander et al. 1975; Wright and Van Dyne 1976; Gibbens and Beck 1987).

Burrograss (*Schleropogon brevifolius* Phil.) and ear muhly (*Muhlenbergia arenacea* [Buckl.] A.S. Hitchc.) are also found on heavy soils that may or may not receive run-in water. These species can compose up to 60% of total cover on these sites. Success of burrograss is related to its ability to begin growth under cool temperatures and to spread rapidly by stolons and seeds. Production of many seeds with high viability followed by dispersal by wind, water, and animals, as well as minimal constraints on seedling establishment, lead to the dominance by this species on heavy soils (Paulsen and Ares 1962).

Tarbush Shrublands

Communities dominated by tarbush are often found on clay loam soils with some gravel near the surface (Paulsen and Ares 1962). These sites may receive some run-in water. Tarbush is a deciduous C₃ perennial shrub with a tar-like odor as a result of secondary compounds in its leaves (Estell et al. 1998). Tarbush has an extensive root system and produces seeds that are wind or water dispersed (Mauchamp et al. 1993; Gibbens and Lenz 2001). Herbaceous species in these communities are similar to the playa grasslands, where tobosa and burrograss are the common grasses.

Creosotebush Shrublands

Communities dominated by creosotebush typically occur on bajada slopes and alluvial fans. Soils vary from well-drained sands to shallow stony soils underlain by cemented calcium carbonate at shallow or deep depths (Gardner 1951). Creosote makes up 28–45% of total cover in these communities (Paulsen and Ares 1962). Creosote is an evergreen, drought-resistant C₃ perennial shrub that can live up to 400 years in the Chihuahuan Desert (Miller and Huenneke 2000). Creosotebush produces many secondary compounds that may influence the growth and survival of other species (Knipe and Herbel 1966). Associated species in these communities include bush muhly (*Muhlenbergia porteri* Scrib.), fluff grass (*Dasyochloa pulchella* [Kunth] Steudel), and black grama, as well as a variety of forbs.

Mesquite Shrublands

Communities dominated by honey mesquite have been referred to as a “moving dune complex” (Campbell 1929). Mesquite is a deciduous, thorny, long-lived (200 years) C₃

shrub. This species is a facultative phreatophyte with very deep and laterally extensive root systems (Gibbens and Lenz 2001). Mesquite occurs on most soil types but is particularly prevalent on sandy soils. Most mesquite-dominated soils are deep sands with a calcium carbonate layer at variable depths. Short, multistemmed mesquite plants accumulate blowing sand until a mound forms around each plant. Interspaces between plants are scoured of loose soil resulting in sparse herbaceous cover. In some sites, the calcium carbonate layer is exposed at the surface, whereas coppice dunes, or nabkhas, can be > 3 m high (Langford 2000). Mesquite typically makes up 30–55% of total cover on these sites (Paulsen and Ares 1962). Associated plants in dunes include saltbush (*Atriplex canescens* [Pursh] Nutt.), broom snakeweed, dropseeds, threeawns, and a variety of forbs.

Vegetation Dynamics

In the Jornada Basin, major changes in plant communities have been documented using a series of vegetation maps and land surveys. The first study to analyze change in vegetation was the classic paper by Buffington and Herbel (1965). General Land Office Survey notes made in 1858 were used to delineate areas covered by shrubs. Collectively, mesquite, tarbush, and creosotebush occurred on 42% of the Jornada Experimental Range (JER) in 1858, and no area was free of shrubs by 1963. Early land survey notes also showed that the increase of shrubs was widespread in southern New Mexico (York and Dick-Peddie 1969).

More detailed vegetation maps have been prepared for the JER for three time periods following the early land surveys: reconnaissance surveys by the U.S. Forest

Service in 1915–16 and 1928–29 and by local Jornada researchers in 1998. The goal of the early field surveys was to determine the number of forage acres using five steps: (1) The Jornada was surveyed by section, and vegetation types were outlined on a map; (2) total plant foliar cover was estimated to the nearest 10% within each vegetation type; (3) percentage composition of species making up each of three broad categories of “weeds,” “grasses and grass-like plants,” and “shrubs” was estimated relative to the total for that area (100%); (4) the palatability rating of each species was multiplied by its percentage cover and summed for all species to obtain a forage-acre factor; and (5) cover was multiplied by the forage-acre factor to result in the number of forage acres in that area.

In 1999–2001, a hand-colored, original 1915–16 vegetation map at a scale of 1 inch = 1 mile and a 1928–29 vegetation map at a scale of 2 inches = 1 mile were digitized, and field data were entered into a database. Dominant species for each vegetation type were obtained from the field forms or determined from the percentage composition. Because the early surveys usually did not distinguish between species of threeawns or species of dropseeds, comparisons of communities over time are limited for these species.

In 1998, a vegetation map of the Jornada was again made using a field survey. Transparent overlays on large-scale (4.5 inches = 1 mile) color infrared prints from aerial photographs taken in 1996 were used as a mapping base for an intensive ground reconnaissance; vegetation was mapped to ~ 8 ha minimum area or grain. Vegetation types were defined in terms of dominant species with usually no more than four species used to characterize any given type. Digitization of polygons delineated on the overlays

permitted construction of vegetation maps based on primary and secondary dominant species (figures 10-1, 10-2), and percentage area calculations for the first four dominance classes through time (figures 10-3, 10-4). Although changes in rank may not reflect all changes in cover, the main results are not affected.

Perennial Grasses

One of the striking features of vegetation change from 1915–16 to 1998 is the large reduction in black grama–dominated grasslands (figures 10-1, 10-2). Although black grama was the first or second dominant on 28% of the Jornada in 1915–16, this species dominated only 4% of the area in 1998 for a net loss of 24% (table 10-1). Black grama occurred on 48% of the area as either a first, second, third, or fourth dominant in 1915–16 (figure 10-3a). By 1928–29, most decreases in area of black grama occurred in the second through fourth dominance classes. In 1998, very little area (< 0.06%) contained black grama as a third or fourth dominant. Many sites where black grama is still a major component of the community were treated for shrub control prior to 1990. Records from $1 \times 1 \text{ m}^2$ quadrats sampled from 1915 until the 1970s indicate that much of the decrease in black grama cover occurred after the severe drought of the 1950s (Gibbens and Beck 1988; Yao et al. 2002a).

Threeawns were much more prominent in 1915–16 than in 1998 (figures 10-1, 10-2), mainly on areas now dominated by mesquite. Those species were a first or second dominant on 23% of the area in 1915–16 and only 4% in 1998 for a net loss of 19% (table 10-1). In 1915–16, these species were mostly first, second, or fourth dominants; in

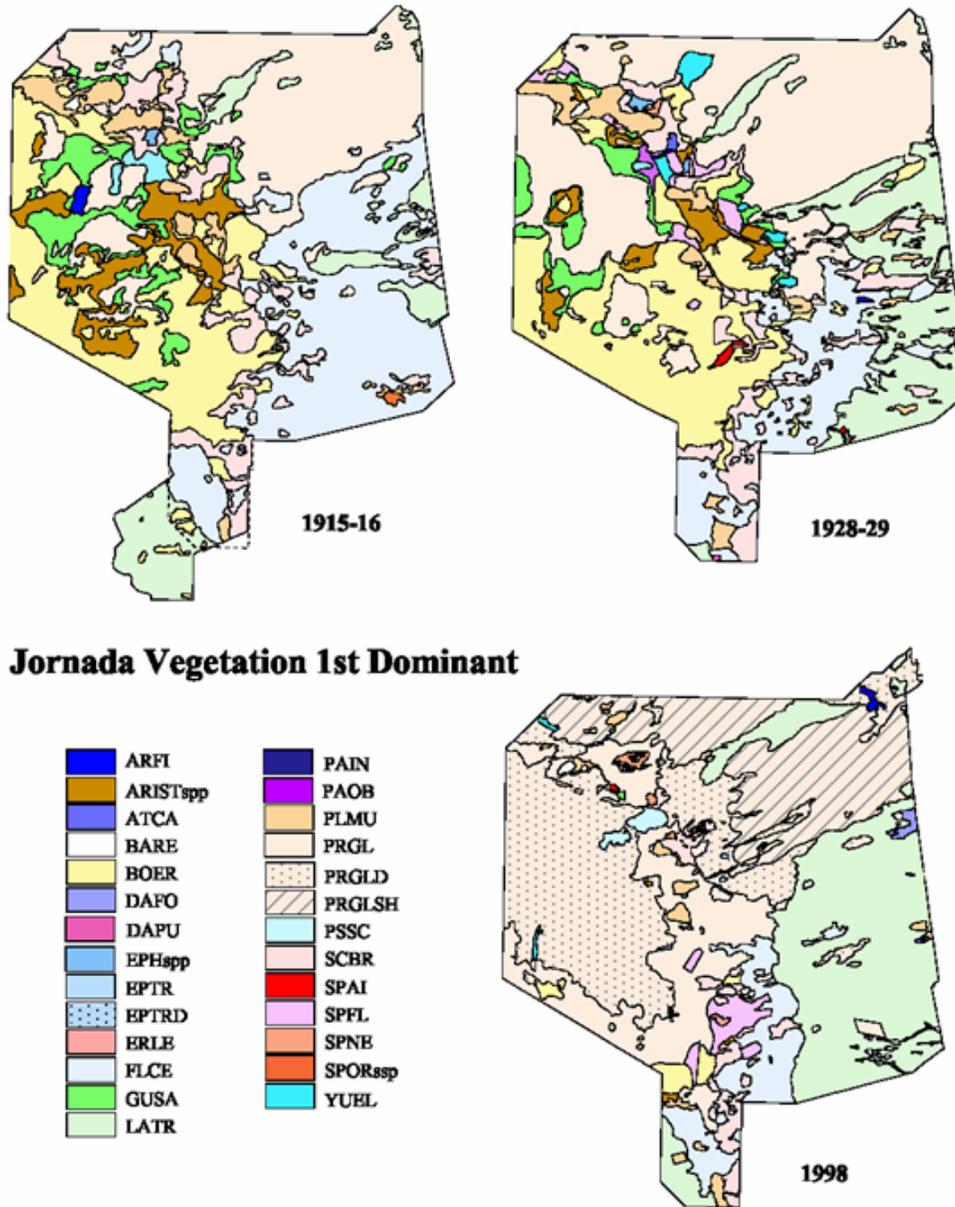
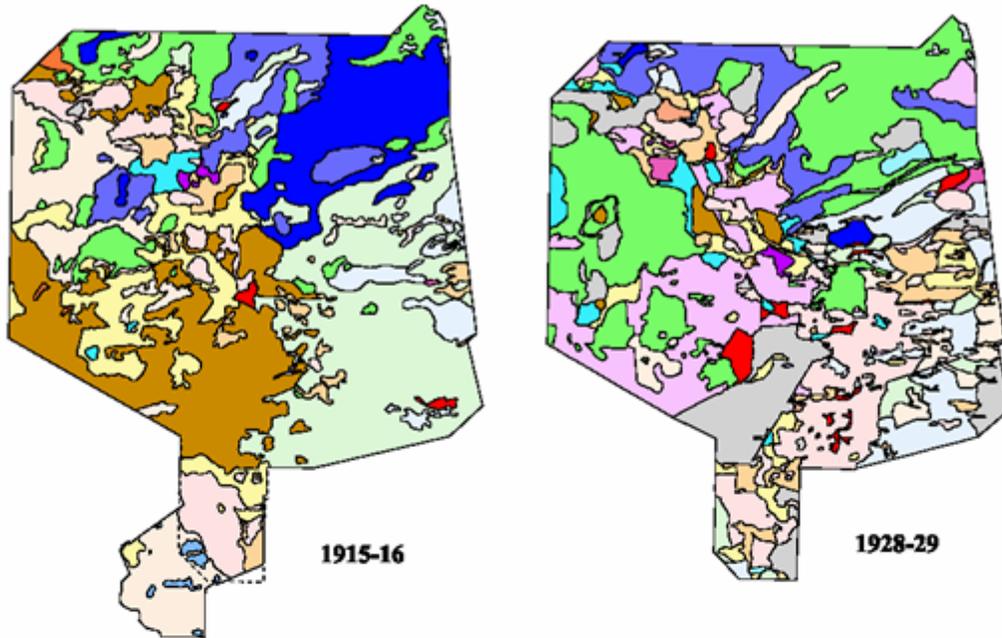


Fig. 10-1. Vegetation maps of the first dominant species derived from reconnaissance surveys of the plains portion of the Jornada Experiment Range in 1915-16, 1928-29, and 1998. Species codes defined in Table 10-1. More area was fenced in 1915-16 than at present but only the area shown by dotted lines and conforming to present boundaries was used in computing areas. The areas dominated by mesquite (*Prosopis glandulosa*) in 1998 were categorized as mesquite (soil accumulations at base of plants 20 cm or less), mesquite dunes (20 cm to about 3 m in height), or mesquite sandhills (greater than 3 m in height, sometimes 6 m or more).



Jornada Vegetation 2nd Dominant

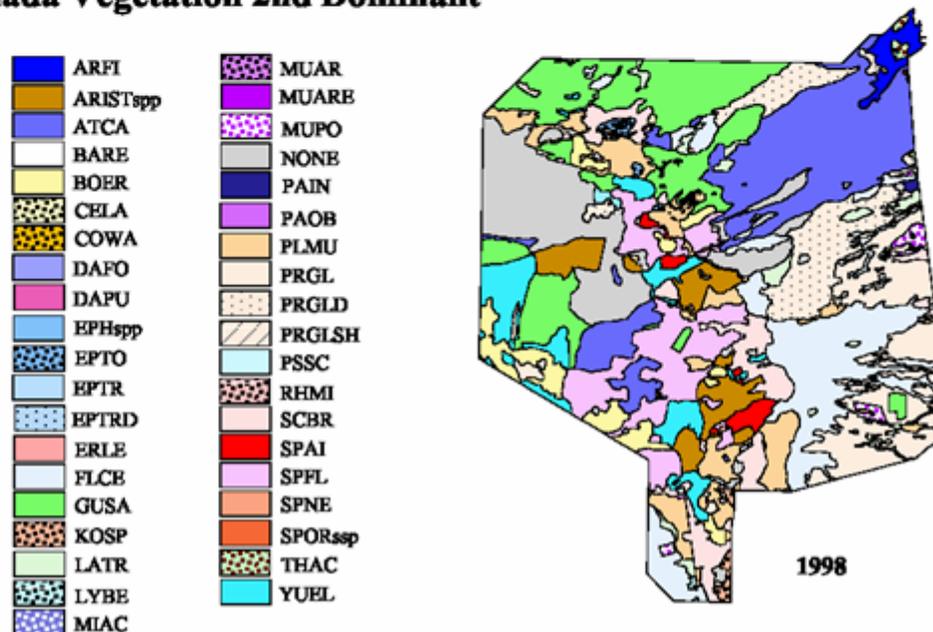


Fig. 10-2. Vegetation maps of the second dominant species derived from reconnaissance surveys of the plains portion of the Jornada Experiment Range in 1915-16, 1928-29, and 1998. Species codes defined in Table 10-1. More area was fenced in 1915-16 than at present but only the area shown by dotted lines and conforming to present boundaries was used in computing areas. The areas dominated by mesquite (*Prosopis glandulosa*) in 1998 were categorized as mesquite (soil accumulations at base of plants 20 cm or less), mesquite dunes (20 cm to about 3 m in height), or mesquite sandhills (greater than 3 m in height, sometimes 6 m or more).

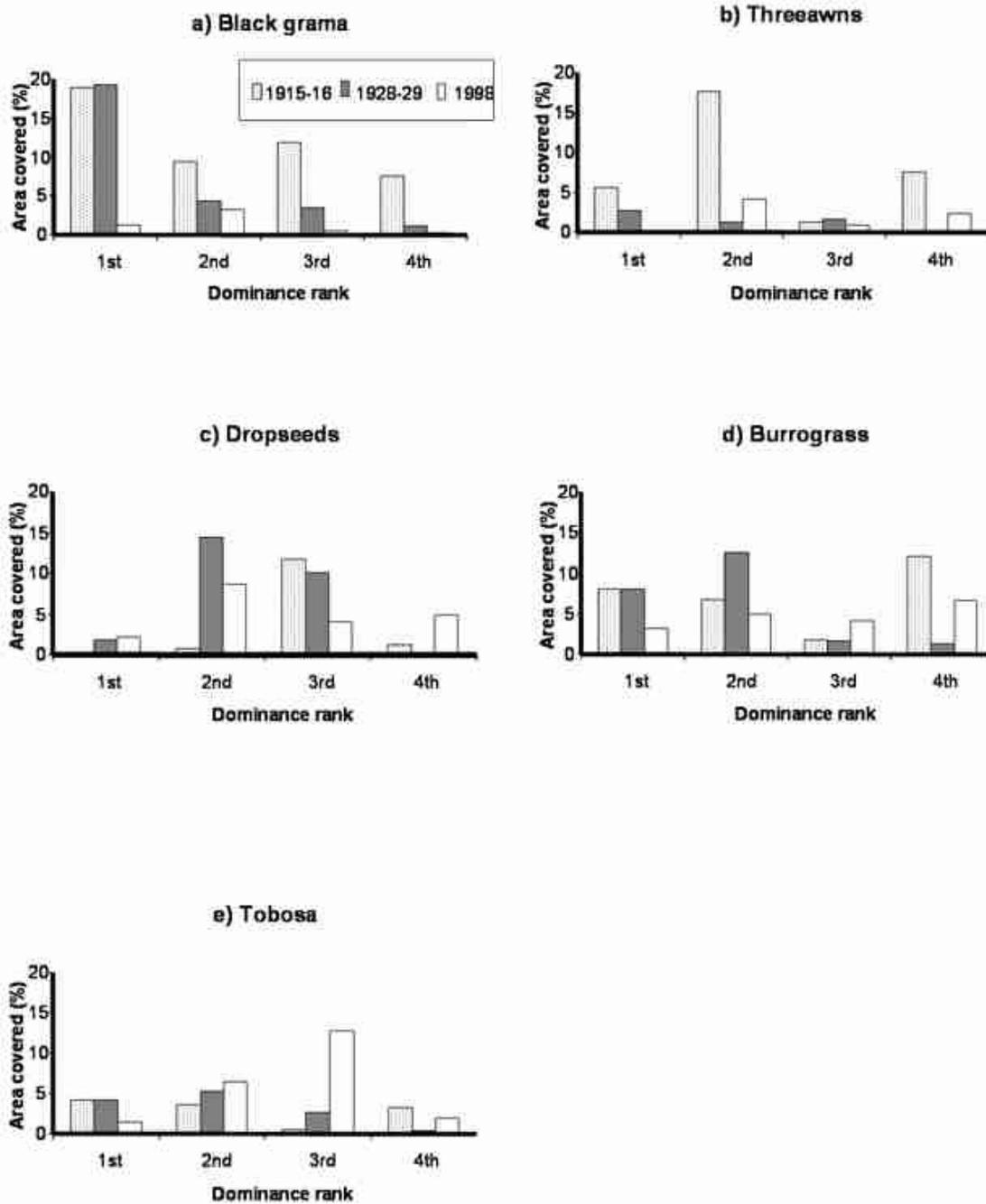


Fig. 10-3. Percentage of area covered for five grass species or genera in three sample dates for four dominance classes: (a) black grama (*Bouteloua eriopoda*), (b) threeawns, (c) dropseeds, (d) burro grass, and (e) tobosa (*Pleuraphis mutica*).

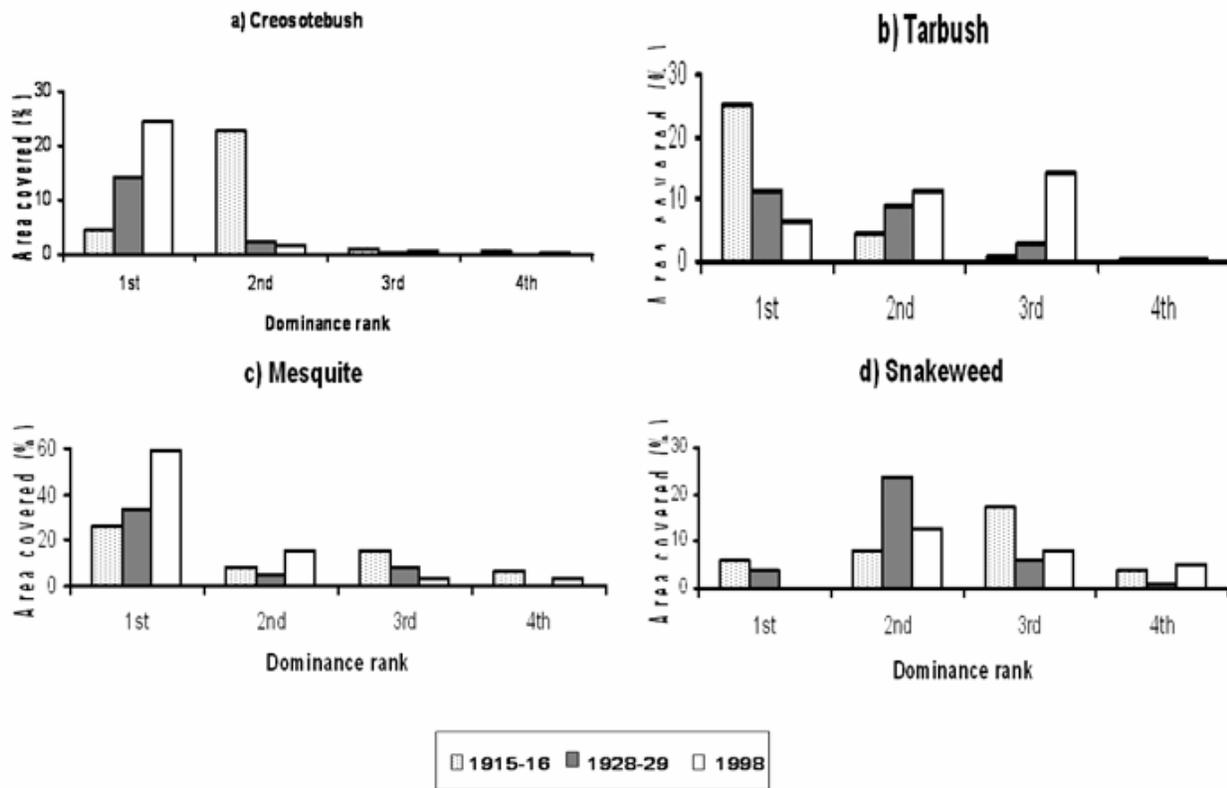


Fig. 10-4. Percentage of area covered for four shrub species in three sample dates for four dominance classes: (a) creosotebush (*Larrea tridentata*), (b) tarbush (*Flourensia cernua*), (c) mesquite (*Prosopis glandulosa*), and (d) snakeweed.

1998, threeawns were the second dominant on most of the area where they occurred (figure 10-3b). Area dominated by dropseeds increased 10% from 1915–16 to 1998 with most of the increase occurring before 1928–29 (table 10-1). These increases in cover were probably due to population fluctuations in these widespread but relatively short-lived species. These species were primarily second and third dominants during all three time periods (figure 10-3c).

Structure and Function of Chihuahuan desert Ecosystem 13
 The Jornada Basin Long-Term Ecological Research Site
 Edited by: Kris Havstad, Laura F. Huenneke, William H. Schlesinger
 Chapter 10. Debra P.C. Peters, Robert P. Gibbens 2006

Table 10-1. Percentage of area covered by each species as a first and second dominant in each of three mapping years, and change in percentage of area from 1915-16 to 1998.

	Species code	1915-16	1928-29	1998	Change in area (%)
Grasses					
Threeawns (<i>Aristida</i> spp)	ARIST spp	23	4	4	-19
Black grama (<i>Bouteloua eriopoda</i>)	BOER	28	24	4	-24
Fluffgrass (<i>Dasyochloa pulchella</i>)	DAPU		0.5		0
Lehmann lovegrass (<i>Eragrostis lehmanniana</i>)	ERLE			0.1	0.1
Sand muhly (<i>Muhlenbergia arenicola</i>)	MUAR,MUARE	0.3	0.3	0.3	0
Bush muhly (<i>Muhlenbergia porteri</i>)	MUPO			0.6	0.6
Vine mesquite (<i>Panicum obtusum</i>)	PAOB		0.3		0
Tobosa (<i>Pleuraphis mutica</i>)	PLMU	8	9	8	0
Burrograss (<i>Schleropogon brevifolius</i>)	SCBR	15	21	8	-7
Dropseeds (<i>Sporobolus</i> spp)	SPAI,SPFL,SPNE SPORssp	1	16	11	10
Dominant shrubs					
Tarbush (<i>Flourensia cernua</i>)	FLCE	30	20	18	-12
Snakeweed (<i>Gutierrezia sarothrae</i>)	GUSA	15	27	13	-2
Creosotebush (<i>Larrea tridentata</i>)	LATR	12	16	26	14
Honey mesquite (<i>Prosopis glandulosa</i>)	PRGL,PRGLD, PRGLSH	34	38	74	40
Other shrubs					
Sand sage (<i>Artemisia filifolia</i>)	ARFI	11	1	1	-10
Four-wing saltbush (<i>Atriplex canescens</i>)	ATCA	6	7	14	8
Winterfat (<i>Krascheninnikovia lanata</i>)	KRLA			0.1	0.1
Feather-plume (<i>Dalea formosa</i>)	DAFO			0.3	0.3
Mormon tea (<i>Ephedra</i> species)	EPHspp,EPTO, EPTR,EPTRD	0.3	0.3	0.4	0.1
Crucifixion thorn (<i>Koeberlinia spinosa</i>)	KOSP			0.3	0.3
Silver wolfberry (<i>Lycium berlandieri</i>)	LYBE		0.1	0	0
Mariola (<i>Parthenium incanum</i>)	PAIN			0.1	0.1
Broom dalea (<i>Psoralea scoparius</i>)	PSSC	0.7	0.6	0.8	0.1
Prickle-leaf dogweed (<i>Thymophylla acerosa</i>)	THAC			0.2	0.2
Soaptree and banana yucca (<i>Yucca</i> spp.)	YUEL	1	3	5	4

Nomenclature follows Allred (2003). Similar species are combined in the table, and denoted by multiple species codes. Areas are calculated for the current extent of the Jornada Experimental Range, and do not include the southwestern extension marked by the dashed line in the 1915-16 map.

Areas dominated by burrograss declined 7% from 1915–16 to 1998, whereas tobosa dominance did not change (table 10-1). Both species occurred frequently in most of the four dominance classes for all three time periods (figures 10-3d, e). Quadrat records indicate that these two species were less affected than black grama by the drought of the 1950s; reduction in dominance was generally due to encroaching shrubs and associated effects of aeolian deposits (Gibbens and Beck 1987). Several minor grass species showed no change in area dominated, including fluff grass, sand muhly (*Muhlenbergia arenicola* Buckl.), and vine mesquite (*Panicum obtusum* Kunth). Bush muhly and the introduced Lehmann lovegrass (*Eragrostis lehmanniana* Nees), on the other hand, have expanded.

Shrubs

Areas in which creosotebush was the first or second dominant increased 14% from 1915–16 to 1998 (table 10-1). In 1915–16, creosotebush was primarily a second dominant, whereas by 1998 this species was a primary dominant on most sites where it occurred (figure 10-4a). Much of this increase in creosotebush occurred at the expense of tarbush on the bajada slopes at the eastern side of the Jornada (figures 10-1, 10-2). Tarbush declined in area (12%) where it was the first and second dominant (table 10-1), although this species also increased on areas formerly dominated by burrograss and tobosa (figures 10-1, 10-2), and remains a second and third dominant throughout much of the area where it was a primary dominant in 1915–16 (figure 10-4b).

Of all shrubs, mesquite made the largest gain in area as a first or second dominant (40%) from 1915–16 to 1998 (table 10-1). Mesquite has been the first dominant on most

areas where it occurred for all three time periods (figure 10-4c). If areas in which mesquite was estimated to occupy a subdominant role are included, this species was a major plant community component on approximately 95% of the Jornada in 1998.

Although mesquite has been the primary object of shrub control measures and about 10,000 ha have been treated on the Jornada, this species continues to increase in density, cover, and importance (Gibbens et al. 1993). Areas occupied by mesquite include the sandhills, where this species was dominant in 1858 (Buffington and Herbel 1965) and in 1915–16 (figure 10-1). There is some correlation between size of mesquite dunes and age (Gadzia and Ludwig 1983). However, depth of material available for dune formation also plays an important role (chapter 4).

The suffrutescent broom snakeweed declined slightly (2%) in areas where it was the first and second dominant from 1915–16 to 1998 (table 10-1). However, total area where this species was a significant component of the plant community varied through time from 15% (1915–16) to 27% (1928–29) and 13% (1998). Similar to the dropseeds, broom snakeweed is relatively short-lived and populations fluctuate widely among years, often in response to winter precipitation. This species was a second or third dominant on most sites where it occurred (figure 10-4d). Of the remaining principal shrub species, only sand sage (*Artemisia filifolia* Torrey) showed a large decrease in area dominated from 1915–16 to 1998 (10%; figures 10-1 and 10-2, table 10-1). Fourwing saltbush and soaptree yucca increased in area dominated (8% and 4%, respectively). The remaining shrub species showed little or no change through time.

Drivers of Vegetation Change

At the Jornada, the widespread expansion of two shrubs (honey mesquite and creosotebush) into perennial grasslands has been particularly important. Much of this expansion has been accompanied by a decrease in cover and abundance of black grama, a key forage species that previously dominated many of the sandy loam uplands in the Chihuahuan Desert. The shrub species were formerly restricted to more localized sites in the area (Gardner 1951; Stein and Ludwig 1979). Because of the widespread expansion of these two shrub species at the expense of black grama, we focus on the key drivers influencing dynamics of these three species, although additional perennial grasses will be included when information is available. Next we summarize the major drivers involved in shrub invasion and the resulting effects on black grama and ecosystem processes. Two major aspects of vegetation dynamics are considered for each driver when possible: (1) the response of vegetation during the time that the driver was operative, and (2) the recovery of the vegetation following the cessation of the driver. The implications of these responses to shrub invasion are also considered.

Livestock

Livestock have often been implicated as important drivers in shrub invasion into desert grasslands. Livestock density in southern New Mexico increased markedly in the 1880s following the American Civil War (Fredrickson et al. 1998). At the Jornada, cattle densities have decreased over the past century (chapter 13). Although the peak in animal numbers in the late 1800s and early 1900s corresponds to a period of rapid invasion by shrubs in the region, other factors interacting with the effects of livestock likely contributed to the invasion process. A number of studies have examined the response of vegetation following livestock removal. In many cases (but not all) perennial grasses

increased following exclusion of livestock. Most studies recognized the importance of other factors, including drought, fire, and small animals, as separate or confounding constraints to grass recovery (Glendening 1952; Branscomb 1958; Humphrey 1958; Schlesinger et al. 1990; Drewa et al. 2001).

Livestock have four major effects on vegetation that differ for grasses and shrubs: (1) herbivory on aboveground biomass (for grasses: tillers, inflorescences, seeds; for shrubs: leaves, stems, seeds), (2) dispersal of seed, (3) trampling of plants and soil, and (4) redistribution of nutrients, particularly nitrogen, through urine and fecal deposition. Herbivory can occur at the seedling or adult stage with different consequences for plant survival and vegetation dynamics. The importance of seed dispersal depends on the palatability of the flowering structures and seeds and the ability of germinable seeds to pass through the digestive tract of animals. Trampling has direct effects on plant mortality, as well as indirect effects on water availability through the modification of soil properties, such as bulk density and infiltration capacity, that influence plant growth. These effects are detailed in chapter 13. Here, we focus on responses of the vegetation to livestock herbivory and dispersal of seed with implications for interactions between grasses and shrubs.

Perennial Grasses

Black grama has been the most well-studied perennial grass in terms of response to grazing by cattle. Basal area and biomass of black grama can decrease as much as 50% in three to four years when utilization is > 40% under seasonal or year-round grazing (Canfield 1939; Valentine 1970). In the absence of cattle or under light to moderate grazing (< 40% utilization), black grama is primarily influenced by precipitation (Paulsen

and Ares 1962). Overgrazing and excessive trampling have negative effects on inflorescence height, as well as the number and length of stolons (Valentine 1970; Miller and Donart 1979). Growth of black grama is further delayed when overgrazing is accompanied by drought: Regrowth of this species was negligible after 13 years of cattle exclusion (Nelson 1934; Canfield 1939). Reductions in biomass and basal area of dominant grasses can have important negative effects on annuals and perennial forbs, likely as a result of increased wind erosion and loss of soil particles (Drewa and Havstad 2001).

Shrubs

In addition to the indirect effects of grazing by cattle on grasses that reduce competition and positively influence shrub growth, grazing also has direct positive effects on shrubs. The most important positive effects of grazing are on shrub recruitment, particularly honey mesquite recruitment. Dissemination of seed by cattle has been invoked as a more important factor than the negative effects of grazing on grasses that influences mesquite invasion into black grama grasslands (Humphrey 1958; Wright 1982; Paulsen and Ares 1962). Cattle readily consume mesquite pods, and large numbers of seeds remain viable after passing through the digestive tracts of cattle (Paulsen and Ares 1962; Mooney et al. 1977). Seeds are often deposited at large distances from where they were consumed (Humphrey 1958; Paulsen and Ares 1962). A favorable microenvironment provided by cattle dung may facilitate germination, particularly if the dung is deposited in the rainy season (Paulsen and Ares 1962). Seedlings of honey mesquite readily become established; within four months following germination, seedlings develop roots to depths of 40 cm (Brown and Archer 1990). Seed germination increased seven to eight times in

Texas prairies when the heights of perennial grasses were clipped to 25 cm compared with unclipped controls (Brown and Archer 1989). Germination, establishment, and survival of honey mesquite were not affected by level of perennial grass density or moderate and heavy grazing (Brown and Archer 1999). By contrast, seedling survival through time was dependent on the presence of large patches of soil without perennial grass cover (Whitford et al. 2001).

Small Animal Activity

Native rodents and lagomorphs are important components of Chihuahuan Desert ecosystems that affect grasslands and shrublands differently with the potential to influence shrub encroachment (chapter 12). These small animals primarily affect plants through their consumption of aboveground material and, in particular, seeds and seedlings. This consumption can have major impacts on the ability of grasses to recover following shrub invasion, as well as on the ability of shrub seedlings to become established in grasslands.

Perennial Grasses

When perennial grasses are abundant, small animals appear to have minimal impact on grassland dynamics (Norris 1950; Buffington and Herbel 1965; Gosz and Gosz 1996). However, in open areas following shrub invasion, jackrabbits (*Lepus californicus*) and rodents are generally more abundant (Vorhies and Taylor 1933), and small animal activity in overgrazed areas can prevent a recovery in perennial grasses (Norris 1950). In some cases, deteriorated rangeland is dominated through time by snakeweed (Parker 1938). Burrowing activities of bannertail kangaroo rats (*Dipodomys spectabilis*) occur more frequently in black grama grasslands compared with mesquite-dominated areas.

These activities can shift species composition toward annuals instead of perennial grasses (Moroka et al. 1982). Granivory by ants may be more important than loss of seeds to rodents for various plant species in black grama grasslands (Kerley and Whitford 2000).

Grass recovery can occur rapidly following the removal of small animals. Basal area and biomass of perennial grasses increased four to five times following the exclusion of small animals for 8 years (Norris 1950). Lagomorphs were found to have differential effects on vegetation in shrub-dominated areas of the Jornada that were evident 50 years after their exclusion. Compared with controls, spike dropseed increased 30 times in plots where rabbits were excluded (Gibbens et al. 1993). Dropseeds are preferred forage for jackrabbits—up to 40% of their diet (Dabo et al. 1982). Fluff grass was more abundant in plots with rabbits, compared to controls, and may be more affected by water availability than grazing pressure (Gibbens et al. 1993). Positive effects of lagomorph exclusion on black grama were expected because this species can comprise up to 54% of the diet of jackrabbits in summer months (Fatehi 1986; Fatehi et al. 1988) and black grama seedlings are readily consumed in shrub-dominated areas (Bestelmeyer and Peters unpublished data). Black grama did not show a response until 51 years of lagomorph exclusion in areas where shrubs had been removed (Havstad et al. 1999). This delayed response is likely due to a limited seed source for recovery because very few black grama plants occurred on plots at the beginning of the study and a stand of black grama is not located near the study site (Havstad et al. 2003).

Shrubs

Small animals can have both negative and positive effects on shrubs, with most impacts occurring at the seed and seedling stage. The diet of jackrabbits is comprised of honey

mesquite, creosotebush, and broom snakeweed stems that are used as sources of food and water (Dabo et al. 1982; Steinberger and Whitford 1983b; Fatehi 1986; Fatehi et al. 1988). High seedling mortality of creosotebush due to jackrabbits and rodents has been observed in several studies (Boyd and Brum 1983; Whitford et al. 2001). Canopy cover of honey mesquite and creosotebush were significantly higher on lagomorph exclusion plots within 10 years after the start of the treatments and persisted for > 40 years (Gibbens et al. 1993; Havstad et al. 1999). Evidence also exists for the positive effects of small animals in promoting shrub invasion. Rodents can aid in the dispersal of honey mesquite seeds into grassland areas in southern Arizona (Reynolds and Glendening 1949^a) and presumably in the Chihuahuan Desert as well. Merriam kangaroo rats (*Dipodomys merriami*) collect seeds and store them in shallow caches; many of these seeds are not consumed and can germinate to contribute to mesquite expansion (Paulsen and Ares 1962). Burrowing activities of kangaroo rats can also have positive effects on the growth, flowering, and survival of creosotebush (Chew and Whitford 1992).

Drought

Periodic drought is a key characteristic of arid regions. Severe drought (Palmer drought index between -3 and -4) of 2-4 years' duration occurs on average every 20-25 years, whereas extreme drought (palmer index < -4) occurs every 50-60 years (Scurlock 1998^b). At the Jornada Basin site, extreme drought occurred in the early 1900s and again in the 1950s when 7 years out of 11 over the > 80-year record were classified as either severe or extreme drought based on annual precipitation. The drought in the 1950s was

^a Reynolds and Glendening 1949 not found in the Refs list. Please add it; or else change this citation. Added

^b Change in date ok? No Scurlock 1995 in the Refs list. 1998 is correct

the most severe recorded over a 350-year period for the Southwestern United States

(Fredrickson et al. 1998), although tree-ring reconstruction shows that similar droughts occurred prior to the seventeenth century (Woodhouse and Overpeck 1998). Studies conducted through time since the early 1900s have documented both small- and large-scale shifts in dominance from perennial grasses to shrubs with much of the change corresponding with the 1950s drought (Hennessy et al. 1983a; Gibbens and Beck 1987). These observations clearly show that drought is a contributing factor in shrub invasion (Herbel et al. 1972). Shifts in dominance from perennial grasses to shrubs occur due to differences in life history traits of species that determine their ability to tolerate drought and to recover following drought. Long-term data are critical in examining the effects of infrequent catastrophic events, such as drought, on ecosystem properties and dynamics (Conley et al. 1992).

Perennial Grasses

In general, basal area of black grama and other perennial grasses decrease during drought with black grama recovering more slowly than other grasses. The susceptibility of black grama to summer drought was noted early in the 1900s (Jardine and Forsling 1922; Nelson 1934). Similar responses were observed during the drought of 1934 when no new growth was reported for black grama and basal cover of this species decreased 77% between 1933 and 1935 (Campbell 1936; Canfield 1939). Most of our information comes from plant responses during and after the drought of the 1950s that are examined in the context of long-term responses beginning in 1915 and postdrought responses continuing to the present. During the drought from 1951 to 1956, growing season precipitation (July 1–October 1) decreased 43–47% from the long-term average; the broad-scale pattern in

vegetation was a reduction in basal cover of black grama by 72–90% from predrought levels (Herbel et al. 1972). The largest reduction in black grama cover occurred on deep sandy soils, and the least reduction occurred on sandy soils with a shallow indurated caliche layer. Grazing intensity was found to have little effect on black grama basal area during extended drought, although recovery was faster for conservatively grazed plots compared with heavy grazing or protected plots (Paulsen and Ares 1962).

Detailed analyses of species responses during the drought of the 1950s have been conducted using a series of 1-m² permanent quadrats located throughout the Jornada starting in 1915. The quadrats were charted annually until 1947 and sporadically since that time. A total of 104 quadrats were located in black grama (57 quadrats), tobosa (22 quadrats), burrograss (12 quadrats), threeawn (6 quadrats), and communities dominated by other species (7 quadrats). Prior to 1950 black grama went extinct on 11 quadrats that were previously dominated by this species (Gibbens and Beck 1988). The most dramatic change in vegetation occurred during 1950–61 when black grama disappeared from an additional 37 quadrats. Recovery of black grama following drought is indicated because this species was present in 9 quadrats in 1979 and in 12 quadrats in 1995 (Yao et al. 2002a). The ability of black grama to persist on 16% of the quadrats and to recover on 5% is likely due to a number of factors. Recent analyses show that black grama persistence on these quadrats is positively related to the distance from the nearest shrub community in 1915 (Yao et al. 2002b). Other characteristics of each plot, including soil texture, annual precipitation, depth to caliche, and elevation, were less important than distance to shrubland. Management practices (e.g., herbicide treatment, grazing history, and distance to water sources) and small-scale redistribution of water that were not

included in these analyses are also expected to be important to black grama persistence.

Temporal variation in black grama basal area was found to be related to long-term precipitation (2–15 years following sampling) for quadrats with and without persistent black grama, although additional factors were more important than precipitation for quadrats where black grama went extinct (Yao et al. 2002a). By contrast, annual growth of black grama was related to short-term precipitation (< 15 months following sampling) for both types of quadrats.

The slow recovery of black grama following drought is supported by a clipping study conducted on the Chihuahuan Desert Rangeland Research Center (CDRRC; Lohmiller 1963). Postdrought measurements made in 1962 showed that yield of black grama had not recovered to predrought levels even though five of the six postdrought years had above-average precipitation. Recent simulation model analyses indicate that the slow recovery of black grama to drought in the 1950s and 1970s was consistent with an inability of seedlings to become established (Peters and Herrick 2001). Other perennial grasses and forbs responded more rapidly and dominated simulated plots until black grama became established and grew to dominate the plots.

Other important grass species were also negatively affected by drought in the 1950s, although generally their recovery was faster than that of black grama. On average, tobosa basal cover was lower in the 1950s compared with the 1930s, 1940s, and 1970s (Gibbens and Beck 1988). However, very few quadrats (< 10) were sampled in any given year. High basal cover of tobosa starting in 1965 indicates rapid recovery. Tobosa grasslands are typically located in low-lying areas with heavy soils that receive some run-in of water from overland flow (Herbel and Gile 1973) that may explain the fast recovery.

Tobosa has also been reported to be more drought-tolerant than black grama, possibly due to its ability to become dormant under low soil-moisture conditions (Herbel et al. 1972). Burrograss in run-in locations showed similar responses to tobosa, both during the 1950s drought and in the following years as basal area recovered to predrought levels in 1960 (Gibbens and Beck 1988). Although only six quadrats were established in threeawn communities, all of them responded similarly to drought in that no threeawn occurred in these quadrats after 1952. Currently, all of these quadrats have converted to mesquite coppice dunes (Gibbens and Beck 1988). In a related study, threeawns as well as dropseeds were more susceptible to drought compared with black grama; the threeawns were eliminated by the drought, whereas the dropseeds made a partial recovery through seedlings (Herbel et al. 1972).

Shrubs

In general, shrubs are less severely impacted by summer drought compared with grasses. Most information is available from short-term experiments, observations on small plots, and aerial photography analyzed over time to indicate rates of invasion. However, long-term studies have not been conducted at a sufficiently large scale. Based on rainfall exclusion studies, both creosotebush and mesquite were found to be well adapted to withstand season-long droughts, in part because of their ability to use near-surface soil water during the summer (Reynolds et al. 1999b). In addition, creosotebush plants were able to shift growth and physiological activity to use temporally available moisture, carry out limited physiological activity during drought, and compensate for drought through enhanced growth in the season following drought. For mesquite, compensation occurred through increased water uptake associated with enhanced physiological activity in the

season following drought. Both species have well-developed lateral and taproot systems that also may be important for survival under conditions of low precipitation (Gibbens and Lenz 2001).

Observations through time suggest that shrubs now dominating former black grama sites became established during or following the 1950s drought. An analysis of changes in dominant species showed that creosotebush, mesquite, and tarbush became dominants on former black grama sites by 1981 (Gibbens and Beck 1987). Although it is not always possible to determine when the shrubs became established, these species were clearly dominant by 1981. In some cases establishment date can be determined. Mesquite plants appeared on quadrats in 1916 and 1924 and persisted until 1981. One tarbush plant appeared on a quadrat in 1956 and persisted until at least 1981.

Several studies have shown the ability of mesquite to survive and even increase in cover and abundance during the 1950s drought. A black grama community that was hand-grubbed in 1939 to remove all mesquite plants had increasing numbers of mesquite, from 285 plants/ha in 1948 to 377 plants/ha in 1955 and 400 plants/ha in 1959 (Wright 1982). Size of mesquite plants also increased during the drought as evidenced by an increase in canopy cover from 0.6% to 2.3% from 1948 to 1959. An ecotone between mesquite coppice duneland and black grama grassland was studied using transects established in 1940 (Wright 1982). The mesquite dune type originally covered 25% of the first transect and 50% of the second transect. For both transects, density of mesquite increased from 1940 to 1948; density decreased but cover increased from 1953 to 1959. The decrease in density may have been due to the loss of small shrubs during the drought. Increases in mesquite cover occurred throughout both transects, whereas increases in

numbers occurred primarily in the transition zone and grassland areas. Differences were also observed in the rate of encroachment along the two transects that were likely due to their different orientations with respect to the prevailing winds, as well as different soil textures. More recently, satellite images have been used to document short-term drought effects with grasslands being the most spectrally responsive to variation in precipitation compared with shrub-dominated areas (Peters et al. 1993).

Fire

Little is known about the role of fire in the Chihuahuan Desert, either in the United States or Mexico (Humphrey 1974; Drewa et al. 2001). Most information on fire in desert grasslands of the United States is from the Sonoran Desert in southeastern Arizona (Humphrey 1958; Wright 1980). In Chihuahuan Desert grasslands, natural fires most likely occurred in June, when the frequency of lightning strikes is high (Gosz et al. 1995), the vegetation is dry, and weather conditions exist to promote the spread of fire (low humidity, high temperatures, and high winds). A characteristic fire return interval is unknown, but a 9–10-year period has been estimated for desert grasslands in southeastern Arizona (Cable 1967; McPherson 1995).

Some have questioned if biomass and fuel load were sufficient prior to European settlement to carry extensive fire in the Chihuahuan Desert (Buffington and Herbel 1965; Dick-Peddie 1993). Prior to a period of intense livestock grazing and subsequent encroachment of shrubs during the late nineteenth century, fuel loads were likely higher than at present. Additionally, despite reduced fuel loads, natural fires are still observed every two to three years in ungrazed, black grama–dominated grasslands in central New Mexico at the Sevilleta LTER, and an extensive natural fire was observed in the early

20th Century on the Jornada . Thus, though fires continue to occur naturally in

Chihuahuan Desert grasslands, it is likely that the size, frequency, and intensity of these fires have decreased over the past 150 years (Bahre 1995).

Perennial Grasses (Black Grama)

In general, effects of fire on perennial grasses are highly variable; grass response may be influenced by soil moisture conditions at the time of the fire, the amount of rainfall received during the growing season immediately following the fire, or the grazing intensity by cattle (Gosz and Gosz 1996). Most research conducted on black grama indicates high mortality following fire under drought conditions that persist into the immediate postfire environment. For example, only 10% of black grama ramets survived a fire under excessively dry conditions in the Sonoran Desert (Cable 1965). At the Jornada, cover of black grama decreased 13% in burned plots and increased 4% in unburned areas four years following a fire that occurred during a summer-long drought in 1995 (Drewa and Havstad 2001). Other recent studies suggest that black grama can recover rapidly from even year-round cattle grazing (utilization < 40%) if growing season precipitation is at least equivalent to the long-term average immediately following a fire (Drewa et al. 2001).

At the Jornada, a June fire conducted in 1999 in a community codominated by black grama and honey mesquite resulted in low mortality of the former species (Drewa and Havstad 2001). Two years following fire, basal cover of black grama was 56% of unburned cover in grazed areas and 64% of unburned cover in ungrazed areas. Grass mortality was a function of the size of individual plants prior to fire. Small plants (basal area < 10 cm²) had a higher probability of fire-induced mortality than larger plants (> 30

cm²). These rapid responses are likely a result of above-average precipitation during the growing season immediately following the fire. Similarly, at the Sevilleta LTER site, a lightning-ignited fire in 1998 resulted in low mortality of black grama (Peters unpublished data). Precipitation was above average in summer 1998. Thus, black grama recovery is not only highly variable 4–8 years to > 50 years (Wright 1980; McPherson 1995; Gosz and Gosz 1996) but may depend more on soil moisture availability during the season of the fire than on grazing intensity when properly managed.

Shrubs

Prior to European settlement, natural fire may have been effective in deterring honey mesquite invasion by top-killing or completely killing plants. The degree of kill depends in part on shrub size, fire season, and intensity of burn. After one year following prescribed fires in June 1999, canopy area of honey mesquite decreased by 22% but increased 24% in unburned areas (Drewa et al. 2001). In the same study, shrub volume decreased 40% following fires and increased 30% after just one year in fire-excluded areas. In addition, only 3 small shrubs (< 65 cm height; ~ 10 years old) of the 210 shrubs were killed completely.

Fire season and intensity were also found to influence the ability of honey mesquite to recover following fire (Drewa et al. 2001). Shrubs were 8% taller and resprouted 16% more after dormant season than growing-season fires. For shrubs clipped to simulate fire, resprouting was 35% greater than that after actual low-intensity fires (fueled by natural vegetation) and 60% greater than that after actual high-intensity fires (artificial fuel additions). In natural settings growing season fires may be more effective than those during the dormant season in reducing the stature of honey mesquite.

Fire may also be effective in limiting the recruitment of mesquite plants into grasslands. Fire can completely kill seeds and seedlings of mesquite (Cox et al. 1993; Brown and Archer 1999). Although complete kill of larger plants is rare, top kill of older life history stages delays reproductive maturity and setting of seed (Drewa et al. 2001). Less information is known about fire effects on other species of shrubs, including creosotebush or tarbush. Fire may be important in limiting recruitment of these species into grasslands, but the probability of adult mortality may be lower compared with mesquite, which is a more aggressive resprouter.

Climate Change

Broad-scale patterns in climate are largely responsible for large-scale patterns in vegetation. The presence of C₄-dominated grasslands in southern New Mexico is a result of high temperatures during the growing season combined with low and variable amounts of precipitation, as well as periodic drought (Schmutz et al. 1992). The region has experienced major changes in climate over geological time that have resulted in several major shifts between grasslands and shrublands over the past 10,000 years (VanDevender and Spaulding 1979; Monger et al. 1998). Historic climate has also been proposed as an explanation for the low ability of black grama to become established under current climatic conditions (Neilson 1986). The current shift from grass- to shrub-dominated ecosystems has likely occurred at a faster rate (50–100 years) compared with geologic changes over hundreds or thousands of years, and the influence of human activities has been particularly important in these rapid rates of change. However, shifts between grasslands and shrublands over geologic time suggest that the current shrub invasion

episode may be reversed if climatic conditions once again become more favorable for the recruitment and growth of grasses.

Elevated concentrations of atmospheric CO₂ are another driver proposed to influence shrub invasion dynamics (Mayeux et al. 1991; Johnson et al. 1993; Polley et al. 1996). Woody plants typically possess the C₃ photosynthetic pathway that may confer an advantage under elevated CO₂ compared with C₄ grasses. Also, widespread encroachment of woody species into grasslands began shortly after atmospheric CO₂ concentration rose above its preindustrial level of 270–280 ppm. Thus the global nature of the increase in CO₂, the multiple benefits of higher CO₂ to C₃ plants, and the near synchrony of the increase in CO₂ and shift in vegetation from C₄ grasses to C₃ woody plants have led some researchers to propose that the historic increase in CO₂ is a major factor contributing to woody plant encroachment (Polley et al. 1992). However, others have questioned the validity of this explanation. Elevated CO₂ may have contributed to the general increase in woody plants globally, but local factors are more likely to be important to the rate, pattern, and extent of invasion at a particular site (Archer et al. 1995). Interactions among elevated CO₂ and other drivers are also likely to be important (Polley et al. 1996).

Directional changes in climate as a result of elevated concentrations of atmospheric CO₂ may have long-term effects on grass–shrub interactions with implications for invasion dynamics. Simulation models have been used to predict long-term responses of grasses and shrubs to directional changes in climate. Effects of climate on the probability of establishment of black grama were investigated along a climatic gradient in the southwestern United States using a daily time step soil water model,

SOILWAT (Minnick and Coffin 1999). Sites were simulated using historical weather data and predicted weather from global climate models for sites spanning southern Colorado to southern New Mexico. Simulated black grama establishment decreased from north to south as historic annual precipitation decreased and temperature increased. Low simulated seedling establishment of black grama at the Jornada is similar to field results for this species (Neilson 1986). A directional increase in year-round temperature and increase in summer precipitation resulted in an increase in establishment of black grama at all sites. The large range in establishment probability along this gradient suggests that seedling establishment may not limit recovery of this species throughout its geographic distribution. Other recruitment processes, such as production of viable seeds and presence of germinable seeds in the soil, may become more important as temperatures decrease and precipitation increases (Peters 2002b). At the Sevilleta LTER, ~ 250 km north of the Jornada, seed production of black grama occurs more frequently (viability > 50%) than at the Jornada (Peters 2002b). Two periods of precipitation are predicted to be critical for black grama recruitment: Precipitation in June is important for seed germination followed by precipitation in July and August that is needed for seedling establishment (Peters 2000).

More recently, a simulation model (ECOTONE) was used to investigate the importance of multiple processes for shifts in species dominance and composition with changes in climate (Peters 2002a). Model results for a site at the northern boundary of the Chihuahuan Desert (Sevilleta LTER) show that black grama and creosotebush ecotones are stable under current climatic conditions without cattle grazing, small rodent activity, fire, or severe drought. However, a change in climate to an increase in summer

precipitation and year-round increase in temperature resulted in a shift to black grama dominance. This shift in dominance was due to an increase in establishment of black grama seedlings followed by more favorable conditions for the growth of this species compared with the growth of creosotebush. These shifts in vegetation are not predicted to occur uniformly across the landscape (Peters and Herrick 1999b). Recovery of black grama is not expected on degraded sites currently dominated by creosotebush where the establishment of black grama has a very low probability of occurring. By contrast, sites that are currently codominated by black grama and creosotebush on soils with a moderate ability to hold water for plants are predicted to shift to black grama dominance. Seed availability is also predicted to influence the ability of black grama to recover on sites where it currently does not occur (Peters and Herrick 1999a; Rastetter et al. 2003).

Conclusions

Shrub invasion consists of a complex suite of processes and drivers that have occurred, in most cases, in combination for many sites worldwide. Within the Jornada Basin, a number of short- and long-term experiments combined with monitoring and simulation models provide one of the best opportunities to investigate shrub invasion processes through time and space. Our studies show that a suite of processes were important in transforming the JER from desert grassland to shrubland over the past 50–100 years. Large numbers of cattle consuming perennial grasses and dispersing mesquite seeds combined with severe drought in the early 1900s and again in the 1950s, along with an increase in small animal herbivory on grasses and a reduction in fire control of shrubs, apparently led to the landscapes that we see today. Elevated concentrations of atmospheric CO₂ may have conferred a growth advantage to shrubs; however, it is

unlikely that this factor alone generated the shift from grasses to shrubs. Predicted directional changes in climate that increase summer precipitation and temperature may promote shifts in vegetation from grass–shrub savannas to grass dominance on certain sites in the future. In addition, changes in the size, timing, and intensity of rainfall events during the growing season may also shift the vegetation with grasses being favored by small, frequent rainfall and shrubs being favored by large rain events with deeper infiltration.