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Mechanisms of Range Expansion and Removal of Mesquite in Desert Grasslands of the Southwestern United States

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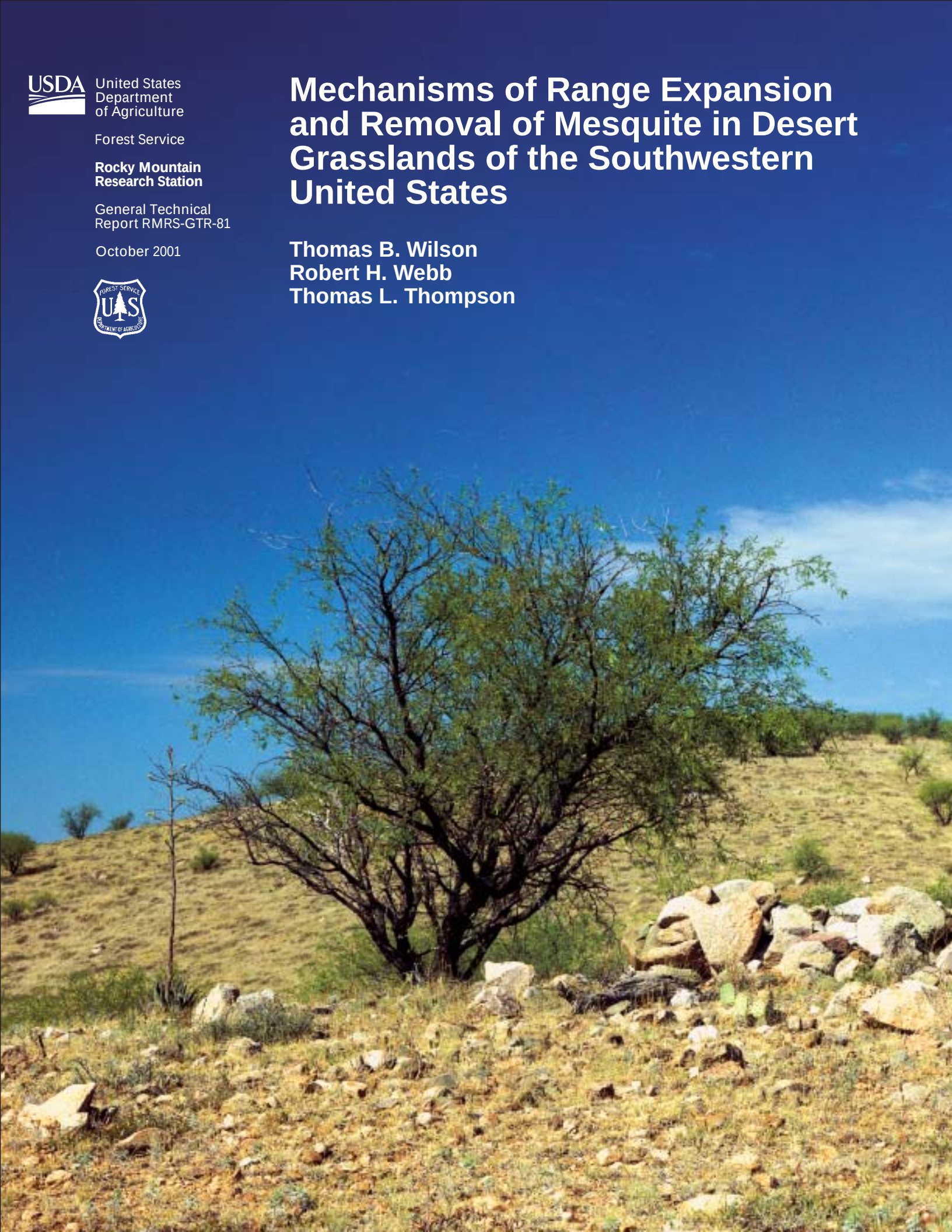

Abstract

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During the last 150 years, two species of mesquite trees in the Southwestern United States have become increasingly common in what formerly was desert grassland. These trees have spread from nearby watercourses onto relatively xeric upland areas, decreasing rangeland grass production. Management attempts to limit or reverse this spread have been largely unsuccessful. This paper reviews studies regarding mesquite natural history and management strategies, emphasizing studies published during the past decade. Mesquite possess a deep root system and are capable of fixing atmospheric N, rendering them capable of accessing resources unavailable to other plants in open rangeland. Their seeds, which remain viable for decades, have a hard exocarp and require scarification before germination. Consumption by cattle provides a means of scarification and seed dispersal, and is a major factor contributing to the spread of mesquite in open rangelands. Increases in atmospheric CO_2 and winter precipitation during the past century also contribute to enhanced seed germination. Removal techniques have included herbicides, prescribed burning, grazing reduction, and mechanical removal. For increased effectiveness of these techniques, management goals must be clearly articulated; these goals include complete removal, no removal, and limited removal. Of these, limited removal appears the most feasible, using an initial herbicide application followed by periodic prescribed burning.

Keywords: mesquite, biological invasions, rangeland ecology, soil nitrogen, rangeland management

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Mechanisms of Range Expansion and Removal of Mesquite in Desert Grasslands of the Southwestern United States

Thomas B. Wilson
Robert H. Webb
Thomas L. Thompson

Introduction

Rangelands in the Southwestern United States have been used for settlement, agriculture, and livestock ranching during the last 150 years. Because of the gentle topography, sufficient available water, and abundant forage, use of this rangeland—especially in southeastern Arizona and southwestern New Mexico (fig. 1)—has been intensive. As a result, much of this area has been transformed to a mixed-phase woodland or shrubland, with no sign of this trend diminishing (Archer and others 1988; Buffington and Herbel 1965; Hastings and Turner 1965; McClaran and Van Devender 1995). Figures 2–6 show repeat photography that document this change at selected sites in the region. The alteration of grassland to shrubland has created considerable concern as land use managers recognize a corresponding decline in available livestock forage. The mesquite tree (*Prosopis* spp.) has played a major role in this change, as it has expanded its range from more sheltered and mesic desert grassland drainage systems and riparian zones to open rangelands.

While the causes that account for this altered distribution—climate change (Grover and Music 1990), livestock grazing (Archer and others 1988; Bahr and Shelton 1993; Schlesinger and others 1990), suppression of wildfires (Bahre 1985; Biggs 1997; Humphrey 1958), or rodent effects (Cox and others 1993; Reynolds and Glendening 1949)—have been investigated for several decades, no single effective strategy has been offered as a means of slowing or reversing mesquite encroachment in desert grasslands. Removal tactics have included fire (Britton and Wright 1970; Wright and others 1976), herbicides (Gibbens and others 1986; Jacoby and others 1982; Warren and others 1996), and mechanical removal (Dodd and Holtz 1971). These have resulted in varying degrees of success, mainly short term.

One key to understanding why mesquite has expanded its range, and why it may be at times impervious to attempts at removal, is through an examination of its natural history. Though this has been studied in the past, many studies concerning intraspecific competition (Ansley and others 1998; Kramp and others 1998), seed germination requirements (Bush and Van Auken 1990; Cox and others 1993), root systems (Ansley and others 1990, 1991; Stromberg 1993), and nitrogen fixation (Johnson and Mayeux 1990; Zitzer and others 1996) have taken place only within the last 10 years.

In this study, we especially refer to the desert grasslands of southeastern Arizona and southwestern New Mexico in the area shown in figure 1. Previous workers (Brown and Lowe 1980) referred to two types of grassland in this region—semidesert grassland and plains and Great Basin Desert grassland—but we prefer the simpler classification of "desert grassland" as used by McClaran and Van Devender (1995). We subdivide the desert grasslands into the desert grasslands of southeastern Arizona, which mostly surround the Santa Rita and Huachuca Mountains, and the desert grasslands of the western Chihuahuan Desert, which spans the area from the Sulfur Springs Valley of southeastern Arizona to the Bootheel of southwestern New Mexico.

The objectives of this study are (1) to describe the natural history of the mesquite species that have increased their distribution within the Southwestern United States, focusing on those attributes that could account for this range expansion, (2) to review the existing research that has addressed this expansion, with an emphasis on research produced within the last decade, (3) to describe management goals, practices, and results, and (4) to propose a management strategy that accounts for regional differences while providing long-term effectiveness.

Mesquite Natural History

Floristics

Three species of mesquite tree are currently recognized as indigenous to the Southwestern United

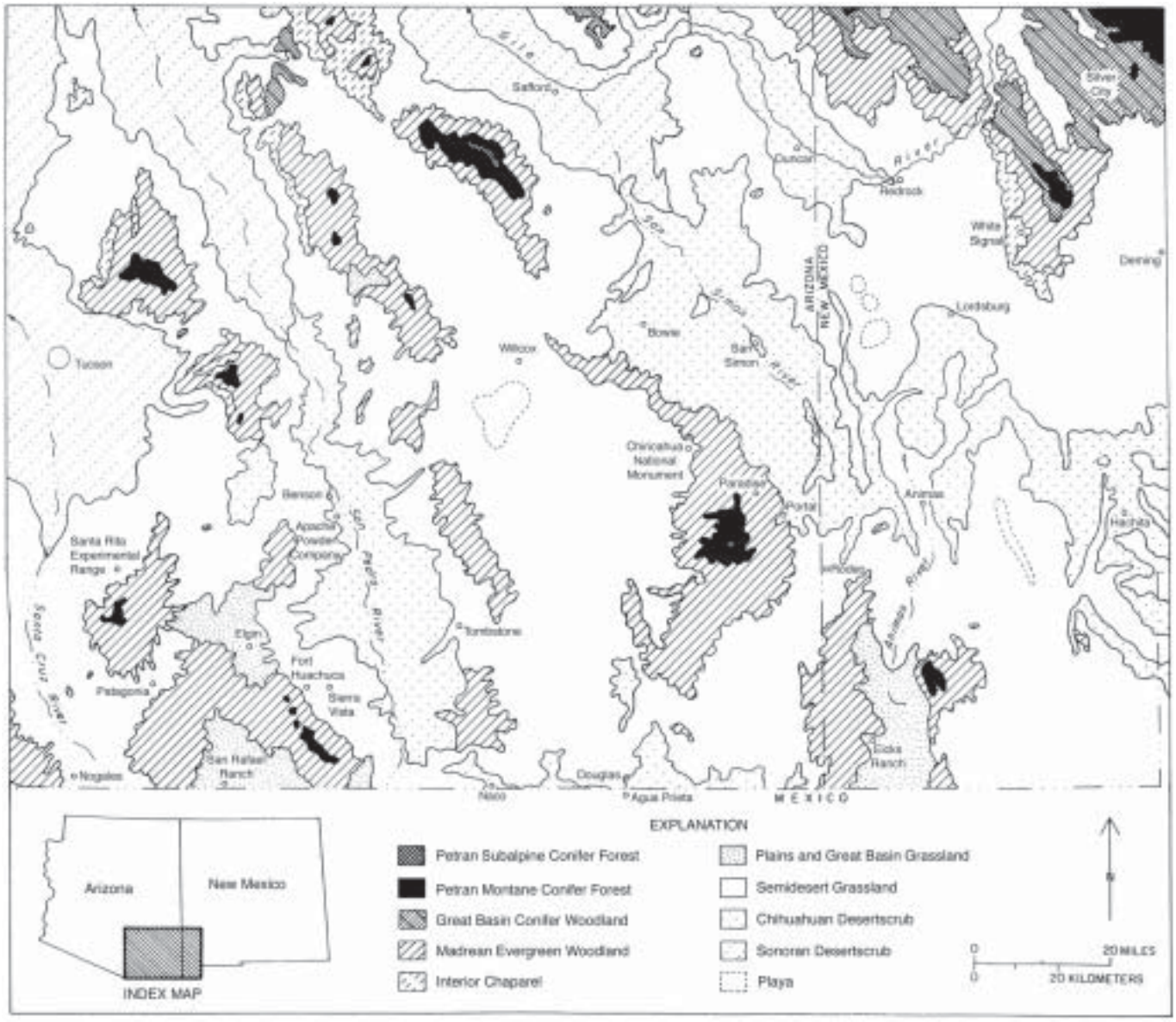


Figure 1—Map showing biotic communities of the region of southwestern New Mexico and southeastern Arizona that contain desert grasslands (from Brown and Lowe 1980). This area includes what we refer to as Sonoran and Chihuahuan Desert grasslands, defined by Brown and Lowe (1980) as semidesert grassland and plains and Great Basin grassland.

States: screwbean mesquite (*Prosopis pubescens* Benth.), velvet mesquite (*Prosopis velutina* Woot.), and honey mesquite (*Prosopis glandulosa* Torr.). Two subspecies of honey mesquite are found in this area: Texas honey mesquite (*Prosopis glandulosa* var. *glandulosa* Torr.) and western honey mesquite (*Prosopis glandulosa* Torr. var. *torreyana* [L. Benson] M.C. Johnston). They are members of the legume family (Fabaceae) and are characterized by pinnate leaves, spiny branches, seedpods, and a central taproot. However, individual variation in physical characteristics as well as hybridization makes taxonomic classification at the species level problematic. In general, *P. glandulosa* can be differentiated from *P. velutina* because the former has glabrous leaflets up to 4 cm long; the latter has pubescent leaflets up to 1.3 cm long. The two varieties of *P. glandulosa* are distinguished by their spines; *P. glandulosa* var. *torreyana* has paired thorns, while *P. glandulosa* var. *glandulosa* has solitary thorns (Isely 1998).

Two of these species, *P. glandulosa* and *P. velutina*, have had the most significant expansion into desert grasslands. While *P. velutina* is restricted in the United States to southern and central Arizona, *P. glandulosa*

Figure 2—The Altar Valley east of the Coyote Mountains (approximately 884 m). (A) October 8, 1903. In 1903, much of the Altar Valley south of what is now known as Three Points, AZ, was open desert grassland with scattered cacti and shrubs. Even at this early date, scattered small mesquite (*P. velutina*) shrubs, along with littleleaf palo verde (*Cercidium microphyllum*), are on the open rangeland. Cattle grazing was pervasive in the Altar Valley in large ranches (photograph by David Griffiths, number 2098, courtesy of the National Archives). (B) February 20, 1999. The Altar Valley is now mostly a mesquite-palo verde woodland with little remaining perennial grass. At this site, creosote bush (*Larrea tridentata*) is also prominent in the foreground along with cholla cacti (*Opuntia* spp.) (photograph by Dominic Oldershaw, stake 3805, courtesy of the Desert Laboratory Photograph Collection).

Figure 3—Railroad Pass on the Munk Ranch north of Willcox, southeastern Arizona (1,250 m). (A) Between 1901 and 1920. Much of the rangeland east of Willcox was grassland punctuated with scattered mesquite trees and yuccas (*Yucca elata*) at the turn of the century. This type of environment was probably maintained by periodic wildfires before the advent of widespread cattle grazing and fire suppression (photograph by J. A. Munk, number A.141.86, courtesy of the Southwest Museum). (B) June 19, 1995. Rangeland east of Willcox now is mostly shrubland, dominated by snakeweed (*Gutierrezia sarothrae*) with locally abundant mesquite (both *P. velutina* and *P. glandulosa* var. *glandulosa*) and yuccas (photograph by Dominic Oldershaw, stake 3350, courtesy of the Desert Laboratory Photograph Collection).

Figure 4—Hooker Ranch in the Dos Cabeza Mountains, southeastern Arizona (1,433 m). (A) Between 1901 and 1919. The headquarters of the Hooker Ranch is in a valley south of the peaks of the Dos Cabeza Mountains. Around the turn of the century, this valley had vegetation similar to that shown in figure 2A just east of Willcox. (photograph by J. A. Munk, number A.142.143, courtesy of the Southwest Museum). (B) June 24, 1995. *Prosopis velutina* is now a dominant tree on the lower slope rangelands in the view. Perennial grasses remain between the trees at this higher-elevation site, however (photograph by Dominic Oldershaw, stake 3355, courtesy of the Desert Laboratory Photograph Collection).

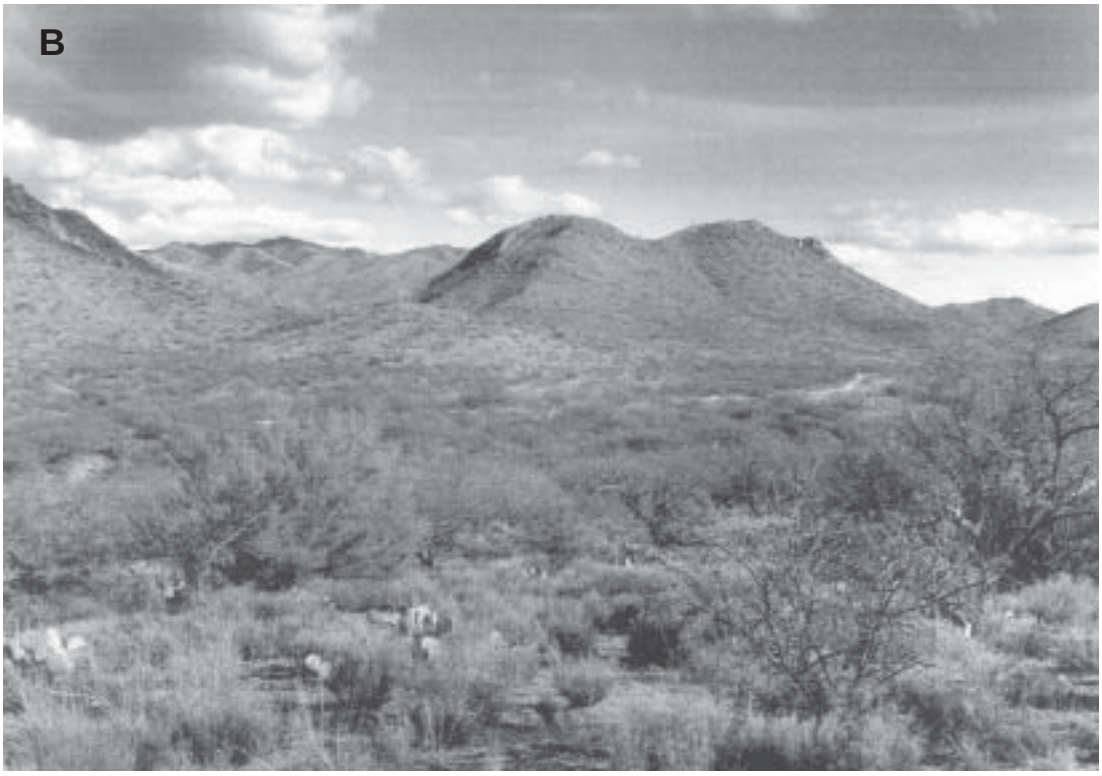


Figure 5—Lincoln Mine Camp in the Sierrita Mountains of southern Arizona (1,091 m). (A) February 25, 1906. The Lincoln Mine is in the foothills of the Sierrita Mountains on the east side of the Altar Valley in southern Arizona. As shown in this view of the former mine headquarters, the valley supported a grassland with scattered mesquite (*P. velutina*) and succulents, including ocotillo (*Fouquieria splendens*) and prickly pear cactus (*Opuntia phaeacantha*) (photograph by D. T. MacDougal, number A1-58, courtesy of the Desert Laboratory Photograph Collection). (B) 1994. Woody vegetation now dominates this valley. Littleleaf paloverde (*Cercidium microphyllum*) has increased as well as mesquite (*P. velutina*), shrubs, and prickly pear cactus. Perennial grasses are difficult to find in most years of the late 20th century (photograph by Robert H. Webb, stake 3114, courtesy of the Desert Laboratory Photograph Collection).

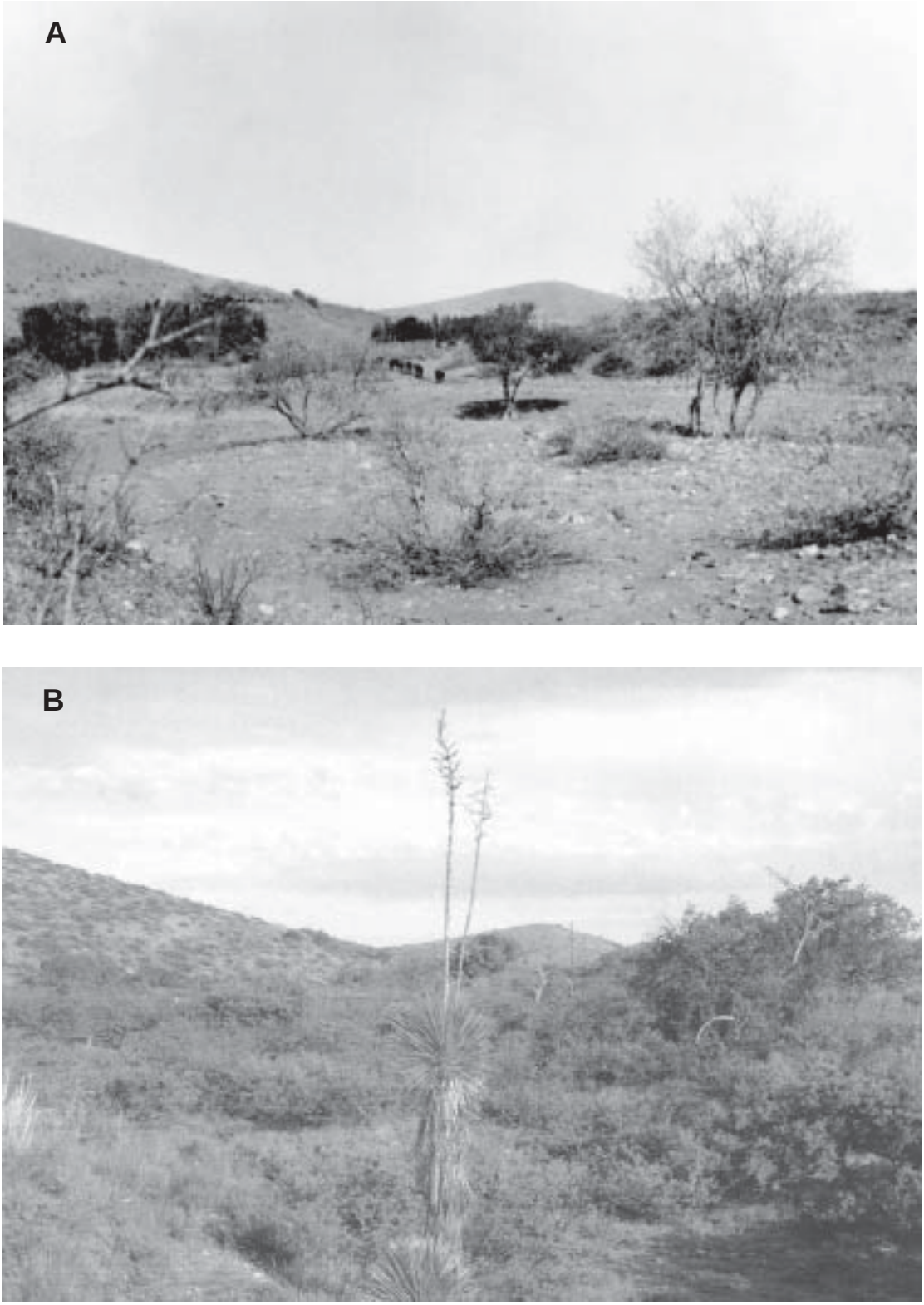


Figure 6—Munk Draw on the Munk Ranch north of Willcox, southeastern Arizona (1,364 m). (A) Between 1901 and 1919. Scattered trees, mostly mesquite, line the shallow watercourse in this photograph of the active Munk Ranch north of Willcox. Note the cattle in the background (photograph by J.A. Munk, number A.141.96, courtesy of the Southwest Museum). (B) June 16, 1995. Woody vegetation, primarily mesquite, has increased along this ephemeral watercourse in the 20th century (photograph by Dominic Oldershaw, stake 3336, courtesy of the Desert Laboratory Photograph Collection).

occurs from Texas to California. *P. glandulosa* var. *glandulosa* is found mainly in Texas east of the Pecos river and north into Oklahoma, while *P. glandulosa* var. *torreyana* is found west of the Pecos river, throughout southern New Mexico and adjacent Arizona, and in southern California, northwestern Arizona, southern Nevada, and southwestern Utah. *P. glandulosa* var. *glandulosa* can also be found along Interstate 10 through New Mexico and Arizona east of Tucson due to cattle transport with subsequent seed dispersal. In this paper we assume that *Prosopis velutina* and the two subspecies of *P. glandulosa* are sufficiently similar in characteristics to be treated together.

Morphology

Mesquite attains its maximum height of over 12 m in sheltered riparian habitats, yet is opportunistic enough to grow on exposed desert slopes where reproductively mature individuals may only be 1.5 m tall. In xeric upland sites, their taproot may reach only 1 m in depth where solid bedrock prevents deeper penetration; however, taproots of *P. velutina* have been recorded at over 53 m depth (Philips 1963) under more favorable conditions.

While mesquite trees are characterized by a massive central taproot, they also possess an extensive lateral root system (Heitschmidt and others 1988). For this reason they are classified as facultative phreatophytes, able to extract permanent ground water when available but also able to extract soil moisture (Ansley and others 1990). Ansley and others (1990, 1991) severed the lateral roots of four *P. glandulosa* var. *glandulosa* trees at two sites in western Texas. They found that stomatal conductance was reduced during the first growing season on the site with less available subsurface water; this reduction disappeared during the second growing season, probably due to root regeneration.

In riparian habitats and desert grasslands, *P. glandulosa* and *P. velutina* are typically single stemmed with a central trunk up to 35 cm in diameter. However, multistemmed individuals are not uncommon, especially as a result of resprouting following fire. Conversely, multistemmed plants are most common in more arid habitats such as the Arizona upland regions of the Sonoran Desert. Aboveground form also appears to be related to subsurface characteristics. For example, Stromberg and others (1993) compared *P. velutina* aboveground characteristics to available water and found that the height of stands in riparian areas was inversely related to depth of the water table; trees were 8 m tall where the ground water depth was greater than 15 m, but grew to 12 m where the ground water was less than 15 m.

Whether single or multistemmed, mesquite trees produce branches that may form a canopy with a diameter twice the height of the plant. Both stems and larger branches may be either smooth or rough textured with a fair degree of individual variation. Branches are typically spiny with considerable variation in thorn length (from 0.5 to over 5 cm) and density.

Finn and others (1994) identified annual growth rings in the wood of *P. glandulosa* at five sites in Texas. Their samples included trees that resprouted vegetatively following cutting; for these plants they noted that ring count would signify age of regrowth, not necessarily the tree itself. They found stems ranging from 7 to 30 years in age, but their data in conjunction with Archer's (1989) growth rate study suggest that the age tree stems may exceed 200 years. Using repeat photography, Bowers and others (1995) documented *P. glandulosa* longevities more than 100 years.

Phenology and Germination

Though climatic conditions vary considerably throughout the ranges of *P. glandulosa* var. *glandulosa* and *P. velutina*, their growing seasons are generally in the spring and in the late summer. This is typical of a C3 species but not the C4 grass species that dominate open rangelands. Mesquite trees are typically deciduous during the winter months, but may also lose their leaves during summer drought (Ansley and others 1992). Leaves produced during the spring may be larger than in late summer (Nilsen 1986), perhaps in response to light intensity and transpiration potential. These leaves form a hydrophobic waxy cuticle that can accumulate during the growing season, providing mesquite some resistance to foliar-applied herbicides (Jacoby and others 1990c).

Flowering occurs in the late spring and typically attracts a variety of flying insect-pollinators, including bees, wasps, and beetles. Seed pods exceeding 30 cm in length are produced through the summer. The seeds have a generally high mortality rate from bruchid beetles (*Algarobius prosopis* and *Neltumius arizonensis*), which bore holes into the fruit and deposit eggs on the seed. Germination occurs in both fall and spring, coincident with peaks in annual precipitation (Brown and Archer 1987).

The seeds have a hard exocarp and must undergo scarification prior to germination. This contributes to their long-term viability, which may exceed 20 years (Martin 1948, 1970). Kramp and others (1998) evaluated the effectiveness of deer, cattle, and coyotes as scarification agents and vectors for *P. glandulosa* var. *glandulosa* seed dispersal. They found that seeds continued to germinate in fecal samples of all species 2 years after deposition, and that an average of 7.8, 5.2, and 4.5 seedlings emerged from deer, cattle, and coyote feces, respectively. These authors concluded that cattle were most effective as seed vectors because cattle feces contained more seed. Brown and Archer

(1989) found that honey mesquite had a survival rate of 74 to 97 percent for individuals that survived 2 weeks after germination in cattle fecal sites. Ingestion by herbivores has the added benefit of eliminating bruchid beetles from the fruit (Burkhart 1976).

Under laboratory conditions, *P. glandulosa* seedlings in a clay loam soil emerged from planting depths between 0.5 and 1.5 cm after 3 to 6 days, with a root-to-shoot ratio of 5:1 within this period (Scifres and Brock 1971). In a similar study of *P. velutina* seedlings, Cox and others (1993) found that a planting depth of 2 to 4 cm in a sandy loam resulted in the highest percent germination; they also determined that seeds planted at this depth were unaffected by fire. Brock (1986) found that unrestricted root growth is critical for the survival of velvet mesquite seedlings. In a laboratory study, he found that the greatest root development and growth rate during the first 30 days was in sandy loam and clay loam soils; after this time aboveground growth exceeded root development.

Emerging seedlings readily survive losses of top growth due to herbivory (Weltzin and others 1998). In a growth chamber experiment, Weltzin and others (1998) evaluated the relative tolerances of seedlings aged 18 and 33 days to repeated clipping above either the first or fourth nodes. They found that the younger seedlings had a 75 percent survival rate after repeated clipping above the first node, verses a 38 percent survival rate for older seedlings.

Insufficient light may limit the survival of emerging seedlings. Bush and Van Auken (1990) observed that seedlings rarely emerge under the canopy of mature *P. glandulosa* trees, despite elevated soil nutrient concentrations. When these authors compared seedling emergence and survival, they found that the largest seedlings were found in areas with full light and herbaceous plant exclusion, while the smallest seedlings were found under adult trees with herbaceous plant competition. Conversely, Brown and Archer (1989) found *P. glandulosa* seed germination and establishment to be independent of herbaceous biomass or moisture conditions, though their survival rate increased with supplemental watering.

Intraspecific competition can limit population densities of either seedlings or reproductively mature individuals. In a survey of establishment rates for *Prosopis glandulosa* var. *glandulosa* in cattle fecal sites in northern Texas, Kramp and others (1998) found that all sites where mesquite had germinated eventually had either a single established plant or none. Ansley and others (1998) noted that access to soil water appears to be the competitive mechanism limiting population densities and individual tree size for this species in areas where lateral root systems provide the main source of water uptake.

Mesquite and Nitrogen

Nitrogen availability is considered to be a major factor limiting plant growth in regions where mesquite occurs in the Southwestern United States (West and Klemmedson 1978). However, several studies have indicated that mesquite in these regions represent a source of nitrogen rather than a sink. In a 3-year study, Barth and Klemmedson (1983) found that soil under *P. velutina* canopies accumulated 11.2 g N/m^2 per meter of tree height; this concentration was inversely related to distance from the trunk and decreased away from the canopy edge. Virginia and Jarrell (1983) found similar results in a study of soil properties under *P. glandulosa* var. *glandulosa* canopies; total N, NH_4^+, NO_3^-, organic C, plant-available P, and K were significantly ($P \leq 0.05$) higher beneath canopies than in adjacent open areas. In California, Rundel and others (1982) found 1,020 g soil total N/m^2 under *Prosopis glandulosa* var. *torreyana* canopies, 160 g soil total N/m^2 total N between canopies, and 45 g soil total N/m^2 in adjacent open areas. At the Fort Huachuca Military Reservation in southeastern Arizona, shallow soil under mesquite canopies had an average of 17 mg NO_3^--N/kg and 2.05 mg/kg in adjacent open areas (Biggs 1997).

The main mechanism responsible for elevated soil nutrient concentrations under mesquite is biological nitrogen fixation by soil Rhizobia followed by litterfall. In a symbiotic relationship, mesquite will transport abundant C into their root systems at a high energy cost to facilitate the establishment of Rhizobia bacteria within the rhizosphere. Subsequently, the roots form nodules around the Rhizobia which proceed to convert N_2 from the soil atmosphere to a form usable by the host plant (NH_3). Eventually this fixed atmospheric N is returned to the soil via litterfall. Though plants resorb leaf nutrients to varying degrees before leaf senescence, fallen *P. glandulosa* leaves can contain 2.6 percent N, a retention rate of over 74 percent (Killingbeck and Whitford 1996). This represents an annually renewed source of soil N which is replenished mainly during the late fall when mesquite become deciduous. Rundel and others (1982) have estimated that 25 to 30 kg N/ha accumulates annually under canopies of *P. glandulosa* var. *torreyana* as a result of fixation, whereas Virginia (1986) found that mesquite litterfall annually returns 135 kg N/ha to the soil. Since litter deposition occurs mainly under the mesquite canopy, adjacent open areas may remain unaffected.

Despite empirical evidence, explicit identification of N fixation by mesquite has remained elusive. Shearer and others (1983) found a lower isotope ratio of $^{15}N/^{14}N$ in leaf tissue of *P. glandulosa* var. *torreyana* compared to similar tissue of unrelated reference plants. This

indicated that mesquite were using atmospheric N, which is naturally more abundant in ^{14}N, rather than mineralized soil N, which is more abundant in ^{15}N. However, these authors could not quantify the amount of N fixed using this method, due to lack of replication and the absence of appropriate non-N-fixing reference plants.

Other researchers have attempted to locate N-fixing nodules in the roots of mesquite. Johnson and Mayeux (1990) recovered brown, leathery textured nodules in the roots of *P. glandulosa* var. *glandulosa* in eastern Texas. They found that 11 of 19 trees possessed nodules within 10 cm of the soil surface; the average length of each nodule was 1.7 mm. These nodules increased in frequency with increasing depth below the surface to their maximum sampling depth of 3 m. The nodules were weakly attached to roots less than 0.5 mm in diameter. These authors also found abundant insect frass and body parts in the vicinity of the roots and suggested that nodule predation by insects may have occurred. Virginia (1986) found that soil Rhizobia populations increased with soil depth to a maximum concentration at the upper margins of ground water. Johnson and Mayeux (1990) suggest that since soil NO_3 can prevent N fixation, nodule formation may occur in deeper soils with lower NO_3 concentrations. Jenkins and others (1988, 1989) found seasonally fluctuating populations of Rhizobia at 0 to 9 m depth in soil columns collected in playas, dunes, arroyos, and grasslands in California and New Mexico. Their data suggest that soil salinity, age of the host plant, and ground water depth and fluctuations determine Rhizobia distribution and type. Presumably, the location and density of nodulation in the mesquite root zone correspond to these populations.

Considerable logistical difficulties must be overcome for field identification of nodules, given their fragility, small size, and the depths at which they are found. Johnson and Mayeux (1990) failed to find nodules under mesquite in western Texas, New Mexico, and Arizona despite $\delta^{15}N$ analysis that suggested that these mesquite were utilizing atmospheric N. These authors speculated that they may have simply failed to locate the soil nodules since nodule formation may be of an ephemeral nature, as has been suggested by Bailey (1976) and Zitzer and others (1996).

Conversely, mesquite seedlings can form nodules under controlled conditions. Bailey (1976) identified root nodules produced by *P. glandulosa* seedlings grown in a growth chamber. Frequency of nodulation was statistically correlated with soil texture, water, and the abundance of Rhizobia; wet sandy soils produced the most nodules, while dry clayey soils produced the least. Felker and Clark (1980) also found nodules formed when both *P. glandulosa* varieties were grown in vermiculite, furnished with a nutrient solution free of N, and inoculated with soil Rhizobia collected from the nodules of a mesquite grown in a separate nodulation experiment (Eskew and Ting 1978).

Historical Range Expansion of Mesquite

Much of the information on mesquite expansion in the Southwestern United States comes from anecdotal observations of ranchers and other rangeland users, published reports, and repeat photography (figs. 2–6). In one of the earliest scientific reports on the subject, Griffiths (1910) reported his observations of increasing mesquite populations on the Santa Rita Experimental Range south of Tucson, AZ, and speculated that overgrazing was one of the primary contributing factors. Hastings and Turner (1965) present repeat photography that documents increases in *P. velutina* on southern Arizona rangelands. They found that much of the increase in mesquite occurred after 1880. A recent update of Hastings and Turner (1965) shows that mesquite has also increased between the mid-1960s and mid-1990s, indicating that the expansion has not ceased (R.M. Turner, written communication, 1999).

Estimates of the rate of recent mesquite establishment in open rangelands vary widely. Hennessy and others (1983) determined that a black grama (*Bouteloua eriopoda*) grassland on the Jornada Experimental Range in southern New Mexico was completely converted to mesquite woodland between 1934 and 1980. Gibbens and others (1992) compared mesquite density on the Jornada in herbicide-treated areas in 1976 and in 1988 and noted an increase from 67 to 494 plants/ha. These authors also estimated that on the College Ranch in New Mexico, *P. glandulosa* increased from 130 plants/ha in 1982 to 147 plants/ha in 1988. Using data provided by Glendening (1952), Gibbens and others (1992) estimated that *P. velutina* increased in a 17-year period on the Santa Rita Experimental Range at the rate of 9.2 plants/ha/year in areas with livestock grazing, and at the rate of 15.7 plants/ha/year in areas where livestock and rodents were excluded. Felker and others (1990) noted that *P. glandulosa* stands can regenerate to a density of 10,000 stems/ha, with an average trunk diameter of 4 cm, 10 years after land has been cleared. To predict future growth of *P. velutina* stands, Chojnacky (1991) developed a model using basal area, stems per stand, trees per stand, and average tree height data from 47 locations in southern Arizona. This model is mainly applicable to short-term projections, since it does not account for mesquite mortality. Using the model with a 30-year projection, this author noted that initial basal area was probably

the most important variable influencing growth rate; for a stand with an initial basal area of 18.5 m^2/ha the stand volume increased from approximately 62 to 80 m^3/ha within 10 years, followed by a reduction to the initial volume in the last 20 years. Implicit in this model is the idea that mesquite stands that occur in locations with abundant resources will experience a rapid increase in size, then decline through intraspecific competition.

Mechanisms of Mesquite Range Expansion

Mesquite have the ability to access ground water using a deep root system, grow in a variety of soil types and in the variety of climatic conditions found in the Southwestern United States, and can indirectly access atmospheric N. Therefore, mesquite can avoid the resource limitations that restrict the establishment and maintenance of competing plants in the majority of the habitats in which they are found. With this relative independence, why have mesquite moved into open grasslands from adjacent riparian or ephemeral channels only within the past century? While much research has been focused on the mechanisms of recent mesquite dispersal into open grasslands (Archer and others 1988; Bahre 1985; Bahre and Shelton 1993; Cox and others 1993; Grover and Musick 1990; Humphrey 1958; Reynolds and Glendening 1949; Schlesinger and others 1990), little attention has focused on why mesquite had not occupied these areas prior to the past 150 years.

Fire

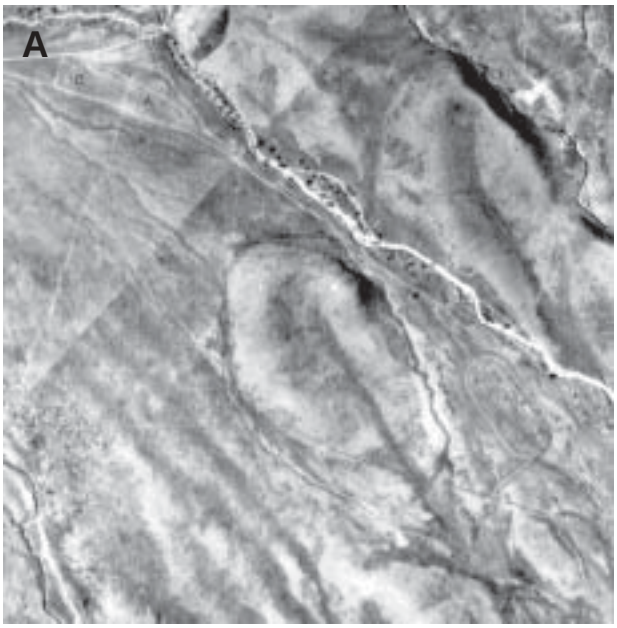
Mesquite range expansion has been attributed to altered land-management practices associated with cattle ranching (Bahre and Shelton 1993). Fires have been actively suppressed during the past century to minimize damage to vegetation, livestock, and property; in addition, cattle grazing has reduced herbaceous fuel loads, thereby reducing fire frequency (Van Auken and Bush 1997). Before widespread settlement by Euro-Americans, Native Americans regularly set wildfires in desert grasslands (Bahre 1985). Over long periods, these fires presumably minimized mesquite seedling establishment in open areas while allowing the continued presence of mesquite in sheltered drainage and riparian areas. Now, occasional fires occur with uncertain long-term effects (fig. 7).

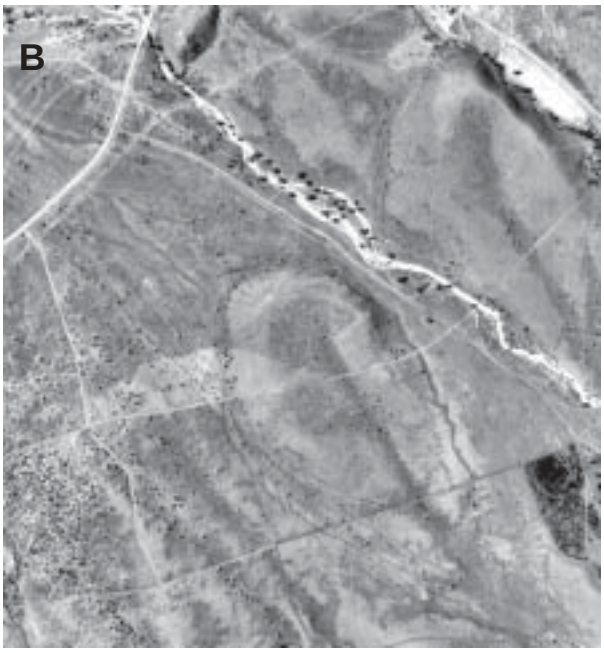
Figure 7—June 1999. Effect of rangeland fire on *Prosopis velutina* woodland on eastern foothills of the Huachuca Mountains, southeastern Arizona. Note the mesquite tree (*P. velutina*) in the right foreground appears to be largely undamaged by fire (photograph by Thomas Wilson).

At the Fort Huachuca Military Reservation, we located three adjacent sites of different fire frequency but equivalent topography and soil type (fig. 8). These sites are separated by a network of roads that function as firebreaks. The site with less than one fire per decade for the past 30 years had 4.75 kg/m^2 of *Prosopis velutina* aboveground biomass; the site with an average of two fires per decade for this time period had 0.52 kg/m^2; and the site with an average of four fires per decade had 0.078 kg/m^2 (Biggs 1997). The ratios of *P. velutina* biomass to grass biomass were 116:1 on the unburned site, 3:1 on the site with two fires per decade, and 1:2 on the site with four fires per decade.

Seed Dispersal

Mechanisms of seed dispersal are likely to play a key role in the dynamics of mesquite distribution (Brown and Archer 1989). Janzen and Martin (1982) suggested that mesquite thrived in open grasslands as recently as 10,000 years ago. During the Pleistocene, horses, elephants, and ground sloths served as the





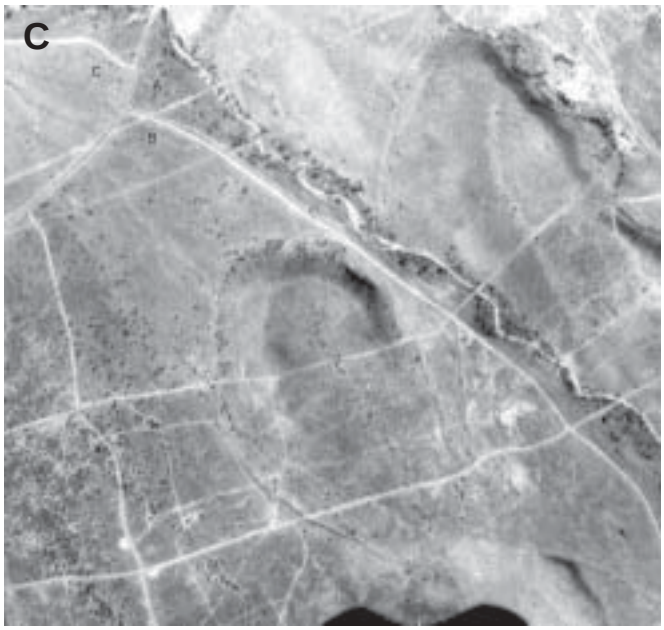


Figure 8—Aerial photographs of Woodcutter's Canyon in the southeastern gunnery ranges at Fort Huachuca Military Reservation in southeastern Arizona. Note that the road system changes through time but the topography is consistent among these photos. The letters A, B, and C refer to plots intensively studied by Biggs (1997), Biggs and others (1999), and Wilson and others (1999) for the effects of fire frequency on soil-nutrient concentrations and mesquite stand densities. (A) 1935. Individual mesquite (*P. velutina*) are mostly confined to washes at the upper right, center, and lower left. A prominent line from upper right to middle left is a fence line, a residual of livestock grazing in the area that ended in the early 1940s. Note that no mesquite occur on sites A, B, and C. (B) November 17, 1956. By 1956, mesquite trees are scattered throughout the view, although large sections of grasslands remain without trees, particularly at right. The modern road system, which also serves as a firebreak system, was established just before this time. The stand density of mesquite on sites A, B, and C is approximately equal; all three sites had disturbances related to World War II training exercises. (C) January 18, 1975. Mesquite

Fig. 8 (con.)

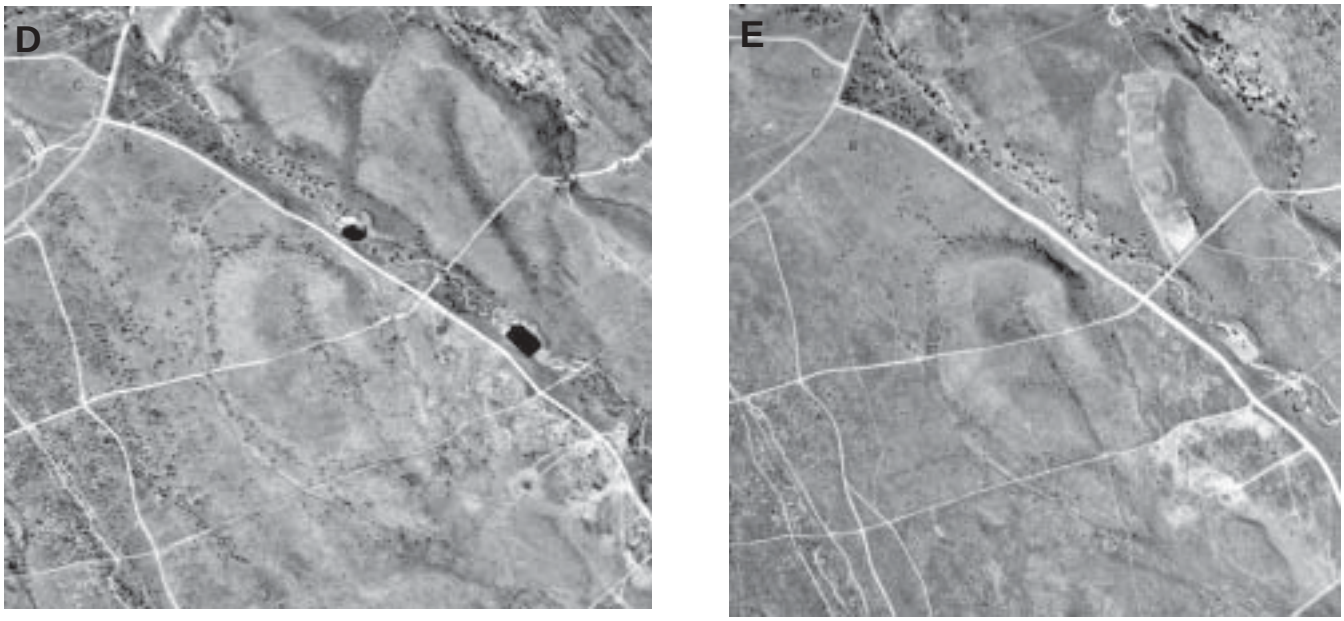


Figure 8 (Con.)

stands have become quite dense in some portions of the view, particularly at lower left. Mesquites have continued to increase on site A, which did not burn in the 20th century. Site C burned shortly before this photograph, resulting in its light color in this photograph, and mesquite trees are not very visible on this site in 1975. (D) January 20, 1985. Mesquite stand densities are highest in 1985, particularly in the rangelands at left. Site C, which had a fire frequency of four fires per decade between the early 1970s and 1989 (Biggs 1997), remains free of significant mesquite. In the same period, site B had a fire frequency of two fires per decade, and mesquite trees are scattered uniformly at a lower density than sites at lower left. Mesquite density on site A continued to increase because of lack of fires. The difference between the burned sites and site A is reflected by differences in albedo. (E) March 31, 1994. Because of wildfires set during military exercises, mesquite stand densities may be significantly lower on much of the rangeland, particularly at lower left. However, the size of individual plants is much lower, reflecting resprouting of trees damaged by fires. Because of the lack of fires, site A consequently has a high stand density and large size of individual mesquite trees (Biggs and others 1999). For these reasons, site A clearly is distinguishable from sites B and C as well as the rest of the rangeland. For these reasons, the Southern Gunnery Range at Fort Huachuca serves as a good example of our management objective C, the limited control of mesquite on rangelands.

primary seed-dispersal agents, ingesting mesquite fruit and subsequently depositing scarified seed at fecal sites. Martin and Burney (1999) also suggest that many of the characteristics of mesquite—sharp spines, waxy leaves, sweet-tasting fruit, and the ability to readily resprout following herbivory—evolved with ancestral megafauna. This prevented overgrazing while promoting fruit consumption and seed dispersal. With the extinction of these large mammalian herbivores, mesquite were found less frequently in open areas but persisted in drainages and riparian areas, where they were more resistant to environmental perturbations such as drought or fire, and where their seeds became dispersed through surface-water transport (Grover and Musick 1990).

Adjacent drainages and riparian areas offer more favorable growing conditions compared to open grasslands: improved moisture and nutrient availability through surface-water transport, reduced maximum air temperatures, and some protection from wind and fire. However, mesquite are currently thriving on open grasslands, and are providing an environment favorable for the establishment of other woody shrubs such as prickly pear cactus (*Opuntia lindheimeri*), desert hackberry (*Celtis pallida*), hog plum (*Colubrina texensis*) (Archer and others 1988), and perennial grasses such as bush muhly (*Muhlenbergia porteri*) (Haque and others 1991). Birds, rodents, and insects acting as seed dispersal agents for shrub species may be attracted to mesquite canopies for shade and reduced visibility, incidentally transporting seed to the soil below (Archer and others 1988). Consequently, the shrubs germinating from these seeds might become established because areas under mesquite canopies provide most of the same resources and protection from the elements as riparian areas.

Livestock Grazing

Cattle grazing is believed to be a major cause of the contemporary range expansion of mesquite trees. Through grazing, cattle limit herbaceous competition for germinating mesquite seedlings, creating more open areas with access to sunlight. Cattle ingest mesquite fruit, consequently transporting the seed, scarifying it, then depositing it in a moist, nutrient-rich microenvironment. Brown and Archer (1987) compared seedling emergence on sites with and without cattle. They found 12 to 15 seedlings/m in the former case and no seedlings in the latter. Brown and Archer (1989) maintain that as seed dispersers, cattle are surrogate megafauna, resuming relationship between mesquite and large mammals that last existed in the latest Pleistocene.

Cattle indirectly facilitate the establishment of other shrubs under mesquite by augmenting soil nutrient concentrations. Cattle tend to congregate under the shade of mesquite trees, where they deposit abundant feces, providing supplemental N to the soil that adds to the elevated N concentrations that result from litterfall. Livestock therefore contribute to the redistribution of nutrients from open rangelands to beneath mesquite canopies.

Livestock grazing facilitates mesquite establishment in open grassland ranges but reduces the biomass of native grasses by at least three mechanisms. First, as mesquite woodlands comprise a larger portion of the aboveground biomass within an area, the grazing intensity on the remaining grasses increases because shrubs and trees are less palatable than grasses (Grover and Musick 1990). Second, mesquite woodlands can form a canopy that inhibits native grass seed germination as suitable microclimates become more spatially restricted. Third, mesquite trees sequester nutrients, making intertree areas relatively nutrient poor (Biggs 1997).

Eventually, mesquite growth may inhibit grazing. Archer and others (1988) used aerial photographs taken in 1941, 1960, and 1983 to monitor closed-canopy woodlands and woody plant groupings centered around *P. glandulosa* within grasslands on the Rio Grande Plains of Texas. Within the grassland, they found that half of the groupings were less than 5 m apart and 95 percent were within 15 m. These authors predicted that these gaps would diminish as individual canopies grew because the mean area for each grouping increased from 494 m^2 to 717 m^2 (+70 percent) between 1941 and 1983. Seedlings, composed mainly of *P. glandulosa,* occupied 85 percent of the open areas (Archer and others 1988). Eventually these trees can form an impenetrable thicket, restricting livestock traffic and increasing the cost of livestock management (Teague and others 1997).

Mesquite stands may continue to increase in size on open ranges after cattle grazing has been eliminated (Brown 1950; Brown and Archer 1989; Glendening 1952). Once seed has been dispersed into open areas and mesquites have become established, a constantly renewed seed bank and seed viability that can last for 20 years (Martin 1970) ensure that mesquite could persist on open rangelands. For example, at the Fort Huachuca Military Reservation in southeastern Arizona, cattle grazing has been eliminated since the mid-1940s. However, aerial photographs of the region from 1935 to 1994 document the continued increase of mesquite in open rangeland 50 years after cattle grazing was terminated, despite periodic grassland fires that appear to affect average canopy size (fig. 8). While maximum stand densities continue to exist within riparian areas, populations of established trees and seedlings in grasslands persist to form woodlands of greater than 80 trees/ha at Fort Huachuca (Wilson 2001).

Climate Fluctuations and Atmospheric Gases

An increase in the relative contribution of winter rains to annual precipitation can favor the germination and establishment of certain shrub species, including mesquite (Sala and others 1997). Mesquite and many common shrubs in the Southwestern United States have a C3 photosynthetic pathway, deciduous habit, a moderate transpiration rate, drought avoidance, low herbivory, high seed production, many germination requirements, high survival following disturbance, and slow recruitment (Diaz and Cabido 1997). Grasses in this region are C4 plants with a high leaf area, a shallow dense fine root system, a high transpiration rate, low to moderate drought resistance, moderate herbivory, moderate seed production, few germination requirements, and low survival after disturbance but rapid reestablishment. Changes in the seasonal pattern of soil-water potential is reflected in the relative abundance of C3 shrubs verses C4 grasslands in a region (Sala and others 1997). Shrubs favor winter precipitation for seed germination and vegetative growth, while grasses are more responsive to warm-season rainfall, suggesting that changes in seasonal precipitation may drive rangeland conversions from grasses to shrubs.

Changes in climate in the Southwestern United States during the 20th century have been documented (Hastings and Turner 1965) and disputed (Bahre 1991). To evaluate climatic variation in southwestern New Mexico and southeastern Arizona, we standardized seasonal precipitation using the technique of Hereford and Webb (1992). We identified the two ecological precipitation seasons of summer

(July through September) and winter (November through March). For winter precipitation, November and December totals were considered part of the following year. For each climate station that we used (tables 1–2), we calculated the standardized seasonal precipitation, P_s, by

$$P_s = \Sigma\{\Sigma[(x_{ij} - \mu_i)/\sigma_i]/k\}/n, \qquad (1)$$

where $x_{i,j}$ = monthly precipitation for climate station i in month j (mm); μ_i = the mean and σ_i = the standard deviation of monthly precipitation for climate station i (mm); k = the number of months in the season; and n = the number of climate stations with data. The value of n varies through the 20th century due to the varying number of available climate stations (for example, tables 1–2) and whether or not data are missing.

Annual and seasonal precipitation in southwestern New Mexico and southeastern Arizona has varied during the 20th century (figs. 9–11). From 1980 through 1998, 15 and 12 years had above-average annual precipitation in southwestern New Mexico and southeastern Arizona, respectively (fig. 9). Annual precipitation from about 1940 to 1980 was generally below average, particularly in the mid-1950s. The results displayed in figure 9 confirm previous work that suggests that annual precipitation in the Southwestern United States is nonstationary (Hereford and Webb 1992; Webb and Betancourt 1992).

Seasonal precipitation also varies between years. In southwestern New Mexico and southeastern Arizona, 12 years had above-average winter precipitation between 1980 and 1998, compared to 12 years of above-average winter precipitation during the previous 40 years (figs. 10–11). Between 1900 and 1998 in southeastern Arizona, winter or summer precipitation (but not both) was above average for 51 years; of these, 28 years had above-average winter precipitation with below-average summer precipitation. The period from 1895 to 1906 included only 3 years of above-average precipitation, and those only occurred during the summer (fig. 11A). However, 10 of the following 11 years had above-average winter precipitation, coinciding with the range expansion of mesquite observed by Griffiths (1910). These weather patterns may have significantly contributed to this expansion by optimizing environmental conditions for enhanced mesquite seed germination. More recent increases in winter precipitation could be manifested in an accelerated rate of mesquite establishment during the past 20 years as observed by ranchers in the Southwestern United States.

The 27 percent increase in atmospheric CO_2 from 1900 to the present has been cited as a contributing

Table 1—Climate stations in the western Chihuahuan Desert grassland.

State	Location	Elevation	Period of record	Annual precipitation
		m		*mm*
Arizona	Bowie	1,149	1-1-1899 to 12-31-1998	273
Arizona	Chiricahua National Monument	1,616	1-1-1909 to 12-31-1998	493
Arizona	Clifton	1,058	1-1-1893 to 12-31-1998	328
Arizona	Douglas	1,232	7-1-1948 to 2-28-1994	371
Arizona	Douglas FAA Airport	1,250	7-2-1948 to 12-31-1998	333
Arizona	Douglas Smelter	1,210	12-1-1903 to 3-20-1973	312
Arizona	Duncan	1,116	5-21-1901 to 12-31-1998	276
Arizona	Paradise	1,655	1-1-1906 to 8-31-1937	484
Arizona	Portal	1,524	1-1-1914 to 3-31-1955	442
Arizona	Portal 4SW	1,643	3-1-1965 to 12-31-1998	546
Arizona	Safford	884	8-1-1998 to 6-30-1973	226
Arizona	Safford Agricultural Station	899	8-1-1948 to 12-31-1998	234
Arizona	San Simon	1,101	3-1-1898 to 12-31-1998	244
Arizona	San Simon 9ESE	1,183	7-19-1962 to 7-31-1986	251
Arizona	Willcox	1,274	6-1-1898 to 12-31-1998	311
New Mexico	Animas	1,345	9-1-1923 to 12-31-1998	280
New Mexico	Columbus	1,268	1-1-1925 to 12-31-1998	242
New Mexico	Deming	1,311	1-1-1914 to 12-31-1998	240
New Mexico	Eicks Ranch	1,619	1-1-1933 to 10-31-1961	373
New Mexico	Hachita	1,375	1-1-1914 to 12-31-1998	269
New Mexico	Lordsburg	1,296	1-1-1914 to 12-31-1998	275
New Mexico	Redrock	1,265	1-1-1914 to 12-31-1998	324
New Mexico	Rodeo	1,256	1-1-1914 to 12-31-1998	285
New Mexico	White Signal	1,851	11-1-1948 to 12-31-1998	381

Table 2—Climate Stations in the southeastern Arizona Desert grassland.

State	Location	Elevation	Period of record	Annual precipitation
		m		*mm*
Arizona	Apache Powder Company	1,125	7-1-1923 to 4-30-1990	335
Arizona	Arivaca	1,105	1-1-1956 to 12-31-1998	455
Arizona	Benson	1,119	6-1-1894 to 5-31-1975	288
Arizona	Elgin	1,494	10-1-1912 to 12-31-1969	383
Arizona	Fort Huachuca	1,424	2-1-1900 to 12-31-1981	397
Arizona	Nogales	1,162	7-1-1948 to 6-30-1983	421
Arizona	Nogales 6N	1,085	10-1-1952 to 12-31-1999	450
Arizona	Old Nogales	1,189	12-1-1892 to 6-30-1948	399
Arizona	Patagonia	1,233	7-1-1921 to 12-31-1998	454
Arizona	San Rafael Ranch	1,445	12-1-1892 to 3-31-1968	439
Arizona	Santa Rita Experimental Station	1,311	7-1-1916 to 12-31-1998	566
Arizona	Sierra Vista	1,402	3-1-1982 to 12-31-1998	374
Arizona	Tombstone	1,405	7-1-1893 to 12-31-1998	354
Sonora	Agua Prieta	1,189	2-1-1961 to 12-31-1986	379
Sonora	Cananea	1,607	1-1-1923 to 10-31-1991	539
Sonora	Naco	1,404	1-1-1923 to 12-1-1995	368

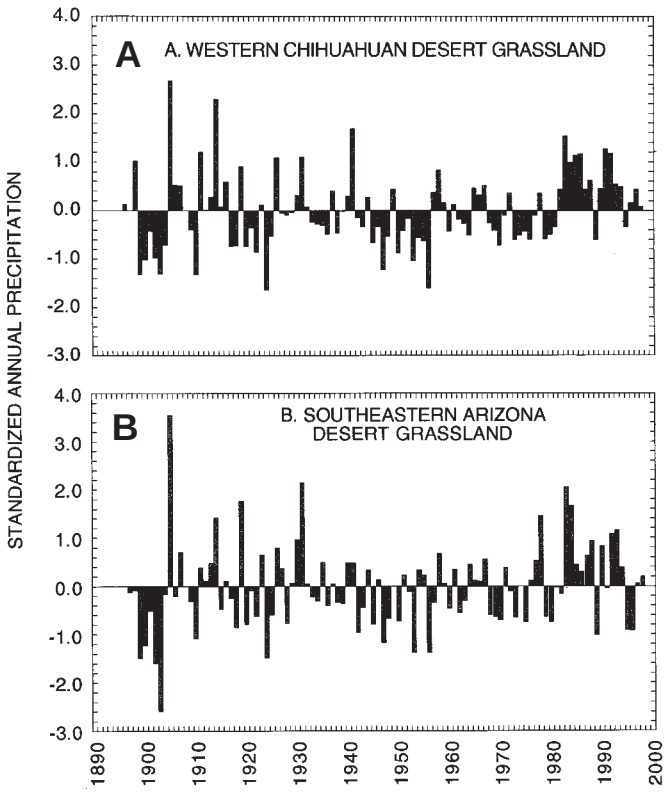


Figure 9—Standardized anomalies of annual precipitation. (A) Grasslands of the western Chihuahuan Desert. (B) Grasslands of southeastern Arizona.

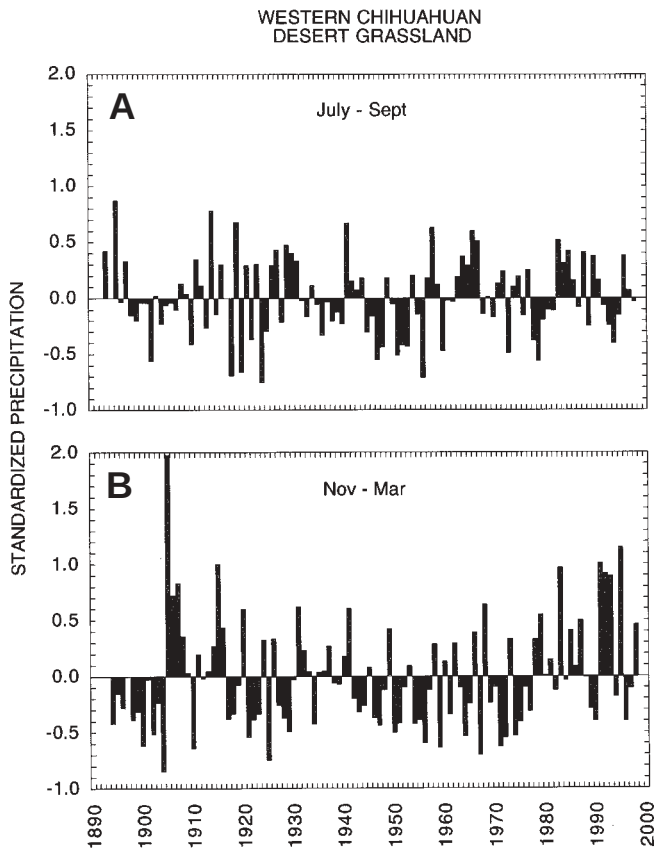


Figure 10—Standardized anomalies of seasonal precipitation in grasslands of the western Chihuahuan Desert (table 1). (A) Summer precipitation (July through September). (B) Winter precipitation (November through March).

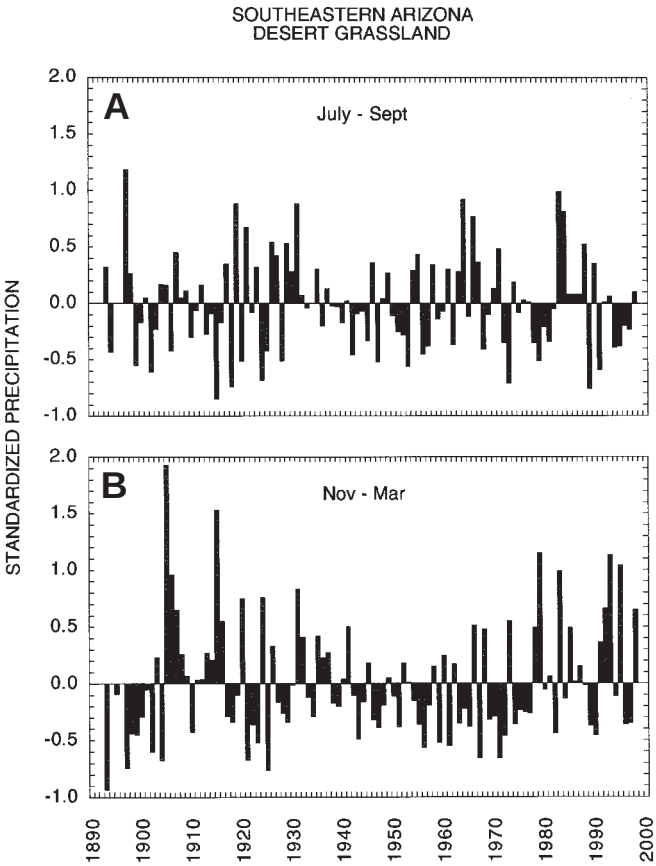


Figure 11—Standardized anomalies of seasonal precipitation in the desert grasslands of southeastern Arizona (table 2). (A) Summer precipitation (July through September). (B) Winter precipitation (November through March).

factor in mesquite range expansion. Polley and others (1994) observed increased nodulation and N fixation when greenhouse-grown *P. glandulosa* seedlings were exposed to elevated CO_2 concentrations. These seedlings also produced more belowground biomass, and their N and water-use efficiencies increased linearly with increasing atmospheric CO_2 concentrations. Conversely, mesquite seedlings grown with little bluestem (*Schizachyrium scoparium*), a C4 perennial grass, manifested none of these characteristics. The authors suggest competition with grasses attenuates the beneficial effects of increased atmospheric CO_2 on mesquite. In the absence of this competition, mesquite seedlings can establish more rapidly.

Mesquite Management Practices

Because of mesquite expansion into open rangelands, with resulting reductions in livestock forage, land-use managers have employed a variety of tactics—fire, herbicide, and physical removal—to completely remove existing trees and limit further spread. These practices all have something in common: logistical difficulties and side effects potentially harmful to habitat restoration. For example, ranchers at the Waggoner Ranch (202,000 ha) in northern Texas have attempted to remove mesquite since the 1950s without effect, and it continues to regenerate in treated areas and spread further. Attempts at control have been largely terminated due to increasing costs (Teague and others 1997).

Prescribed Burning

Fire has been used as a management tool to control mesquite distribution for decades (Humphrey 1949). However, mesquite trees can survive fire while still relatively young. Wright and others (1976) determined that while *P. glandulosa* seedlings up to 1.5 years of age were easy to kill with medium intensity fires, 2.5-year-old trees survived with severe damage, and 3.5-year-old trees were tolerant; these authors recommended against using fire as a management tool in overgrazed areas. Archer and others (1988) found similar results. Martin (1983) determined that within 5 years of a fire in southern Arizona *P. velutina* biomass had attained preburn levels. In these cases cattle grazing could increase mesquite survival rates by not only lowering fire frequency through fuel removal (Van Auken and Bush 1997), but fire intensity as well. Hobbs and others (1991) found that grazing reduced fire temperature and energy release in a tallgrass prairie.

Livestock grazing alters rangeland fire characteristics in the following ways. Consumption and trampling by livestock can lower the density and average height of herbaceous biomass. In turn, this can affect the average height and duration of a fire; in many cases, flames may not reach the canopies of reproductively mature mesquite. After a fire, mesquite below a certain size class can be reduced in numbers; however, given the survival rate of larger reproductively mature trees, recruitment would continue as the larger trees replenish the mesquite seed bank.

Since mesquite trees appear largely impervious to individual fires, repeated burning has been recommended (Wright and others 1976). In this case, the fires would need to occur at a frequency that would prevent the recovery from damage inflicted by previous fires, and it assumes that sufficient fuel would accumulate in the periods between fires. While this might provide an effective management tool to limit the distribution of mesquite of certain size classes, it could also provide the conditions that facilitate the establishment of exotic plant species better adapted

than native grass species to cope with frequent disturbance, such as Lehmann lovegrass (*Eragrostis lehmanniana*) (Martin 1983; Wilson and others 1999). This is an important point to consider when attempting to restore desert grasslands to historic species compositions.

Herbicide Application

Herbicides have also been employed to control the spread of mesquite. In a 3-year study, aircraft applied 1.12 kg/ha of 3,6-dichloropicolinic acid (clopyralid) (Jacoby and others 1981). Subsequent monitoring over a 2-year period showed that this agent was significantly more effective at killing mesquite than 2,4,5-T and picloram applied at the same rate, with 60 to 68 percent mortality. Jacoby and others (1981) observed that clopyralid was not effective in killing associated shrub and succulent plants such as saltbush (*Atriplex* sp.) or prickly pear (*Opuntia* sp.). In another study, Jacoby and others (1982) determined that dead mesquite serves to protect germinating forage plants from grazing, allowing significant increases in forage production.

Subsequent studies have attempted to quantify the effects of herbicide treatment based upon mesquite morphology. Jacoby and others (1990b) determined that mesquite with multiple stems were significantly more resistant to mortality from a variety of herbicides including clopyralid, triclopyr, picloram, and 2,4,5-T. Though they determined that clopyralid was the most effective herbicide, mortality decreased from 55 percent for single-stemmed trees, 35 percent for three- to five-stemmed trees, and 19 percent for trees with greater than five stems. These authors suggest that the greater canopy coverage for multiple-stemmed trees is more effective in preventing herbicides from penetrating the soil under the canopies. In contrast, they did not find a significant relationship between tree height and herbicide-induced mortality (Jacoby and others 1990a).

The epicuticular wax found on mesquite leaves can minimize the effects of foliage-absorbed herbicides. Mayeux and Wilkinson (1990) suggest that herbicides applied in an oil spray are more effective than aqueous sprays. Jacoby and others (1990c) found that leaf epicuticular wax increased through the growing season, then stabilized or decreased in late summer. These authors also found individual differences in the amount of leaf epicuticular wax within populations and suggest that over time these trees could represent a greater portion of the population as the selective pressure of foliage-absorbed herbicide applications eliminated trees with less leaf epicuticular wax.

Jacoby and Ansley (1991) evaluated the effects of herbicide applications during various seasons. They found the most effective herbicide—clopyralid—induced the greatest mortality (92 percent) when applied during September. These authors suggested that herbicide applications during the late summer are most effective, and nearby agricultural areas are less susceptible to treatment effects at that time.

One negative effect of herbicide treatment is the potentially deleterious effects on the environment and biodiversity within open rangeland. Nolte and Fulbright (1997) monitored plant and animal biomass for 2 years following treatment of mesquite with a mixture of picloram and triclopyr. They found no differences in vegetation, rodent, and avian species richness between control plots and treatment areas, although they noted that annual precipitation was 16 percent above average during this period, possibly attenuating the deleterious effects of the herbicide.

This study and the ones previously mentioned (Jacoby and others 1981, 1982, 1990a,b,c, 1991) were conducted within a 10-year period or less, and only monitored the effects of a single herbicide application. To completely remove mesquite or at least limit its spread in open rangeland using herbicides only, multiple treatments are required; otherwise, the long-term viability of mesquite seeds and their abundance within the seed bank would ensure continual recruitment.

These multiple applications could create adverse side effects to rangeland species diversity and biomass not recognized from the results of a single treatment. In a study that evaluated impacts of repeated herbicide applications on biodiversity, Gibbens and others (1986) applied 2,4,5-T to *Prosopis glandulosa* within dunelands in southern New Mexico during 3 consecutive years. They found mesquite mortality to be 54 percent, without specifying if any specific age class of mesquite were particularly susceptible. These authors also determined that residual 2,4,5-T in the soil dissipated rapidly, and was not detected 131 days after treatment. While they found lower indices of microbial activity on treated areas, they attributed this to lower carbon availability as the mesquite trees were defoliated. Overall, the authors found a decrease in avian species diversity on treated areas but no differences in arthropod or rodent diversity. Since this was a 3-year study, no data were presented on the rate of mesquite recruitment following the herbicide treatment. Although these results appear promising, mesquite mortality after 3 consecutive years of herbicide applications accounted for just over half of the trees in the study area. This implies that these treatments would have to continue at a fairly regular interval for many years to create a significant long-term reduction in mesquite populations. With the attendant costs of herbicides and aerial application over large areas, a viable long-term management strategy using only herbicides may be impractical.

Mechanical Removal

Mesquite physical removal is another management tactic. Roller chopping and shredding can reduce plant density, stature, and canopy cover immediately following treatment, but subsequent basal resprouting can create greater stem densities (Dodd and Holtz 1971). Other techniques include root plowing, chaining, and dozing. While these tactics may kill existing mesquite, the woody debris is often left in place, therefore impeding navigation through these areas and limiting available space for livestock forage (McPherson and Wright 1986). In addition, mechanical removal may negatively affect other plant and animal species. For example, driving large mechanical equipment through rangeland can cause soil compaction, crush animals, destroy animal burrows, and uproot desirable plant species such as perennial grasses. The extent of these effects remains unknown.

Mesquite Management Objectives

This paper has mainly discussed the negative impacts of mesquite population expansion onto open rangeland. However, mesquite wood is prized as a material for furniture, and the wood is also used for cooking, with an estimated value of $400/ton as barbeque chips (Felker 1996). Some characteristics of the wood, such as hardness and shrinkage, are considered equivalent or superior to mahogany, oak, and walnut (Felker and others 1990), with lower rates of expansion and contraction due to changes in ambient humidity. While still nascent, the mesquite lumber industry in Texas generates $5 to 10 million per year (Felker 1996).

Mesquite seed pods are high in carbohydrates, providing a rich energy source for wildlife, livestock, and humans (Felker 1998). Mesquite trees also provide habitat for birds, small mammals, reptiles, and insects, increasing biodiversity and recreational opportunities (McPherson 1997). Therefore, completely removing mesquite trees from open rangeland may not only be an unrealistic objective, it may actually lower the profitability of this rangeland to land-use managers. For this reason, management objectives and their implications should be clearly articulated when formulating a management strategy.

For example, if the management objective is the complete removal of mesquite trees from open rangeland, the long-term commitment of resources to this task might not be a realistic goal for many land-use managers. Instead, a compromise may have to be reached, whereby the density of mesquite stands are reduced to the point that land-use activities such as cattle ranching may be efficiently practiced, while recognizing that these trees will continue to exist on open rangeland. Periodic burning of this open rangeland may therefore not entirely remove mesquite, but will lower its density to the point that cattle may find sufficient forage, and ranchers may avoid navigating within dense woodland. Overall, land-use managers have a choice of three management objectives. They are described as follows, with the specific procedure or combination of procedures that may be most effective.

Objective 1: Complete Mesquite Removal From Desert Grassland

This option is considered by those who wish to restore desert grasslands to their historic (within the past 150 years) species compositions. To completely remove mesquite trees, two points need consideration. First, one has to consider the prodigious commitment of resources in terms of personnel, materials, time, and expense. Second, complete removal of mesquite does not necessarily result in the restoration of desert grassland. If mesquite range expansion represents a form of disturbance to the grassland plant community, then efforts to remove it represent another. Exotic plant species better adapted to various disturbance regimes may have a competitive advantage over native grasses in exploiting this disturbance. For this reason, a management strategy would have to include continual monitoring and persistent removal of mesquite and other undesirable plant species. Where possible, documentation of the rate and extent of mesquite spread in the management area could help determine the extent of management efforts necessary for removal. This documentation would include dated aerial photographs and interviews with local residents.

A suggested management tactic is a combination of mechanical removal and/or herbicide treatment followed by prescribed burning. If prescribed burning is scheduled after allowing the mechanically displaced woody debris to dry sufficiently for combustion, then this may allow the surviving mesquite to resprout. These resprouts could then be killed back by the subsequent fire. McPherson and Wright (1986) recommended that areas to be burned should be suspended from livestock grazing for at least a previous growing season so that herbaceous dry matter could accumulate. They also recommended conducting a small test burn to verify the efficacy of a prescribed burn within a given time period. Over time, periodic prescribed fires could be used to destroy emerging mesquite seedlings. The rate of mesquite reestablishment in this area would depend on the size of the existing seed bank, the density and distribution of mesquite stands in adjacent areas, and the mechanisms of seed dispersal from those adjacent areas.

To satisfy this objective, land-use managers could identify and protect rangelands that are currently devoid of mesquite, such as the desert grassland north of Sonata in southeastern Arizona (fig. 1). Since the seed bank in these areas would be largely devoid of mesquite, potential seed dispersers would have to be monitored and controlled. Due to the high rate of mesquite establishment in rangelands, these mesquite-free areas are becoming more limited in size. Preventing mesquite establishment is less difficult than removing it, though this may be unrealistic in areas that contain livestock.

Objective 2: Continued Mesquite Establishment in Desert Grassland

This objective may be implemented by ranchers who lack the resources necessary for range control or by researchers who wish to study the current and future rate and extent of mesquite establishment on open rangelands. Because the N-fixing capability of mesquite can elevate soil N concentrations within the rangeland, exotic plants that have higher N requirements could become established. Even a management objective of nonintervention would have to include continued monitoring of rangeland for potentially invasive species.

The implementation of any of the other management objectives will become more difficult with time as the mesquite alter soil-nutrient concentrations and create a long-lasting seed bank. Therefore, a long-range forecast of land use in these rangelands is advisable before implementing this objective.

Objective 3: Limited Mesquite Removal From Desert Grassland

This objective is probably the most feasible alternative for most land-use managers, including those who have limited resources for rangeland control, and/or those who wish to profit from the beneficial aspects of limited mesquite establishment on rangeland. Prescribed fires combined with limited grazing and an initial herbicide application are recommended management tactics in this case. Ansley and others (1996) determined that while intense fires may kill all aboveground portions of mesquite, basal resprouting may quickly produce an impenetrable grove. These authors suggested that lower intensity fires may kill small mesquite while allowing larger individuals to survive with intact upper canopies; this can create a park effect with enhanced visibility beneath stand canopies. Since the main stems of the larger mesquite remain intact, resprouting would be minimized.

By minimizing multistemmed resprouting, the average stem diameter of mesquite stands would be larger, increasing the commercial lumber value. Ansley and others (1998) thinned sections of a dense mesquite woodland from 300 to 80 trees/ha; within 5 years of thinning, trees within this section had significantly greater basal stem diameters, canopy diameters, and leaf area. Felker and others (1990) have suggested that limited removal of mesquite from rangeland may actually increase its value as lumber, as stands below maximum density tend to produce larger individuals with thicker main stems. They predicted that a spacing of 10 m per tree would produce an optimum yield. Limited grazing intensity would slow the rate of mesquite seed establishment and would also allow grasses to retain viable populations between mesquite canopies.

The parklike stands resulting from periodic prescribed fires would become more aesthetically appealing, creating opportunities for recreation and tourism while maintaining an increased biodiversity of wildlife. Ultimately, this land management system could increase the commercial value of rangeland for ranchers; commercial utilization of these areas for mesquite lumber and tourism and recreation would offset any losses in revenue from limited livestock grazing. Since this management tactic is relatively inexpensive to implement (Teague and others 1997), it can be used over a long period to ensure that these thinned mesquite stands remain stable in density.

Conclusions

After Euro-American settlement in rangelands of the Southwestern United States, mesquite moved from predominantly riparian and ephemeral-channel locations to adjacent xeric grasslands. The exact causes for this range expansion are complex and may never be fully determined. Although mesquite is native to the geographic region, its expansion into more xeric habitats resembles that of exotic invasive species, and warrants an inspection of its life history strategies, as discussed in this paper.

Although many plant species lack common features that determine whether they are invasive or potentially invasive, mesquite is uniquely qualified to occupy areas that are resource-limited to many other C3 plants. As C3 plants, they can utilize winter precipitation that is unused by C4 grasses, and their deep root system ensures that they have access to soil moisture unavailable to shallow-rooted grasses. Mesquite can indirectly access atmospheric N, a resource that is severely limited in xeric environments.

Two interdependent factors may account for increased mesquite distribution in open rangelands within the last 150 years. Seed dispersal has increased due to ingestion by livestock, and to a lesser extent by rodents. Germination and establishment of seeds has

been enhanced by increases in winter precipitation, particularly since about 1960, and decreases in interspecific competition due to livestock grazing. Ultimately, mesquite stands may increase until mesquites are only competing with each other for resources. In the absence of a land-management strategy, intraspecific competition may be the main mechanism limiting their densities in this habitat.

It is ironic that livestock grazing is one of the main dispersal mechanisms for seed, while at the same time increasing mesquite stand densities limits future grazing potential of this region. For continued use of these areas for livestock grazing, a land-management strategy is therefore mandated. This strategy must contain clearly defined objectives after determining how these areas will be used.

Of the three management objectives offered, complete removal of mesquite from open rangelands would be the most difficult to accomplish and to maintain. In contrast, nonintervention would be the easiest to implement. However, this could have undesirable consequences as exotic plant species may become established, and the biodiversity of native plants become diminished. Limited removal of mesquite from these rangelands is potentially the most realistic objective for most land use managers, as it may be relatively cheap to implement (Teague and others 1997), while actually increasing the commercial potential of this landscape.

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