

FIRE, GRAZING, AND HONEY MESQUITE INVASION IN BLACK GRAMA-DOMINATED GRASSLANDS OF THE CHIHUAHUAN DESERT: A SYNTHESIS

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ABSTRACT

Prior to European settlement, the Chihuahuan Desert comprised, in part, grasslands dominated by the perennial grass, black grama (*Bouteloua eriopoda*), as well as by other herbaceous species. Honey mesquite (*Prosopis glandulosa*) was mostly abundant in adjacent lower-lying areas of water runoff and intermittent streambeds. Since the late 19th century, however, cattle have been directly responsible for increased abundances and expanded distributions of honey mesquite through consumption and dissemination of seed. Additionally, a period of overgrazing and interactive effects with other factors such as drought and small mammal herbivory, resulted in reduced abundances of black grama. As a result of decreased fuel abundance, lightning-initiated fires that likely occurred just prior to and throughout the growing season, have decreased in size, intensity, and frequency. Despite reductions in herbaceous fuels following European settlement, we hypothesize that fire remains effective in topkilling shrubs of honey mesquite and in so doing, may directly interfere with its development toward reproductive maturity and its ability to set seed. Based on information from the literature and results from our research, complete kill of honey mesquite is rare, though fire is effective in topkilling and returning shrubs to an immature life history stage. Fire remains an effective deterrent in slowing honey mesquite invasion. However, the recurrence of fire is highly contingent on the degree and rate of black grama recovery that may be determined by the timing and amount of precipitation immediately following fires as well as the degree of livestock grazing.

keywords: black grama, *Bouteloua eriopoda*, cattle, Chihuahuan Desert, fire, grasslands, grazing, honey mesquite, livestock, *Prosopis glandulosa*, shrubs.

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INTRODUCTION

Distributions and abundances of tree and shrub species in the Chihuahuan Desert have increased appreciably since the late 19th century (Glendening 1952, Humphrey 1958, York and Dick-Peddie 1969, Gibbens et al. 1986, 1993). In particular, honey mesquite was restricted mostly to low-lying drainage areas with sandy soils prior to European settlement (Humphrey 1958). However, its invasion or encroachment into black grama-dominated grasslands, located on nearby level uplands, coincided with the advent of intense livestock grazing during the late 1800s (Branscomb 1956). At the same time, natural fire regimes were altered in Chihuahuan desert grasslands because the size, frequency, and intensity of fires were reduced (Humphrey 1974, McPherson 1995). Overgrazing by livestock decreased cover and biomass of herbaceous species that are necessary to carry fires (Humphrey 1974, Wright 1980).

By combining information from the literature with results from our research, we hypothesize that honey mesquite invasion and success in Chihuahuan desert grasslands are the result of a number of interactive factors, including livestock grazing and exclusion of

fire. In this paper, we first provide background information on various aspects of Chihuahuan desert ecosystems (vegetation, soils, climate, grazing, fire), with an emphasis on black grama-dominated grasslands. We then discuss the role of grazing, climate, and fire in invasion by honey mesquite. Results of a recent study in southcentral New Mexico examining grazing and fire effects on this leguminous shrub are then presented. Finally, we develop a conceptual model to synthesize this information and to propose that the reintroduction of fires, in combination with proper management of livestock, may be an effective approach to deter further honey mesquite invasion in Chihuahuan desert grasslands. Encroachment of other woody species, such as creosotebush (*Larrea tridentata*) and tarbush (*Flourensia cernua*), has also occurred in the Chihuahuan Desert (see Paulsen and Ares 1962, Buffington and Herbel 1965). Additionally, other invasive species such as Lehmann lovegrass (*Eragrostis lehmanniana*) are abundant in other desert systems; however, this is not yet the case in the Chihuahuan Desert. Honey mesquite is the most pervasive, dominant invasive species in black grama-dominated grasslands of the Chihuahuan Desert; thus, these other species will not be discussed here.

BACKGROUND

Vegetation and Soils

The Chihuahuan Desert covers 450,000–629,000 km² (Henrickson and Straw 1976, Morafka 1977, Dinerstein et al. 2000), and is located primarily in the Mexican states of Sonora, Chihuahua, and Coahuila, extending 1,500 km south into parts of Durango, Nuevo Leon, Zacatecas, and San Luis Potosi as well as parts of Queretaro and Hidalgo (Schmutz et al. 1991, Dinerstein et al. 2000). The Chihuahuan Desert reaches its northern limit in the southern Rocky Mountains of the United States, largely in southcentral New Mexico and much smaller areas of southwestern Texas, southwestern New Mexico, and southeastern Arizona (Humphrey 1974, Lauenroth 1979). At an average elevation of 1,400 m (Medellín-Leal 1982), the Chihuahuan Desert frequently occurs in broad basins or flat valleys, interspersed with swales and old lake beds where the terrain is mostly flat or gently undulating with no permanent streams or surface drainage outlets (Paulsen and Ares 1962, Buffington and Herbel 1965). The Chihuahuan Desert is discontinuous regionally and frequently interrupted by mountain ranges and by anthropogenic development (Humphrey 1974, Martin 1975, Bunting 1978, McClaran 1995).

Much of the Chihuahuan Desert comprises unconsolidated Pleistocene detritus (J.O. Veatch. 1918. The soils of the Jornada Range Reserve, New Mexico. U.S. Bureau of Soils, unpublished document.). This alluvial fill, from igneous and limestone mountains, can be as deep as 91 m, of which coarser soil particles are found near mountain foothills, and finer particles are characteristic of lower-lying areas (Paulsen and Ares 1962, Buffington and Herbel 1965). In general, soils are immature and continue to aggrade, showing little difference in texture between surface and subsoil layers (Paulsen and Ares 1962, Buffington and Herbel 1965). Soils tend to be light colored, low in organic matter (Bunting 1978, Schmutz et al. 1991), and are generally underlain by an impervious layer of calcium carbonate or caliche at soil depths varying from a few centimeters to >1 m (Canfield 1939, Valentine 1970, Martin 1975, Gibbens et al. 1986).

Mixed grass–shrub vegetation constitutes much of the Chihuahuan Desert (Humphrey 1974, McClaran 1995 and references therein). Herbaceous species composition is often closely associated with subtle differences in soil texture and structure that influence moisture dynamics, aeration, and plant root development (Canfield 1939, Paulsen and Ares 1962). On upland areas that are characterized by well drained, deep, loamy sands and sandy loams, black grama typically comprises 75% of the plant cover (Canfield 1939, Paulsen and Ares 1962, Buffington and Herbel 1965). In these black grama-dominated grasslands, associated perennial grasses include red (*Aristida purpurea* var. *longiseta*), purple (*A. purpurea*), and Wootton (*A. pansa*) three-awns, as well as sand (*Sporobolus cryptandrus*) and mesa (*S. flexuosus*) dropseeds that may constitute up to 45% of plant cover especially in less compact, sandier soils (Nelson 1934, Paulsen and Ares

1962). Long-lived (>3 years) perennial forbs are common, including desert marigold (*Baileya multiradiata*), leatherweed (*Croton pottsii*), zig-zag morning-glory (*Evolvulus nuttallianus*), and silver-leaf nightshade (*Solanum elaeagnifolium*). Abundant also are short-lived perennial forbs (2–3 years) (e.g., spectacle-pod [*Dimorphocarpa wislizenii*] and white stem [*Mentzelia multiflora*]). Prominent annuals include spike spiderling (*Boerhavia spicata*), espanta vaquero (*Tidestromia lanuginosa*), six-weeks three-awn (*Aristida adscensionis*), as well as needle (*Bouteloua aristidoides*) and six-weeks (*B. barbata*) grama (Nelson 1934). Associated shrubs include soap tree yucca (*Yucca elata*), ephedra (*Ephedra* spp.), honey mesquite, and the suffrutescent, broom snakeweed (*Gutierrezia sarothrae*) (Paulsen and Ares 1962).

Honey mesquite dunes share similar soils to adjacent, upland black grama-dominated plant communities (Buffington and Herbel 1965), but tend to form in areas of water runoff and intermittent streambeds (Schlesinger et al. 1990). Blowing sand accumulates in dense patches of honey mesquite. Much of this sand comes from inter-shrub spaces where cover of dominant perennial grasses is often reduced because of overgrazing and trampling, prolonged drought conditions, and depletion of soil moisture by honey mesquite. Through time, soils in these inter-shrub spaces become increasingly unstable and heavily wind-eroded, and surviving vegetation consists of short-lived perennials and annuals (Paulsen and Ares 1962). This desertification process also results in the accumulation of nutrients within these shrub-dominated patches, largely through the symbiotic fixation of atmospheric nitrogen (see Schlesinger et al. 1990). Species commonly found in black grama-dominated communities are occasionally encountered on these nutrient-rich mesquite islands and include dropseeds, threeawns, and spectacle pod (Paulsen and Ares 1962). However, black grama rarely occurs in mesquite dunelands (W.H. Schlesinger, Duke University, personal communication).

Climate

In the Chihuahuan Desert, between 50 and 80% of annual precipitation occurs from July to September as intense, localized convective thunderstorms of short duration (Paulsen and Ares 1962, Humphrey 1974, Hennessy et al. 1983). During this time, precipitation tends to be highest in August followed by July and then September (Paulsen and Ares 1962, Warren et al. 1996). Winter rainfall (December to March) originates from frontal storms of lower intensity, but covers larger areas (Gibbens et al. 1992, Kelt and Valone 1995). For the remainder of any given year (i.e., late fall and late spring), rainfall occurs infrequently (Paulsen and Ares 1962, Cable 1967) and may make up only 27% of the annual total (Drewa and Havstad 2001).

Mean annual precipitation is generally low and spatially variable, both at regional and localized scales. It ranges from 76.2 mm in Coahuila to 305–406 mm in western and southern regions of the Chihuahuan

Desert in Mexico (Humphrey 1974). In parts of southeastern Arizona, mean annual precipitation is 350 mm (Kelt and Valone 1995). In contrast, average yearly precipitation (1918–1999) is 227 mm on the Jornada Experimental Range, representing 78,266 ha of the Chihuahuan Desert in southcentral New Mexico (Drewa and Havstad 2001). Within these regions, mean annual precipitation can be extremely variable because of highly localized storms during the summer (Gosz et al. 1995). For example, average yearly precipitation (1916–1953) varied between 176 mm and 273 mm among 21 rain gauges located across the Jornada Experimental Range (Paulsen and Ares 1962). In any single year, annual precipitation within the northern most region of the Chihuahuan Desert in central New Mexico can be as little as 100 mm, but as much as 3 times that amount <30 km away (Gosz et al. 1995).

Annual precipitation can be extremely variable over time; drought conditions are common (Nelson 1934, Canfield 1939, Miller and Donart 1979). Based on long-term records prior to 1920 on the Jornada Experimental Range, lower than average annual precipitation was expected for 3–4 years within cycles of 8–10 years (Jardine and Forsling 1922). In the same area, summer rainfall was within 15% of the average in only 13 years and >35% above or below the average in 12 years during 1916–1953 (Paulsen and Ares 1962). During 1951–1956, the most severe drought of the past 350–400 years occurred throughout the southwestern United States (Fredrickson et al. 1998, Swetnam and Betancourt 1998). During 1974–1976, growing season precipitation varied from 107% above and 28% below the mean in southcentral New Mexico (Miller and Donart 1979). The degree to which patterns of precipitation are spatially and temporally variable may be inversely related to the average amount received in any given area of the Chihuahuan Desert (Gosz et al. 1995).

In contrast to humid environments, the length of the growing season in black grama-dominated grasslands may be determined more by patterns of precipitation than by temperature (Canfield 1939, Paulsen and Ares 1962, Buffington and Herbel 1965). Air temperature can vary from –23 to 42 °C, and daily temperature fluctuations can be as much as 30 °C (Warren et al. 1996). On average, temperature is 24 °C, and mean monthly maximum and minimum temperatures occur in June (36 °C) and January (13 °C), respectively (Paulsen and Ares 1962, Gibbens et al. 1986, 1992). Further, the number of frost-free days averages 200 days/year (Gibbens et al. 1986). However, infrequent precipitation during April, May, and June results in negligible growth of perennial grasses (Canfield 1939). Moisture limitations are enhanced by low humidity (<10%) and increased evaporation, especially in June (>34.3 cm; Buffington and Herbel 1965). Thus, the growing season for perennial grasses is mostly confined to 90 days from July through September when soil moisture is available, along with warm temperatures, higher humidity (40–50%), and reduced evaporation (26 cm/month) (Paulsen and Ares 1962, Buffington and Herbel 1965, Gibbens et al. 1986).

Compared with other North American grasslands, southwestern desert grasslands comprise a greater proportion of C₄ grasses (e.g., black grama) because of year round high temperatures and a relatively later growing season when precipitation is most likely to occur (Nelson 1934, McClaran 1995, Epstein et al. 1997). Additionally, life cycles of winter and summer annuals are synchronized with the distribution of yearly precipitation that may permit their coexistence (Davidson et al. 1985, Gutierrez and Whitford 1987, Kelt and Valone 1995, Guo and Brown 1997). A narrow window for growth of dominant perennial grasses and low annual precipitation are 2 major reasons why Chihuahuan and all other desert grasslands produce the lowest total biomass of any North American grassland type (Sims and Singh 1978).

Cattle Grazing

Grasslands of the Chihuahuan Desert have a history of livestock grazing that can be traced back to the 16th century (Fredrickson et al. 1998). During the late 1800s, severe year-round cattle grazing contributed to the marked reduction of dominant perennial grasses such as black grama (Humphrey 1958). When utilization is >40% and occurs seasonally or year round, basal area and biomass of black grama can decrease as much as 50% during 3–4 years (Canfield 1939, Valentine 1970). In the absence of cattle or when conservatively grazed, black grama is influenced mostly by patterns of precipitation (Paulsen and Ares 1962). Though apical dominance is often removed under conservative grazing, basal area of black grama can increase through the lateral spread of stolons (Canfield 1939). In contrast, overgrazing and excessive trampling directly interfere with reproductive activity; seedstalk height growth is reduced 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. During a 13-year study (1915–1927) on the Jornada Experimental Range, droughts during 1916–1918 and 1921–1926 resulted in negligible growth of black grama under conditions of overgrazing (Nelson 1934, Canfield 1939). Similar findings have been reported in other desert grasslands of the southwestern United States (Cable and Martin 1975). Today, overgrazing in black grama-dominated grasslands is not as prevalent as it once was during the late 19th century (Fredrickson et al. 1998). However, severe reductions in the past have accelerated wind erosion of soils and loss of fine soil particles that continue to make re-establishment, growth, and reproduction of black grama difficult in the Chihuahuan Desert (Nelson 1934, Schlesinger et al. 1990). Reductions in biomass and basal area of dominant perennial grasses can result in increased abundances of annuals and perennial forbs (Kelt and Valone 1995, Drewa and Havstad 2001). However, short life cycles of these functional groups of species probably interact more with highly variable patterns of precipitation (Guo and Brown 1997).

Native Mammal Herbivory

Native small mammals may also contribute to the deterioration of Chihuahuan desert grasslands that have been overgrazed by livestock (Norris 1950). Where perennial grasses are abundant, these herbivores may have little effect on desert grassland dynamics (Norris 1950, Buffington and Herbel 1965, Gosz and Gosz 1996). However, in open areas of reduced perennial grass cover, jackrabbits (*Lepus californicus*) and rodents, for example, are generally more abundant (Vories and Taylor 1933). Small mammal presence in severely overgrazed areas can almost eliminate herbaceous vegetation, especially during drought (Vories and Taylor 1933, Norris 1950).

Grass recovery can occur rapidly with the removal of small mammals. After 8 years, basal area and biomass of perennial grasses increased 4–5 times following exclusion of both rabbits and rodents in degraded Chihuahuan desert grasslands of southcentral New Mexico (Norris 1950). Reduced soil disturbance and seed predation resulted after >12 years of kangaroo rat (*Dipodomys* spp.) exclusion in Chihuahuan desert grasslands of southeastern Arizona. As a consequence, abundances of perennial and annual grasses (e.g., Lehmann lovegrass and six-weeks three awn, respectively) increased (Brown and Heske 1990, Heske et al. 1993, Curtin et al. 2000). Over 50 years, lagomorphs had differential effects on vegetation in shrub-dominated areas in the Chihuahuan Desert. Compared to unfenced control areas, basal area of spike dropseed was 30 times greater and mariola (*Parthenium incanum*) canopy cover increased more in plots from which jackrabbits were excluded. In contrast, species such as black grama and bush muhly (*Muhlenbergia porteri*) exhibited no differential response to the presence or absence of jackrabbits (Gibbens et al. 1993).

Native herbivores can influence woody vegetation. As an example, the diet of jackrabbits comprises honey mesquite, creosotebush, and broom snakeweed stems that are utilized as both a food and water source during the drier winter months (Vories and Taylor 1933, Dabo et al. 1982, Steinberger and Whitford 1983, Fatehi 1986). Leaves, however, are generally not consumed because they often contain toxic chemicals. Thus, rabbit activity not only affects the growth morphology of shrubs, but uneaten, removed leaves provide energy inputs of litter that contain a higher content of toxic chemicals than naturally senescent material (Fowler and Whitford 1980). At the northwestern extent of the Chihuahuan Desert, climatically induced increases in woody vegetation coverage have been greater in granivore exclosures compared with control areas over almost 2 decades (Curtin et al. 2000, Curtin and Brown 2001).

Large ungulates such as pronghorn (*Antilocapra americana*), muledeer (*Odocoileus hemionus*), and elk (*Cervus elaphus*) were once common in Chihuahuan desert grasslands of central New Mexico prior to increased anthropogenic activity during the mid-19th century. At present, these wide-ranging species tend to be more restricted to montane areas, but venture into

lower-elevation desert grasslands as winter approaches. Reduced populations of native ungulates likely have minimal impact on total production of desert vegetation. However, they do create small soil disturbances prior to the excretion of waste products. Additionally, their carcasses provide a pulse of soil nutrients resulting in increased abundances of grasses and forbs (see Parmenter and Van Devender 1995).

Fire

Historically, natural fire was most likely to occur during June when a high frequency of lightning strikes ignited dry vegetation (Wootton 1916, Humphrey 1958). Following the dry period from April through May, convective thunderstorms accompanied by lightning occur from June through September. In June, however, dry conditions persist because of high winds and low relative humidity. As a result, precipitation usually evaporates in the atmosphere before reaching the ground, making the initiation of fires likely. Higher humidity and rainy conditions, fostered by moisture from the Gulf of Mexico, does not occur until July (Gosz et al. 1995). Though highly speculative, the historical fire return interval for any point on the landscape may have been 9–10 years (Wright 1980, Minnich 1983, McPherson 1995), coinciding with the time required for herbaceous vegetation fuels to reach pre-fire levels of biomass (Cable 1967). In addition, fires may have been extensive and burned hundreds of hectares of land (Humphrey 1949, Bahre 1991).

Little is known about the role of fires in Chihuahuan desert grasslands, either in the United States or in Mexico (Humphrey 1974). Most historical evidence of fire comes from the Sonoran Desert in southeastern Arizona (Wright 1980) that can be traced back to the 1500s (Humphrey 1958). Despite floristic differences, the 2 desert systems have been presumed to be very similar with respect to the prevalence of fire (Humphrey 1974). In contrast, reduced abundances of black grama since the late 19th century, the lack of historical evidence of fire, and black grama mortality following prescribed fire has made many question its historical significance in the Chihuahuan Desert (Wright 1960, Buffington and Herbel 1965, York and Dick-Peddie 1969). However, observations from the past 100 years at specific research sites suggest that fire occurs in the Chihuahuan Desert. According to a news bulletin, a natural fire was observed by J.T. Jardine just prior to 1914 on the Jornada Experimental Range (U.S. Forest Service 1928). In the same area over 1 growing season, small fires have occurred adjacent to yucca plants that were struck by lightning (P.B. Drewa, personal observation). Further, fire is an important component of ungrazed black grama grasslands at the Sevilleta National Wildlife Refuge located at the northern most extent of the Chihuahuan Desert in central New Mexico. Aside from the presence of critical synoptic weather during the growing season, characteristics of natural fire regimes prior to European settlement (especially fire frequency) remain unknown in black grama-dominated grasslands of the Chihuahuan Desert.

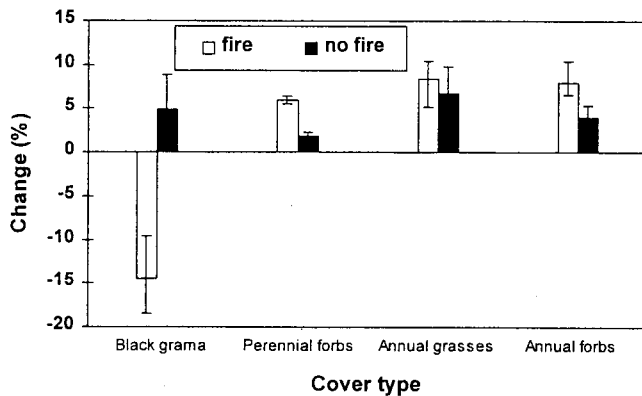


Fig. 1. Change in cover of black grama (dominant perennial grass), perennial forbs, annual grasses, and annual forbs, 4 years following prescribed head fires during 1995 on the Jornada Experimental Range, New Mexico.

Perennial grass recovery following fire may be contingent on patterns of precipitation (Wright 1980). When a June fire was prescribed during drought in 1952, basal cover of perennial grasses decreased 1 year later in the Sonoran Desert of southeastern Arizona. However, after 1 year following a June fire that was accompanied by average summer precipitation, basal cover of perennial grasses was equivalent to pre-fire levels (Cable 1967). Prior to an accidental fire in June, 1963 in the same area, no precipitation had fallen for 64 days. Again, a combination of fire and drought may explain why survivorship of black grama ramets was only 10% (Cable 1965). Four years following a June fire in the Chihuahuan Desert, cover of black grama decreased almost 15%, but increased 5% in fire-excluded areas (Figure 1; Drewa and Havstad 2001). In the year of these fires, the study area received no precipitation during April and May, and June precipitation was only 16% of the long-term average. Further, only 50% of expected precipitation occurred in July. Thus, black grama recovery to pre-burn levels may take more than 4 years and possibly as long as 8 years during drought (Wright 1980, Gosz and Gosz 1996). Though speculative, recovery may take even longer (up to 50 years) if fire and drought occur concomitantly with livestock grazing (Wright 1980, Martin 1983, McPherson 1995).

Decreased abundances of perennial grasses are sometimes associated with increases in perennial forbs and annuals after fire (Cable 1972, Valone and Kelt 1999). Greater increases in annual grass production in burned versus unburned areas has occurred only when above-average rainfall occurred during the summer immediately following prescribed June fires (Cable 1967). With the delayed recovery of black grama, annual forbs and grasses collectively increased regardless of fire, although perennial forb cover was 4% greater in burned than unburned areas (Figure 1; Drewa and Havstad 2001).

HONEY MESQUITE INVASION

Honey mesquite has encroached into many Chihuahuan desert grasslands located mostly on sandy

soils. For example, honey mesquite occurred on 11,777 ha in 1858, but was present on 37,126 ha by 1963 on the Jornada Experimental Range (Buffington and Herbel 1965). More specifically, the number of mesquite plants increased 125%, and canopy area increased 74% from 1936 to 1951 (Paulsen and Ares 1962). Expanded distributions and increased abundances of shrubs have ultimately resulted in the expansion of mesquite dunes at the landscape scale, regardless of subtle differences in edaphic factors (Paulsen and Ares 1962, Buffington and Herbel 1965). The major factors that influence honey mesquite invasion include effects of domestic livestock and native herbivore activity, climate, and fire. These factors have important independent as well as interactive effects with other factors on shrub invasion and persistence in Chihuahuan desert grasslands.

Animal Activity

Cattle are primarily responsible for the invasion of honey mesquite through the dissemination of seed (Humphrey 1958, Wright 1960, Paulsen and Ares 1962). Mature honey mesquite pods are palatable, and cattle consume them in large quantities (Paulsen and Ares 1962, Mooney et al. 1977). Further, seeds pass through the digestive tract and are eliminated in cattle droppings, often at locations several kilometers from where they were consumed (Humphrey 1958, Paulsen and Ares 1962, Buffington and Herbel 1965, Brown and Archer 1987). A favorable microenvironment provided by cattle dung may facilitate mesquite germination (Humphrey 1958, Paulsen and Ares 1962). This supposition has been questioned in floristically similar Texas prairies where seedling survival was comparably high (up to 97%) between dung sites and areas where seeds were experimentally sown away from cattle droppings (Brown and Archer 1987, 1989).

In addition to livestock, rodents and other mammals may also contribute to the dissemination of honey mesquite seeds (Reynolds and Glendening 1949, Kramp et al. 1998). In black grama-dominated grasslands of the Chihuahuan Desert, the Merriam kangaroo rat (*Dipodomys merriami*), for example, collects seeds and stores them in shallow caches. Many seeds that are not consumed may germinate in the caches and thus contribute to mesquite expansion (Paulsen and Ares 1962). At the northwestern extent of the Chihuahuan Desert, however, mesquite establishment was less in experimental plots where many seedlings may have been subject to kangaroo rat herbivory as opposed to areas where kangaroo rats were excluded up to 21 years (Valone and Thornhill 2001).

Perennial grasses that are grazed by livestock may have little effect on establishment of honey mesquite. High levels of seedling establishment were reported in both grazed and ungrazed areas (Smith and Schmutz 1975, Meyer and Bovey 1982). In particular, seedling germination increased 7–8 times in Texas prairies where the heights of perennial grasses were experimentally clipped to 25 cm compared with ungrazed controls. However, it was not enhanced in heavy de-

foliated treatments (clipped to 10 cm; Brown and Archer 1989). More recently, establishment, germination, and survival of honey mesquite were not significantly affected by either varying levels of perennial grass density (nonmanipulated or reduced 50%) or by moderate and heavy grazing (grass clipped to heights of 20 cm and 10 cm, respectively) and no defoliation (Brown and Archer 1999). Honey mesquite seedlings can quickly access soil moisture in zones that are inaccessible to perennial grasses and other nonwoody vegetation that possess shallow root systems. Within 4 to 12 months of germination, honey mesquite roots can rapidly develop and penetrate soil depths of >40 cm and >90 cm, respectively (Brown and Archer 1990).

Climate

Prolonged dry conditions result in perennial grass mortality and thus may foster honey mesquite invasion (Humphrey 1958, Buffington and Herbel 1965, York and Dick-Peddie 1969). During the early 1930s, a fenced, 259-ha area on the Jornada Experimental Range was established to exclude livestock and encompassed black grama-dominated grassland and adjacent mesquite dunes (Buffington and Herbel 1965). After 45 years, honey mesquite was the most abundant species within the entire enclosure (Hennessy et al. 1983). Drought conditions, especially during the early 1950s, and subsequent wind erosion resulted in mortality of black grama in the enclosure. Honey mesquite may have become established following drought (Fredrickson et al. 1998) with the low cover of nonwoody vegetation (Buffington and Herbel 1965). Seedlings of honey mesquite may be very drought tolerant. During drought in arid savannas of Texas, seedling emergence remained high (i.e., 42%), and seedling survival was not different between excessively dry areas and those that received supplemental watering (Brown 1987).

Encroachment of mesquite may increase as a result of long-term changes in patterns of precipitation. Mesquite cover has more recently increased in the northwestern extent of the Chihuahuan Desert (Curtin et al. 2000), and is associated with winter precipitation that has been several times greater than the 100-year mean for much of the Southwest since the 1970s (Brown et al. 1997, Swetnam and Betancourt 1998). In turn, much higher than average winter rainfall corresponds to numerous El Niño Southern Oscillation events from 1977 to 1992 (Brown et al. 1997).

Fire

Prior to European settlement, natural fires may have limited honey mesquite invasion from sandy bottomlands into grasslands (Humphrey 1958). Following fire, mature honey mesquite often resprout from basal stem buds just below the soil surface where they are well insulated from heat (Cable 1965, 1972). Although topkilling does not kill the individual, it inhibits flowering and seed set (Humphrey 1958). Mesquite establishing from seed may take 10–13 years before reaching reproductive maturity (Chew and Chew 1965,

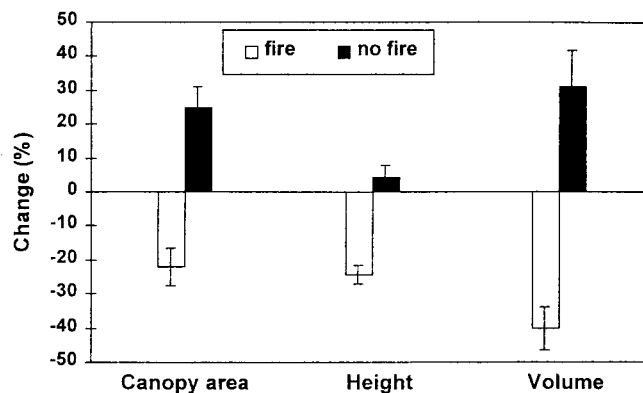


Fig. 2. Change in canopy area (m^2), height (m), and volume (m^3) of honey mesquite, 1 year following prescribed head fires during June, 1999 on the Jornada Experimental Range, New Mexico. In total, 478 shrubs were sampled, of which 210 were encountered in burned experimental units.

Martin 1975, Wright 1980). Thus, if fire occurred every 10 years in this region, it may have been effective in reducing mesquite seed production (Humphrey 1958).

Degree of complete kill and topkill of honey mesquite depends, in part, on shrub size as well as fire season and intensity. Fire may be effective in killing mesquite seeds (Cox et al. 1993). Additionally, honey mesquite, ranging from 1.5 to 2.5 years old and 9 to 21 cm in height, may be vulnerable to complete kill (Wright et al. 1976). When June fires were 104 °C at the soil surface, 20–60% mortality occurred; fires that burned at >223 °C resulted in 40–100% complete kill. Conversely, complete kill was rare among shrubs >3.5 years old. Only 8% mortality occurred following fire temperatures ranging from 104 to 601 °C (Wright et al. 1976). Similarly, 60% mortality occurred among shrubs <1.3 cm in stem diameter. Mortality decreased with larger stem diameter classes (e.g., 11% mortality for trees >12.7 cm stem diameter) (Cable 1972). Similar relationships exist between shrub size and topkill of mesquite (Martin 1983). Prescribed fires conducted outside the lightning season are not as effective as June fires in damaging shrubs. While summer fires resulted in 86–97% topkill of honey mesquite, only 11–70% topkill occurred following winter fires in Texas prairies (Ansley and Jacoby 1998).

Despite current low levels of herbaceous biomass, our research shows there is sufficient fuel to topkill honey mesquite in Chihuahuan desert grasslands. On the Jornada Experimental Range, we examined the effect of June fires on honey mesquite morphology in 1999. Because vegetation was spatially discontinuous and variable in biomass, fires had to be re-ignited on numerous occasions over a 2-week period to ensure that areas were burned in their entirety. Thus, fire temperatures at the soil surface were highly variable (<80–1037 °C). After 1 year, canopy area decreased 22% in burned plots, but increased 24% in unburned areas (Figure 2; $P < 0.001$). Similarly, shrub height decreased 24% following fire, but changed little over 1 year in unburned plots ($P < 0.001$). Overall, shrub

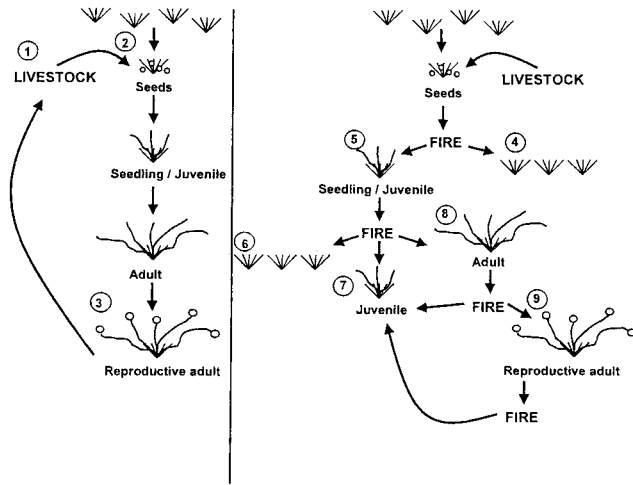


Fig. 3. Conceptual model to illustrate how growing season fire might be used as an effective means of deterring honey mesquite invasion.

volume decreased 40% following fires and increased 30% after just 1 year in fire-excluded areas ($P < 0.001$). Of the 210 shrubs that were burned in our study, only 3 were completely killed. On average, these shrubs were 61.8 cm (± 0.7 cm SE) in canopy diameter and 79.2 cm (± 8.3 cm SE) in height. Given their size, these shrubs were ca. 10 years old (R.P. Gibbens, Jornada Experimental Range, personal communication). This age exceeds the 3.5-year threshold found previously in Texas prairies (Wright et al. 1976). On average, these shrubs burned at 592 °C (± 155 °C SE) in dense herbaceous fuels (almost 80% ground cover) that may explain their mortality.

CONCEPTUAL MODEL OF FIRE, GRAZING, AND HONEY MESQUITE INVASION

We developed a conceptual model to illustrate how prescribed fire might be used as an effective means of deterring further honey mesquite invasion in the presence of low and variable herbaceous biomass (Figure 3). Dissemination of honey mesquite seeds into black grama-dominated grasslands by cattle initiates shrub invasion (1; left panel). In the absence of fire (2), establishment and growth of honey mesquite plants results in a shrub-dominated community over time. Individuals that reach reproductive maturity (3) provide seed sources for dissemination by livestock and the spread of mesquite across the landscape.

With the use of fire (Figure 3, right panel), mesquite invasion can be decreased in numerous ways. Fire that kills mesquite seeds can allow the persistence of grasslands through time (4). On some sites, seeds of honey mesquite may survive fires and subsequently become established (5). Where complete kill of young plants occurs, these sites may return to a grassland stage (6). Alternatively, fires may be effective in topkilling smaller shrubs of honey mesquite to maintain an immature stage (7). For large shrubs (8), topkill is

more likely following fire as well as a subsequent return to an immature stage. Where fires were either of very low intensity or did not occur, other shrubs may reach reproductive maturity (9). Fire may ultimately topkill these shrubs and return them to a juvenile stage.

The effectiveness of fire is expected to be contingent on the amount and spatial distribution of herbaceous biomass as well as shrub size and status. Recovery of perennial grasses is expected to depend on patterns of precipitation and the degree of livestock grazing before and after fire. Managing the number and distribution of livestock and use of growing season fire is expected to provide an effective strategy for controlling invasion of honey mesquite and maintaining black grama-dominated grasslands through time.

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