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A Bibliography of Important Plant Species in the Chihuahuan Desert of North America (1904 – 2002)

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Foreword

This study was conducted for the Office of the Directorate of Environmental Programs (DAIM), Assistant Chief of Staff (Installation Management) (ACS[IM]) under project 622720896, "Environmental Quality Technology"; Work Unit CNN-T081, "ATTACC/EDYS Integration." The technical monitor was Dr. Vic Diersing, DAIM-ED-N.

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1 Introduction

Background

Army User Requirements

Documentation of the Army's environmental technology requirements has been an iterative process that began with a series of meetings in 1993 and the Office of the Directorate of Environmental Programs' publication, *U.S. Army Environmental Requirements and Needs*. The Army's environmental technology requirements describe the critical research, development, test, and evaluation needs for accomplishing the Army's mission with the least impact or threat to the environment. These requirements are Army-level requirements that were reviewed for their impacts to readiness and quality of life, impact or threat to the environment, and timeliness needed for the Army to maintain compliance with environmental regulations. All major commands, major subcommands, the Office of the Deputy Chief of Staff for Operations, and the Office of the Deputy Chief of Staff for Logistics were involved in establishing the prioritized and validated list of the Army's environmental technology requirements.

Land Capacity and Characterization is the third priority conservation user requirement. This user requirement defines the Army's need to estimate training land carrying capacity. Twenty-eight exit criteria were identified in the *Land Capacity and Characterization* user requirement. Each exit criteria defines a specific product required to address a specific aspect of the overall requirement. Several of the exit requirements require detailed understanding of installation natural resources. A comprehensive bibliography of current research in this area aids synthesis of the available data and analysis and is important to the success of the project.

Chihuahuan Desert Region

The warm deserts of North America cover an area of about 868,000 km² (MacMahon 1988). Within this area three different deserts are distinguished according to climatic and biogeographic criteria: the Mojave, the Sonoran, and the Chihuahuan deserts. The Chihuahuan Desert is the largest of the three, covering an area of 453,000 km² in the United States and Mexico. It is charac-

terized by pronounced summer precipitation (generally about 60 to 90 percent of the annual precipitation falls in summer) and relatively high elevation (generally over 1200 m) (MacMahon 1988). Generally the Chihuahuan desert is cooler than the other warm deserts of North America and has more rainfall. The yearly mean temperature for a suite of stations across the whole desert is 18.6° C (14-23° C), and the average precipitation is 235 mm (150-400 mm) (Schmidt 1986). Outwash plains, valleys, and foothills of the Chihuahuan desert have historically been dominated by grasslands (Schmutz et al. 1992). These grasslands merge at lower elevations into desert shrublands and at higher elevations into shortgrass or plains grasslands, and piñon-juniper, oak woodlands or chapparal. Over the past century, extensive areas of these desert grasslands have been encroached by shrubs (Van Auken 2000). The species of focus in this bibliography were selected because of their importance in the desert grassland and shrubland communities of the North American Chihuahuan desert. In this area, desert grassland communities are generally dominated by *Bouteloua eriopoda* (black grama) on sandy loams to clay loams, whereas in the clay rich soil in floodplains and swales (playas) extensive grasslands dominated by *Pleuraphis mutica* (= *Hilaria mutica*, *tobosa*) can be found (Schmutz et al. 1992). Desert shrublands can be dominated or co-dominated mainly by the following three shrubs: *Larrea tridentata* (creosotebush), *Prosopis glandulosa* (honey mesquite), and *Flourensia cernua* (tarbush).

Objective

The objective of this work was to assemble as much published ecological information as possible about five dominant arid land species found in the Chihuahuan Desert of North America.

Chapter 2 contains selected references that significantly contribute to the understanding of arid land ecology, but do not specifically speak about the species of interest. Chapter 3 contains reference information on *Bouteloua eriopoda* (black grama). Chapter 4 contains references on *Pleuraphis mutica* (= *Hilaria mutica*, *tobosa*). Chapter 5 contains *Larrea tridentata* (creosotebush). Chapter 6 contains *Prosopis glandulosa* (honey mesquite). Chapter 7 contains *Flourensia cernua* (tarbush). Furthermore, information gathered on an important subdominant half-shrub, *Gutierrezia sarothrae* (= *Xanthocephalum sarothrae*, broom snakeweed), is presented in Chapter 8. Chapter 9 contains reference information on the ecology of annual species.

Even though the selection of the species was based on their importance in the North American Chihuahuan desert, the literature search done for this bibliog-

raphy was not restricted to this particular geographic area. Both work completed in vegetation dominated by the species of interest as well as work investigating some aspect of their ecology was included in this bibliography. Because these species dominate such big areas in the warm deserts of North America, understanding their ecology is extremely important for land managers in this region. This bibliography, as any other bibliographical work, is not exhaustive. However, at this point in time it is important to summarize this long history of research such that a more comprehensive understanding of these species can be attained. The references here assembled will be summarized into conceptual models illustrating the differences in the ecological roles of these species. Furthermore, they can be used to parameterize simulation models that support land management decisions and can help to validate such models. The long history of research done on these species may also help us understand how shift in the emphasis of research over time affected our understanding of these species.

Approach

This bibliography was assembled using online electronic databases to find both references and abstracts (AGRICOLA, BIOSIS, Current Contents, JSTOR, Jornada LTER bibliography). Furthermore, university library catalogues from New Mexico State University, Arizona State University, and a combined catalogue of all the universities of California were searched for unpublished dissertations and theses. Several individuals at the Jornada Experimental Range (USDA-ARS) and New Mexico State University in Las Cruces contributed to this work with their knowledge concerning these species (John Anderson, Robert Gibbens, Laurie Abbott, Ed Fredrickson) and references obtained from them were used here. Some of the abstracts presented in this bibliography have been scanned with character recognition software from photocopies and originals of the references.

Scope

The literature review is limited to the Chihuahuan Region of North America and is constrained by the available documented information base. As with all bibliographies, new references become available even as this publication is being printed. We welcome your suggestions. Please email to:

jeffrey.s.fehmi@erdc.usace.army.mil.

Mode of Technology Transfer

The report and the information it contains are made available with land managers and research personnel as the primary intended audience.

This report will be made accessible through the World Wide Web (WWW) at URL:

<http://www.cecer.army.mil>

2 Community Structure and Dynamics in Arid Lands

Agnew, A. D. Q. 1997. Switches, pulses and grazing in arid vegetation. *Journal of Arid Environments* 37: 609-17.

Allred, K. W. 1996. Vegetative changes in New Mexico rangelands. *New Mexico Journal of Science* 36: 168-231.

Abstract: Rangelands in New Mexico comprise vegetative communities of woodlands, grasslands, and shrublands, and occupy about 80% of the land area of New Mexico. Composed of elements from the ancient Arcto-Tertiary and Madro-Tertiary geofloras, they have been in their present configuration only since the close of the Pleistocene; earlier rangelands experienced dramatic shifts in distribution and species composition in response to the glacial advances and retreats and were not always reconstituted in their former patterns. Vegetative changes of the last 200 years have been comparatively rapid and were sometimes in response to a suite of factors different from prior environments. Early 19th century vegetation, surmised from the writings of travelers and explorers, is contrasted with the rangeland vegetation of present day New Mexico. There has been dramatic increase, in areal extent or in density, of shrub-dominated communities, generally at the expense of grass-dominated ecosystems. The primeval occurrence of shrublands scattered throughout New Mexico is also noted, however. Introduction of numerous exotic plant species has contributed to vegetative change, as well as extirpation of plant species. Primary agents of change are reviewed, such as human activities, fire, herbivory, climate, and drought.

Archer, S. 1978. Woody plant encroachment into Southwestern grasslands and savannas: rates, patterns and proximate causes. In *Ecological implications of livestock herbivory in the West*. Editors M. Yavra, W. A. Laycock, and R. D. Pieper. Denver, CO: Society for Range Management.

Abstract: Warm temperature grasslands and savannas which characterized many landscapes in southwestern North America at the time of European settlement have been replaced by shrublands and woodlands. These changes in plant life-form composition were coincident with the introduction of large numbers and high concentrations of livestock. While a cause-effect relationship is implied, it is difficult to demonstrate, since most evidence is based on anecdotal historical accounts or descriptions from localized long-term studies, many of which are conflicting. Case studies documenting the rate, pattern and extent of vegetation change are summarized and used to illustrate how historical inconsistencies might be resolved. Where vegetation history is reasonably known, causes for changes are evaluated.

Explanations for the proliferation of weedy plants and the associated decline of graminoids have typically centered around alterations in climatic, grazing and fire regimes. Each of these factors is addressed individually and in combination. It is argued that: (1) Atmospheric CO₂ enrichment and directional shifts in climate may have occurred, but have not been sufficient, to cause the vegetation changes observed to

date: (2) Fire is not necessarily required to maintain grasslands or savannas; and (3) Although herbivory, lack of fire, atmospheric CO₂ enrichment and climate have interacted to produce recent vegetation change, selective grazing by large numbers and high concentrations of livestock has been the primary force in altering plant life-form interactions to favor unpalatable woody species over graminoids. Conceptual models illustrating the role of grazers in directing plant succession are presented in the context of ecosystem resilience, multiple steady states and positive feedbacks.

Archer, S., T. W. Boutton, and K. A. Hibbard. 2001. Trees in grasslands: biogeochemical consequences of woody plant expansion: Global biogeochemical cycles in the climate system. In *Global biogeochemical cycles in the climate system*. Editors Ernst-D. Schulze, S. P. Harrison, M. Heimann, E. A. Holland, J. Lloyd, I. C. Prentice, and D. Schimel, 115-37. San Diego: Academic Press.

Bailey, Oran F. 1967. "Water availability and grass root distribution in selected soils." M. S. Thesis, New Mexico State University.

Barbour, M. G. 1973. Desert dogma reexamined: root/shoot productivity and plant spacing. *American Midland Naturalist* 89: 41-57.

Barnard, C. M., and L. D. Potter. 1984. *New Mexico grasses. A vegetative key*. Albuquerque, NM: University of New Mexico Press.

Binggeli, P. 1996. A taxonomic, biogeographical and ecological overview of invasive woody plants. *Journal of Vegetation Science* 7: 121-24.

Branscomb, Bruce L. 1958. Shrub invasion of a southern New Mexico desert grassland range. *Journal of Range Management* 11: 129-32.

Abstract: The grazing value of a large portion of the desert grassland in southwestern United States has been greatly reduced during the last 100 to 150 years by the invasion of undesirable shrubs. Although much of the present area is now lightly infested, infestation does not have to be heavy before range productivity is seriously damaged. As the economic welfare of the Southwest depends in large measure upon its grazing and soil resources, investigations to determine the extent of shrub invasion, rate of range deterioration, and possible reasons for this retrogression in plant cover are important. In this study, records of vegetational changes, environmental conditions, and forage utilization were compiled and analyzed in an attempt to determine the extent of shrub invasion on a southern New Mexico semidesert grassland range over a thirty-year period.

Brown, J. R., J. C. Scanlan, and J. G. McIvor. 1998. Competition by herbs as a limiting factor in shrub invasion in grassland: a test with different growth forms. *Journal of Vegetation Science* 9: 829-36.

Abstract: We tested the hypothesis that seedling establishment, the critical stage in the invasion of grassland by shrubs, is limited by competition with perennial grasses in seasonally wet/dry savannas. We placed seeds of two invasive exotic shrubs - *Cryptostegia grandiflora*, a woody vine, and *Acacia nilotica*, an arborescent legume - into pots with a wide range of existing above- and below-ground herbaceous biomass provided by either a tussock or a stoloniferous perennial grass. We also imposed different levels of watering frequency (5, 10 and 21 d), nutrient addition (+ and -) and grass clipping intensity (no clipping, clipped to 5 cm and clipped to 25 cm). There was no effect of any treatment on shrub seedling emergence or survival and all of the seedlings that emerged survived the 90-d growing period. Herbaceous competition also failed to have an effect on biomass accumulation in shrub seedlings. More frequent watering significantly increased above- and below-ground biomass accumulation for both shrub species and nutrient addition significantly increased *Cryptostegia* biomass accumulation. Based on these results, we question the proposition that reduction in competition by herbs via livestock grazing has been a significant factor in determining the rate or pattern of exotic shrub increase in the seasonally wet/dry tropics. We also question the suitability of the two-layer soil moisture hypothesis as a basis for management practices to control the ingress of woody species into grasslands and open savannas.

Cable, D. R. 1969. Competition in the semidesert grass-shrub type as influenced by root systems, growth habits, and soil moisture extraction. *Ecology* 50: 27-38.

Abstract: Measurements of phenological development, herbage production, basal area, and density of annual and perennial grasses and of the half-shrub burroweed (*Aplopappus tenuisectus* (Greene) Blake), over a 4-year period show that production of each class of plant was affected to some extent by each of the others, except that annual grasses had no effect on burroweed crown area. Production of Arizona cottontop (*Trichachne californica* (Benth.) Chase), the dominant perennial grass, was restricted about 25% on plots with annual grass or burroweed competition and 46% by both together. Annual grass production averaged 18% lower with burroweed competition and 44-54% lower with perennial grass competition. Burroweed crown area increased 220% on plot with no perennial grass, but only 111% on plots with perennial grass competition. Presence of burroweed reduced perennial grass yield only moderately, because the root systems of burroweed and grass do not overlap greatly, and their main growth periods are at different seasons. High evaporation rates during the summer growing season masked most differences in moisture extraction between species. During the winter-spring growing period, on the other hand, burroweed depleted the available soil water rapidly, while water loss on perennial grass plots was little more than from bare soil.

———. 1980. Seasonal patterns of soil water recharge and extraction on semidesert ranges. *Journal of Range Management* 33: 9-15.

Caldwell, M. M. 1987. Competition between root systems in natural communities. In *Root development and function*. Editors P. J. Gregory, J. V. Lake, and D. A. Rose, 167-85. Cambridge: Cambridge University Press.

Abstract: Plants invest heavily in root systems, partly to compete effectively for below-ground resources. An investment in increased root length per unit volume of soil appears to be particularly important. In the last example cited, the presence of an effective competitor reduced the resource gain by the shrub relative to that removed in the presence of a weaker competitor even though the shrub was apparently investing the same in root systems. Thus, the presence of competing roots can increase the cost of root system investment in order to obtain the same quantity of resource. Although information is scant and controversial, root systems of neighbouring plants may frequently intermingle and competition between individual roots of neighbours is probably an important phenomenon. Even when shoots are competing for light, competition below-ground may be more severe in many instances. Although limited by many assumptions, theoretical models of root system activity may provide some insight into the nature of competition for soil resources and the characteristics of root systems that may enhance competitive potential.

Cannon, W. A. 1911. *The root habits of desert plants*. 96 pp. Washington: Carnegie Institution of Washington.

Cepeda-Pizarro, Jorge G., and Walter G. Whitford. 1990. Decomposition patterns of surface leaf litter of six plant species along a Chihuahuan Desert watershed. *The American Midland Naturalist* 123, no. 2: 319-30.

Abstract: Mass losses from litter bags of surface creosote bush litter placed along a Chihuahuan Desert watershed were measured to answer the following questions: (1) Do edaphic factors affect organic matter losses? (2) Are there differences in mass losses between the litter of the site-dominant plant species and creosote bush leaf litter? We hypothesized that (1) mass losses of all litter types would be higher at the base of the watershed and lower on the upper portions of the watershed and (2) mass losses of the litter of the site-dominant plants would be higher than those of creosote bush leaf litter in the same site. Mass losses from creosote bush leaf litter did not follow the moisture-organic matter gradient present in the watershed. Mass losses were higher at mid-slope run-on areas than in upper-slope erosional sites and the dry lake basin. Mass losses were highest where subterranean termite activity was the highest. There were differences between losses from the litter of the site-dominant and creosote bush leaf litter in some instances, but these differences were not attributable to differences in lignin content nor C:N ratio. Mass losses of litter of site-dominant species were not always higher than that of creosote bush leaf litter in the same site. Mass losses were best described by the double exponential model.

Connin, Sean L., R. A. Virginia, and C. P. Chamberlain. 1997. Carbon isotopes reveal soil organic matter dynamics following arid land shrub expansion. *Oecologia* 110, no. 3: 374-86.

Abstract: Over the past century, overgrazing and drought in New Mexico's Jornada Basin has promoted the replacement of native black grama (*Bouteloua eriopoda* Torr.) grass communities by shrubs, primarily mesquite (*Prosopis glandulosa* Torr.). We investigated the effects of shrub expansion on the distribution,

origin, turnover, and quality of light (LFC) and heavy (HFC) soil organic matter (SOM) fractions using delta-¹³C natural abundance to partition SOM into C₄ (grass) and C₃ (shrub) sources. Soil organic matter beneath grasses and mesquite was isotopically distinct from associated plant litter, providing evidence of both recent shrub expansion and Holocene plant community changes. Our delta-¹³C analyses indicated that SOM derived from mesquite was greatest beneath shrub canopies, but extended at least 3 m beyond canopy-margins, similar to the distribution of fine roots. Specific ¹⁴C activities of LFC indicated that root litter is an important source of SOM at depth. Comparison of turnover rates for surface LFC pools in grass (7 or 40 years) and mesquite (11 or 28 years) soils and for HFC pools by soil depth (approx. 150-280 years), suggest that mesquite may enhance soil C storage relative to grasses. We conclude that the replacement of semiarid grasslands by woody shrubs will effect changes in root biomass, litter production, and SOM cycling that influence nutrient availability and long-term soil C sequestration at the ecosystem level.

Cornelius, J. M., P. R. Kemp, J. A. Ludwig, and G. L. Cunningham. 1991. The distribution of vascular plant species and guilds in space and time along a desert gradient. *Journal of Vegetation Science* 2: 59-72.

Cornet, A. F., C. Montana, J. P. Delhoume, and J. Lopez-Portillo. 1992. Water flows and the dynamics of desert vegetation stripes. In *Landscape boundaries. Consequences for biotic diversity and ecological flows*. Editors A. J. Hansen, and F. di Castri, 327-45. New York: Springer Verlag.

Cross, A. F., and W. H. Schlesinger. 1999. Plant regulation of soil nutrient distribution in the northern Chihuahuan desert. *Plant Ecology* 145, no. 1: 11-25.

Abstract: Vegetation throughout the southwestern United States has changed from perennial grassland to woody shrubland over the past century. Previous studies on the development of 'islands of fertility' focused primarily on only the most limiting, plant-essential element, soil nitrogen (N). The research presented here addressed the question of whether other plant-essential elements, namely phosphorus (P) and potassium (K), showed similar concentration gradients under the desert shrub *Larrea tridentata*, creosotebush. It also examined whether the spatial distribution of N, P, and K differed from that of essential, but non-limiting nutrients, namely calcium (Ca), magnesium (Mg), and sulfur (S), and non-essential elements, namely sodium (Na), chloride (Cl), and fluoride (F). Within adjacent grassland and shrubland plots, surface soils were collected under and between vegetation and analyzed for a suite of soil nutrients. Soil nutrient distribution followed a uniform pattern that mirrored the spatial homogeneity of bunchgrasses in the grassland, but followed a patchy distribution that mirrored the spatial heterogeneity of individual shrubs in the shrubland. The main differences were that in the grassland, all elements were uniformly distributed, but in the shrubland the plant-essential elements, nitrogen, phosphorus, and potassium, were concentrated under the shrub canopy, and the non-limiting and non-essential elements were either concentrated in the intershrub spaces or were equally concentrated under shrubs and in the interspaces. Our results show how vegetation shifts from grassland to shrubland contribute to long-term, widespread change in the structure and function of desert ecosystems.

- Davis, S. D. 1991. Lack of niche differentiation in adult shrubs implicates the importance of the regeneration niche. *Trends in Ecology and Evolution* 6: 272-74.
- Dick-Peddie, W. A. 1993. *New Mexico vegetation: Past, present, and future*. Albuquerque: University of New Mexico Press.
- Ehleringer, J. R. 1993. Carbon and water relations in desert plants: an isotopic perspective. In *Stable isotopes and plant carbon/water relations*. Editors James R. Ehleringer, Anthony E. Hall, and Graham D. Farquhar, 155-72. San Diego: Academic Press.
- Ehleringer, J. R., S. L. Phillips, W. S. F. Schuster, and D. R. Sandquist. 1991. Differential utilization of summer rains by desert plants. *Oecologia* 88: 430-434.
- Evenari, M. 1975. Adaptive mechanisms in desert plants. In *Physiological adaptation to the environment*. Editor F. J. Vernberg, 111-29. New York: Intext Educational Publishers.
- Fischer, R. A., and N. C. Turner. 1978. Plant productivity in the arid and semiarid zones. *Annual Review of Plant Physiology* 29: 277-317.
- Fonteyn, P. J., and B. E. Mahall. 1978. Competition among desert perennials. *Nature* 275: 544-45.
- Franco-Pizaña, J. G., T. E. Fulbright, D. T. Gardiner, and A. R. Tipton. 1996. Shrub emergence and seedling growth in microenvironments created by *Prosopis glandulosa*. *Journal of Vegetation Science* 7: 257-64.
- Franklin, Janet, Jeff Duncan, and Debra L. Turner. 1993. Reflectance of vegetation and soil in Chihuahuan desert plant communities from ground radiometry using SPOT wavebands. *Remote Sensing of Environment* 46: 291-304.
- Abstract: The spatially averaged reflectance of a partially vegetated land surface can be modeled as an area-weighted mixture of the reflectances of different components or classes of objects (plants, shadow) of the background (soil, grass). We sampled the spectral reflectance of the shaded and unshaded components of Chihuahuan desert plant communities (shrubs, soil, subshrubs, and perennial grasses) in the SPOT wavebands using a hand-held radiometer. We examined the mean reflectance differences between components to evaluate their spectral separability. Shrub canopy and shaded components have similar reflectance in the visible wavebands. However, in the near-infrared band, which is strongly scattered by green plant canopies, the shaded canopy and shaded background components were similar to each other and lower than either sunlit background or sunlit canopy. When reflectance measurements were

transformed to normalized ratio (NDVI, SAVI) and orthogonal green vegetation indices, the shaded and sunlit portions of each component (canopy and soil) were similar, but the shaded components were intermediate between their sunlit counterparts. Different soil types and plant species with different life forms (e.g., shrubs, grasses) and phenologies exhibited different reflectance characteristics. However, the broadband reflectances of the three dominant shrub species were similar at the end of the growing season, in spite of their differences in morphology.

Galeano-Popp, R. 1996. Conserving New Mexico's biodiversity on public lands. In *New Mexico's Natural Heritage*. Editors: E. A. Herrera, and L. F. Huenneke, 300-326. Las Cruces: New Mexico Academy of Science.

Gibbens, Robert P., Reldon F. Beck, and W. G. Whitford. Unpublished book chapter. Long-term vegetation trends in the Jornada Basin: The 1950's drought in historical perspective.

Gosz, J. R. 1995. Edges and natural resource management: future directions. *Ecology International* 22: 17-34.

Guo, Q., P. W. Rundel, and D. W. Goodall. 1998. Horizontal and vertical distribution of desert seed banks: patterns, causes, and implications. *Journal of Arid Environments* 38: 465-78.

Abstract: This study examined small-scale seed distribution using published data collected using the same techniques and the same group of observers in four locations in North American deserts (Curlew Valley, Utah in the Great Basin Desert; Rock Valley, Nevada in the Mojave Desert; Silverbell, Arizona in the Sonoran Desert; and Jornada, New Mexico in the Chihuahuan Desert). The distribution patterns were examined horizontally (under shrub canopy to open areas) and vertically (measured at the soil surface and at four depth intervals) in relation to seed morphology. At all four sites, seed distribution of individual species was positively related to seed abundance. Horizontally, total number of seeds per unit area decreased from under the shrub canopy to intershrub areas. Vertically, total number of seeds declined as soil depth increased. Most species were only present in a small proportion of samples. Small seeds were either abundant and broadly distributed or rare and found in a few samples, but larger seeds were always low in abundance and restricted to a small proportion of samples. For annual species, significantly higher proportions of larger seeds than smaller seeds were found deeper in the soil. However, when much larger-seeded species, i.e. herbaceous perennials and shrubs, were included in the analyses, most very small or very large seeds were found in the upper-most layers of soils and intermediate to large-sized seeds deeper in the soils. Such seed distribution related to seed morphology and soil factors may have significant ecological implications in plant population dynamics and community structure in desert ecosystems.

———. 1999. Structure of desert seed banks: comparisons across four North American desert sites. *Journal of Arid Environments* 42: 1-14.

Abstract: The similarities and differences in seed bank structure across four locations in the North American deserts (Curlew Valley, Utah in the Great Basin; Rock Valley, Nevada in the Mojave Desert;

Silverbell, Arizona in the Sonoran Desert; and Jornada, New Mexico in the Chihuahuan Desert) were compared using published data. Species composition at Curlew Valley was most distinctive among the four study sites. In all four sites, average seed size decreased in this order: shrub, herbaceous perennial, and annual species. Mean seed sizes were similar across the Curlew Valley, Rock Valley and Silverbell sites but much smaller at the Jornada site. Most species have small seeds, but the number of seeds varied greatly among these small-seeded species; i.e. seeds of these species could be highly abundant or very rare in the seed banks. In contrast, very few species have large seeds and the seeds of these species were always rare. The possible roles of underlying soil and climatic factors in structuring desert seed bank structure are discussed.

Gutterman, Y. 1994. Strategies of seed dispersal and germination in plants inhabiting deserts. *The Botanical Review* 60, no. 4: 373-425.

Harrington, G. N. 1991. Effects of soil moisture on shrub seedling survival in a semi-arid grassland. *Ecology* 72, no. 3: 1138-49.

Abstract: Grazing of wooded grasslands by domestic stock has led to dominance by woody plants, in many parts of the world. In semi-arid grasslands in Australia *Dodonaea attenuata* is a common, invasive shrub of perennial grasslands on sandy soils. There is evidence that cohorts of *D. attenuata* establish infrequently in vigorous grasslands and more frequently where the perennial grass has been damaged by overgrazing. This study examined the influence of herbaceous growth on mortality of *D. attenuata* seedlings, by growing them in plots with controlled moisture input. The herbaceous layer in the plots was either natural, clipped, or killed. Without summer irrigation all the seedlings in the natural grassland died. Seedling survival was inversely related to the amount of herbaceous growth on the other treatments. Summer irrigation maintained *D. attenuata* seedlings and produced a large biomass of perennial grass, which left the seedlings susceptible to grass fires. A water-balance model was run for the experimental site for the 97 yr of climatic records. The soil-moisture patterns associated with the establishment of three known cohorts of *D. attenuata* were identified. The model output was interrogated for similar soil moisture patterns in other years. It was estimated that only six widespread *D. attenuata* establishment events have occurred in 97 yr. In intact grasslands *D. attenuata* rarely establishes densely, and when it does so it is susceptible to grass fires. Modern management has increased establishment frequency by increasing the availability of summer soil moisture by overgrazing the grasslands and has suppressed grass fires. This has changed open grassland to dense shrubland.

Hastings, James R., and Raymond M. Turner. 1965. *The changing mile: An ecological study of vegetation change with time in the lower mile of an arid and semiarid region.* 317 pp. Tuscon, AZ: University of Arizona Press.

Havstad, K. M. 1998. An overview of arid grasslands in the Northern Chihuahuan Desert. In *The future of arid grasslands: identifying issues, seeking solutions*, Editors B. Tellman, D. M. Finch, C. Edminster, and R. Hamre. Proc. RMRS-P-3, Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Abstract: The intent of this paper is to outline information on four topics regarding grasslands of the Chihuahuan desert: 1) general aspects of their ecological dimensions, 2) recent vegetation dynamics, 3) current threats, and 4) common ground with other desert grasslands. The Chihuahuan desert is a region of about 350,000 square kilometers. There are at least fifteen different definitions of the boundaries of this desert. Figure 1 is from Schmidt (1979) and its boundaries are based on an aridity index. Generally, this index reflects an area of <250 mm of average annual precipitation, an average mean annual temperature of 17° C, and an elevation of >1200 m. This paper will focus on the northern region of the Chihuahuan desert, an area called the Trans-Pecos which extends from Southeast Arizona across New Mexico into Texas. A small portion of the Trans-Pecos occurs in west Texas on the upper Pecos River below the Guadalupe Mountains. The western border of the Chihuahuan Desert in Arizona is defined by the amount of precipitation occurring during the summer monsoonal months. East of this line in the Sonoran desert >55% of the annual precipitation occurs during the summer. West of this line in the Chihuahuan desert <55% of the annual precipitation occurs during the summer months.

Henrickson, J., and M. C. Johnston. 1986. Vegetation and community types of the Chihuahuan desert. In *Second symposium on resources of the Chihuahuan desert region*. Editors: J. C. Barlow, A. M. Powell, and B. N. Timmermann, 20-39. Alpine, Texas: Chihuahuan Desert Research Institute.

Abstract: A classification of plant communities of the Chihuahuan desert region, inclusive of all montane habitats is presented. A total of 16 intergrading communities is recognized including eight Desert Scrub and Woodland communities: Chihuahuan Desert Scrub (with 5 facies), Lechuguilla Scrub, Yucca Woodland, Prosopis-Atriplex Scrub, Alkali Scrub, Gypsophilous Scrub, Arborescent Cactus Scrub, and Riparian Woodland; three Grassland communities: Grama Grassland, Sacaton Grassland, and Tobosa Grassland; a Chaparral community: Montane Chaparral; and four Montane Woodland communities: Juniper-Pinyon Woodland; Oak Woodland, Pine Woodland, and Mixed Fir Forest. Representative species in each are listed.

Herbel, C. H. 1979. Utilization of grass- and shrublands of the southwestern United States. In *Management of semi-arid ecosystems*. Editor B. H. Walker, 161-203. Amsterdam, Netherlands: Elsevier Scientific Publishing Company.

———. 1985. Vegetation changes on arid rangelands of the Southwest. *Rangelands* 7: 19-21.

Abstract: Change, an inherent characteristic of ecosystems, is a recognized feature of vegetation in the arid and semiarid portions of the southwestern United States. Territorial surveys in the 19th century and terrestrial photography in the 19th century and early 20th century have been used to establish a base for vegetation conditions and then for recording variations from this base. All evidence indicates a dramatic shift from land with a high proportion of grassy vegetation to one dominated by shrubs. Most of these

changes have occurred in the last 50-100 years. Following are some of the reasons and possible solutions to problems resulting from these changes that would be applicable to parts of Arizona, New Mexico, and Texas, with possible use in other arid and semiarid regions of the world.

Hochstrasser, T., G. Kröel-Dulay, D. P. C. Peters, and J. R. Gosz. in press. Vegetation and climate characteristics of arid and semi-arid grasslands in North America and their biome transition zone. *Journal of Arid Environments*.

Abstract: The objective of this study was to investigate the relationship among species richness, functional group composition, and climate for three sites representing the shortgrass steppe, the Chihuahuan desert grasslands and their biome transition zone. We found that perennial species richness increased as the climate became more favorable for plant growth. The biome transition zone was more similar to the Chihuahuan desert grassland site in most climate and vegetation characteristics, partly because of the shorter biogeographic distance between the two sites. This study clarified the ecological position of the biome transition zone site with respect to the adjacent biomes.

Huebner, C. D., J. L. Vankat, and W. H. Renwick. 1999. Change in the vegetation mosaic of central Arizona USA between 1940 and 1989. *Plant Ecology* 144: 83-91.

Humphrey, R. R. 1958. The desert grassland a history of vegetational change and an analysis of causes. *The Botanical Review* 24, no. 4: 193-252.

Idso, S. B. 1992. Shrubland expansion in the American southwest. *Climatic Change* 22: 85-86.

Jackson, R. B., J. Canadell, J. R. Ehleringer, H. A. Mooney, O. E. Sala, and E. D. Shulze. 1996. A global analysis of root distributions for terrestrial biomes. *Oecologia* 108: 389-411.

Johnson, A. R., S. J. Turner, W. G. Whitford, A. G. de Soyza, and J. W. Van Zee. 2000. Multivariate characterization of perennial vegetation in the northern Chihuahuan desert. *Journal of Arid Environments* 44: 305-25.

Abstract: We surveyed vegetation at 100 sites in southern New Mexico to establish a benchmark for monitoring vegetation change. Sites were selected in a stratified random design, based on a classified AVHRR image. Two shrubs (*Larrea tridentata* and *Prosopis glandulosa*) are the most important contributors to perennial cover in the area. Principal components analysis (PCA) and detrended correspondence analysis (DCA) both clearly delineate these shrublands from the smaller number of compositionally-varied grassland sites. A latitudinal trend in DCA axis 1 scores suggests that encroachment of shrubs into grasslands is most pronounced in the southern portion of the study area.

Kieft, T. L., C. S. White, S. R. Loftin, R. Aguilar, J. A. Craig, and D. A. Skaar. 1998. Temporal dynamics in soil carbon and nitrogen resources at a grassland-shrubland ecotone. *Ecology* 79, no. 2: 671-83.

Abstract: Plant communities of large portions of the southwestern United States have changed from grassland to desert shrubland. Previous studies have demonstrated that soil nutrient resources become spatially more heterogeneous and are redistributed into islands of fertility with the shift in vegetation. The research presented here addressed the question of whether soil resources become more temporally heterogeneous as well as more spatially heterogeneous when grassland undergoes desertification to form shrubland. Within adjacent grassland and creosotebush sites, soil profiles were described at three soil pits, and samples were collected for description of nutrient resources within the profile. Relative abundance of plant cover and bare soil was determined within each site using line transects. Surface samples (0-20 cm depth) of bare soil and soil beneath the canopies of grasses and creosotebush were collected 17 times during 1992-1994. Soil samples were analyzed for moisture, extractable ammonium and nitrate, nitrogen mineralization potential, microbial biomass carbon, total organic carbon, microbial respiration, dehydrogenase activity, the ratio of microbial C to total organic C (C_{mic}/C_{org}), and the ratio of microbial respiration to biomass carbon (metabolic quotient). The major differences in the structure of soils between sites were the apparent loss of 3-5 cm depth of sandy surface soil at the creosotebush site and an associated increase in calcium carbonate content at a more shallow depth. Soils under plants at both sites had greater total and available nutrient resources, with higher concentrations under creosotebush than under grasses. Greatest temporal variation in available soil resources was observed in soils under creosotebush. When expressed on the basis of area, available soil resources were higher in the grassland than in the creosotebush shrubland, primarily due to the difference in plant cover (45% in grassland, 8% in creosotebush shrubland).

Lee, C. A. 1990. "The spatial distribution of roots for three plant lifeforms in the shortgrass steppe." M. S. Thesis, Colorado State University.

Little, E. L. Jr., and R. S. Campbell. 1943. Flora of Jornada Experimental Range, New Mexico. *American Midland Naturalist* 30: 626-70.

Abstract: The Jornada Experimental Range is an area of 302 square miles in Dona Ana County, southern New Mexico. Most of it is in the plain of Jornada del Muerto, 4,000 to 4,600 feet above sea level, with semidesert (Lower Sonoran) grass and shrubs vegetation; part is on the San Andres Mountains and foothills that rise into the woodland (Upper Sonoran) zone to a maximum elevation of 8,000 feet. A collection of specimens of 528 species of ferns and seed plants representing 301 genera and 82 families, together with a few lower plants, was made here by the Forest Service from 1915 to 1939. A list of the species is included. The families having greatest representation, with the numbers of species in each, are. Compositae, 87; Gramineae, 80; Leguminosae, 33; Cactaceae, 16; Cruciferae, 15; and Euphorbiaceae, 15. A few are State records and extensions of known range. The flora is western and more distinctly southwestern in distribution. More than two-fifths of the species occur from western Texas to southern Arizona and northern Mexico and more than two-fifths additional range widely in the western half of the United States. When the species were classified on the basis of Raunkiaer's life forms, hemicryptophytes

and therophytes showed the greatest excesses in percentages over Raunkiaer's normal spectrum, and the percentage of phanerophytes was far below that standard. Approximately half the species are perennial herbs, one-fourth annual herbs, and one-fourth woody plants, mainly semidesert shrubs. Only 13 species here have the size and habit of trees. Most of the plants have unusually small leaves. A statistical analysis of the vegetation is presented, based upon data compiled from range surveys and listing the species that make up nearly all the vegetation. Only about one-third of the vegetation has high value and the rest is of low forage value or none. The native vegetation is valuable chiefly as forage for livestock, which in this locality are mainly cattle grazed yearlong.

- Ludwig, J. A. 1977. Distributional adaptations of root systems in desert environments. In *The belowground ecosystem: a synthesis of plant-associated processes*. Range Science Department Science Series No. 26. J. K. Marshall, 85-91. Fort Collins, Colorado: Range Science Department, Colorado State University.
- Abstract: Early studies on the distribution patterns of root systems of desert plants are reexamined in view of recent IBP studies. Unpublished studies on root habits of desert plants in North America are used along with studies from other deserts of the world to support conclusions. The question of occupation of the subterranean space in a desert introduces the hypothesis that through time plants should distribute their root systems in order to obtain the necessary volume of water for maximal growth. Evidence is presented to suggest this hypothesis holds. Excavation studies showed the horizontal distribution of perennial roots is such that during periods of maximal growth, the extension of temporary fine roots could occupy all available root space. In documented cases where the spacing of plants is such that it is impossible for roots to extend the great distance, the openness may be caused by past and present domestic grazing. Exceptions are extremely arid and unstable dune desert regions. Root:shoot ratios in desert shrub species have been thought to be high as an adaptive mechanism for drought resistance. Evidence is reviewed and presented which shows that desert species do not possess high root:shoot ratios. Root:shoot ratios are highly variable within and between species. Root:shoot ratios do not increase with increasing aridity as has been suggested; in fact, evidence indicates the reverse is true. Much of the variation in root:shoot ratio in a desert shrub species is age dependent. Desert shrub species with the broadest local and geographical distribution have a generalized type of root system, where a tap root and lateral roots are both capable of extensive horizontal and vertical distribution. This appears to be an adaptation where these species can establish on the highly varied desert soils. However, this distribution adaptation is probably not unique to desert shrubs and thus is not a special adaptive mechanism for drought resistance. Other anatomical, morphological, and physiological adaptations exhibited by desert shrubs are probably of greater importance to their establishment and long-term survival.

- . 1987. Primary productivity in arid lands: myths and realities. *Journal of Arid Environments* 13: 1-7.
- Abstract: We tend to view arid environments as harsh and water-limited, due to low amounts of precipitation. In fact, many sites within desert regions receive considerable amounts of water due to run-on; for example, washes (arroyos, wadis). The productivity of these can be high. However, in reality, their extent is small. We often assume productivity of deserts to be only water-limited. Recent research in arid ecosystems indicates, however, that nutrients can be critical to production. We also think of desert

precipitation as being unpredictable, in addition to low in quantity. Nevertheless, many of the major arid lands of the world are characterized by highly seasonal patterns of precipitation. Native plant and animal populations have evolved numerous tactics which capitalize on the predictable timing of precipitation. Humans have learned to exploit this predictability by growing crops and raising livestock that can gain from seasonal patterns. Humans also manipulate arid environments by removing the limits to productivity through irrigation and fertilization and, while some cases of agricultural production are noteworthy, the reality is that the cost/benefit ratio is not favorable. Furthermore, extensive arid and semi-arid areas are undergoing rapid desertification. Monitoring desertification is essential to our future understanding of arid and semi-arid land productivity.

Lyford, F. P., and H. K. Qashu. 1969. Infiltration rates as affected by desert vegetation. *Water Resources Research* 5: 1373-76.

MacMahon, James A. 1988. Warm deserts. In *North American terrestrial vegetation*. Editors Michael G. Barbour, and William Dwight Billings, 231-64. Cambridge; New York: Cambridge University Press.

MacMahon, J. A., and F. H. Wagner. 1985. The Mojave, Sonoran and Chihuahuan deserts of North America. In *Hot deserts and arid shrublands. Ecosystems of the world*. 12A Editors M. Evenari, I. Noy-Meir, and D. W. Goodall, 105-201. Amsterdam: Elsevier.

McClaran, M. P., and T. R. Van Devender 1995. *The desert grassland*. Tucson: The University of Arizona Press. Chapters: Desert grasslands and grasses (Mitchel P. McClaran), Desert grasslands, mixed shrub savanna, shrub steppe, or semidesert shrub? The dilemma of coexisting growth forms (Tony L. Burgess); 3- Desert grasslands history: changing climates, evolution, biogeography, and community dynamics (Thomas R. Van Devender); 4- Landscape evolution, soil formation, and Arizona's desert grasslands (Joseph R. McAuliffe); 5- The role of fire in the desert grasslands (Guy R. McPherson); 6- Diversity, spatial variability, and functional roles of invertebrates in desert grassland ecosystems (Walter G. Whitford, Gregory S. Forbes, Graham I. Kerley); 7- Diversity, spatial variability, and functional roles of vertebrates in the desert grassland (Robert R. Parmenter, Thomas R. Devender); 8- Human impacts on the grasslands of southeastern Arizona (Conrad J. Bahre); 9- Revegetation in the desert grassland (Bruce A. Roundy, Sharon H. Biedenbender).

McClaran, M. P., and M. Umlauf. 2000. Desert grassland dynamics estimated from carbon isotopes in grass phytoliths and soil organic matter. *Journal of Vegetation Science* 11: 71-76.

Abstract: We document the potential for using carbon isotopes in both soil organic matter (SOM) and grass phytoliths in soil to increase the temporal and taxonomic resolutions of long term vegetation dynamics. Carbon isotope values from both SOM and phytoliths are expected to describe both the age of material through ^{14}C dating, and the photosynthetic pathway of the source plant material through ratios of $^{12}\text{C}/^{13}\text{C}$.

Taxonomic resolution is increased because the phytoliths examined are specific to grasses, whereas the SOM reflects the contribution of all the vegetation. Temporal resolution is increased because phytoliths are less mobile in the soil profile than SOM, and can therefore provide older dates from the same soil depth. Our results, from a desert grassland site in southwestern North America, largely confirm these expectations and show that C₄ species have dominated the grass composition for the last 8000 yr. C₃ non-grass vegetation increased about 100-350 yr BP, and no significant C₃ grass or non-grass vegetation existed between 350-2000 yr BP.

McLaughlin, S. P. 1986. Floristic analysis of the Southwestern United States. *Great Basin Naturalist* 46: 47-65.

Abstract: A study was made of the distributions of native, terrestrial, vascular plants occurring in 50 local floras from throughout the Basin and Range and Colorado Plateau physiographic provinces of the southwestern United States. The objectives of the study were to objectively define and describe the floristic elements-assemblages of species with roughly coincident geographic distribution-occurring in the southwestern United States and to determine what such assemblages reveal about the floristic history of the region. The total flora (native, terrestrial species only) of the Southwest is estimated at 5,458 species, 77% of which were recorded in 1 or more of the local floras. Nearly 2296 of these species are endemic to the study region. A majority of the species were found to be relatively rare. The average range of a species included only 4 floras, and 90% of the species were recorded from 11 or fewer floras; only 81 species (1.5%) were recorded from 50% or more of the floras. Trees constitute 2% of the regional flora and have the widest average distribution; perennial herbs constitute 59% of the flora and have the most restricted distributions. Factor analysis was used to identify seven floristic elements for the region: a Great Basin element, a Mojavean element, a Colorado Plateau element, a Chihuahuan element, an Apachian element, and a Mogollon element. This factor analysis solution was shown to satisfy criteria of interpretability and consistency. The Mojavean, Colorado Plateau, and Apachian elements are believed to be autochthonous. The other four elements show high overlap in species composition with one or more adjacent regions. Each floristic element is mapped to show its geographic form and distribution. Analysis of these maps shows how the existence of objectively defined floristic elements is not contradictory to either the individualistic view of the distribution of a species or local continuity of vegetation and flora. The rarity of the majority of species and the clear association of floristic elements with rather narrowly circumscribed Holocene environments suggests that many Southwestern species have migrated little and are of rather recent, probably postglacial origin. Geographic "principles" derived from the distribution patterns of relatively few, widespread, dominant, usually woody species may not be applicable to entire, regional floras.

Noy-Meir, I. 1979-1980. Structure and function of desert ecosystems. *Israel Journal of Botany* 28: 1-19.

Paulsen, Harold A. Jr. 1953. A comparison of surface soil properties under mesquite and perennial grass. *Ecology* 34, no. 4: 727-32.

Abstract: Samples from the surface inch of soil from native black grama- Rothrock grama grassland areas and interspersed areas recently invaded by mesquite were analyzed for physical and chemical properties.

The samples were obtained from the foothill vegetation type on the Santa Rita Experimental Range in southeastern Arizona. The soil of the sampling area is typed as a Tumacacori coarse sandy loam. The laboratory analyses indicate the soil under the mesquite cover to be deteriorated in both chemical and physical properties. The latter is believed of greater importance since the indicated reduction in the nutrient capital is not believed to have reached the minimal requirements of the grasses. Physically, the soil under the mesquite was coarser, lower in pore volume, and higher in volume-weight. Soil structure and moisture relations were apparently less favorable and there was shown to be more instability of the surface soil.

Paylore, P. 1969. Bibliographical sources for arid lands research. *Arid lands in perspective*. W. G. McGinnies, and B. J. Goldman, 249-75. Tucson, AZ: University of Arizona Press.

Persson, H. and I. O. Baitulin (Editors) 1996. *Plant root systems and natural vegetation*. Uppsala: Opulus Press.

Pieper, R. D., J. C. Anway, M. A. Ellstrom, C. H. Herbel, R. L. Packard, S. L. Pimm, R. J. Raitt, E. E. Staffeldt, and J. G. Watts. 1983. Structure and function of North American Desert Grassland ecosystems. *Special Report. Agricultural Experiment Station. New Mexico State University* 39: 1-298.

Pilmanis, A. M., and W. H. Schlesinger. 1999. Spatial assessment of desertification in terms of vegetation pattern and available soil nitrogen. In *Proceedings of the Fifth International Conference on Desert Development*, Editors Idris Rhea Taylor, Harold Dregne, and Kary MathisLubbock, Texas: Texas Tech University Press. Abstract: The objective of this study was to use spatial statistics to quantify the effects of desertification on the distribution of biomass and available nitrogen in Chihuahuan desert black grama (*Bouteloua eriopoda*) grassland, which has been invaded by honey mesquite (*Prosopis glandulosa*) shrubland. This research is a portion of analysis of spatial patterns and interrelationships of ecological variables across a desertification gradient, with the larger goal of being to improve our understanding of the mechanisms underlying desertification in southwestern ecosystems. This study tested the sensitivity of "Geostatistics" and "Spatial statistics" to detect subtle differences between ecosystems, such as those occurring across a continuous gradient of desertification.

Reynolds, J. F., P. R. Kemp, and J. D. Tenhunen. 2000. Effects of long-term rainfall variability on evapotranspiration and soil water distribution in the Chihuahuan Desert: A modeling analysis. *Plant Ecology* 150: 145-59. Abstract: We used the patch arid land simulator (PALS-FT) -- a simple, mechanistic ecosystem model -- to explore long-term variation in evapotranspiration (ET) as a function of variability in rainfall and plant functional type (FT) at a warm desert site in southern New Mexico. PALS-FT predicts soil evaporation and plant transpiration of a canopy composed of five principal plant FTs: annuals, perennial forbs, C₄ grasses, sub-shrubs, and evergreen shrubs. For each FT, the fractional contribution to transpiration depends upon

phenological activity and cover as well as daily leaf stomatal conductance, which is a function of plant water potential, calculated from root-weighted soil water potential in six soil layers. Simulations of water loss from two plant community types (grass- vs. shrub-dominated) were carried out for the Jornada Basin, New Mexico, using 100 years of daily precipitation data (1891-1990). In order to emphasize variability associated with rainfall and fundamental differences in FT composition between communities, the seasonal patterns of cover of perennials were held constant from year to year. Because the relative amount of year to year cover of winter and summer annual species is highly variable in this ecosystem, we examined their influence on model predictions of ET by allowing their cover to be variable, fixed, or absent. Over the entire 100-yr period, total annual ET is highly correlated with total annual rainfall in both community types, although T and E alone are less strongly correlated with rainfall, and variation in transpiration is nearly 3 times greater than evaporation and 2 times greater than variation in rainfall (CV of rainfall = 35%). Water use shows a relatively high similarity between the grass- and shrub-dominated communities, with a 100-yr average T/ET of 34% for both communities. However, based on a year-by-year comparison between communities, T/ET was significantly greater in the grass-dominated community, reflecting the fact that over the long term more than half of the rain occurs in the summer and is used slightly more efficiently (T>E) by the C₄-grass community than the shrub community, although we found some rainfall patterns that resulted in much greater T/ET in the shrub community in a given year. Percent of water lost as transpiration (T/ET) suggests that while there is a general trend toward increased T/ET with rainfall in both community types, T/ET is extremely variable over the 100-yr simulation, especially for normal and below normal amounts of rainfall (T/ET values range from 1 to 58% for the grass-dominated site and 6 to 60% for the shrub-dominated site). These predictions suggest that because of the relatively shallow distribution of soil water, there is little opportunity for vertical partitioning of the soil water resource by differential rooting depths of the plant FTs. However, functional types may avoid competition by keying on particular "windows" of moisture availability via differences in phenologies. We found very little differences in average, long-term model predictions of T, E, and ET when annual plant cover was variable, fixed, or absent. The results of our simulations help reconcile some of the disparate conclusions drawn from experimental studies about the relative contribution of transpiration vs. evaporation to total evapotranspiration, primarily by revealing the great year-to-year variability that is possible.

Reynolds, J. F., R. A. Virginia, and W. H. Schlesinger. 1997. Defining functional types for models of desertification. In *Plant functional types. Their relevance to ecosystem properties and global change*. Editors T. M. Smith, H. H. Shughart, and F. I. Woodward, 195-216. Cambridge, UK: Cambridge University Press.

Schlesinger, William H., and Adrienne M. Pilmanis. 1998. Plant-soil interactions in deserts. *Biogeochemistry* 42: 169-87.

Abstract: Geostatistical analyses show that the distribution of soil N, P and K is strongly associated with the presence of shrubs in desert habitats. Shrubs concentrate the biogeochemical cycle of these elements in "islands of fertility" that are localized beneath their canopies, while adjacent barren, intershrub spaces are comparatively devoid of biotic activity. Both physical and biological processes are involved in the formation

of shrub islands. Losses of semiarid grassland in favor of invading shrubs initiate these changes in the distribution of soil nutrients, which may promote the further invasion and persistence of shrubs and cause potential feedbacks between desertification and the Earth's climate system.

Schlesinger, W. H., J. F. Reynolds, G. L. Cunningham, L. F. Hueneke, W. M. Jarrell, R. A. Virginia, and W. G. Whitford. 1990. Biological feedbacks in global desertification. *Science* 247: 1043-48.

Schlesinger, William H., T. J. Ward, and John Anderson. 2000. Nutrient losses in runoff from grassland and shrubland habitats in southern New Mexico: II. Field plots. *Biogeochemistry* 49: 69-86.

Abstract: Losses of dissolved nutrients (N, P, K, Ca, Mg, Na, Cl, and SO₄) in runoff were measured on grassland and shrubland plots in the Chihuahuan desert of southern New Mexico. Runoff began at a lower threshold of rainfall in shrublands than in grasslands, and the runoff coefficient averaged 18.6% in shrubland plots over a 7-year period. In contrast, grassland plots lost 5.0 to 6.3% of incident precipitation in runoff during a 5.5-year period. Nutrient losses from shrubland plots were greater than from grassland plots, with nitrogen losses averaging 0.33 kg ha⁻¹yr⁻¹ vs. 0.15 kg ha⁻¹yr⁻¹, respectively, during a 3-year period. The greater nutrient losses in shrublands were due to higher runoff, rather than higher nutrient concentrations in runoff. In spite of these nutrient losses in runoff, all plots showed net accumulations of most elements due to inputs from atmospheric deposition. Therefore, loss of soil nutrients by hillslope runoff cannot, by itself, account for the depletion of soil fertility associated with desertification in the Chihuahuan desert.

Schmidt, R. H. Jr. 1979. A climatic delineation of the 'real' Chihuahuan desert. *Journal of Arid Environments* 2: 243-50.

Abstract: The Chihuahuan Desert is one of the least-known regions in North America. The lack of scientific investigation by any discipline is reflected by the vague and inconsistent boundaries assigned to this arid zone. Placing the Chihuahuan Desert into a regional framework is further complicated by the lack of studies which extend across the international boundary between the United States and Mexico. This investigation was undertaken to provide a more detailed and definitive map of the Chihuahuan Desert. Mean annual temperatures and precipitation values, obtained for nearly 800 weather stations, were utilized to delineate the Chihuahuan Desert based upon the de Martonne aridity index. Using an aridity index ≤ 10 , it was found that the Chihuahuan Desert occupies approximately 350,000 km², and includes 115 weather stations. As large areas exist where climatic data are not available, or where long-term climatic records are non-existent, twelve other delineations of this arid zone were mapped at the same scale to make possible a comparison, and provide additional basis for establishing relatively firm boundaries for North America's least known desert.

———. 1986. Chihuahuan climate. In *Second symposium on resources of the Chihuahuan desert region*. Editors J. C. Barlow, A. M. Powell, and B. N. Timmermann, 40-63. Alpine, Texas: Chihuahuan Desert Research Institute.

- Schmutz, E. M., E. L. Smith, P. R. Odgen, M. L. Cox, J. O. Klemmedson, J. J. Norris, and L. C. Fierro. 1992. Desert grassland. *Ecosystems of the world. Natural grasslands*. 8a ed., R. T. Coupland, 337-62. Amsterdam: Elsevier Scientific Press.
- Shmida, A. 1985. Biogeography of the desert flora. In *Hot deserts and arid shrublands. Ecosystems of the world*. 12A Editors M. Evenari, I. Noy-Meir, and D. W. Goodall, 23-77. Amsterdam: Elsevier.
- Shreve, F. 1934. Rainfall, runoff and soil moisture under desert conditions. *Annals of the Association of American Geographers* 24: 131-56.
- Shreve, F. 1942. The desert vegetation of North America. *The Botanical Review* 8: 195-246.
- Sims, P. L., and J. S. Singh. 1978. The structure and function of ten western North American grasslands. III. Net primary production, turnover and efficiencies of energy capture and water use. *Journal of Ecology* 66: 573-97.
- Sims, P. L., J. S. Singh, and W. K. Lauenroth. 1978. The structure and function of ten western North American grasslands. I. Abiotic and vegetational characteristics. *Journal of Ecology* 66: 251-85.
- Smith, S. D., D. T. Patten, and R. K. Monson. 1987. Effects of artificially imposed shade on a Sonoran desert ecosystem: microclimate and vegetation. *Journal of Arid Environments* 13: 65-82.
Abstract: Artificial shading was provided to a Sonoran Desert ecosystem with an array of 12 regularly spaced, opaque structures. Shading resulted in a cooler, moister microhabitat below and behind each structure. Open gaps between structures also exhibited moister soils relative to a control. Ephemeral plants increased in species diversity and showed a shift in species composition in shaded microsites, but exhibited decreased total biomass relative to controls. A deciduous shrub, *Ambrosia deltoidea*, had more mesophytic leaves, higher leaf area, carbon dioxide assimilation and growth in shaded microsites. An evergreen shrub, *Larrea tridentata*, had highest carbon dioxide assimilation and growth in sunny microsites within the array of shading structures. The plant responses observed in this study illustrate the contrasting adaptations of different desert life forms from the same habitat.
- Soriano, A., and O. Sala. 1983. Ecological strategies in a Patagonian arid steppe. *Vegetatio* 56: 9-15.
Abstract: The vegetation in the Coironal arid steppe consists of grasses and shrubs. The objective of this paper was to test Walter's hypothesis that woody vegetation and grasses compete for water in the upper layers of the soil, but woody vegetation has exclusive access to a source of water at deeper levels. Analysis of root profiles and patterns of leaf and soil water potential led us to accept the hypothesis for this arid

steppe. Additional information on phenology and on the ability of the major grass species to respond to watering permitted to identify two ecological strategies corresponding to grasses and shrubs. Grasses behave as opportunists having always leaves ready to grow as soon as water becomes available. They have a shallow root system and are able to respond very rapidly to increases in soil water availability. In contrast, woody species have a clear-cut periodic pattern of growth and dormancy. They possess thick horizontal roots running below 35-40 cm and utilized water stored in lower layers of the soil. A diagrammatic model summarizes the role of periodic and opportunistic species upon water circulation in the ecosystem. The effect of changes in the proportion of the two groups upon water dynamics is also discussed.

Stein, Rebecca A., and John A. Ludwig. 1979. Vegetation and soil patterns on a Chihuahuan desert bajada. *American Midland Naturalist* 101, no. 1: 28-38.

Abstract: Vegetation and soils were sampled along a 1100-m transect on a bajada, in southern New Mexico to determine if present vegetation patterns can be interpreted from soil patterns. Species cover was measured in 66 plots, each 50.3 m². Of these, 22 were randomly chosen as sites for soil pits, which were described and analyses conducted on the top (A1) horizon. The plots were clustered into four communities: *Erioneuron pulchellum* desert grassland transition, *Larrea tridentata* desert shrub, *Bouteloua curtipendula* semidesert grassland and *Bouteloua eriopoda* desert grassland. Soils of these communities differ significantly in pH, Mg, organic carbon and total nitrogen. These soil chemistry differences could be due to relatively recent changes from *Bouteloua* grassland to *Larrea* shrubland, as indicated by our dead shrub data and as documented for many bajadas in southern New Mexico. However, soil series and geomorphic surface patterns, which are not readily affected by recent vegetation changes, suggest that *Larrea* may always have been an important shrub on shallow calcareous soils (of erosional surfaces) in southern New Mexico. Its importance as a mosaic type in the once extensive desert grasslands has probably been underestimated.

Sun, G., D. P. Coffin, and W. K. Lauenroth. 1997. Comparison of root distributions of species in North American grasslands using GIS. *Journal of Vegetation Science* 8: 587-96.

Syvertsen, J. P., G. L. Nickell, R. W. Spellenberg, and G. L. Cunningham. 1976. Carbon reduction pathways and standing crop in three Chihuahuan desert plant communities. *Southwestern Naturalist* 21: 311-20.

Teeri, J. A., and L. G. Stowe. 1976. Climatic patterns and the distribution of C₄ grasses in North America. *Oecologia* 23: 1-12.

Abstract: A stepwise multiple regression analysis was used in an attempt to correlate statistically the geographic patterns in the abundance of C₄ grasses with patterns in climatic variables. The percent of grasses having the C₄ pathway was computed for the total grass flora in twenty-seven widely spaced regions of North America. From long-term climatic records seasonal and annual values for solar irradiance, water supply, heat availability, and combinations of these variables were assigned to each of the twenty-

seven regions. The results of the analysis suggest that high minimum temperatures during the growing season have the strongest correlation with the relative abundance of C₄ grass species in a regional flora. It appears that the deleterious effects of low temperatures during growth negate the advantages of possessing the C₄ pathway in cooler habitats.

Thompson, J., and L. F. Huenneke. 1996. Nurse plant associations in the Chihuahuan Desert shrublands. In *Proceedings: symposium on shrubland ecosystem dynamics in a changing environment*, Compilers J. R. Barrow, E. D. McArthur, R. E. Sosebee, and R. J. Tausch, 158-64 Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station.

Abstract: Spatial studies in the Chihuahuan Desert of associations with *Larrea* shrub islands found juveniles more often associated with shrub islands than unassociated. The spatial structure of the shrub islands points to Nurse Plant facilitation of seedlings. Experiments tested the effects of canopy, shrub islands, and understory on five perennials' germination. Longer survival times, but not higher germination, of *Zinnia acerosa* were found beneath artificial canopies in intershrub areas and cleared shrub islands as compared to intact shrub islands. Therefore, *Zinnia* may be poor competitor, preferring germination microsites with few competitors, regardless of Nurse Plant effects.

USDA NRCS. 1999. "The PLANTS database." Web page. Available at <http://plants.usda.gov/>.

Van Devender, T. R. 1986. Pleistocene climates and endemism in the Chihuahuan desert flora. In *Second symposium on resources of the Chihuahuan desert region*. Editors J. C. Barlow, A. M. Powell, and B. N. Timmermann, 1-19. Alpine, Texas: Chihuahuan desert research institute.

Van Devender, T. R., and W. G. Spaulding. 1979. Development of vegetation and climate in the Southwestern United States. *Science* 204: 701-10.

Abstract: Plant macrofossils in ancient packrat middens document the presence of woodland communities in most of the present Chihuahuan, Sonoran, and Mojave deserts in the southwestern United States during the late Wisconsinan (22,000 to 11,000 years before present by radiocarbon dating). Warm desert species were common in the woodlands at lower elevations and mixed conifer and subalpine forests were present at high elevations. Inferred mild, wet winters and cool summers produced unusual plant and animal associations compared to those of today. Montane communities acquired modern aspects and more mesophytic species disappeared from lower woodlands about 11,000 years ago. Early Holocene xeric woodlands and an inferred winter precipitation regime persisted until about 8000 years ago. The present circulation patterns, rainfall regimes, and biotic distributions probably formed as a result of the melting of the continental ice sheets. Southwestern communities appear to have responded quickly to climatic changes compared to the gradual responses of central and eastern United States forest communities.

Vora, R. S., and J. F. Messerly. 1990. Changes in native vegetation following different disturbances in the lower Rio Grande valley, Texas, USA. *Texas Journal of Science* 42, no. 2: 151-58.

Abstract: Permanent plots established in 1981 were censused again in 1986 at the Palmview tract of the Rio Grande Valley National Wildlife Refuge in southern Texas. Successional changes from bareground to communities dominated by dry-land willow (*Baccharis neglecta*) and huisache (*Acacia smallii*) were documented. In formerly grazed woodlands, overstory honey mesquite (*Prosopis glandulosa*) trees grew an average of 2.5 meters in height over the five-year period. Understory honey mesquite trees were dying, and cover of herbaceous vegetation declined. Cover of woody species such as coma (*Bumelia celastrina*), granjeno (*Celtis pallida*), brasil (*Condalia hookeri*), and Texas ebony (*Pithecellobium flexicaule*) were increasing beneath honey mesquite.

Walker, B. H., and I. Noy-Meir. 1982. Aspects of the stability and resilience of savanna ecosystems. *Ecology of tropical savannas*. B. J. Huntely, and B. H. Walker, 556-90. New York: Springer Verlag.

Went, F. W. 1955. The ecology of desert plants. *Scientific American* 192: 68-75.

Westoby, M. 1979-1980. Elements of a theory of vegetation dynamics in arid rangelands. *Israel Journal of Botany* 28: 169-94.

Abstract: Under grazing pressure the vegetation of rangelands is often altered. Range managers traditionally have thought of these changes as retrogression or disturbance, setting climax vegetation back to a seral stage. Unfortunately, removing the grazing pressure often does not reverse the changes in the way the succession model would predict. Here four elements are sketched out of a theory which can deal with these exceptions. First, which plant growth-forms win competition often depends not only on the growth-forms but also on which is present as established adults, or on which is most abundant. Second, vegetation changes can sometimes induce soil changes. The extent to which reversing a vegetation change depends on soil restoration varies greatly, and the speed with which soil structure can be restored varies from rapid to negligible. Third, the impact of grazing on different life-forms varies greatly in different situations; in particular, the nature of and scope for selectivity is very different in dense grasslands, where much of the primary production is being removed, compared to open arid vegetation. Fourth, a new model is outlined for the adaptation of plant growth-forms to different arid climates. This model shows that different growth-forms can coexist stably in arid regions because they use different growth opportunities in complex weather sequences. Climates with the same general level of aridity can offer very different mixtures of growth opportunities, because of patterning of rainfall in time; accordingly different mixtures of growth-forms are found. These growth-forms are adapted demographically, not just physiologically. After particular weather sequences, some species may be present only as seeds or seedlings, while others are present as adults; thus above-ground vegetation can vary even while the mixture of populations present is stable. One growth-form, such as annuals, can include several distinct demographic strategies, with different responses both to drought and to gazing. These four elements of a theory, taken in different combinations, can explain both classical cases of range succession and the important exceptions.

Whitford, W. G., K. Stinnett, and J. Anderson. 1988. Decomposition of roots in a Chihuahuan desert ecosystem. *Oecologia* 75: 8-11.

Wierenga, P. J., J. M. H. Hendrickx, M. H. Nash, J. Ludwig, and L. A. Daugherty. 1987. Variation of soil and vegetation with distance along a transect in the Chihuahuan Desert. *Journal of Arid Environments* 13: 53-63.

Wilson, J. B., and A. D. Q. Agnew. 1992. Positive-feedback switches in plant communities. *Advances in ecological research*. 23 ed., M. Begon, and A. H. Fitter, 263-336. London: Academic Press.

Wondzell, Steven Michael. 1984. "Recovery of desert grasslands in Big Bend National Park following 36 years of protection from grazing by domestic livestock." M. S. Thesis, New Mexico State University.

Wondzell, Steven M., Gary L. Cunningham, and Dominique Bachelet. 1996. Relationships between landforms, geomorphic processes, and plant communities on a watershed in the northern Chihuahuan Desert. *Landscape Ecology* 11, no. 6: 351-62.

Abstract: The close correlation of plant communities to landforms and geomorphic surfaces resulted from differences in the redistribution of water and organic matter between landforms in the northern Chihuahuan Desert. Biotic processes are limited by water and nitrogen, and the interactions between landforms, geomorphic processes, soils, and plant communities control the redistribution of these limiting resources within internally drained catchments. Geomorphic processes are regulated by the geologic structure and gross topographic relief of internally drained catchments over geological time scales. Land forming processes can be viewed as static at the time scales of 10's to 100's of years, with individual landforms regulating geomorphic processes, namely erosion and deposition resulting from the horizontal redistribution of water within the catchment. The vegetation composition is a critical feedback, reinforcing the erosional or depositional geomorphic processes that dominate each landform.

The Jornada Long-Term Ecological Research site may be one of the simplest cases in which to decipher the relationship between landforms, geomorphic processes and plant communities. However, these geomorphic processes are common to all internally drained catchments throughout the Basin and Range Province, and result in the development of characteristic landforms and associated vegetation communities. Although the patterns may be modified by difference in parent material, watershed size, and land use history - erosional, depositional, and transportational landforms can still be identified.

The sharpness of ecotones between plant communities on individual landforms is related to the degree to which landforms are linked through the flow of water and sediment. Sharp ecotones occurred at the transition from depositional to erosional landforms where little material was transferred and steep environmental gradients are maintained. Gradual ecotones occurred at the transition from erosional to depositional landforms where large quantities of material were transferred leading to the development of a gradual environmental gradient.

The relationships between geomorphic processes and vegetation communities that we describe have important implications for understanding the desertification of grasslands throughout semi-arid regions of North America. Disturbances such as grazing and climate change alter the composition of plant communities, thereby affecting the feedbacks to geomorphic processes, eventually changing drainage patterns and the spatial patterns of plant communities supported within the landscape.

Wood, J. C., M. K. Wood, and J. M. Tromble. 1987. Important factors influencing water infiltration and sediment production on arid lands in New Mexico. *Journal of Arid Environments* 12: 111-18.

Abstract: Factors influencing infiltration rates and sediment production were evaluated on representative study areas of four watersheds in New Mexico under various land management practices. Multiple regression analysis was used to determine the most important factors influencing infiltration and sediment production. Factors found important were soil texture, soil organic matter, soil bulk density, plant cover, biomass production, time to runoff and time to ponding. Of all variables studied, total ground cover was considered to be the most important single variable influencing infiltration and sediment production.

Wright, Robert A. 1982. Aspects of desertification in *Prosopis* dunelands of southern New Mexico, USA. *Journal of Arid Environments* 5: 277-84.

Abstract: Mesquite shrubs in long-established plots registered increases in numbers and cover for most observation periods, in spite of drought, herbicide treatment and protection from grazing. The few decreases noted seem to be accounted for by drought and herbicide. Changes in the biotic and physical environment are incorporated into a model that shows their respective roles in effecting the conversion from grass- to shrub-dominated ecosystems.

Yool, Stephen R. 1999. Multi-scale analysis of disturbance regimes in the northern Chihuahuan Desert. *Journal of Arid Environments* 40, no. 4: 467-83.

Abstract: Remote sensing facilitates cross-scale validation, enables analysis of processes and patterns in time and space, and is thus viable for the conduct of earth system science. Multi-scale analyses of natural vegetation patterns and processes in the northern Chihuahuan Desert show that natural vegetation is capable of recovering from short-term, high intensity disturbances such as an atomic bomb blast. In contrast, mesquite dunelands persist on other sites grazed before the blast, showing the Chihuahuan is less resilient to long-term low intensity disturbances. A geographic information system (GIS) was used to register historical Landsat Multi-Spectral Scanner (MSS) data acquired over Trinity National Historic Site (TNHS), New Mexico, and the vicinity. Aerial and ground photography provide supporting detail, at finer scales, regarding the distribution and pattern of natural vegetation at TNES Ground Zero and adjacent weapons impact targets. Aside from initial mechanical or thermal damage to vegetation from the first atomic test over a half century ago, analyses of vegetation at satellite and airphoto scales show no apparent persistent blast effects around TNHS.

York, J. C., and W. A. Dick-Peddie. 1969. Vegetation changes in southern New Mexico during the past hundred years. *Arid lands in perspective*. W. G. McGinnies, and B. J. Goldman, 155-66. Tucson, AZ: University of Arizona Press.

Abstract: The mesas of southern New Mexico were covered by grass in the middle of the last century. This grass was primarily grama grass (*Bouteloua* sp.). Mesquite occurred in limited areas on shallow sandy soil, but more importantly it occurred around Indian campsites. Creosotebush was restricted to well-drained gravelly hilltops and narrow patches in the foothills of mountains. Juniper stands were on mountain foothills usually higher or further north than creosotebush. The area was correctly classified desert grassland. All the other species have greatly expanded their ranges during the past hundred years, usually in response to a reduction in grass cover. The grass has not completely disappeared or even changed its boundaries in all cases. In one instance a secondary replacement of mesquite by creosotebush has taken place. The speed of the recent occupation by mesquite may be attributed to the effects of cattle in the presence of ideal source pockets of mesquite around old Indian campsites. The speed with which this almost complete replacement of grass has taken place in southern New Mexico coupled with the fact that isolated areas are unchanged indicates that climate has not been a factor. The topography and biomass potential of southern New Mexico make it highly unlikely that the area could ever have carried a fire. The appearance of the grazing industry is the only factor which coincides with the time of this spectacular change. Although the grasslands of southern New Mexico were extensive and dominated the area, they were on the xeric edge of the continental Grassland Formation. A single factor such as grazing was evidently enough to set in motion a series of relatively rapid events which culminated in a desert shrub vegetation. Even though the climate is virtually unchanged, the surface horizon which 100 years ago supported grassland is undoubtedly long gone down the arroyos or formed into dunes. Until there is a climatic change, therefore, most of southern New Mexico can be considered to be a desert climax rather than a desert grassland climax as it was 100 years ago.

3 *Bouteloua eriopoda* (Torr.) Torr. (Black grama)



Black grama is a stoloniferous, drought tolerant, C4 perennial grass. It is characterized by its hairy internodes. Even though in southern New Mexico reproduction by seeds is infrequent under the current climatic conditions (Neilson 1986), vegetative reproduction by stolons is common in this species. Black grama has a maximum lifespan of 35-40 years (Wright and Van Dyne 1976). Timing of inflorescence emergence varies with rainfall and can occur as early as June and as late as September (Gibbens 1989). The roots of black grama spread radially from the canopy for about 0.75 – 1 m and they can be found to around 1 – 1.5 m depth (Gibbens and Lenz 2001). Black grama is the dominant of desert grasslands in the Sonoran and Chihuahuan deserts. In the United States it is distributed throughout New Mexico and Arizona, as well as in parts of Colorado, Utah, Western Texas and Eastern California (Utah State University 2002). The range of elevation it generally occurs in is between 900 and 1,800 m (Simonin 2000). Soils are usually sandy loams to clay loams (Schmutz et al. 1992). Black grama is generally considered a prime forage species, especially because of its relatively high nitrogen content during the winter (Wright and Streetman 1958).



Atwood, Terence L. 1987. "Influence of livestock grazing and protection from livestock grazing on vegetational characteristics of *Bouteloua eriopoda* rangelands." Ph. D. Dissertation, New Mexico State University. Abstract: This study, conducted on *Bouteloua eriopoda* rangelands in southern New Mexico, was initiated in an attempt to quantify the effects of livestock grazing and protection from grazing on the vegetational characteristics of these ranges. Four study sites were examined, each of which had a livestock enclosure erected previous to the study. Ages of the enclosures in 1985 were 17, 22, 32, and 48 years. Vegetational attributes measured were density and frequency of perennial grasses and forbs, annual grasses and forbs, and density, frequency and canopy frequency of shrubs. At the site protected for 17 years, no differences ($P \leq 0.05$) were found in *Bouteloua eriopoda* density between the grazed and protected treatments. *Bouteloua eriopoda* density was greater ($P \leq 0.05$) on the grazed treatment than on the ungrazed treatment at the 22-year-old site, as was that of *Sporobolus* spp. Density of *Bouteloua eriopoda* was greater ($P \leq 0.05$) on the protected treatment at the site protected for 32 years, possibly due to favorable rainfall on the study site in preceding years. Density of *Bouteloua eriopoda* on the 48-year-old study site was greater on the protected than the grazed treatment at the time of, and for nine years following, the construction of the enclosure. In 1985, density of the species was greater ($P \leq 0.05$) on the grazed area. Density and frequency of perennial and annual forbs, and shrubs showed no relationship to either protection or grazing. It was concluded that livestock grazing is an important management tool in maintaining *Bouteloua eriopoda* rangelands, probably due to the species low tolerance to, and slow recovery from drought when ungrazed.

Atwood, T. L., R. F. Beck, and R. P. Gibbens. 1987. Vegetation parameters inside and outside livestock enclosures on three Chihuahuan Desert grassland communities. *40th Annual Meeting, Soc. Range Manage.* Abstr. No. 34.

Baggs, Joanne Elizabeth. 1997. "The role of *Bouteloua eriopoda* in the community structure and ecosystem function of a semi-arid grassland." M. S. Thesis, New Mexico State University.

Beck, Reldon F. 1978. A grazing system for semiarid lands. In *First International Rangeland Conference*, Editor Donald N. Hyder, 569-72 Society of Range Management.

Abstract: A seasonal suitability grazing system was started on semiarid grassland in 1967. Ten years of data have not shown it to be superior to yearlong grazing with which it was compared. Livestock performance was similar on the two systems. Drought and conservative stocking rates were primarily responsible for the lack of differences between the systems. Flexibility, a primary component of the seasonal suitability system, allows for specific management of perennial grasses. Sampling of vegetation was not intensive enough to detect the observable improvement on the seasonal suitability pastures.

Beck, R. F., T. L. Atwood, and R. P. Gibbens. 1986. Vegetation changes following 20 years of protection on black grama sites originally grazed at four intensities. *39th Annual Meeting, Soc. Range Manage.* Abstr. No. 110.

Beres, Lisa Ann. 1993. "Response potential of three perennial desert grasses to various disturbances." M.S. Thesis, New Mexico State University.

Abstract: Increasing desertification of the northern Chihuahuan semidesert grasslands is linked, in part, with the decline or disappearance of perennial grasses. While vegetational changes have been well documented since the early 1900's, no clear cause for these changes has been determined. Although many disturbances have been linked to these changes, this study focuses only on grazing, microsite, and competition effects. By measuring the growth potential, establishment potential, and germination rates of *Bouteloua eriopoda*, and *Sporobolus flexuosus*, and *Aristida wrightii*, the study provided insights into potential response to these disturbances. In these dominant perennial grasses, grazing effects were measured in three major ways. A descriptive survey assessed differences between plants and populations with a history of livestock grazing and those without. Secondly, a clipping experiment measured regrowth potential in response to biomass removal from selected plants within these areas. Finally, differences in clonal spread in *Bouteloua eriopoda* were measured in grazed and ungrazed locations. In all three species, microsite effects were assessed through the survivorship and growth of clonal transplants planted into open and vegetated patches within shrubland and grassland communities. For competition effects, survivorship and growth responses were measured for the three species growing together in pots that were either in full sunlight or shade. In these studies, growth and establishment potential was measured by assessing plant height, plant size, stolon length, number of tillers or stolons, number of nodes, and flowering seed production. Germination rates were determined in a lab study, using seeds of the three grass species. Results indicated there were some significant grazing effects for the variables studied in some of the species. However, there was no significant effect of grazing history on response to clipping for any of the study species. Clonal spread was significantly different between sites and treatments in *Bouteloua eriopoda*. Survivorship was low for the clonal transplants. However, two of the three grass species had a higher survivorship within the vegetated microsite patches. In contrast, in the greenhouse

experiment, the transplants that were in full sunlight had more tillers and increased height than those in the shade. *Aristida wrightii* had the highest seed production and germination rate.

Bock, C. E., and J. H. Bock. 1993. Cover of perennial grasses in southeastern Arizona in relation to livestock grazing. *Conservation Biology* 7, no. 2: 371-77.

Bridges, J. O. 1941. "Reseeding trials on arid range land." Bulletin 278. New Mexico State University, Agricultural Experiment Station, Las Cruces, New Mexico.

———. 1942. "Reseeding practices for New Mexico ranges." Bulletin 291. New Mexico State University, Agricultural Experiment Station, Las Cruces, New Mexico.

Buxbaum, C. A. 1997. Soil heterogeneity controls Chihuahuan desert and Colorado shortgrass prairie species distribution in a desert-grassland ecotone. *Supplement to Bulletin of the Ecological Society of America* 78: 62.

Cable, Dwight R. 1965. Damage to mesquite, Lehmann lovegrass, and black grama by a hot June fire. *Journal of Range Management* 18: 326-29.

Abstract: Twenty-five percent of mesquite trees were killed on an area with Lehmann lovegrass ground cover compare to eight percent on an area with black grama. Ninety percent of black grama plants and more than 98% of lovegrass plants were killed. Many new lovegrass seedlings became established on both areas.

———. 1975. Influence of precipitation on perennial grass production in the semidesert Southwest. *Ecology* 56, no. 4: 981-86.

Abstract: Perennial grass production in the semidesert grass-shrub type (with and without a velvet mesquite (*Prosopis juliflora* var. *velutina* [Woot.] Sarg.) overstory) was dependent primarily on current summer rainfall and previous summer rainfall. The influence of previous summer rainfall was an interaction effect--not a direct effect. The best overall relationship involved current August rainfall, previous June through September rainfall, and the interaction product of these two. However, in interaction product along yielded estimates essentially as good as the multiple regression, and explained 64%-91% of the year-to-year variability in grass production. Winter precipitation had no consistent effect on perennial grass production the following summer. The degressing effect of mesquite on perennial grass production was most noticeable at low rainfall levels, but became minor at high rainfall levels

Campbell, R. S. 1935. After the drought. *Amer. Cattle Producer* 17: 3-5.

———. 1935. Management of black grama ranges. *American Hereford Journal* 26, no. 9: 74-76.

Campbell, R. S., and E. H. Bomberger. 1934. The occurrence of *Gutierrezia sarothrae* on *Bouteloua eriopoda* ranges. *Ecology* 15, no. 1: 49-61.

See abstract under *Gutierrezia sarothrae*

Campbell, R. S., and Edward C. Crafts. 1939. How to keep and increase black grama on southwestern ranges. Leaflet No. 180, U.S. Department of Agriculture.

Abstract: Black grama (*Bouteloua eriopoda*), also known locally as woollyfoot or crowfoot grama, is by far the most important forage grass on the 89 million acres of semidesert grasslands in Arizona, New Mexico, southwestern Texas, and southern Utah. Although not as common now as in the early days, black grama can be maintained on the range and even brought back by management based on careful consideration of its forage and soil-protection values, its methods of spreading, and its ability to stand up under drought and grazing.

As a prime indicator of range utilization, black grama ranks second only to blue grama (*Bouteloua gracilis*) over the entire Southwest. The two sometimes occur together in mixed stands, but blue grama typically grows in pinon-juniper woodlands and on the heavier soils of the short-grass plains, whereas black grama is found on the better-drained soils in the short-grass country and the warmer and lower semidesert grasslands. Black grama may be easily distinguished from other grammas by its widely creeping runners or stolons, which root at the joints and send up new shoots that later become separate plants.

Canfield, R. H. 1933. Solid and hollow stemmed grasses of the Jornada Experimental Range. *Science* 78: 342.

———. 1934. Stem structure of grasses on the Jornada Experimental Range. *Botany Gazette* 95: 636-48.

———. 1938. How closely may black grama and tobosa grass be grazed year after year? *Cattlemen* 23, no. 7: 1-3.

———. 1938. Vegetational density and composition of black grama type ranges as influenced by semideferred grazing. *USDA, Forest Service, Southwest Forest and Range Exp. Sta. Res. Note 35*: 2 pp.

———. 1939. Ways and means to minimize the ill effects of drought on black grama ranges. *USDA, Forest Service, Southwest Forest and Range Exp. Sta. Res. Note 82*: 7 pp.

———. 1939. Maintaining the balance between summer and winter forage on black grama ranges. *USDA, Forest Service, Southwest Forest and Range Exp. Sta. Res. Note 81*: 4 pp.

———. 1939. *The effect of intensity and frequency of clipping on density and yield of black grama and tobosa grass*. Technical Bulletin , no. 681. Washington : U.S. Dept. of Agriculture.

See abstract under *Pleuraphis mutica*

———. 1948. New grass for old. *Amer. Cattle Producer* 30: 30-31.

———. 1957. Reproduction and life span of some perennial grasses of southern Arizona. *Journal of Range Management* 10, no. 5: 199-203.

Cornelius, Joe Malcolm. 1988. "Fire effects on vegetation of a northern Chihuahuan Desert grassland (New Mexico)." Ph. D. Dissertation, New Mexico State University.

Abstract: It has been hypothesized that fire was important in maintenance of southwestern US desert grasslands, and that decreased fire frequency and intensity caused by lowered fuel levels from livestock grazing may be one cause of desertification of these desert grasslands. This research examines fire effects in a black grama (*Bouteloua eriopoda*) grassland, and assesses the potential historical role that fire may have had in these grasslands. Permanent plots were located on a northern Chihuahuan Desert grassland study site (south-central New Mexico). Selected plots were burned in May 1984 and May 1985. Plant canopy cover was estimated within plots in spring 1984 (preburn) and fall 1984 through 1986. Following burning, cover increase of perennial grass (primarily *Bouteloua eriopoda*) was slow (6-8 years estimated to return to preburn cover), and variation between years was high. Shrub (primarily *Ephedra trifurca*) mortality was low, cover increased slightly faster than perennial grass (4-5 years estimated to return to preburn cover), and there was little variation between years. Cactus (primarily *Opuntia violacea*) mortality was low and cover was little affected by burning. Subshrub (primarily *Xanthocephalum microcephalum*) mortality was high, but the rate of seedling reestablishment afterwards was also high, thus, fire likely has little long-term effect on cover. There was increased species diversity even three years after burning due to decreased grass cover and increased cover of perennial forbs and annuals. These results suggest that fire was not important in maintenance of black grama Chihuahuan Desert grasslands. Instead a widespread, intense fire would likely have been a severe disturbance that could have caused decreased abundance of grasses and increased abundance of shrubs, thus possibly enhancing desertification rather than preventing it

DeGarmo, H. C.Jr. 1966. "Water requirement and production of eight desert plant species under four soil moisture levels." M. S. Thesis, New Mexico State University.

Drewa, Paul B., and Kris M. Havstad. 2001. Effects of fire, grazing, and the presence of shrubs on Chihuahuan desert grasslands . *Journal of Arid Environments* 48, no. 4: 429-43.

Abstract: Responses of herbaceous and suffrutescent species to fire, grazing, and presence of *Prosopis glandulosa* were examined in a Chihuahuan desert grassland in south-central New Mexico. Treatments

were assigned randomly to eight 12×8 m plots within each of two blocks. Following fires in June 1995, unfenced plots were exposed to livestock grazing over 4 years. Plots were established that either included or excluded *P. glandulosa*. Perennial grass cover, primarily *Bouteloua eriopoda*, decreased by 13% in burned plots but increased 5% in unburned areas. Conversely, perennial forb cover was 4% greater after fire. Perennial grass frequency decreased 30% more and perennial forb frequency increased 10% more following burning. Further, increases in evenness after fire resulted in a 225% increase in species diversity. Grazing also resulted in a decrease in perennial grass cover while frequency decreased 22% more in grazed than ungrazed plots. Only frequency and not cover of perennial forbs and annual grasses increased more following grazing. Presence of *P. glandulosa* had no differential effect on responses of non-shrub species. Fires were conducted during near drought conditions while grazing occurred during years of precipitation equivalent to the long-term average. Precipitation immediately following fire may be critical for recovery of *B. eriopoda*-dominated desert grasslands; relationships between fire and post-fire precipitation patterns require future investigation.

Drewa, Paul B., Debra P. C. Peters, and Kris M. Havstad. 2001. Fire, grazing, and honey mesquite invasion in black grama-dominated grasslands of the Chihuahuan desert: a synthesis. In *Proceedings of the invasive species workshop: the role of fire in the control and spread of invasive species. Fire conference 2000: the first national congress on fire ecology, prevention, and management*. Editors K. E. M. Galley, and T. P. Wilson, 31-39. Tallahassee, Florida: Tall Timbers Research Station.

See abstract under *Prosopis glandulosa*

Dugas, William A., Ralph A. Hicks, and Robert P. Gibbens. 1996. Structure and function of C3 and C4 Chihuahuan desert plant communities. Energy balance components. *Journal of Arid Environments* 34, no. 1: 63-79.

See abstract under *Larrea tridentata*

Dwyer, Don D., and Harlan C. DeGarmo. 1970. Greenhouse productivity and water-use efficiency of selected desert shrubs and grasses under four soil-moisture levels. *New Mexico Agricultural Experiment Station Bulletin* No. 570.

El Shahaby, Ahmed F. 1988. "Associative nitrogen fixation with C4 grasses of the northern Chihuahuan Desert variant ." Ph. D. Dissertation, New Mexico State University.

Abstract: Increasing evidence has been accumulating supporting significant grass-diazotrophic associations. However, characterization of these associations in hot desert grasses is lacking. Nitrogenase activity was measured in excised roots amended with glucose. Grass roots had up to 18-fold greater nitrogenase activity than soil cores. This confirms association between N₂-fixing bacteria and the plant species. The C4 perennial grasses tested had greater nitrogenase activity than the C3 annual herb, *Baileya multiradiata*, desert marigold. Nitrogenase activity was highly variable among plant species and within a species. Higher rates of nitrogenase activity were associated with higher soil water contents. The

phenophase of the plant species affected nitrogenase activity. Nitrogenase activity was greatest during vegetative and flowering phases of the grass phenology. Nitrogenase activity was higher during the hot wet season than during the cold season or warm dry season suggesting that climatic conditions or plant growth affected nitrogen fixation activity. Nitrogen fixation associated with intact plant-soil systems was studied in the greenhouse. There were no significant differences in acetylene reduction among grasses. Plant phenology had a significant effect on nitrogenase activity. The highest nitrogenase activity was observed during vegetative growth. The study confirmed that N₂ is fixed in soil and in the rhizosphere of grasses tested. Inoculation studies were conducted on the C₄ perennial grass, *Sporobolus cryptandrus*, under greenhouse conditions. In the first experiment, inoculated plants had greater height, more tillers, longer flag leaf length, greater root length, more biomass, greater nitrogenase activities, and higher N content than control plants. The nitrogenase activity was greater during the vegetative phase than reproductive phases of the grass. In the second experiment, clipping after inoculation had similar significant effects on plant parameters and N content. However, nitrogenase activity and N concentration in plants and soil were lower than in the first experiment. The mixed culture treatment had the major positive effect on the grass in both experiments. The results indicated that associative N₂ fixation may be ecologically important in N₂ fixation and cycling in the Chihuahuan Desert.

Ewing, David Lugene. 1977. "Topographic factors affecting utilization of black grama in southwestern Arizona ." M. S. Thesis, University of Arizona.

Fernández, R. J., and J. F. Reynolds. 2000. Potential growth and drought tolerance of eight desert grasses: lack of trade-off? *Oecologia* 123, no. 1: 90-98.

Abstract: Eight perennial C-4 grasses from the Jornada del Muerto Basin in southern New Mexico show five-fold differences in relative growth rates under well-watered conditions (RGR_{max}). In a controlled environment, we tested the hypothesis that there is an inverse relationship (trade-off) between RGR_{max} and the capacity of these species to tolerate drought. We examined both physiological (gas exchange) and morphological (biomass allocation, leaf properties) determinants of growth for these eight species under three steady-state drought treatments (none=control, moderate, and severe). When well watered, the grasses exhibited a large interspecific variation in growth, which was reflected in order-of-magnitude biomass differences after 5 weeks. The species had similar gas-exchange characteristics, but differed in all the measured allocation and morphological characteristics, namely tiller mass and number, root:shoot ratio, dry-matter content, and specific leaf area (SLA). Drought affected tillering, morphology, and allocation, and reduced growth by 50 and 68% (moderate and severe drought, respectively) compared to the well-watered controls. With the exception of SLA, none of these variables showed a significant species-by-treatment interaction. We calculated three indices of drought tolerance, defined as the ratio in final biomass between all the possible "dry"/"wet" treatment pairs: severe/moderate, moderate/control, and severe/control. We found no significant correlation between these drought tolerance indices, on the one hand, and three indices of growth potential (greenhouse RGR_{max} , final biomass in the control treatment, and final:initial biomass ratio in controls), on the other. Based on these controlled-environment results, we hypothesize that the commonly reported correlation between plant growth potential and drought tolerance

in the field may in some cases be explained by differential effects of plants on soil-water content rather than by differences in species responses to drought.

Fields, M. J., D. P. Coffin, and J. R. Gosz. 1999. Burrowing activities of kangaroo rats and patterns in plant species dominance at a shortgrass steppe-desert grassland ecotone. *Journal of Vegetation Science* 10: 123-30.

Gadzia, Kirk Leslie. 1979. "Growth and development patterns of black grama in southern New Mexico." M. S. Thesis, New Mexico State University.

Abstract: The objectives of this study were to 1) provide an accurate description of growth and development of black grama; 2) determine reproductive potential of all stem types within this species; and 3) distinguish the most important factors influencing new plant establishment by vegetative means. Three years of black grama shoot production were classified according to their position of growth during a two-year period. Horizontal shoots, which have generally been referred to as stolons included shoots growing along or near the soil surface. Vertical shoots, generally classified as flower stalks or floral culms, included shoots in a position +/- 25 degrees from the vertical; while angular shoots included those shoots which occur throughout the plant at approximately a 45 degree angle and have been referred to as either stolons or floral culms. Shoots were permanently marked with non-restricting color rings and changes in development and position were evaluated over a two-year period.

No apparent morphological differences were noted between the three categories of shoots. All shoots followed the general phenological pattern of vegetative growth, floral development, quiescence and senescence. The period of time shoots remained in these phases appeared to depend upon prevailing conditions of precipitation, temperature and day length. Amounts of axillary branching, which are the potential for vegetative reproduction in black grama, were nearly equal for all categories.

Of the three categories of shoot position, proportions of axillary branches which became rooted during the study period were greatest for the horizontal category. Angular shoots rooted about 30% of the total, while vertical shoots only rarely contributed to vegetative reproduction. Differences in proportion of positional change within the three categories appeared responsible for the observed difference in rooted axillary branching. These differences were also related to the amount of time axillary branches were in position to take advantage of the relatively short periods during the growing season when conditions were favorable for rooting.

Comparison of grazed and ungrazed plants suggests that the chances for establishment of axillary branches on shoots in the horizontal position are not severely impaired under a moderate grazing regime, although a greater percentage were broken by trampling. Angular shoots were less susceptible to trampling, but about 30% were consumed during the 1978 growing season. Practically all vertical shoots were removed under moderate grazing. Hoof action may improve the chances for establishment of rooted axillary branches by covering their crown bases with loose soil and providing more favorable rooting conditions through breakup of the hard-surfaced soil crust.

Gibbens, Robert P. 1989. Phenology of native and introduced grasses in southern New Mexico. *42nd Annual Meeting of the Society of Range Management*, Abstract No. 061.

Gibbens, Robert P., and Reldon F. Beck. 1987. Increase in number of dominant plants and dominance-classes on a grassland in the northern Chihuahuan desert. *Journal of Range Management* 40, no. 2: 136-39.

Abstract: Between 1915 and 1932, 104 permanent 1 x 1-m quadrats were established on grasslands of the Jornada Experimental Range in southern New Mexico. Primary- and secondary-dominant species were determined from the first quadrat records and each quadrat was reevaluated in 1981 to determine current dominants. The first records showed that 13 species of perennial grasses occupied all primary- and secondary-dominant positions on all quadrats. In 1981, there were 12 perennial grass species as primary- or secondary-dominants. Six shrub species occurred as primary- or secondary-dominants on 47% of the quadrat sites in 1981. Dominance-classes, i.e., single-species dominance or two-species dominant combinations, increased from 24 to 43. Thus, vegetation on this range has become more diverse and this diversity must be considered in grazing management.

———. 1988. Changes in grass basal area and forb densities over a 64-year period on grassland types of the Jornada Experimental Range. *Journal of Range Management* 41, no. 3: 186-92.

Abstract: Between 1915 and 1932, permanent 1 x 1-m quadrats were established on grasslands of the Jornada Experimental Range in southern New Mexico. Quadrat records accumulated from 1915 to 1979 on grasslands dominated by black grama [*Bouteloua eriopoda* (Torr.) Torr.], poverty threeawn (*Aristida divaricata* Willd.), tobosa [*Hilaria mutica* (Buckl.) Benth.], and burrograss (*Scleropogon brevifolius* Phil.) were used to examine changes in perennial grass basal area and forb densities. Quadrats originally dominated by black grama had large reductions in basal area during droughts, and basal area increased slowly following droughts. By 1979, black grama no longer occurred on 77% of the quadrats. Quadrats originally dominated by poverty threeawn changed to a mesquite (*Prosopis glandulosa* Torr. var *glandulosa*) type. Perennial grass basal area on quadrats dominated by tobosa and burrograss decreased during droughts, but recovery was relatively rapid. Antecedent precipitation was associated with only 10 to 38% of the variation in perennial grass basal area. Perennial forb densities were low and fluctuated among years in all types. Annual forbs and grasses displayed large fluctuations in densities among years. The necessity of basing management of Chihuahuan Desert ranges on the perennial grasses is borne out by the low densities of palatable perennial forbs, and the extreme fluctuations and unpredictability in densities of annual forbs and grasses.

Gibbens, Robert P., Ralph A. Hicks, and William A. Dugas. 1996. Structure and function of C3 and C4 Chihuahuan desert plant communities. Standing crop and leaf area index. *Journal of Arid Environments* 34, no. 1: 47-62.

See abstract under *Flourensia cernua*

Gibbens, R. P., and J. M. Lenz. 2001. Root systems of some Chihuahuan desert plants. *Journal of Arid Environments* 49, no. 2: 221-63.

Abstract: Root systems of 11 shrub or shrub-like species, 11 grass species, 19 perennial forb species and four annual forb species were excavated on the Jornada Experimental Range in the northern Chihuahuan Desert in southern New Mexico, U.S.A. Maximum radial horizontal spread of shrub root systems usually occurred above calcic and petrocalcic horizons at depths above 1 m. With one exception, all shrub species roots were traced through calcic and petrocalcic horizons to depths down to 5 m. Upward growing roots reaching very shallow depths (<10 cm) were common for most shrub species. Thus, the shrubs can readily access soil water and nutrients from both surface and deep soil horizons. Grass root systems on sandy soils extended radially up to 1.4 m, perhaps an adaptation to capture more soil water from the frequent small rainfall events. Grass roots did not extend through calcic or petrocalcic horizons and none penetrated deeper than 1.6 m. Perennial forb root systems varied in depth of branching but often penetrated into or through calcic and petrocalcic horizons and, like shrubs, have an advantage over grasses during droughts. Root systems of the annual forbs, excavated at the end of a season of above average precipitation, reached depths of 0.5-1.2 m. At each of the 18 excavation sites the roots of all the plant life forms were highly intermingled in the upper soil horizons, indicating that competition for water and soil nutrients is intense. It is believed that the plasticity and architecture of the shrub root systems, enabling them to compete with the grasses for soil water in the upper soil horizons and also access soil water at depths beyond the reach of grass roots, has been a major reason for the increase of shrubs during the historical period in this arid environment

Gill, Richard A., and Ingrid C. Burke. 1999. Ecosystem consequences of plant life form changes at three sites in the semiarid United States. *Oecologia* 121, no. 4 : 551-63.

See abstract under *Larrea tridentata*

Glendening, G. E. 1942. Germination and emergence of some native grasses in relation to litter cover and soil moisture. *Journal of the American Society of Agronomy* 34: 797-804.

Abstract: 1. During the summer of 1938 seeds of 10 native perennial grasses were planted in replicated plots under eight different treatments, including cultivation and covering of the surface soil with various kinds of litter on a depleted semidesert grassland range south of Tucson, Ariz. At the same time provision was made on an adjacent plot to obtain moisture samples at surface-inch, 6-inch, and 12-inch depths of bare soil, soil covered with straw litter, and soil covered with open-mesh gauze fabric. 2. Results showed that moisture content at all levels was consistently greater under the straw and gauze than on the bare ground and that the length of time during which moisture content of the surface soil was above the calculated W. C. was greatest under the straw litter. 3. Germination and emergence of grass seedlings was increased from 4 to more than 20 times over that on the bare ground by the various surface-soil treatments.

Gosz, R. J., and J. R. Gosz. 1996. Species interactions on the biome transition zone in New Mexico: response of blue grama (*Bouteloua gracilis*) and black grama (*Bouteloua eriopoda*) to fire and grazing. *Journal of Arid Environments* 34: 101-14.

Gross, Bryan D. 1984. "Demographic sensitivity of two perennial desert grasses (*Bouteloua eriopoda* Torr. and *Sporobolus flexuosus* Thurb.) with inferences toward ecological dominance and subdominance." Ph. D. Dissertation, New Mexico State University.

Abstract: The objective of this study was to determine if differences in ecological role of two perennial grasses, in a southern New Mexico desert grassland, could be explained by species demography. It was hypothesized that demographic insensitivity to the environment favors dominance, while sensitivity results in subdominance. Analysis of black grama (*Bouteloua eriopoda* Torr.) and mesa dropseed (*Sporobolus flexuosus* Thurb.) was conducted on a cohort basis for 42 years of data. Species demography was analyzed on a life table basis and by regression analysis, with intraspecific density and various environmental components used as causal variables. Results indicated few differences in mean demography of the species, although black grama was characterized by a more constant age-specific mortality risk and mesa dropseed by high reproduction. The demographic feature unique to the species was variability of survival and reproduction. Mesa dropseed was characterized by greater variability of both fitness parameters. Environmental dependence results showed that each species was characterized not by overall unique sensitivity, but instead by age-dependent patterns. Sensitivity to short-term environmental events was greatest for first- and second-year age-states, and was more pronounced in mesa dropseed than in black grama. Older plants of each species were sensitive to longer-term environmental events. The sensitivity of adults of each species was similar. Survival sensitivity to intraspecific density was also age-dependent. Highest density sensitivity occurred in mature and first-year plants of both species, while lowest sensitivity to density occurred in second year plants. Black grama was more sensitive to density than was mesa dropseed. This was also true for reproduction. Results did not firmly support the initial hypotheses. Each species did not demonstrate overall uniqueness of demography since this was strongly age-dependent. Species demographic behavior, and perhaps relative ecological roles, are strongly dependent upon variability of population age structure.

Gross, Bryan D., and Robert P. Gibbens. unpublished manuscript. Life history comparison of two perennial desert grasses with inferences toward dominance and opportunism. 31 pp.

Abstract: A study was conducted to determine if differences in ecological role of two perennial grasses could be explained by species life history. It was hypothesized that insensitivity of survival and reproduction to environmental variability, and demographic inflexibility, leads to ecological dominance, while life history sensitivity and flexibility results in a subdominant ecological role. Analysis of life histories of black grama (*Bouteloua eriopoda*), a dominant, and mesa dropseed (*Sporobolus flexuosus*), a subdominant, was conducted on a cohort basis using 42 years of data from annually charted quadrats on a southern New Mexico desert grassland. Species demography was compared on a life-table basis and by various non-linear techniques. Results indicated few differences in mean demography. The demographic feature unique to each species was variability of survival and reproductive rates. Greater variability of survival and

reproduction, and greater age-dependency, were demonstrated by the subdominant species. Variable life history may have a major effect upon ecological roles of coexisting species, and may affect vegetation patterns along successional gradients.

Haque, Zahoorul, Amade Younga, Kirk C. McDaniel, and Rex D. Pieper. 1991. Two-phase pattern in mesquite-herbland vegetation in southern New Mexico. *The Southwestern Naturalist* 36, no. 1: 54-59.

See abstract under *Prosopis glandulosa*

Havstad, K. M., R. P. Gibbens, C. A. Knorr, and L. W. Murray. 1999. Long-term influences of shrub removal and lagomorph exclusion on Chihuahuan Desert vegetation dynamics. *Journal of Arid Environments* 42: 155-66.

Abstract: Cover of perennial species in long-term experimental plots in a creosotebush dominated community in the Chihuahuan Desert was monitored for 56 years. Sixteen 21.3 x 21.3 m plots were established in 1938-39 to evaluate the effects of lagomorph exclusion and shrub removal. Major dominant shrubs were individually severed at ground level and removed by hand in 1939, and this process was repeated after measuring plant cover in 1947, 1956, 1960, 1967, 1989, and 1995. Lagomorphs were excluded with poultry wire fencing. Shrub removal increased the basal cover of two major desert grass species, black grama (*Bouteloua eriopoda* Torr.) and spike dropseed (*Sporobolus contractus* A.S. Hitch.) between 1939 and 1995, but differences were not evident until 50 years after initial treatment. Temporal effects of lagomorph exclusion were less pronounced than shrub removal. Clearly, shrub dominance has an extremely important and lasting role in determining vegetation community structure in this arid environment, even when aboveground shrub structures are periodically removed.

Herbel, Carlton H., Fred N. Ares, and Robert A. Wright. 1972. Drought effects on a semidesert grassland range. *Ecology* 53, no. 6: 1084-93.

Abstract: A vegetational survey on the Jornada Experimental Range in southern New Mexico, taken annually from 1941 through 1957, is the basis for a study of the effects of the great drought of 1951 through 1956. Both cover and yields were studied. Observations were stratified into seven classes based on a consideration of land form and soil characteristics. Seasonal and annual precipitation during the drought averaged 55% of the pre-drought average. The most severe drought years were 1951, 1953, and 1956. Both the cover and yield of *Bouteloua eriopoda* (Torr.) Torr., the dominant species on the upland sandy soils, were greatly reduced by drought. However, drought damage was much more severe on the deep than on shallow sands. When the impermeable caliche layer occurred at shallow depths, moisture relations during drought were apparently much better than when caliche occurred at greater depths. Another result of drought was the invasion of *Prosopis juliflora* (Sw.) DC. in areas where grass stands have been thinned by drought. *Sporobolus* spp. and *Aristida* spp., minor components of the climax, were more susceptible to drought damage than *Bouteloua eriopoda*. Yields of perennial grasses per unit cover were as great during the drought as prior to the drought. Both winter-spring and summer precipitation are important in

preventing death losses of black grama. In arid areas it seems necessary to consider both cover and species composition in arriving at a potential for a site

Herbel, Carlton H., and Robert P. Gibbens. 1996. Post-drought vegetation dynamics on arid rangelands in southern New Mexico. *New Mexico Agricultural Experiment Station Bulletin No. 776*.

Abstract: The severe drought of 1951-1956 greatly changed vegetation on some arid rangeland sites of the Southwest. This study presented vegetation cover and yield for various sites for several years following the drought. Perennial grasses were the most prominent portion of the herbaceous plants. The sites dominated by tobosa and burrograss did not have the drastic changes as did some of the sandy sites, but there can be a tenfold increase or decrease of the basal cover of those two species within two years. Black grama cover was substantially reduced on deep sands by severe drought and did not recover during this study. These deep sands are subject to wind erosion because they lost much of their protective cover. Drought effects on black grama were not as severe on shallow sands, and its cover increased in wetter years on these sites. Because of prolific seed production, mesa dropseed's cover increased rapidly on sands following drought; but it decreased substantially during the dry years in the 1960s. Propagules of annual grasses and forbs, and short-lived perennial forbs were abundant from previous populations, allowing them to increase rapidly when environmental conditions were appropriate for certain species to establish. Results indicated that protection from rodents and rabbits increased the cover of annual grasses, whereas their presence increased the cover of annual forbs. However, protecting herbaceous plants from rodents, rabbits, or cattle did not give a major response. Broom snakeweed increased on sandy soils in wetter years. Honey mesquite's increase following drought was greater on deep sands than on shallow sands, but there also was a rapid increase on shallow sands. Apparently, the absence of cattle increased honey mesquite cover, but the presence of cattle did not prevent honey mesquite increase. Perennial grass yields were higher on shallow sands, where there was a mixture of black grama and mesa dropseed, than on deep sands dominated by mesa dropseed. The factors affecting perennial grass yields were precipitation, soil water, soil characteristics, plant species, and plant cover. The variation in annual perennial grass production on all sites was sometimes dramatic and has management implications. This study shows that large vegetation changes occurred because of severe drought and these changes are persistent on some sites.

Herbel, Carlton H., and Ronald E. Sosebee. 1969. Moisture and temperature effects on emergence and initial growth of two range grasses. *Agronomy Journal* 61: 628-31.

Abstract: This research, conducted in controlled light-temperature chambers, studied the effects of two temperature regimes and five moisture levels on early growth of black grama (*Bouteloua eriopoda* (Torr.) Torr.) and boer lovegrass (*Eragrostis chloromelas* Steud.). The maximum daily soil temperatures ranged from 53 to 67 C in the high temperature regime, and from 38 to 51 C in the low temperature regime, depending on moisture level. The daily minimum temperatures were about 25 C in all treatments. The five soil moisture levels were determined as a portion of the volume required to maintain field capacity conditions. Level A was approximately field capacity; level B and C were watered as level A on the planting day, and then reduced to about a half and a third of level A for the remainder of the 21-day trial. Levels D

and E were watered as level A for the first 3 days, and then reduced to about a half and a third of level A for the remainder of the trial.

In the high temperature regime black grama did not emerge at moisture levels B and C; and boer lovegrass did not emerge at levels B, C, and E. In addition, boer lovegrass did not emerge in the low temperature regime at moisture level C. Survival of emerging seedlings ranged from 0 to 4.7% in the high temperature regime at all moisture levels except A. Reduced soil moisture, a day after planting, was more detrimental to survival than reducing soil moisture on the third day after planting. Survival of black grama at moisture level A in the high temperature regime was not adversely affected by the high leaf temperatures (81 C). The shoot lengths and weights of surviving black grama seedlings were always greater than those of boer lovegrass. Survival and growth of seeded species in the Southwest would be enhanced if soil temperatures and evaporation from the soil surface were reduced. Under the conditions of this 21-day trial it took about 70 mm of water for either species to survive in the low temperature regime and about 231 mm to survive in the high temperature regime.

Herman, R. Peter, Kerri R. Provencio, Ruben J. Torrez, and Gwen M. Seager. 1993. Effect of water and nitrogen additions on free-living nitrogen fixer populations in desert grass root zones. *Applied and Environmental Microbiology* 59, no. 9: 3021-26.

Abstract: In this study we measured changes in population levels of free-living N₂-fixing bacteria in the root zones of potted *Bouteloua eriopoda* and *Sporobolus flexuosus* plants as well as the photosynthetic indices of the plants in response to added nitrogen, added water, and added water plus nitrogen treatments. In addition, N₂ fixer population changes in response to added carbon source and nitrogen were measured in plant-free soil columns. There were significant increases in the numbers of N₂ fixers associated with both plant species in the water and the water plus nitrogen treatments. Both treatments increase the photosynthetic index, suggesting that plant exudates were driving N₂ fixer population changes. Population increases were greatest in the water plus nitrogen treatments, indicating that added nitrogen was synergistic with added water and suggesting that nitrogen addition spared bacteria the metabolic cost of N₂ fixation, allowing greater reproduction. Plant-free column studies demonstrated a synergistic carbon-nitrogen effect when carbon levels were limiting (low malate addition) but not when carbon was abundant (high malate), further supporting this hypothesis. The results of this study indicate the presence of N₂ fixer populations which interact with plants and which may play a role in the nitrogen balance of desert grasslands.

Hickman, Gary Wayne. 1974. "Some effects of carbamate insecticide on primary producers in a desert grassland ecosystem." M.S. Thesis, New Mexico State University.

Abstract: Field and greenhouse studies were undertaken to determine some effects of a carbamate insecticide on primary producers in a desert grassland ecosystem. A 2500 m² field area was sprayed with Sevin and periodically sampled over a period of one year to obtain density, cover and biomass data. These results were compared to an untreated control area. Over the study period, no significant differences developed in the above parameters between treatment and control areas.

In the greenhouse, field transplanted *Bouteloua eriopoda* plants received various concentrations of insecticide and were sampled over a period equivalent to the growing season for vegetative and reproductive biomass. No significant differences developed among the various treatments and control. The only study that produced significantly different results was the germination experiment. *B. eriopoda* seeds were soaked in various concentrations of insecticide and allowed to germinate in moistened petri plates. The medium concentration tested, 0.01%, produced significantly higher germination percentages than the water only control.

Hochstrasser, Tamara. 2001. "Pattern and process at a desert grassland-shrubland ecotone." Ph. D. Dissertation, Colorado State University.

See abstract under *Larrea tridentata*

Holechek, Jerry L., Ackim Tembo, Alipayou Daniel, Michael J. Fusco, and Manuel Cardenas. 1994. Long-term grazing influences on Chihuahuan desert rangeland. *Southwestern Naturalist* 39, no. 4: 342-49.
Abstract: Vegetation composition and forage productivity were studied on two Chihuahuan desert ranges with different management histories. They involved the conservatively grazed New Mexico State University College Ranch, and adjoining intermediately grazed Bureau of Land Management (BLM) ranges north of Las Cruces in southcentral New Mexico. Conservative and intermediate grazing involved about 30 and 50% average use by livestock of the key forage species, respectively. A major focus of this study was the influence of stocking rate on recovery of native perennial grasses on rangeland with moderate amounts of honey mesquite (*Prosopis glandulosa* Torr.) (College Ranch) compared to areas heavily dominated by mesquite (BLM). In fall of 1982 total perennial grass standing crop averaged 182 kg/ha and 36 kg/ha on the long-term conservatively (CG) and intermediately grazed (IG) ranges, respectively. By the fall of 1990 perennial grass standing crop had increased to 349 kg/ha and 159 kg/ha on the CG and IG ranges, respectively. Mesa dropseed (*Sporobolus flexuosus* Thurb. Rybd.) and black grama (*Bouteloua eriopoda* Torr.), two important Chihuahuan Desert forage species, had greater standing crop on the CG than IG range throughout the 1982-1991 study period. Our data indicate that some mesquite-dominated ranges in the Chihuahuan Desert are responsive to both favorable rainfall and conservative stocking if residual perennial grasses remain, and that livestock grazing is sustainable under utilization levels that involve removal of one-third of the current year's growth of key forage species (black grama, dropseeds, threeawns). On course sandy soils with a high canopy cover of honey mesquite, brush control may be necessary to initiate range recovery.

Huenneke, L. F., J. P. Anderson, M. Remmenga, and W. H. Schlesinger. 2002. Desertification alters patterns of aboveground net primary production in Chihuahuan ecosystems. *Global Change Biology* 8, no. 3: 247-64.
Abstract: The Chihuahuan desert of New Mexico, USA, has changed in historical times from semiarid grassland to desert shrublands dominated by *Larrea tridentata* and *Prosopis glandulosa*. Similar displacement of perennial grasslands by shrubs typifies desertification in many regions. Such structural vegetation change could alter average values of net primary productivity, as well as spatial and temporal

patterns of production. We investigated patterns of aboveground plant biomass and net primary production in five ecosystem types of the Jornada Basin Long-Term Ecological Research (LTER) site. Comparisons of shrub-dominated desertified systems and remnant grass-dominated systems allowed us to test the prediction that shrublands are more heterogeneous spatially, but less variable over time, than grasslands. We measured aboveground plant biomass and aboveground net primary productivity (ANPP) by species, three times per year for 10 years, in 15 sites of five ecosystem types (three each in *Larrea* shrubland, *Bouteloua eriopoda* grassland, *Prosopis* dune systems, *Flourensia cernua* alluvial flats, and grass-dominated dry lakes or playas). Spatial heterogeneity of biomass at the scale of our measurements was significantly greater in shrub-dominated systems than in grass-dominated vegetation. ANPP was homogeneous across space in grass-dominated systems, and in most growing seasons was significantly more patchy in shrub vegetation. Substantial interannual variability in ANPP complicates comparison of mean values across ecosystem types, but grasslands tended to support higher ANPP values than did shrub-dominated systems. There were significant interactions between ecosystem type and season. Grasslands demonstrated higher interannual variation than did shrub systems. Desertification has apparently altered the seasonality of productivity in these systems; grasslands were dominated by summer growth, while sites dominated by *Larrea* or *Prosopis* tended to have higher spring ANPP. Production was frequently uncorrelated across sites of an ecosystem type, suggesting that factors other than season, regional climate, or dominant vegetation may be significant determinants of actual NPP.

Huenneke, Laura F., Dennis Clason, and Esteban Muldavin. 2001. Spatial heterogeneity in Chihuahuan desert vegetation: implications for sampling methods in semi-arid ecosystems. *Journal of Arid Environments* 47, no. 3: 257-70.

Abstract: Patchiness of above-ground vegetation, such as that in semi-arid grasslands and shrublands, can pose problems in sampling plant cover, biomass and productivity. We present a method of measuring above-ground plant biomass and production that can be applied consistently among vegetation types and that generates seasonal, spatially-explicit results. Results from 15 sites within the Jornada Basin (Chihuahuan Desert, New Mexico, USA) confirm considerable patchiness and non-normal distributions of plant biomass, even in grasslands. However, tests of adequacy of sample size and of sample error associated with the regression-based estimates of biomass confirmed that the estimates of above-ground net primary productivity are sufficiently precise to be useful in comparisons of both shrub-dominated and grassland sites.

Hyder, Paul W. 2001. "Total phenolics, condensed tannins, and nordihydroguaiaretic acid (NDGA) as potential allelopathic compounds in creosotebush (*Larrea tridentata* (Sess. & Moc. ex DC.) Cov.) and tarbush (*Flourensia cernua* DC) in the northern Chihuahuan Desert ." Ph. D. Dissertation, New Mexico State University.

See abstract under *Flourensia cernua*

Johnsen, T. N. Jr., and H. L. Morton. 1991. Long-term tebuthiuron content of grasses and shrubs on semiarid

rangelands. *Journal of Range Management* 44, no. 3: 249-53.

Jordan, Gilbert L., and Marshal R. Haferkamp. 1989. Temperature responses and calculated heat units for germination of several range grasses and shrubs. *Journal of Range Management* 42, no. 1: 41-45.

Kemp, Paul R. 1983. Phenological patterns of Chihuahuan desert plants in relation to the timing of water availability. *Journal of Ecology* 71, no. 2: 427-36.

Abstract: (1) Phenology, density, and cover of plant species occurring in a single Chihuahuan desert habitat were studied for 2 years as a function of habitat moisture with the objective of relating plant species diversity to water partitioning. (2) Much of the temporal variation in growth and phenology between species was correlated with differences in life form and photosynthetic pathway. (3) The annual plant species consisted of a winter-spring group containing only species with the C3 photosynthetic pathway which utilize the moisture from frontal storms of winter, and a summer group containing a large majority of species with the C4 photosynthetic pathway which utilize the moisture from convectional storms of late summer. (4) The perennial plant species consisted of C3 and C4 forbs, C4 grasses, C3 shrubs and CAM shrubs. The C3 forbs showed greatest activity in spring or autumn while the C4 forbs and grasses were most active in the summer and autumn. The C3 shrubs and CAM shrubs were active at various times from spring to autumn and not as dependent as the other groups on available soil moisture. (5) There was above average precipitation in late summer and autumn during the first year of study and an early and prolonged drought in autumn of the second year. Some species of perennial C3 forbs and C4 grasses responded to the abundant precipitation of the first autumn with increased density or cover in the second year, but there was little change in the shrub species. The drought in the second year caused a reduction in the number of species and individuals of both C3 and C4 annual plants. (6) The results suggest that the high species diversity in this habitat is partly a result of the different life form and photosynthetic pathway groups, each being adapted for utilizing a particular phase of the seasonally and yearly variable water.

Knipe, D., and C. H. Herbel. 1960. The effects of limited moisture on germination and initial growth of six grass species. *Journal of Range Management* 13: 297-302.

Abstract: Two hundred caryopses each of black grama, bush muhly, tobosa, mesa dropseed, Lehmann lovegrass, and boer lovegrass were germinated in petri dishes on blotter paper moistened with water-mannitol solutions of 0.3, 3.0, 7.0, 11.0, 15.0, and 20.0 atm. osmotic concentration (degrees of moisture stress). The object of the study was to determine differences, within and among species, in time required to germinate, total germination, and initial growth of seedlings under various conditions of moisture stress. With the exception of Lehmann lovegrass, time required to germinate was not greatly increased by increasing osmotic concentration from 0.3 to 7.0 atm. However, total germination of Lehmann lovegrass, boer lovegrass, and mesa dropseed was significantly reduced by increasing osmotic concentration from 0.3 to 7.0 atm., and reduction in total germination of all species was very nearly significant under these

conditions. Generally, the growth of seedlings was significantly decreased by increasing osmotic concentration from 0.3 to 7.0 atm. Of the species tested, black grama and bush muhly seem best adapted to survival under conditions of limited moisture. Seedlings of these species were the only ones which attained measurable growth when germinated and grown at 11.0 atm osmotic concentration. None of the species developed measurable seedlings at 15.0 and 20.0 atm. osmotic concentration, but the caryopses of black grama and bush muhly germinated surprisingly well at these levels of moisture stress.

Kröel-Dulay, G. 1998. Stepwise transformation of phytosociological data: a case study in the semiarid grasslands of New Mexico. *Abstracta Botanica* 22: 95-100.

Abstract: A stepwise data transformation procedure is proposed. By applying a series of cover thresholds, low cover values are gradually deleted, whereas the remaining data are used in binary form after each step of deletion. The method does not aim at the selection of a single optimal weighting of cover-abundance data; instead, it provides a simple tool to investigate how different weightings of species of low vs. high performance influence the results of an analysis. The method is used to compare the species compositions of two grassland types in the semiarid region of New Mexico, USA. In an area where two grass species (*Bouteloua eriopoda* and *Bouteloua gracilis*) grow predominantly intermingled, patches dominated exclusively by either of the two grasses were sampled. The dissimilarity of their species composition was expressed by the complement of the Kulczynski index. Randomisation was used to test for significance. The two grassland types were different in species composition, and the stepwise data transformation procedure showed that this difference increased while gradually deleting the species of low cover and species of low frequency. Although most species can establish in both types, several of them reach higher cover or frequency in either of the two types.

Lauenroth, W. K., D. P. Coffin, I. C. Burke, and R. A. Virginia. 1997. Interactions between demographic and ecosystem processes in a semi-arid and an arid grassland: a challenge for plant functional types. *Plant functional types. Their relevance to ecosystem properties and global change*. T. M. Smith, H. H. Shugart, and F. I. Woodward, 234-54. Cambridge, UK: Cambridge University Press.

Ludwig, John A., Esteban Muldavin, and K. Rosalind Blanche. 2000. Vegetation change and surface erosion in desert grasslands of Otero Mesa, Southern New Mexico: 1982 to 1995. *American Midland Naturalist* 144, no. 2 : 273-85.

Abstract: Desert grasslands that skirt mountain ranges in northern Mexico and the southwestern United States were once common. These grasslands have largely been replaced by shrublands and their soils have become eroded. The most frequently cited causes of these changes are livestock overgrazing, fire and increasing aridity. Studies have not separated grazing and fire from climate effects. Our aim was to determine whether desert grasses are being replaced by shrubs and how rapidly soil surfaces are eroding on unburnt Otero Mesa desert grasslands, where livestock overgrazing has not been a significant factor in historic or recent times. In this article we describe how vegetation and soil surface levels changed from 1982 to 1995 on six permanent transects. Vegetation was measured by charting canopy cover and stem

bases of perennial plants in quadrats. Soil surface levels were surveyed in reference to benchmarks placed in nearby bedrock. Vegetation quadrats and surface levels were re-measured in 1995. From 1982-1983 to 1995 the canopy cover of the desert shrubs, *Larrea tridentata* and *Gutierrezia microcephala*, declined by 1.5% and 5.8%, respectively. Canopy cover of the C4 xeric grass *Bouteloua eriopoda* declined by 5.3%. This decline in xeric grass cover was offset by a 1.2% increase in the C4 mesic grass *Bouteloua curtipendula* and a 4.0% increase in the C3 mesic grass *Stipa neomexicana*. From 1983-1984 to 1995 soil surfaces along transects eroded an average of 0.4 mm. Thus, desert shrubs were not replacing desert grasses, but mesic grass species were replacing xeric species. These changes were associated with a 15-y period of relatively wet cool-seasons and moist warm-seasons from 1981 through 1995. These results document that, even in the absence of livestock grazing and fire, desert grassland vegetation is very responsive to precipitation change over relatively short time periods.

Martin, S. C., and D. R. Cable. 1974. Managing semidesert grass-shrub ranges: vegetation response to precipitation, grazing, soil texture, and mesquite control. 1-45 Government Printing Office.

McClaran, M. P. 1995. Desert grasslands and grasses. In *The desert grassland*. Editors M. P. McClaran, and T. R. Van Devender, 1-30. Tucson: University of Arizona Press.

McGinnies, W. J. 1960. Effects of moisture stress and temperature on germination of six range grasses. *Agronomy Journal* 52: 159-62.

Abstract: Increased moisture stress delayed germination, reduced rate and 28-day total of germination. Highest average germination was at 20° C. Under high moisture stress all species germinated better at 20 than at 10 or 30° C. Seed size showed positive correlation with germination at a stress of 15 atmospheres.

McPherson, G. R. 1995. The role of fire in the desert grasslands. In *The desert grassland*. Editors T. R. Van Devender, and M. P. McClaran, 130-151. Tucson: The University of Arizona Press.

Merkin, E. B. 1995. Competition and physiological response of *Bouteloua gracilis* and *Bouteloua eriopoda* to variable soil moisture in a biome transition zone. *REU Paper*.

Abstract: Field measurements of gas exchange were conducted on two species of C4 bunchgrasses, *Bouteloua eriopoda* and *Bouteloua gracilis*, in response to simulated low and high moisture events. Physiological measurements including photosynthesis, stomatal conductance, intercellular carbon dioxide concentration, and water-use-efficiency were taken on four days in a biome transition zone community at the Sevilleta National Wildlife Refuge in central New Mexico. The physiology of these species was compared and considered in light of competition between the two species for a limiting resource, water. Although significant differences were found between days and treatments for the parameters measured, only stomatal conductance was significantly different ($F = 35.61$, $P = 0.0001$) between species. However, means reveal a trend toward a higher photosynthetic rate and water-use-efficiency for *B. eriopoda*, which

suggests that their physiology not only reflects differences in root morphology between the grasses, but differences in their life histories as well. No significant difference was found between the physiological activity of these species to high and low moisture events, suggesting that these species, especially *B. eriopoda*, have had to make ecological tradeoffs in order to respond to moisture efficiently and rapidly and survive long periods of drought. Thus, this study indicates that *B. eriopoda* may be a better competitor in this ecotone community for small moisture events. Future studies need to be broader in scope, of longer duration, and need to include a consideration of morphological aspects of these grasses in order to elucidate differences in physiological capacity that may exist between *Bouteloua eriopoda* and *Bouteloua gracilis*.

Miller, Richard F., and Gary B. Donart. 1979. Response of *Bouteloua eriopoda* (Torr.) Torr. and *Sporobolus flexuosus* (Thurb.) Rybd. to season of defoliation. *Journal of Range Management* 32, no. 1: 63-67.

Abstract: Production, total nonstructural carbohydrates, and crown diameters were measured to evaluate the effects of season of clipping on black grama and mesa dropseed. Vegetative reproduction was also monitored for black grama. Early defoliation of both black grama and mesa dropseed had less impact on plant vigor than continuous defoliation or defoliation during the last half of the growing season. Black grama plants clipped during or after flowering, or continuously through the growing season, produced less herbage in the following year than those plants clipped during the vegetative stage. Removal of 65% of the current year's growth any time during the growing season significantly reduced stolon numbers on black grama. Mesa dropseed clipped during maturity, during flowering, or clipped continuously throughout the growing season was negatively affected on one or more of the plant parameters measured. Clipping during the vegetative state had little apparent effect on plant vigor.

Minnick, Tamera Jo. 1998. "Abiotic factors affecting distribution and dominance patterns of two C4 perennial grass species." Ph. D. Dissertation, Colorado State University.

Abstract: I investigated abiotic effects on demographic processes, particularly recruitment, of two important North American forage grasses and related these results to their distribution and dominance patterns. *Bouteloua gracilis* dominates shortgrass steppe; *B. eriopoda* dominates desert grasslands. I addressed questions at site- and regional-level scales by combining field and growth chamber experiments, and simulation modeling. I predicted recruitment rates for these species at 16 sites along a climatic gradient using a daily time step, multi-layer model of soil water dynamics. Predicted recruitment decreased from north to south for *B. gracilis*, but increased from north to south for *B. eriopoda*. Recruitment was dependent on amount and timing of precipitation and temperature. The latitude at which recruitment rates were similar for the two species moved north under three climate change scenarios, indicating a possible northward expansion of *B. eriopoda*. A common garden study revealed possible mechanisms for *B. eriopoda* exclusion from northern Colorado and allowed comparisons between two populations of *B. gracilis*. Throughout the two year study, *B. eriopoda* survived and grew. Significant quantities of germinable seed were produced by non-native plants only after hand pollination. Native plants initiated flowering earlier in the season than non-native plants, suggesting day length cues for reproduction. I examined effects of soil texture, which varies at the landscape-scale, and precipitation on emergence and growth of *B. gracilis*. Two principle results were 1) seedling emergence was lowest on the soil with highest clay content, and 2)

seedling growth was lowest on the soil with lowest clay content, regardless of precipitation. Thus, soil texture can have important influences on seedling emergence and growth. Results of these studies indicate seed production and seedling establishment may be key processes affecting distributions of *B. gracilis* and *B. eriopoda*. Climate had important effects on large-scale patterns. Within a site, soil texture may influence recruitment through effects on plant available soil water. However, if production of germinable seed is limited by some other variable, such as day length, range expansion is unlikely regardless of the degree to which future climates change.

Minnick, T. J., and D. P. Coffin. 1999. Geographic patterns of simulated establishment of two *Bouteloua* species: implications for distributions of dominants and ecotones. *Journal of Vegetation Science* 10, no. 3: 343-56. Abstract: Our overall objective was to use a soil water model to predict spatial patterns in germination and establishment of two important perennial C-4-bunchgrasses across the North American shortgrass steppe and desert grassland regions. We also predicted changes in establishment patterns under climate change scenarios. *Bouteloua gracilis* dominates the shortgrass steppe from northeastern Colorado to southeastern New Mexico. *Bouteloua eriopoda* dominates desert grasslands in central and southern New Mexico. Germination and establishment for each species were predicted at 16 sites along the gradient using a daily time step, multi-layer soil water model (SOILWAT) to determine the percentage of years that temperature and soil water criteria for germination and establishment were met. Percentage of years with predicted establishment decreased from north to south for *B. gracilis*, but increased from north to south for *B. eriopoda*, comparable to observed dominance patterns. The 95% confidence interval around the point at which simulated establishment were equal for the two species was near the location of the shortgrass steppe-desert grassland ecotone where both species are abundant. The intersection in percentage of years with establishment for the two species was predicted to move further north when climate was scaled using three Global Circulation Models (GCMs), indicating a possible northward expansion of *B. eriopoda*. Our results suggest that recruitment by seed may be an important process in determining, at least in part, the geographic distribution of these two species. Changes in climate that affect establishment constraints could result in shifts of species dominance that may or may not be accompanied by changes in species composition.

Molinar-Holguin, Francisco. 1999. "Effect of honey mesquite (*Prosopis glandulosa* Torr) cover and soil depth on forage production in the Chihuahuan desert ." Ph. D. Dissertation, New Mexico State University. Abstract: Honey mesquite (*Prosopis glandulosa* Torr) invasion of Chihuahuan Desert grasslands is an important concern for both ranchers and range managers. In the last 100 years, extensive areas of the Chihuahuan Desert have been invaded by mesquite. In New Mexico, Arizona and Texas, it is estimated that more than twenty million hectares are covered by this species. Since mesquite has low forage value for livestock, its control may be required to improve forage production on degraded rangelands. There are several factors involved in the proliferation of mesquite, among the most important are severe drought periods and the presence of deep sandy soils. To develop range management plans it is necessary to have ecological information about the factors that contribute to the proliferation of this species on desert rangelands, and the influence of mesquite on forage production. Thus, the objectives of this study were (1)

To determine the possible relationships between forage production and three levels of mesquite (based on canopy cover), (2) To determine if soil depth (shallow < 40 cm, and deep > 41 cm) and previous methods of shrub control (low and high levels) have influenced mesquite cover in the study area, and (3) To determine how climatic fluctuations influenced mesquite cover and forage production, and the direction and trend during the study period. The results indicate that there was a main effect of soil depth on black grama production, with shallow soils being more productive than deep soils. Similarly, mesquite canopy cover was much higher in deep soils across the study area. The magnitude of mesquite canopy cover increase appeared to be more a function of soil depth, than past mesquite control with herbicides. Data pooled across years showed that increases of total grasses and total standing crop production was primarily a function of the interaction soil depth with year. Generally forage production was most increased in wet years and least increased in dry years in shallow soils compared to deep soils. Moreover, soil depth had more influence on forage production than mesquite canopy cover at least at levels below 17%. Total standing crop and snakeweed were higher on low than high mesquite kill areas in 1997. These data and that from previous studies on the Chihuahuan Desert Rangeland Research Center indicate that plant responses to long term (10 or more years) mesquite control are somewhat erratic and site dependent.

Neilson, R. P. 1986. High-resolution climatic analysis and Southwest biogeography. *Science* 232: 27-34.

Nelson, Enoch W. 1934. *The influence of precipitation and grazing upon black grama grass range*. Technical Bulletin , no. 409. Washington : U.S. Dept. of Agriculture.

Olmsted, C. E. 1943. Growth and development in range grasses. III. Photoperiodic response in the genus *Bouteloua*. *Botanical Gazette* 105: 165-81.

Pan, Jean J. 1996. "The effects of grazing history, plant size, and plant density on growth and reproduction in black grama grass (*Bouteloua eriopoda* (Torr.) Torr.)." M. S. Thesis, New Mexico State University.

Paulsen, Harold A. Jr., and Fred N. Ares. 1962. *Grazing values and management of black grama and tobosa grasslands and associated shrub ranges of the Southwest*. Technical Bulletin , no. 1270. Washington : U.S. Dept. of Agriculture, Forest Service.

Abstract: Ecology of range plants, grazing capacity of the forage resource, and techniques of management most suited to black grama and tobosa grasslands and associated shrub ranges of the Southwest have been interpreted from records of vegetation, climate, and livestock on the Jornada Experimental Range. The experimental range is located 23 miles north of Las Cruces, N. Mex.. Research, which has application to more than 60 million acres, has been underway on this area since 1916.

1. Annual rainfall at the Jornada Experimental Range headquarters from 1916 to 1953 averaged 9.02 inches; more than 50 percent of this amount was received in July, August, and September. Precipitation records showed no significant longtime trend in amount, but alternate periods of generally higher or lower

rainfall were apparent at intervals of approximately 20 years. Rainfall alternately averaged about 10 percent above or below the overall mean in these intervals; however, individual years were often much more divergent.

2. Vegetation types on the experimental area include black grama, tobosa, mesquite sandhills, creosotebush, and tarbush. Perennial grasses furnish the bulk of the forage in all types except the mesquite sandhills, where grasses are sparse and palatable browse plants yield more forage. Most forage growth is made from July through September. Growth characteristics and maintenance of black grama and tobosa are given primary consideration in the management of the experimental area. Black grama grows in open stands on the more coarse-textured, sandy soils. It is palatable throughout the year and can advantageously be reserved for use during the dormant or winter season. Tobosa grows on the fine-textured soils that usually receive some flood water. It is highly palatable when actively growing and can withstand moderate grazing at that time.

3. The basal area of grasses on meter-square quadrats charted yearly from 1916 to 1953 was found to fluctuate with precipitation received in a 15-month period, which includes the previous grazing year (July 1-June 30), plus the current growing season (July, August, and September). The basal area of black grama was more closely related to this 15-month precipitation under conservative grazing than under other intensities of grazing use and nonuse. Conservative grazing removes up to 40 percent of the herbage; intermediate use removes between 40 and 55 percent of the herbage; and heavy grazing, more than 55 percent. Basal area of black grama during extended dry periods was reduced to about the shear minimum irrespective of the degree of grazing; however, recovery was greatest on quadrats conservatively grazed. Heavier grazing than was experienced on the quadrats very likely would result in greater decimation of the stand. Where tobosa was dominant, its basal area was highest on intermediately grazed quadrats. During periods of above- and below-average precipitation, the basal area of tobosa varied in a manner similar to that of black grama; however, it is less sensitive than black grama to changes in precipitation.

4. Herbage production of perennial grasses varied widely from year to year in response to fluctuations in precipitation during the growing season. In dry years production was reduced to approximately 100 pounds an acre, air-dry. In favorable years herbage production in the black grama type averaged 500 pounds to the acre. Production of tobosa averaged much higher than black grama; it yielded 1,000 to 1,900 pounds of herbage an acre.

5. Shrubs became more numerous on many area in the black grama and tobosa types during the period of record. As this happened, the grasses and grazing capacity were materially reduced. Mesquite was the primary invader of the black grama type, and creosotebush and tarbush encroached into tobosa grasslands. Creosotebush invades other grass and shrub types except on areas of unstable, sandy soils. Grass associates of the tarbush type were often abundant until the brush thickened considerably. Under the conditions observed, continual invasion of grasslands by shrubby species is inevitable unless control measures are used. Creosotebush and tarbush have quickly reinvaded areas where conversion to grassland has been attempted.

6. On three experimental pastures, which were predominantly covered by shrub types, grazing capacity average 4.8 animal units per section in contrast to 10.9 animal units on 3 pastures that were mostly grass. The brush pastures showed a consistent decline in grazing capacity over the years, but the grass pastures exhibited no such trend. Grazing capacity fluctuated widely in all pastures as a result of annual variations in the forage crop.

7. For the best use and maintenance, tobosa range should be grazed during the growing season and black grama areas should be reserved for fall-winter-spring use when the grasses are dormant.
8. Other features of management included constant improvement of the herd through careful culling, selection of good-quality cows, the use of bulls either registered or eligible for registration, the use of numerous inexpensive water developments in the tobosa areas, salting away from water on black grama range and fencing to obtain better distribution of the cattle. A mixture of cottonseed meal and salt fed to the stock away from water improved the grazing use in the outer reaches of the winter-spring pastures and also supplemented forage deficiencies in protein and phosphorus.
9. Because of the wide fluctuations in forage production, it was advantageous to maintain the number of breeding cows at approximately 60 percent of the entire herd. This permits stocking reductions of as much as 40 percent through selling all yearlings and heifer replacements in years of poor forage growth. When abundant forage is produced, the herd can be increased by retaining weaned calves and forage purchasing additional yearlings.
10. The cow-yearling herd arrangement increased beef production per animal unit grazed, and it also increased the value of the beef produced because of the higher percentages of animals sold as yearlings. During the period 1927-34 when the herd was managed as a cow-calf operation, 377 pounds of beef were sold per animal unit grazed; average annual value was \$23.21. When the cow-yearling herd was maintained from 1940 to 1951, 495 pounds of beef per animal unit were sold, valued at \$64.51. Comparable value of the beef sold during the 1927-34 period averaged \$45.09 per animal unit grazed.
11. Despite application of the best known techniques of range management, ranchers and land administrators of semidesert grass-shrub range areas often face periods of low forage production when stocking must be reduced. In severe drought periods a large part of the stand of perennial forage plants will be killed and livestock must be removed for one year or more to permit general range recovery.

———. 1961. Trends in carrying capacity and vegetation on an arid southwestern range. *Journal of Range Management* 14, no. 2: 78-83.

See abstract under *Pleuraphis mutica*

Pease, D. S., and J. U. Anderson. 1969. Opal phytoliths in *Bouteloua eriopoda* Torr. roots and soils. *Soil Science Society of America Proceedings* 33: 321-22.

Peters, D. P. C. 2000. Climatic variation and simulated patterns in seedling establishment of two dominant grasses at a semi-arid-arid grassland ecotone. *Journal of Vegetation Science* 11: 493-504.

Abstract: The objective of this study was to predict the effects of climatic variation at multiple temporal frequencies on seedling establishment by two congeneric C₄ perennial grasses (*Bouteloua gracilis* and *B. eriopoda*) at the ecotone between shortgrass steppe grassland and Chihuahuan desert grassland in central New Mexico, USA. The approach was to use a daily time-step simulation model to determine the occurrence of a recruitment event in each year based upon the amount and timing of soil water required for establishment. Historical weather data were used to predict effects of seasonal and interdecadal variation in climate on establishment. A sensitivity analysis was used to predict effects of directional climate change

on establishment. *Bouteloua gracilis* had a broad pattern of simulated establishment from May through September that included periods with high year-to-year variation in precipitation. *B. eriopoda* establishment events occurred primarily in July when precipitation amounts were most reliable. Climatic conditions from 1949 through 1968 were more favorable for *B. eriopoda* establishment compared to the cooler, wetter conditions from 1969 through 1988 that favored *B. gracilis*. Establishment of *B. eriopoda* was lowest in El Nino years whereas *B. gracilis* establishment was highest in La Nina years. Establishment of *B. gracilis* was most sensitive to temperature when precipitation was higher than current amounts. The greatest response to temperature by *B. eriopoda* for all precipitation amounts occurred at cooler temperatures than found currently. These results indicate that climatic variation at multiple frequencies has differential effects on seedling establishment for these two perennial grasses, and may account at least in part for patterns in dominance at this biome transition zone.

Pieper, Rex D., and Carlton H. Herbel. 1982. Herbage dynamics and primary productivity of a desert grassland ecosystem. *New Mexico Agricultural Experiment Station Bulletin* No. 695: 42.

Abstract: Primary production was determined for a desert grassland in southern New Mexico with and without grazing. The ungrazed treatment was represented by *Bouteloua eriopoda* grassland, and the grazed treatment was represented by a grassland deteriorated because of drought and grazing pressure. Sampling was conducted approximately biweekly during the growing season and monthly during the dormant season.

Efficiency of aboveground net primary productivity averaged 0.08% of the useable solar radiation reaching the surface during the thermal growing season for the ungrazed treatment and 0.05% for the grazed treatment. Calculations of compartmental transfer rates indicate that these systems are relatively stable with regard to standing live, recent and old dead, aboveground mulch and belowground biomass.

Pieper, Rex D., Carlton H. Herbel, Don D. Dwyer, and Roger E. Banner. 1974. Management implications of herbage weight changes on native rangeland. *Journal of Soil and Water Conservation* 29, no. 5: 227-29.

Abstract: Range researchers and technicians often calculate herbage production from clippings or estimates made once a year, commonly at the end of the growing season. Such estimates may lead to serious miscalculations unless seasonal changes in herbage weight and differential growth of individual species and plant parts are recognized. Data from black grama and blue grama vegetation types show that peak herbage weight lasts only a short time and that the amount of herbage available for grazing animals for most of the year is considerably less than that present at the peak. In addition, leaves and inflorescences, which are the most palatable and nutritious plant parts, deteriorate more rapidly during the dormant season than culms, the least palatable and nutritious plant parts. These changes have major implications in determining stocking rates, comparing treatments and years, determining utilization, and planning grazing systems.

Reese, Michael Edward. 1980. "Seasonal utilization of Lehmann lovegrass and black grama in the desert grassland ." M. S. Thesis, University of Arizona.

- Reynolds, J. F., P. R. Kemp, and J. D. Tenhunen. 2000. Effects of long-term rainfall variability on evapotranspiration and water distribution in the Chihuahuan desert: a modeling analysis. *Plant Ecology* 150: 145-59.
- Roundy, B. A., and S. H. Biedenerger. 1995. Revegetation in the desert grassland. In *The desert grassland*. Editors T. R. Van Devender, and M. P. McClaran, 265-303. Tucson: The University of Arizona Press.
- Sabo, D. G., G. V. Johnson, W. C. Martin, and E. F. Aldon. 1979. Germination requirements of 19 species of arid land plants. 26 pp. Res. Pap. RM-210. Fort Collins, CO: Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station.
Abstract: Tables 3 and 4 summarize temperature, moisture, and procedural recommendations for germination of the 19 species of grasses and shrubs. It is important to note that these recommendations are valid for seeds collected in the areas noted in this study. Subsequent testing of seed collected from various locations has indicated a high degree of ecotypic variability in optimum temperatures for most species. Various articles discussed lend support to this observation.
- Schwartz, A., and D. Koller. 1975. Photoperiodic control of shoot-apex morphogenesis in *Bouteloua eriopoda*. *Botanical Gazette* 136, no. 1: 41-49.
- Senock, R. S., D. L. Devine, W. B. Sisson, and G. B. Donart. 1994. Ecophysiology of three C4 perennial grasses in the Northern Chihuahuan desert. *Southwestern Naturalist* 39: 122-27.
See abstract under *Pleuraphis mutica*
- Simonin, K. A. 2000. *Bouteloua eriopoda*. U.S. Department of Agriculture, Forest Service Rocky Mountain Research Station Fire Sciences Laboratory. 2001. "Fire effects information system." Web page. Available at <http://www.fs.fed.us/database/feis/> .
- Sims, P. L., and J. S. Singh. 1978. The structure and function of ten western North American grasslands. II. Intra-seasonal dynamics in primary producer compartments. *Journal of Ecology* 66: 547-72.
Abstract: (1) Intra-seasonal dynamics of the various above-ground and below-ground primary producer compartments for ten central and western North American grassland sites are presented. (2) The seasonal peak values of the primary producer compartments are examined as indicative of the net accumulation of organic material and the relationships of these peak values to various abiotic regimes at the sites are investigated. (3) Seasonal live biomass followed either a unimodal or a bimodal growth pattern. In general, grasslands with only cool-season or only warm-season plants showed a unimodal pattern, while grasslands dominated by both cool- and warm-season species had a bimodal seasonal growth pattern. There were no significant differences between grazed and ungrazed treatments in seasonal live biomass, although there

was a significant site x treatment interaction. (4) Peak live biomass ranged from 84 to 336 g m⁻², and showed a linear increase with increasing amounts of growing-season precipitation up to 450 mm. at higher values of precipitation increases in live biomass tended to level out. (5) Maximum rates of accumulation of live biomass ranged from 0.4 to 6.5 g m⁻² day⁻¹ Ungrazed grasslands had a peak rate of 4.2 g m⁻² day⁻¹ compared with 3.2 g m⁻² day⁻¹ for grazed grasslands. (6) Generally the recent-dead compartment showed maximum values soon after the peak in the live compartment. Material in the old-dead compartment, however, was at a maximum early in the growing season, and a general decline in the standing crop of old dead material followed as material was transferred to the litter compartment. (7) Litter dynamics responded closely to precipitation events, and showed a rather erratic pattern. (8) Root biomass generally reached a maximum about midway through the growing season. On the cooler grasslands, grazed treatments typically had a larger peak in root biomass: in contrast, the warmer grasslands did not show a marked response in root biomass to grazing.

Smith, S. E., M. R. Haferkamp, and P. W. Voigt. 2002. *Grama grasses*. University of Arizona, Tucson, AZ: School of Renewable Natural Resources. (unpublished dissertation chapter in progress)

Sosebee, Ronald E., and Carlton H. Herbel. 1969. Effects of high temperatures on emergence and initial growth of range plants. *Agronomy Journal* 61: 621-24.

Abstract: The daily soil temperatures used in this light chamber study were patterned after observations made under field conditions: 18 to 39C where the surface was sparsely shaded by brush, and 18 to 53C where the surface was left bare. The soil moisture was maintained at field capacity. Emergence of sacaton (*Sporobolus wrightii* Munro), vine mesquite (*Panicum obtusum* HBK.), bush muhly (*Muhlenbergia porteri* Scribn.), and fourwing saltbush (*Atriplex canescens* (Pursh) Nutt.) was adversely affected by the high temperature regime. Survival of all 14 accessions except rhodesgrass (*Chloris gayana* Knuth), 'Vaughn' sideoats grama (*Bouteloua curtipendula* (Michx.) Torr.), and black grama (*B. eriopoda* (Torr.) Torr.) was reduced by the high temperature regime. At the close of the 21-day trial most species had stopped growing or were growing very slowly under the high temperature regime. The shoot weights for the plants growing in the low temperature regime averaged nearly twice as much as those growing in the high temperature regime. There was no significant difference in root weight per seedling between temperature regimes. The root lengths of black grama, 'Vaughn' sideoats grama, tobosa (*Hilaria mutica* (Buckl.) Benth.), Lehmann lovegrass (*Eragrostis lehmanniana* Nees), and alkali sacaton (*Sporobolus airoides* (Torr.) Torr.) were not reduced significantly by the high temperature regime. The high temperatures were detrimental, in one way or another, to all species even when moisture was adequate but black grama and sideoats grama performed satisfactorily.

Stephens, Gracelet A. 1989. "Response of black grama grass, *Bouteloua eriopoda*, to water and nitrogen in a northern Chihuahuan Desert grassland." M.S. Thesis, New Mexico State University.

Abstract: The response of black grama grass, *Bouteloua eriopoda*, to irrigation and fertilization was examined to test the hypothesis that desert grassland ecosystems are co-limited by water and nitrogen in

the same manner as the adjacent shrublands. The studies carried out during the growing season of black grama have shown that the growth of the tiller is directly controlled by the availability of water ($P < 0.03$) and not by nitrogen, whereas the biomass increase was marginally improved by the addition of nitrogen ($P < 10$). Nitrogen induced early flowering but water had a greater effect during the various phenological stages of black grama ($P < 0.03$) affecting the flowering, longevity, controlling insect damage, and increasing the canopy area in a statistically significant level.

Nitrogen by itself ($P < 0.001$) or in combination with water ($P < 0.03$) reduced the root length of the experiment plants. The short and mat-like roots would have made use of the small rainfall events more efficiently than the plants which received only irrigation (46 out of 61 precipitation events were < 6 mm in size). Since there was no difference in the total biomass production for the nitrogen-treated or water-nitrogen-treated subplots statistically, we conclude that the most important driving variable of the grassland ecosystems is water and not nitrogen. This experiment was carried out on the third successive year of precipitation averaging 315 mm per year. Still irrigation showed significant effect. Nitrogen effect being very marginal suggests that desert black grama grasslands are mainly water-driven ecosystems. As for irrigation, there is differential response, depending on the growing season precipitation.

Stephens, G., and W. G. Whitford. 1993. Responses of *Bouteloua eriopoda* to irrigation and nitrogen fertilization in a Chihuahuan Desert grassland. *Journal of Arid Environments* 24: 415-21.

Abstract: The response of *Bouteloua eriopoda*, black grama, to irrigation and nitrogen fertilization was examined to test the hypothesis that, in desert grasslands, nitrogen availability is greater than in adjacent shrublands. Tiller growth was greater in irrigated plots ($P < 0.05$) while nitrogen had no significant effect on growth ($P > 0.05$). Nitrogen induced early flowering but water had a greater effect during the various phenological stages. Water affected flowering, mortality, insect damage, and biomass production. Nitrogen and nitrogen plus water reduced root length of the experimental plants ($P < 0.05$). The short and mat-like roots of fertilized plants may allow use of the small rainfall events more efficiently than the plants which received only irrigation (46 out of 61 precipitation events were < 6 mm in size). There were no differences in the total biomass production of nitrogen-treated or water-nitrogen-treated subplots compared to controls. There was a higher nitrogen content of stems and leaves on plants from the irrigated-fertilized plots, but no significant differences among other treatments. Based on the large effects of irrigation in a third wet year (> 300 mm year⁻¹) and marginal nitrogen effects, we conclude that productivity in Chihuahuan Desert *Bouteloua eriopoda* grasslands is less nitrogen limited than that of the *Larrea* shrublands. Further, productivity in this perennial desert grassland appears to be closely linked to rainfall with no temporal lags due to nitrogen immobilization.

Streetman, L. J. 1959. "A study of the chromosome number, microsporogenesis, megasporogenesis, embryo sac development, and embryogeny in black gramagrass, *Bouteloua eriopoda* (Torr.) Torr." Ph. D. Dissertation, University of Arizona.

Sundt, P. C., and K. R. Vincent. 1999. Influences of geomorphology on vegetation in the Animas Creek Valley, New Mexico. In *Toward integrated research, land management, and ecosystem protection in the Malpai Borderlands: conference summary*, 25-43. Proceedings RMRS-P-10, U.S. Forest Service, Rocky Mountain Research Station.

Abstract: Affinity or disaffinity for particular geomorphic surfaces or topographic positions were rated for blue grama, three-awn grasses, black grama, hairy grama, plains lovegrass, tobosa, vine mesquite grass, aparejo grass, sideoats grama, wolftail grass, mesa dropseed, and shrubby buckwheat

Toole, V. K. 1939. Germination requirements of the seed of some introduced and native range grasses.

Proceedings of the Association of Official Seed Analysts 13th annual meeting: 227-43.

Abstract: *Poa macrantha* germinated best at an alternating temperature of 20° to 30°C with the use of potassium nitrate. Germination was complete in 21 days. *Eragrostis curvula* required for maximum germination an alternation of temperature which includes a high temperature. The alternating temperatures Room to 35°C, 20° to 40°, and 25° to 40° gave a germination of 94% or above in six days. *Eragrostis lehmannia* germinated best at 15°C constant with the use of potassium nitrate. *Eragrostis abyssinica* is nitrate-sensitive. A germination of approximately 95% was obtained at high temperature alternations. *Eragrostis secundiflora* and *E. trichodes* are nitrate-sensitive. The best results were obtained by prechilling for a period of 14 days before germinating at a Room to 35° alternation. *Polypogon monspeliensis* is benefited by potassium nitrate and light. With water, the seed germinates well only at a high alternating temperature, but with the use of potassium nitrate the range of favorable alternating temperatures is widened. *Muhlenbergia racemosa* germinated best at the alternating temperatures 20° to 35°C and 10° to 30° with the use of potassium nitrate. The constant temperature, 35°, gave almost as high results as the above alternating temperatures. *Muhlenbergia porteri* germinated best at an alternating temperature of 20° to 35°C. *Muhlenbergia rigens* gave about equal results at alternating temperatures of 20° to 30°C, 10° to 35°, 15° to 35°, 20° to 35° and 20° to 40°. *Bouteloua curtipendula* germinated best at the cooler alternating temperatures, 20° to 30°C with light, 10° to 35°, 10° to 30° and 15° to 25°, and at the constant temperature, 20°. This species is light sensitive. *Bouteloua chondrosioides* germinated best at the alternating temperatures of 25° to 40°C and 20° to 35°, with the use of nitrate. *Bouteloua filiformis* germinates over a wide range of alternating and constant temperatures. It is not benefited by the use of light or nitrate. *Bouteloua gracilis* germinated best at alternating temperatures of 20° to 30°C and 15° to 25°. *Bouteloua eriopoda* germinates best with the use of nitrate at an alternating temperature of room to 35°C. *Bouteloua parryi*, *B. rothrockii*, and *Eragrostis brizantha* germinated 5% or less under various conditions tried. Of the species tested at a series of constant temperatures, *Bouteloua curtipendula*, *Polypogon monspeliensis*, and *Eragrostis lehmannia* gave decreasing germination as the temperature was raised, while *E. curvula*, *Muhlenbergia racemosa* and *M. rigens* showed an increase of germination with increase of temperatures.

- Utah State University, The Utah Agricultural Experiment Station and the following units within the U. S. Government ARS, APHIS, USFS, NRCS, BLM, NPS. "Manual of Grasses for North America." Web page. Available at <http://herbarium.usu.edu/webmanual/default.htm>.
Abstract: Distribution maps of grasses in North America based on floras, herbarium specimens, and accounts.
- Valentine, K. A. 1970. Influence of grazing intensity on improvement of deteriorated black grama range. *New Mexico Agricultural Experiment Station Bulletin* No. 553.
Abstract: The objective of the work reported in this bulletin was to determine the level of use of black grama that will permit satisfactory recovery of deteriorated range
- Valentine, K. A., and J. J. Norris. 1964. A comparative study of soils of selected creosotebush sites in southern New Mexico. *Journal of Range Management* 17: 23-32.
See abstract under *Larrea tridentata*
- Vera-Cruz, Maria Teresa R. P. 1990. "Interception of water by range plants and evaporation from soils in southwest New Mexico." M. S. Thesis, New Mexico State University.
- Watkins, W. E. 1939. Monthly variation in carotene content of two important range grasses, *Sporobolus flexuosus* and *Bouteloua eriopoda*. *Journal of Agricultural Research* 58: 695-99.
Abstract: The monthly carotene content of two important southern New Mexico range grasses, black grama and mesa dropseed, has been presented. Both grasses are moderately high in carotene during the growing season. The mesa dropseed loses all of its carotene soon after the fall freezes end the growing season. The black grama grass, whose upright stems remain green for a distance of from 4 to 6 inches of their base throughout the winter, contain an amount of carotene that seems to be ample to satisfy the vitamin A requirements of range cattle.
- Watts, J. G. 1963. Insects associated with black grama grass, *Bouteloua eriopoda*. *Annals of the Entomological Society of America* 56: 374-79.
Abstract: Collections from black grama grass, *Bouteloua eriopoda* Torrey, were made throughout the year by a variety of techniques, on a ranch in southern New Mexico, and 9 orders, 55 families, 109 genera, and 120 species of insects were taken. They included grass feeders, parasites and predators, and casual visitors. Four species of Thysanoptera accounted for considerably more than 50% of the total insect population and 97% of the thrips were *Chirothrips falsus* Hood. Insect populations were translated by use of broad-spectrum insecticides. The reproduction of the *C. falsus* population by 80% or more resulted from consistent and substantial increase in seed set which in a few cases, increased 6 or 7 times. Other insects were at such low levels that no significant change in their numbers could be measured.

———. 1965. *Chirothrips falsus* on black grama grass. *New Mexico Agricultural Experiment Station Bulletin* No. 499.

Abstract: This study was undertaken to determine the biology and ecology of *Chirothrips falsus* Priesner and its relationship to the typically poor seed set of black grama. The work was conducted on native range, principally at the University Ranch near Las Cruces, and on irrigated plots at the Middle Rio Grande Branch Station near Los Lunas.

Tests showed that seed yields can be significantly increased by thrips control. SD 4402 (Telodrin) gave the best control and the greatest increase in seed yield, although dieldrin and Guthion gave good control and substantial seed increases. The granulated systemics, di-syston and phosphamidon, were significantly inferior to dieldrin spray for thrips control and the resulting seed increase of black and blue grama. A series of three spray applications of Bidrin at weekly intervals, begun shortly before the grass began to bloom, reduced thrips numbers and increased seed yields more effectively than similar schedules begun one and two weeks earlier.

Webb, Warren, Stan Szarek, William Lauenroth, Russell Kinerson, and Milton Smith. 1978. Primary productivity and water use in native forest, grassland, and desert ecosystems. *Ecology* 59, no. 6: 1239-47.

Abstract: The relationship between aboveground net primary production (ANPP) and water use varied significantly among ecosystem types. For both hot deserts and shortgrass prairie-cold deserts which are water limited, ANPP is linearly related to annual water use above a minimum amount of water, estimated at 38 to 170 mm, respectively, needed annually to sustain each system. Once the minimum water to sustain ANPP is reached, ANPP increases an estimated 0.38 g and 1.09 g per 1000 g of additional water in the hot desert and the shortgrass prairie-cold desert. In forest systems not water stressed, ANPP was not related to water use. For grasslands representing a gradient from water stressed toward not water stressed, ANPP correspondingly declined per unit of water used. Classically evaluating water-use efficiency as annual ANPP divided by annual evapotranspiration, forests are the most efficient, 0.9 to 1.8 g ANPP/1000 g water, followed by shortgrass prairie, 0.2 to 0.7, then hot deserts, 0.1 to 0.3.

Webb, Warren L., W. K. Lauenroth, Stan R. Szarek, and Russell S. Kinerson. 1983. Primary production and abiotic controls in forest, grassland, and desert ecosystems in the United States. *Ecology* 64, no. 1: 134-51.

Abstract: This paper, a synthesis based on data generated by the International Biological Program, deals with the relationships among biotic factors at the ecosystem level. Emphasis is placed on aboveground net primary production (ANPP), a major component of energy that drives ecosystem processes, and on potential evapotranspiration (PET), the abiotic variable most often used to explain variation in ANPP. The question addressed is: can ANPP be related to combinations of biotic and abiotic factors such that the relationships are independent of ecosystem type, whether it be forest, grassland, or desert? ANPP as a function of peak foliar standing crop (FSC) was best explained by models which showed a reduction in ANPP/FSC as FSC increased. Thus, deserts had a higher ANPP per unit of FSC than did other systems. As expected, photosynthetic efficiency (PE) was highest for forests, @?100 times greater than for deserts. However, when PE was evaluated per unit of foliage, the differences in PE of ecosystems were much less. In fact, a hot-desert site had the highest PE/FSC. In terms of a theoretical maximum, the PE of forests was only 6-25% of

the maximum value. Systems with nearly steady-state aboveground standing crop (ASC) showed an exponential decrease with decreased water availability (potential evapotranspiration minus precipitation). For these same systems, the ratio of ANPP to ASC increased with decreased water availability, suggesting that water-stressed systems need more energy from ANPP to drive internal processes. A model predicting ANPP of desert-shortgrass steppes was structured in terms of FSC, water availability, and temperature. The predictive power was found to be very high, and the model was successfully validated in two of three cases with an independent data set. A model predicting ANPP of forests was structured in terms of FSC, radiation, ASC, and temperature. The deviation of the observed ANPP relative to that calculated was 17%. Deviations from predicted values were highest for deciduous stands with high ANPP and low FSC. Most relationships exhibited good correlations between ANPP and the various independent variables including both biotic, abiotic, and combinations of the two. However, in many instances the data tended to be grouped by ecosystem type, suggesting that variation in ANPP can be reduced if ecosystem type is an added independent variable. It was surprising to find that, with the limits of our data, differences in ANPP at the ecosystem level are not glaring, especially considering that soil factors were not included in our analyses. When considering the broad range of genotypes in each ecosystem, and the much broader genotypic range representing all ecosystems, the control that native ecosystems have over abiotic factors in producing ANPP is evident but not large.

Whitfield, Charles J., and Hugh L. Anderson. 1938. Secondary succession in the desert plains grassland. *Ecology* 19, no. 2: 171-80.

Whitfield, C. J., and E. L. Beutner. 1938. Natural vegetation in the desert plains grassland. *Ecology* 19, no. 1: 26-37.

Williams, Patrick Thomas. 1976. "Grass production changes with mesquite (*Prosopis juliflora*) reinvasion in southern Arizona " M. S. Thesis, University of Arizona.

Wondzell, Steven M., and John A. Ludwig. 1995. Community dynamics of desert grasslands: Influence of climate, landforms, and soils. *Journal of Vegetation Science* 6, no. 3: 377-90.

See abstract under *Flourensia cernua*

Wood, M. K., T. L. Jones, and M. T. Vera-Cruz. 1998. Rainfall interception by selected plants in the Chihuahuan Desert. *Journal of Range Management* 51: 91-96.

Abstract: Forb, grass, and shrubs of ten species were evaluated. The weight of water intercepted per weight of green or dry plant weight appears to be a function of plant growth form and surface characteristics rather than seral position. Plants included cane bluestem, lehmann lovegrass, mesa dropseed, red awn, bush muhly, black grama, side oats grama, russian thistle, broom snakeweed, and fourwing saltbush.

Wooton, E. O., and P. C. Standley. 1912. The grasses and grass-like plants of New Mexico. *Agricultural Experimental Station Research Report Bulletin* no 81.

Wright, N. 1964. Influence of management practices on seed-set, seed yield, seed weight, germination, and insects of black gramagrass, *Bouteloua eriopoda* (Torr.) Torr. *Agronomy Journal* 56: 57-60.

Wright, Neal, and A. A. Baltensperger. 1964. Influence of temperature, light radiation, and chemical treatment on laboratory germination of black gramagrass seed, *Bouteloua eriopoda* Torr. *Crop Science* 4: 168-71.

Abstract: The influence of 6 alternating-temperatures, 5 constant temperatures, light radiation, and several chemical treatments on the germination of black gramagrass caryopses and spikelets was studied. The tests with various temperatures showed that the highest total germination percent (1% level of significance) was at 20-35°C alternating temperature. Light and dark for the temperature experiments (A through K) were not significantly different, however, light and dark treatments were significantly higher than the potassium nitrate treatments. An examination of the daily germination counts showed a different influence for the dark and light treatments for all temperature experiments. Seed germinated more rapidly in the dark. Germination was retarded one day by light at optimal temperature. Germination was retarded when temperatures were less favorable. For example, germination occurred on the second day in the dark at 20-35°C compared with the sixth day in the dark at 15°C.

Twenty-eight light radiation and chemical treatments were studied at the alternating-temperature, 20-35°C. No single treatment was significantly outstanding. Highest germination was 72.0% in the dark with 50 ppm gibberellic acid. The two treatments using spikelets rather than caryopses were lowest suggesting that spikelets will need further study. Light radiation was not effective in increasing germination. Light and dark alone were low; however, with chemicals, particularly gibberellic acid, light and dark gave the highest germination percentages.

The results suggested the alternating-temperature (20-35°C) alternating 16 hours dark and 8 hours light, respectively, with 50 ppm gibberellic acid to be the optimum laboratory conditions for germination of black gramagrass caryopses.

Wright, Neal, and L. J. Streetman. 1958. Past performance and future potential of black grama for southwestern ranges. *Journal of Range Management* 11, no. 5: 207-14.

Abstract: Black grama possesses many desirable characteristics, making it an outstanding range grass of the arid and semiarid grasslands of southwestern United States. Black grama is a well adapted native, long-lived perennial. It can be maintained on the range. Although it is not as abundant as in previous years, its spread can be slowly accomplished by proper utilization and management practices. Black grama's soil protection qualities are most desirable due to the ability of the stem joints to take root, resulting in new plants, making not only a valuable soil protector but providing a means for spreading and revegetation. The drought tolerance of this grass is exceptional in that this characteristic is effectively demonstrated through all growth stages; however, continued use and drought can seriously deplete stands. It is a dependable forage plant with the ability to perform well under grazing. The literature indicates

highest yield performance and persistence when deferred grazing is used, as compared to nonuse or heavy grazing.

The grass is characteristically nutritious at all times of the year, and in comparison with other forage species, the winter and spring nutritional values make black grama outstanding. It is a palatable forage and highly relished throughout the year, and is of particular importance during the dry spring period when other range species are harsh and parched. Unlike most of its associates, black grama is a natural source of reserve feed, since the ungrazed stems remain green for two or more seasons. This feature, coupled with management, minimizes drought hazard and provides a more stable carrying capacity.

This review indicates that many of the principles of black grama range management have been studied and that there has been a minimum of research on the more basic aspects of growth and reproduction. An evaluation of this information indicates that the one characteristic limiting the widespread use of this grass for range reseeding is its extremely poor and unreliable seed setting capabilities. Obviously, the key to its widespread use for reseeding hinges on the improvement of seed production.

In this instance the aim of the plant breeder should be to maintain the many desirable characters while improving seed production. Once the factor or factors limiting seed set can be determined, research will be needed on the cultural techniques necessary to produce seed in sufficient quantity for an economic product. There is need for further investigation of the physiology, cytology, mode of reproduction, breeding behavior, and cultural practices of this grass in order to utilize the most advantageous breeding procedures.

There are no recorded data on the use of fertilizer in relation to reseeding or the effect on yield and nutritive value of black grama. Seed quality factors such as purity, germination, and longevity, reseeding practices, management techniques, and seed processing problems should be considered following the improvement of seed setting along with the development of breeding procedures. The elimination of seed production barriers, which at present are limiting, along with methods of establishing stands in hot, dry areas would allow black grama to take a prominent role in revegetation of the desert grasslands of the southwestern United States.

Wright, R. G. Jr. 1972. Computer processing of chart quadrat maps and their use in plant demographic studies. *Journal of Range Management* 25, no. 6: 476-78.

Abstract: Chart quadrat maps offer a unique source of data on long-term trends in grasslands. Through the use of film scanning computer systems, this information can be more easily processed and used in plant demographic studies.

Wright, R. G., and G. M. Van Dyne. 1976. Environmental factors influencing semidesert grassland perennial grass demography. *Southwestern Naturalist* 21: 259-74.

Abstract: Maximum life spans varied from 28 years for *Bouteloua eriopoda* to only 7 years for *Hilaria mutica*. For newly established plants with shallow root systems, the precipitation the immediate growing season was more important than precipitation for longer antecedent intervals.

———. 1981. Population age structure and its relationship to the maintenance of a semidesert grassland undergoing invasion by mesquite. *The Southwestern Naturalist* 26, no. 1: 13-22.

Abstract: Data from long-term chart quadrats recorded from the Jornada Experimental Range in south-central New Mexico were used to develop demographic measurements for black grama and mesa dropseed. These measurements included mean and maximum lifespans, survival probabilities, and rates of establishment and were used to derive the stable age structure for black grama. They were combined with factors such as climate and grazing in a model designed to simulate the long-term dynamics of a stable perennial grassland. Using the stable age structure as a starting point, the model was perturbed by differentially lowering the age-specific survival rates in an effort to mimic the effect of mesquite competition. A stable age structure for black grama was achieved after a period of 40 years. A similar structure for mesa dropseed could not be derived. Output of the model run over a 47-year period in the absence of mesquite shows that stability of numbers in each class can be achieved over the entire time period. Grazing does not appear to disrupt this stability, but only decreases the number of plants established each year. Simulation of increased mesquite competition showed that in the first 12 years there may be a concomitant decline in the number of new individuals. By the 25th year, the survival rates for all but the oldest individuals have been adversely affected and there are few individuals alive.

Young, Steve A. 1980. "Phenological development and impact of season and intensity of defoliation on *Sporobolus flexuosus* (Thurb.) Rhydb. and *Bouteloua eriopoda* (Torr.) Torr." Ph. D. Dissertation, New Mexico State University.

Abstract: The objectives of this study were to determine how eight seasonal defoliation patterns affect regrowth of dry matter yield and basal diameter of mesa dropseed (*Sporobolus flexuosus* [Thurb.] Rhydb.) and black grama (*Bouteloua eriopoda* [Torr.] Torr.); determine how these defoliation patterns affect the reproductive potential of black grama; quantify seasonal phenological stages of growth in both species; and interpret the data in terms of management application. The eight defoliation patterns consisted of a continuous treatment, an early, late, and total (early plus late) vegetative treatments, boot, flowering, predormant, and dormant treatments. There were two defoliation levels. Light use was defined as removal of 30 percent of annual production and heavy use when 60 percent of annual production was removed. Criteria used to measure plant response to defoliation were regrowth yields by increments, basal diameter changes, and plant growth characteristics. Phenological and morphological characteristics were also measured in both species. Phenological development of mesa dropseed and black grama was gradual through the vegetative growth stages. Internode elongation, sheath length, and plant height increased rapidly in mesa dropseed after floral induction. The slow growth process continued in black grama with a gradual increase in internode length, sheath length, and an increase in plant height commensurate with floral development. Defoliations prior to flowering on black grama and mesa dropseed did not influence regrowth yield by the end of the growing season, regardless of intensity of use. Amount of residual material and changes in basal diameter were variable. Clipping repeatedly reduced diameter and regrowth after four defoliations. A one-time clipping at flowering was the most detrimental to vigor of mesa dropseed and black grama, regardless of intensity of use. This resulted in minimal regrowth, either within a growing season or after a year of nonuse. Basal diameter again varied. This clipping treatment caused a significant decrease in stolon numbers in black grama after a year of nonuse. Regrowth and basal diameter of both

species clipped to remove 30 percent the first year during vegetative growth had increased after two growing seasons. Therefore, for continued forage production, light use prior to floral development is recommended. Regrowth, basal diameter, and stolon numbers increased over two growing seasons in black grama plants clipped to simulate light use at dormancy. Therefore, light use of black grama during the winter is encouraged.

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4 *Pleuraphis mutica* Buckl. (Tobosa)



Pleuraphis mutica Buckl. is the newly accepted scientific name of *Hilaria mutica* (Buckl.) Benth or tobosa grass (Uchytel 1988). Tobosa is a highly productive, drought tolerant, C4 perennial grass. Tobosa can spread vegetatively by short rhizomes which is a slow but very effective process of colonization (Neuenschwander, Sharrow, and Wright 1975). Tobosa is highly competitive on clay rich soils of floodplains and swales, which receive run-on water. These areas can temporarily flood (Uchytel 1988, Paulsen and Ares 1962). The lifespan of individual plants is relatively short (max. 7 years) (Wright and Van Dyne 1976), but tobosa dominance can be stable over time (Gibbens and Beck 1987). Tobosa occurs

both in the Chihuahuan and Sonoran desert and is distributed throughout Arizona, Southern New Mexico and Western Texas in the United States (Utah State University 2002). In northern Mexico it is the dominant herbaceous species in vegetation arcs on slightly sloping, clay loam soils (Montaña, Lopez-Portillo, and Mauchamp 1990). The wealth of dead biomass in its canopy makes tobosa unpalatable during the winter (Paulsen and Ares 1962). However, during its growing season, it can be good feed for livestock.

Anderson, D. M. 1982. Seasonal grazing of semidesert tobosa rangeland in southern New Mexico. In *Proceedings of the National Conference on Grazing Management and Technology*, Editors D. D. Briske, and M. M. Kothmann, 137-42 Department of Range Sciences, Texas A&M University.

———. 1988. Seasonal stocking of tobosa managed under continuous and rotation grazing. *Journal of Range Management* 41: 78-82.

Abstract: Tobosa (*Hilaria mutica* [Buckl.] Benth.) was seasonally grazed with cattle under high-density (2.1 to 5.1 animal unit/hectare [AU/ha]) rotation and low-density (0.33 and 0.39 AU/ha) continuous stocking in 1980 and 1981, respectively. Tobosa leaf and culm color were used to evaluate forage quality. At the end of the 1980-81 growing seasons, crude protein was highest in green tobosa (8.4%) and lowest in gray tobosa from the previous seasons (4.7%). Grazing strategies did not influence the proportion of green tobosa within the standing crop; however, flexible rotation produced a more uniform use of green tobosa within the cell when compared to grazing with fixed intervals between rotations. Grazing patterns result from improper utilization of green tobosa which in future years will senesce into gray colored tobosa that composed 46-91% of the standing crop. In this study, flexible rotation of cattle among paddocks, based on a 30-35% reduction of tobosa standing crop height, reduced gray tobosa within the standing crop more than did continuous stocking. Total heifer liveweight gain per ha in 1980 and 1981, respectively, was 43 and 24% less under continuous stocking compared to rotation grazing management.

Ares, Fred N. 1939. Cutting tobosa grass for hay. *Cattleman* 25, no. 9: 47-50.

Briones, Oscar, Carlos Montaña, and Exequiel Ezcurra. 1996. Competition between three Chihuahuan desert species: evidence from plant size-distance relations and root distribution. *Journal of Vegetation Science* 7, no. 3: 453-60.

Abstract: Using size-distance data we tested the intensity and importance of competition between *Hilaria mutica* (a tussock grass), *Larrea tridentata* (a microphyllous shrub) and *Opuntia rastrera* (a succulent) in the Chihuahuan desert. We also compared the vertical and horizontal distribution of roots to assess the potential degree of overlap in the use of soil resources. The relationships between sizes and distances of nearest-neighbour plants suggested that intraspecific competition is generally more important than interspecific competition. However, evidence of stronger inter than intraspecific competition was found in some cases. Species combinations showing significant interspecific competition involved always *Opuntia*,

whereas *Larrea* and *Hilaria* did not influence each other. The analysis of the symmetry of competition showed that *Opuntia* was adversely affected by the presence of *Hilaria* or *Larrea*. Although differences were found in the distribution of roots, the results of the size-distance study support the idea that, (particularly) *Opuntia*, below-ground niche differentiation is not sufficiently important to totally avoid the negative effects of plant competition

- . 1998. Competition intensity as a function of resource availability in a semiarid ecosystem. *Oecologia* 116, no. 3: 365-72.

Abstract: Two field experiments were conducted using three dominant perennial species of the Chihuahuan Desert: *Hilaria mutica* (a tussock grass), *Larrea tridentata* (a microphyllous shrub) and *Opuntia rastrera* (a flat-stemmed succulent cactus). Two hypotheses concerning competition in arid plant communities were tested. (1) Marked resource partitioning with no interspecific competition could be expected since the three species belong to different life-forms, and that plant growth in deserts is basically limited by harsh environmental conditions. (2) Alternatively, resource scarcity (particularly water) will result in strong plant competition. In a 1-year removal experiment, water status and plant growth of the three species were monitored in twelve 10 m X 10 m plots randomized in three blocks and assigned to the following treatments: (a) removal of all species, except *H. mutica*; (b) removal of all species, except *L. tridentata*; (c) removal of all species, except *O. rastrera*, and (d) control without any manipulation. In a watering experiment, under two neighbourhood conditions (growing isolated or in associations of plants of the three species in plots of 20 m²), the water status of the three species and the growth of *H. mutica* and *L. tridentata* were studied for 32 days after an irrigation equivalent to 30 mm of rain, similar to a strong storm event at the site. In the removal experiment, where plants were free to capture water, no evidence of competition was observed. However, during the watering experiment, in which water was forced into the soil, competitive effects were observed. Associated individuals of *L. tridentata* had lower xylem water potentials and osmotic potentials (OPs) and produced shorter twigs and less leaves and nodes. Although less pronounced, neighbours also had a negative effect on the OP in *O. rastrera*. According to these results, the intensity of the interspecific competition for water seems to depend on the level of resource availability in the soil. Thus, the validity of the two hypotheses tested in this study also depends on the level of resources. Competition could be absent or very low in years of low precipitation, as in the year of this study (173 mm against a 25-year average of 264 mm). However, when soil water availability is high, e.g. following heavy rain, the negative interactions between species could be more intense.

- Britton, C. M., and A. A. Steuter. 1983. Production and nutritional attributes of tobosagrass following burning. *Southwestern Naturalist* 28, no. 3: 347-52.

Abstract: Tobosagrass (*Hilaria mutica*) was prescribed burned in mid-February and late March. Sequential harvests were used to compare growth curves from different burn dates to an unburned control. Crude protein concentration, moisture content, and digestible organic material were determined for all samples. Final yields taken in late July were 2,357, 1,950, and 620 kg/ha for the mid-February burn, late March burn, and control respectively. At growth, initiation, crude protein concentration for new growth varied from about 15 to 20% then decreased to about 7% by July. Moisture content of tobosagrass from

burned areas decreased from about 65% early in the growing period to below 30% in July. Moisture content of the control (old standing dead + new growth) increased to a high of over 30% in early May, then decreased below 20% by July. Digestibility of new growth from all treatments were similar by sampling date and varied from about 40 to 60%. Old standing dead digestibility varied from 14 to 23%.

Campbell, R. S. 1931. Plant succession and grazing capacity on clay soils in southern New Mexico. *Journal of Agricultural Research* 43, no. 12: 1027-51.

Canfield, R. H. 1938. How closely may black grama and tobosa grass be grazed year after year? *Cattleman* 23, no. 7: 1-3.

———. 1939. *The effect of intensity and frequency of clipping on density and yield of black grama and tobosa grass*. Technical Bulletin , no. 681. Washington : U.S. Dept. of Agriculture.

Abstract: Clipping experiments on semidesert black grama range indicate clearly that persistent cropping of all herbage of this grass to a 2-inch height or less eventually results in destructive reduction of tuft area regardless of frequency of seasonal harvesting; it reduces forage yield to zero; it prevents revival and even establishment of reproduction of the forage grass; it entirely outweighs all beneficial effects of above-average rainfall; and the end result is rapid and critical deterioration of the black grama site through excessive wind and water erosion.

Cunningham, G. L., F. R. Balding, and J. P. Syvertsen. 1974. A net CO₂ exchange model for C₄-grasses. *Photosynthetica* 8, no. 1: 28-33.

Abstract: A mathematical model was developed for predicting net CO₂ exchange rates of grasses with C₄-dicarboxylic acid pathway of CO₂ reduction. Model coefficients for two Chihuahuan desert playa species were determined. This was done using net CO₂ exchange rate data and an intrinsically non-linear regression algorithm.

de Alba Avila, Abraham. 1983. "Comparative germination ecology of *Sporobolus airoides* and *Hilaria mutica* from Mapimi Biosphere Reserve and other Mexican and United States locations ." M. S. Thesis, University of Arizona.

Abstract: Germination of *Hilaria mutica* and *Sporobolus airoides* from the Mapimi Reserve were compared with four *S. airoides* accessions. Light effects on germination of the six accessions under four temperatures showed that American accessions had a lower optimum and a greater light effect on other temperatures than Mexican accessions. Establishment of six accessions at four depths showed that surface sowings had higher establishment in cracking clay than in sand. New Mexico and Mapimi *S. airoides* accessions had the highest establishment percent at 10 and 20 days. The effect of osmotic and matric potentials on the germination of *H. mutica* was significant at -9 bars. Matric potentials of -6 and -9 bars and osmotic potential of -9 bars decreased germination of Mapimi *S. airoides*. *Sporobolus airoides* is recommended for

reseeding sites with high moisture availability, using a thin mulch. Mexican accessions are recommended for summer sowings, while the American accessions for late spring or early fall. *Hilaria mutica* is not recommended.

De la Torre, Raul. 1970. "Chemical composition and digestibility of tobosa ." M. S. Thesis, New Mexico State University.

DeGarmo, H. C.Jr. 1966. "Water requirement and production of eight desert plant species under four soil moisture levels." M. S. Thesis, New Mexico State University.

Devine, Donald L. 1987. "A tobosa grass-burro grass mosaic community pattern in the northern Chihuahuan desert." M.S. Thesis, New Mexico State University.

Devine, Donald L., M. Karl Wood, and Gary B. Donart. 1998. Runoff and erosion from a mosaic tobosagrass and burrograss community in the northern Chihuahuan desert grassland. *Journal of Arid Environments* 39, no. 1: 11-19.

Abstract: A mosaic plant community pattern was studied in the northern Chihuahuan Desert grassland region of southern New Mexico. The principal plant species of the mosaic were tobosagrass (*Hilaria mutica* (Buckl.) Benth.) and burrograss (*Scleropogon brevifolius* Phil.). Water runoff, sediment concentration, incremental sediment, and plant and soil properties of both species aggregations were measured. The study site was a large aggregation of burrograss plants in a tobosagrass matrix. Water runoff was three times greater from the burrograss aggregation than from the tobosagrass aggregation both before and after the growing season. Sediment concentration and cumulative sediment loss were also greater from the burrograss than the tobosagrass, except under wet conditions in the early autumn when sediment concentrations were similar. Differences are attributed to greater cover, phytomass, and surface roughness in the tobosagrass aggregation

Dugas, William A., Ralph A. Hicks, and Robert P. Gibbens. 1996. Structure and function of C3 and C4 Chihuahuan desert plant communities. Energy balance components. *Journal of Arid Environments* 34, no. 1: 63-79.

See abstract under *Larrea tridentata*

Dwyer, Don D. 1972. Burning and nitrogen fertilization of tobosa grass. *New Mexico Agricultural Experiment Station Bulletin*. No. 595

Abstract: Tobosa grass (*Hilaria mutica* Buckl. Benth.) is a characteristic species dominating the flood plains of southern New Mexico. During rainstorms these flood plains often receive additional water from surrounding slopes and produce considerably more herbage than nearby sites. The accumulation of past

growth which frequently occurs on the flood plains provides excellent fuel for fires. In the Southwest, lightning from summer electrical storms frequently ignites the dry tobosa which has accumulated. Also, ranchers occasionally burn tobosa flood plains to remove the unwanted accumulation of old growth. Little is known of the effects of fire on subsequent tobosa grass production.

In general, tobosa grass is considered to be low in palatability for livestock. The accumulation of old growth tends to repel the grazing animal, and burning the old growth increases livestock preference for tobosa.

This study was designed to determine the effect that burning tobosa at different times of the year has on subsequent production, with nitrogen fertilization and without.

Dwyer, Don D., and Harlan C. DeGarmo. 1970. Greenhouse productivity and water-use efficiency of selected desert shrubs and grasses under four soil-moisture levels. *New Mexico Agricultural Experiment Station Bulletin* No. 570.

Fernández, R. J., and J. F. Reynolds. 2000. Potential growth and drought tolerance of eight desert grasses: lack of trade-off? *Oecologia* 123, no. 1: 90-98.

See abstract under *Bouteloua eriopoda*

Gibbens, R. P. 1994. Root systems of desert plants. *Sonorensis* 14, no. 1.

Gibbens, Robert P., and Reldon F. Beck. 1987. Increase in number of dominant plants and dominance-classes on a grassland in the northern Chihuahuan desert. *Journal of Range Management* 40, no. 2: 136-39.

See abstract under *Bouteloua eriopoda*

———. 1988. Changes in grass basal area and forb densities over a 64-year period on grassland types of the Jornada Experimental Range. *Journal of Range Management* 41, no. 3: 186-92.

See abstract under *Bouteloua eriopoda*

Gibbens, Robert P., Ralph A. Hicks, and William A. Dugas. 1996. Structure and function of C3 and C4 Chihuahuan desert plant communities. Standing crop and leaf area index. *Journal of Arid Environments* 34, no. 1: 47-62.

See abstract under *Flourensia cernua*

Gibbens, R. P., and J. M. Lenz. 2001. Root systems of some Chihuahuan desert plants. *Journal of Arid Environments* 49, no. 2: 221-63.

See abstract under *Bouteloua eriopoda*

Herbel, Carlton H. 1963. Fertilizing tobosa on flood plains in the semidesert grassland. *Journal of Range Management* 16, no. 3: 133-38.

Abstract: Tobosa (*Hilaria mutica* (Buckl.) Benth.), a drought resistant grass of the arid Southwest, occurs primarily on heavier textured soils, but is not limited to them. It is relatively unpalatable to livestock during the dormant season but is readily grazed during the growing season. Therefore, where possible, tobosa flood plains should be fenced separately and grazed during the growing season while the upland pastures are deferred. These flood plains supporting tobosa in high density and receiving additional water as run-in from adjacent mountains can produce several times the herbage of upland sites. On ranches where the area of tobosa flood plains is limited, increased yields of tobosa will enable the operator to defer the upland pastures more completely and for a longer time in the growing season. The objective of this study was to determine tobosa herbage yields and quality on flood plains as influenced by fertilizer treatments in relation to the effects of available moisture.

Herbel, Carlton H., and Robert P. Gibbens. 1989. Matric potential of clay loam soils on arid rangelands in southern New Mexico. *Journal of Range Management* 42, no. 5: 386-92.

Abstract: The matric potential of soil water is presented for 6 clay loam sites on floodplains of arid rangelands. Gypsum resistance blocks impregnated with plaster of paris were placed at 6 soil depths to 122 cm. At 4 locations, blocks were placed inside and outside a buried sheet metal cylinder so that estimates could be obtained of matric potential due to precipitation and due to precipitation plus run-in. The average annual precipitation during the approximate 20-year study period was 242 mm, slightly above the long-time average. Haplargids dominated by tobosa [*Hilaria mutica* (Buckl.) Benth.] had a greater probability of the matric potential greater than or equal to -1.5 MPa (wet soil) than the Calciorthids dominated by burrograss (*Scleropogon brevifolius* Phil.). The probability of matric potential greater than or equal to -1.5 MPa (wet soil) was as great or greater in winter as during the summer growing season. The factors affecting matric potential were amount and nature of precipitation, amount of run-in water, soil and vegetation type, position on the landscape, and microrelief

Huenneke, L. F., J. P. Anderson, M. Remmenga, and W. H. Schlesinger. 2002. Desertification alters patterns of aboveground net primary production in Chihuahuan ecosystems. *Global Change Biology* 8, no. 3: 247-64.
See abstract under *Bouteloua eriopoda*

Jurado, P., and D. B. Wester. 2001. Effects of biosolids on tobosagrass growth in the Chihuahuan desert. *Journal of Range Management* 54, no. 1: 89-95.

Abstract: Little information is available about seasonal application and carry-over effects of biosolids application to semi-arid grasslands. Biosolids rates of 0 (control), 7, 18, or 34 Mg ha⁻¹ were topically applied to tobosagrass (*Hilaria mutica* (Buckl.) Benth.) experimental plots in a Chihuahuan desert grassland in western Texas. Biosolids were applied twice in 1994, for one-year-only, either in winter-and-summer (WS), or spring-and-summer (SS) seasons. Half of the plots were irrigated every summer for 4 years (1994-1997). Tobosagrass standing crop (herbage yield) and total Kjeldahl nitrogen concentration

(plant %TKN) were measured every year during the 4 years of the study (1994-1997). An increase in biosolids rate increased tobosagrass herbage yield linearly during the 4 growing seasons. Linear and quadratic responses to biosolids rates were observed in %TKN during the experiment. Irrigation increased tobosagrass herbage yield. Irrigation decreased %TKN in 1995 and 1996 and had no influence during the other years. Winter-and-summer applications increased herbage yield more than spring and summer applications in 3 out of 4 years. Spring-and-summer applications increased %TKN more than winter and summer applications only in 1996. Carry-over effects on tobosagrass herbage yield and %TKN were observed in the second, third, and fourth growing seasons after biosolids application. Twice-a-year application of biosolids for 1-year-only offers an excellent means to improve tobosagrass productivity and forage quality.

Kiesling, Herman Ernst. 1968. "Intake and digestibility of tobosa (*Hilaria mutica*) by grazing steers." M.S. Thesis, New Mexico State University.

Abstract: Esophageal-fistula samples of dormant tobosa (*Hilaria mutica* (Buckl.) Benth.) contained significantly more silica, ash protein, ether extract, detergent fiber and detergent lignin, but less A.O.A.C. fiber than hand-plucked grass samples collected in each of seven pastures used in grazing studies at the Jornada Experimental Range. Except for ash, the differences were apparently due to selective grazing by the steers.

Kone, Daouda. 1989. "Tiller defoliation of *Hilaria mutica* (Buckl.) Benth. under seasonal high-density rotation and continuous stocking." M.S. Thesis, New Mexico State University.

Abstract: *Hilaria mutica* (Buckl.) Benth. commonly called tobosa, is a warm-season, native perennial grass. Spread of this grass under arid conditions occurs mainly from rhizomes. Tobosa was seasonally grazed with cattle under high-density (4.83 AU/ha) rotation and low-density (0.35 AU/ha) continuous management strategies in 1986 and 1987 to evaluate patterns of utilization. Each year 80 tillers were monitored under each grazing strategy to evaluate frequency and intensity of defoliation. Under high-density rotational grazing, 92% of the tillers were grazed at least once with a mean height reduction of 31% or 53 mm and an average of 2 leaves removed per tiller. Under low-density continuous grazing only 29% of the tillers were grazed at least once. This resulted in a 14% mean reduction in tiller height or 25 mm mean height reduction and one leaf removed per grazing event. There were a similar number of tillers defoliated at least once in 1986 (51%) compared to 1987 (65%), averaged over both treatments within years. These defoliations contributed to a mean height reduction of 41% or 3 leaves/tiller removed in 1986 compared to a height reduction of 12% or 2 leaves/tiller removed in 1987. During the first grazing cycle, 55% of the tillers averaged over grazing strategies and years were grazed more than once. This contributed to a mean plant height reduction of 27% or 49 mm compared to 61% of the tillers being grazed more than once (36% reduction or 53 mm) during the second grazing cycle. The overall correlation coefficient ($r = 0.26$) indicated height removed did not affect number of leaves removed. Nevertheless, high-density rotation stocking increased frequency and intensity of defoliation. Between grazing cycles in 1987, mean plant height decreased 29 mm under low-density stocking compared to a mean increase in plant height of 68 mm under high-density stocking. The mean number of green leaves decreased by 1 under low-density stocking

compared to high-density stocking in which there was a mean increase of 1. The mean number of brown leaves per culm was greater under high-density stocking (1) compared to low-density stocking (<1).

Montaña, C. 1992. The colonization of bare areas in two-phase mosaics of an arid ecosystem. *Journal of Ecology* 80: 315-27.

Abstract: Two-phase mosaics (densely vegetated patches regularly alternating with almost bare areas) occur on smooth slopes of many arid lands of the world as a result of rainwater redistribution through sheet-flow run off. This paper reports the vegetation dynamics (through synchronic and diachronic approaches) of both the upslope and downslope fringes of vegetated patches (vegetation arcs) located in the Chihuahuan Desert, Mexico. Ten vegetation arcs were used in a synchronic study and one of them in an 8-year diachronic study (1982-90). Data gathered in 2-m-wide, 8-15-m-long grids of 25-cm X 25-cm contiguous quadrats were used to study the variation of species richness, life-form dominance, dominance-diversity relationships and species composition across the fringes. A colonization process developed in the upslope fringes; (i) species richness increased gradually to a peak and then decreased, as would be expected in an ecotone; (ii) this peak coincided spatially with a change in life form and floristic dominance; and (iii) communities with geometric-like distributions of abundance were replaced by communities with log-normal-like distributions of abundance, which are common in successional processes. The diachronic study showed that the peak of species richness had moved upslope with a concomitant colonization of new space in that direction. The displacement of that peak, coupled with changes over time in the dominance of life forms and in the dominance-diversity relationships, provided additional evidence that a successional process of colonization develops. Likewise, long-term variations in floristic composition of the upslope quadrats were explained by time, position along the grid and rainfall, in order of decreasing importance. There was a determinism both in the life form and in the floristic replacement processes observed upslope, suggesting a general scheme of obligatory succession. The bare area was colonized by short-lived perennials and/or facultative therophytes that almost never appear in the main body of the arcs. These species are gradually replaced by tussock grasses and seedlings of woody species which are the dominants in the main body of the arcs. A different process can be inferred from the structural variability in space observed in the downslope fringes. A spatially non-contagious variation in species richness, a spatially non-patterned variation in life-form dominance, and a constancy in geometric-like dominance-diversity relationships suggested that colonization processes were not developing. A long-term decrease in species richness as well as in life-form diversity and a reduction in the abundance of tussock grasses suggested that a process of senescence without new recruitments was occurring. Analysis of the variation of floristic data through time showed the floristic impoverishment of a grassland community dominated by, *Hilaria mutica* coupled with a reduction in the abundance of that species. The dynamics of colonization of bare areas in two-phase mosaics offers an example of succession in arid lands that is probably present in all the world areas where these two-phase mosaics have been reported (the Middle East, Africa, Australia and North America)

Montaña, C., B. Cavagnaro, and O. Briones. 1995. Soil water use by co-existing shrubs and grasses in the Southern Chihuahuan Desert, Mexico. *Journal of Arid Environments* 31: 1-13.

See abstract under *Flourensia cernua*

Neuenschwander, L. H., S H. Sharrow, and H A. Wright. 1975. Review of Tobosa grass (*Hilaria mutica*).

Southwestern Naturalist 20, no. 2: 255-63.

Abstract: This description includes distribution, soils, succession, taxonomy, growth and development, fodder value and chemical composition

Neuenschwander, L. H., and H. A. Wright. 1984. Edaphic and microclimate factors affecting tobosagrass regrowth after fire. *Journal of Range Management* 37, no. 2: 116-22.

Abstract: The plant-air layer and soil surface structure affect regrowth succession following burning in the tobosagrass (*Hilaria mutica*) mesquite (*Prosopis glandulosa*) community in West Texas by altering the microenvironment. Data are presented for the plant-air layer and the soil surface structure as they are related to the recovery of the tobosagrass and the successional response of the annuals. Changes in plant-air layer and the soil surface structure alter the microenvironment and affect plant growth and species composition. A conceptual model is developed illustrating vegetational development as affected by the plant-air layer and the soil surface structure.

Nobel, P. S., and M. J. Linton. 1997. Frequencies, microclimate and root properties for three codominant perennials in the northwestern Sonoran desert on north vs. south-facing slopes. *Annals of Botany* 80: 731-39.

Paulsen, Harold A. Jr., and Fred N. Ares. 1961. Trends in carrying capacity and vegetation on an arid southwestern range. *Journal of Range Management* 14, no. 2: 78-83.

Abstract: During years of low precipitation on black grama and tobosa grasslands and associated shrub ranges of the Southwest, herbaceous cover is reduced and in years of more favorable rainfall it recovers. During a series of dry years on the Jornada Experimental Range in south-central New Mexico basal area of black grama was reduced to approximately the same point irrespective of grazing intensity. Recovery of black grama was greatest where grazing usually removed less than 40 percent of the herbage. Tobosa maintained its greatest basal area under somewhat heavier grazing, which removed 40 to 55 percent of the annual herbage growth.

———. 1962. *Grazing values and management of black grama and tobosa grasslands and associated shrub ranges of the Southwest*. Technical Bulletin , no. 1270. Washington : U.S. Dept. of Agriculture, Forest Service.

See abstract under *Bouteloua eriopoda*

Pinkney, Fred Coatsworth. 1972. "Carbohydrate reserves and photosynthesis in the *Hilaria* genus." Ph. D.

Dissertation, University of Arizona.

Roberts, F. H., C. M. Britton, D. B. Wester, and R. G. Clark. 1988. Fire effects on tobosagrass and weeping lovegrass. *Journal of Range Management* 41, no. 5: 407-9.

Abstract: Fireline intensity (kW/m) was measured on 61 plots of weeping lovegrass [*Eragrostis curvula* (Schrad.) Nees.] and tobosagrass [*Hilaria mutica* (Bucks.) Benth.] burned as headfires and backfires during late winters of 1982 and 1983 in western Texas. Relative humidity, air temperature, wind speed, soil moisture, soil temperature, and fuel moisture were measured at time of burning. Vegetation response was based on plant yield, plant height, and number of seed stalks. Plant responses were not correlated with fireline intensity or any of the environmental parameters measured. Although fireline intensity is an important fire behavior measurement, high fireline intensities did not cause a negative impact on either weeping lovegrass or tobosagrass. Therefore, range managers can conduct high intensity fires to damage or burn down shrubs and not damage these grasses.

Scifres, C. J., J. H. Brock, and R. R. Hahn. 1970. Changes in a tobosagrass-buffalograss community after 27 years of protection from grazing. Texas Agricultural Experiment Station, 2801/2828. College Station, TX.

Senock, R. S., D. M. Anderson, L. W. Murray, and G. B. Donart. 1993. Tobosa tiller defoliation patterns under rotational and continuous stocking. *J. Range Manage.* 46, no. (6): 500-505.

Senock, R. S., D. L. Devine, W. B. Sisson, and G. B. Donart. 1994. Ecophysiology of three C4 perennial grasses in the Northern Chihuahuan desert. *Southwestern Naturalist* 39: 122-27.

Abstract: Despite changes in the relative abundance of C-4 perennial grasses that have occurred in the northern portion of the Chihuahuan desert, no comparative physiological studies on these grasses have been reported. Concurrent measurements were made of leaf physiology, gas exchange, chlorophyll and nitrogen content for mature *Bouteloua eriopoda*, *Sporobolus contractus*, and *Hilaria mutica* during the spring period following an unusually long winter drought. Except for a brief period following rain, midday photosynthesis (A) in *Bouteloua* was below 10 $\mu\text{mol m}^{-2} \text{s}^{-1}$. *Sporobolus* also had low midday A early in the season but had the greatest increase in A following rain when rates approached 25 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and maintained the higher rates through the subsequent dry period. In contrast to the other species, *Hilaria* exhibited higher A early in the season but a more moderate response to increased soil water. Results for the individual species are discussed in the context of speculations contained in published literature concerning varying degrees of drought resistance among the species. Future field studies on these grasses must be broader in scope to fully elucidate differences in drought resistance and the importance of any adaptive physiological mechanisms to past or present vegetation patterns.

Sosebee, Ronald E., and Carlton H. Herbel. 1969. Effects of high temperatures on emergence and initial growth of range plants. *Agronomy Journal* 61: 621-24.

See abstract under *Bouteloua eriopoda*

- Steinberger, Yosef, and Walter G. Whitford. 1985. Microarthropods of a desert tobosa grass (*Hilaria mutica*) swale. *The American Midland Naturalist* 114: 225-34. Abstract: We examined soil microarthropod populations inhabiting a clay-silt soil of a tobosa grass (*Hilaria mutica*) swale in southern New Mexico.... Overall densities of microarthropod groups were correlated with soil moisture but many individual taxa were not. The most numerous and frequently occurring taxa [nanorchestid, tydeid and bdellid mites (Progtigmata); *Aphelacarus* sp. and *Cosmochthonius* sp. (Cryptostigmata)] are common in all Chihuahuan desert habitats examined to date and are common in other North American desert areas.
- Sundt, P. C., and K. R. Vincent. 1999. Influences of geomorphology on vegetation in the Animas Creek Valley, New Mexico. In *Toward integrated research, land management, and ecosystem protection in the Malpai Borderlands: conference summary*, 25-43. Proceedings RMRS-P-10, U.S. Forest Service, Rocky Mountain Research Station.
See abstract under *Bouteloua eriopoda*
- Tadingar, Toloumbaye. 1982. "Utilization of standing crop by cattle under seasonal short duration grazing and seasonal continuous grazing on a semidesert tobosa rangeland." M.S. Thesis, New Mexico State University. Abstract: The purpose of this study was to compare and contrast a seasonal short duration grazing (SDG) treatment, using a ten-paddock cell grazed in sequence by a single herd, and a seasonal continuous grazing treatment. A homogeneous tobosa (*Hilaria mutica*) range located on the Jornada Experimental Range in southern New Mexico was managed under these methods during the 1980 and 1981 grazing seasons. The SDG paddock had significantly higher tobosa composition compared to the continuous paddock during both years (P<0.05). Grouping paddocks according to size indicated that small paddocks had significantly more plants which were defoliated compared to the two large SDG paddocks and the continuous paddock during both years (P<0.05). The degree and amount of change in height imposed on tobosa by grazing animals varied between treatments during both years. There was no significant difference between treatments with regard to average daily gains of livestock during both years (P<0.05).
- Uchtyl, R. J. 1988. *Pleuraphis mutica*. In: U.S. Department of Agriculture, Forest Service Rocky Mountain Research Station Fire Sciences Laboratory. 2001. "Fire effects information system." Web page. Available at <http://www.fs.fed.us/database/feis>
- Ueckert, D. M., T. L. Whigham, and B. M. Spears. 1978. Effect of burning on infiltration, sediment, and other soil properties in a mesquite-tobosagrass community. *Journal of Range Management* 31, no. 6: 420-425.
See abstract under *Prosopis glandulosa*

Utah State University, The Utah Agricultural Experiment Station and the following units within the U. S.

Government ARS, APHIS, USFS, NRCS, BLM, NPS. "Manual of Grasses for North America." Web page.

Available at <http://herbarium.usu.edu/webmanual/default.htm>.

Abstract: Distribution maps of grasses in North America based on floras, herbarium specimens, and accounts.

Wooton, E. O., and P. C. Standley. 1912. The grasses and grass-like plants of New Mexico. *Agricultural Experimental Station Research Report* Bulletin no 81.

Wright, R. G., and G. M. Van Dyne. 1976. Environmental factors influencing semidesert grassland perennial grass demography. *Southwestern Naturalist* 21: 259-74.

Abstract: Maximum life spans varied from 28 years for *Bouteloua eriopoda* to only 7 years for *Hilaria mutica*. For newly established plants with shallow root systems, the precipitation the immediate growing season was more important than precipitation for longer antecedent intervals.

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5 *Larrea tridentata* (DC.) Cov. (Creosotebush)



Creosotebush is the most wide-spread dominant of the North American deserts (Reynolds 1986). It is an evergreen, highly drought resistant, C3 perennial shrub. This species exhibits several chromosome races in North America, which can help to identify postglacial colonization paths (Yang 1970; Hunter et al. 2001). Photosynthesis in creosotebush can occur even during times of very low soil water content (Oechel, Strain, and Odening 1972). Creosotebush flowers opportunistically, whenever there is water available (Abe 1982). Its seeds have no particular adaptation for dispersal (Boyd and Brum 1983), which contributes to its relatively slow and sporadic spread. In the Mojave desert very long-lived (thousands of years) individuals have been found, which makes this species one of the longest-lived plants on earth (Vasek 1980). The Mojave desert ecotype spreads clonally, whereas this has not been observed in the Chihuahuan desert. Furthermore, the lifespan of the Chihuahuan desert ecotype is probably somewhat shorter (about 400 years) (Miller and Huenneke 2000). A multitude of insects, especially bees, are specialized on creosotebush (Hurd and Linsley 1975). Creosotebush produces many secondary compounds that have antimicrobial characteristics (Botkin and Duisberg 1949). For this reason it was sometimes considered allelopathic (Knipe and Herbel 1966).



Abe, Yoko. 1982. "Phenology of tetraploid creosotebush, *Larrea tridentata* (DC.) Cov., at the northeastern edge of the Sonoran desert." Ph. D. dissertation, University of Arizona.

Ackerman, T. J. 1979. Germination and survival of perennial plant species in the Mojave desert. *Southwestern Naturalist* 24: 399-408.

Abstract: Germination and survival of 11 perennial plant species were documented in an undisturbed shrub community in southern Nevada. Only one seedling (0.5%) of 201 germinating between 1971 and 1975 survived until the spring of 1977. *Larrea tridentata* and *Ambrosia dumosa* germinated after rains of 25 mm between mid-June and September. *Atriplex confertifolia*, *Ceratoides lanata*, *Ephedra nevadensis*, *Grayia spinosa*, and five other species germinated between October and March after rains of 16 mm.

Adams, Susan, B. R. Strain, and M. S. Adams. 1970. Water-repellent soils, fire, and annual plant cover in a desert scrub community of southeastern California. *Ecology* 51, no. 4: 696-700.

Abstract: Surveys relating soil wettability and the establishment of annual plants were conducted on soil hummocks under burned and unburned shrubs and trees in a desert scrub community 4 years following a fire. Hummocks under burned and unburned individuals of *Larrea divaricata*, *Prosopis juliflora*, and *Cercidium floridum* were nearly devoid of established annual vegetation, whereas the surrounding soil was densely populated with several species of annual plants, predominately *Sphaeralcea emoryi*. Hydrophobic (water-repellent) layers of soil were found at various depths in the barren hummocks. In general, the layers were further below the soil surface under burned shrubs or trees, and the degree of water repellency was greater. The soil surrounding the hummocks did not contain hydrophobic layers. The mosaic of annuals in the desert scrub vegetation is probably the result of a reduction of available soil moisture due to the formation of water-repellent soils under the shrubs. The effect was more pronounced following fire.

Anderson, D. J. 1971. Pattern in desert perennials. *Journal of Ecology* 59, no. 2: 555-60.

Abstract: Evidence for regularity of distribution in three populations of desert shrubs is reviewed and evaluated. It is argued that the common interpretation of the mechanism underlying distributional regularity--competition between adjacent shrubs for a limited water supply--is not justified in the light of data available for pattern in *Larrea divaricata* populations in relation to mean annual rainfall. Some of the assumptions which underlie this usual interpretation are reviewed and discussed.

Barbour, M. G. 1967. "Ecocline patterns in the physiological ecology of a desert shrub, *Larrea divaricata*." Ph.D. Dissertation, Duke University.

Abstract: The ecology of *Larrea divaricata* Cav., a dominant shrub ubiquitous in the warm desert regions of North and South America, was studied in an attempt to satisfy two objectives: 1) to determine how it has physiologically adapted in germination and early growth behavior to a variety of desert environments, and 2) to estimate the phylogenetic relationships between *Larrea* populations in North and South America. Laboratory and greenhouse experiments were made on seedlings grown from seed collected from 34 United States and 4 Argentina sites. All collection sites were grouped into four desert regions: Argentina, Chihuahuan, Sonoran, Mojave. In general, germination and early root growth behavior did not show differences between desert groups or clinal patterns which correlated strongly with variation in site environment. Requirements for germination and early root growth were such that it was judged unlikely that large-scale germination and survival occur often in nature. It is suggested that optimum field conditions for germination are as follows: seed covered shallowly in soil which remains moist for at least 48 hours, soil moisture level such that osmotic pressure of the soil solution is near zero, temperature around the seed at 23-26° C, soil pH near or below neutrality, and previous exposure of the seed to winter but not summer soil temperatures. Presence of leaf and twig aqueous extract around the seed did not inhibit germination, but cycles of soaking and drying of the seed did increase subsequent germination. In contrast to germination and early root growth, later plant growth response to several factors showed significant differences between desert groups or strong clinal correlation with variation in site environment. Chihuahuan Desert plants exhibited fastest rate of leaf emergence, lowest heat- and salt-tolerance, and onset of wilt at the most negative leaf moisture potentials. Populations from the Mojave Desert were at the opposite ends of these gradients and Sonoran populations were intermediate. Recovery from cold damage correlated positively with latitude and elevation, and plants from very dry sites exhibited less growth reduction at higher levels of competition for soil moisture (or at lower levels of soil moisture) than did plants from more mesic sites. Shoot growth was not affected by root competition in soils with water potential as low as -12.5 atm. Due to seed abortion, non-germination, and mortality over six months' growth, only 20 seedlings survive for every 100 mericarps sown. It is probable that many fewer would survive in nature. Age-frequency distributions of stands of *Larrea* in the relatively mesic Chihuahuan Desert were less often abnormal than those of the more arid Mojave and Sonoran Deserts. Abnormal distributions exhibited several scattered peaks of high frequency or one very narrow peak. Pattern analyses of 23 stands tended to show that *Larrea* shrubs of the Mojave and Sonoran Deserts were distributed regularly, while those of the Chihuahuan Desert were distributed at random or in aggregations. In general, presence or absence of *Larrea* was not reflected in topsoil changes in salinity, pH, or sodium or calcium concentration on alluvial substrata. From field observations, timing of flowering and fruit

maturation seemed to be temperature-, rather than daylength, dependent. Average $2n$ chromosome counts were 25 for Argentina plants, 26 for Chihuahuan, 48 for Sonoran, and 66 for Mojave. These averages should be taken only as indications of increasing ploidy from east to west, rather than as true chromosome numbers. Almost all morphological, physiological, and anatomical traits of *Larrea*, which showed significantly different desert group means, exhibited east-west clines in the United States. Argentina plants were most similar to Chihuahuan plants. Divergence from the Argentina-Chihuahuan genotype increased westward. Many of the clines of values correlated significantly with clines of site environment; however, it is not possible at this time to say whether the strong east-west pattern of genetic divergence indicates adaptation to divergent environments, path of historic plant migration from the Chihuahuan region westward, or both. A hypothesis was developed that the present disjunct range of *Larrea divaricata* originated when *Larrea* of the Chihuahuan and Argentina types evolved from a common trans tropic prototype which then became extinct. The hypothetical prototype was a minor element of the early Madro-Tertiary flora.

- . 1968. Germination requirements of the desert shrub *Larrea divaricata*. *Ecology* 49, no. 5: 915-23.
Abstract: Germination requirements of *Larrea divaricata* Cav. were studied in the laboratory using seed collected at 34 United States sites. Collection sites were grouped into three desert regions (Chihuahuan, Sonoran, Mojave) of increasing aridity from east to west. Optimum laboratory conditions for germination were: darkness, 23 C, leaching the mericarps with running water, wetting and drying cycles, exposure to cold temperatures prior to sowing, and maintaining the medium about the seeds near-zero in osmotic pressure and low in NaCl. Exposure of dry seeds to warm temperatures (37-71 C) prior to sowing resulted in marked reduction of germination. Maximum root growth was obtained at 29 C in a slightly acidic medium low in NaCl and near-zero in osmotic pressure. There were no regional differences in germination behavior. Due to seed abortion, non-germination, and mortality over 6 months' growth, only 20 seedlings survive for every 100 mericarps sown under optimum conditions in the greenhouse. It is unlikely that large-scale germination and survival occur often in nature.
- . 1969. Age and space distribution of the desert shrub *Larrea divaricata*. *Ecology* 50, no. 4: 679-85.
Abstract: Field observations of *Larrea divaricata* Cav. throughout its United States range were used to determine: (1) the age distribution of stand members; (2) the spatial distribution of stand members; and (3) the magnitude of certain soil changes across abrupt community boundaries. Significant non-central tendencies in age distribution of most stands indicated that germination and survival are rare events, contributing to one-age or several-age stands. Shrubs were distributed at random, in clumps, or at regular intervals depending on the environment. Soil pH and salinity changes across ecotones were neither predictable nor usually great enough to affect germination and early growth of *Larrea*.
- . 1974. Plant-plant interactions. In *Arid-land ecosystems: structure, functioning and management*. Editors D. W. Goodall, R. A. Perry, and K. M. W. Howes, 33-49. Cambridge: Cambridge University Press.
Abstract: The objective of this chapter is to review briefly what is currently understood to be the degree of

interaction between desert plants. Much of this information has been gained during the past 20 years. Examples are drawn from throughout the world, but this review remains biased towards North American deserts and *Larrea divaricata* Cav. (= *L. tridentata* (D. C.) Cov.) as a case-study organism.

Barbour, M. G., G. Cunningham, W. C. Oechel, and S. A. Bamberg. 1977. Growth and development, form and function. *Creosotebush. Biology and chemistry of Larrea in New World deserts*. US/IBP Synthesis Series No. 6 ed., T. J. Mabry, J. H. Hunziker, and D. R. Jr. DiFeo, 48-91. Stroudsburg, Pennsylvania: Dowden, Hutchinson and Ross, Inc.

Abstract: The structural contribution of *L. tridentata* to Mojave, Chihuahuan, and Sonoran communities and of *L. cuneifolia* to Argentine communities was summarized in terms of *Larrea* density, absolute, and relative cover, and biomass. These parameters in general were correlated to site annual precipitation, but local factors-especially those related to soil-could completely mask that relationship. The pattern of *Larrea* shrub distribution was shown to include regular, random, and clumped types. Asexual reproduction could create tight clumps of shrubs. The causes of larger-scale pattern were attributed to nonuniformity of habitat, type of sampling method and data analysis used, and seedling survival. The population age (size) structures showed more than one age (size) peak and an absence of young (small) shrubs in arid sites, in contrast to a single peak, or no peak at all, and many young (small) shrubs in mesic sites. In Argentina, *L. cuneifolia*-rather than the relatively more mesophytic, weedy, phreatophytic *L. divaricata*-was shown to be the ecological analog of Sonoran *L. tridentata*. The relationship of site precipitation and soil texture to *L. cuneifolia* cover, density, pattern, and age structure was shown to parallel the pattern shown for Sonoran *L. tridentata*.

Barbour, M. G., and D. V. Diaz. 1973. *Larrea* plant communities on bajada and moisture gradients in the United States and Argentina. *Vegetatio* 28: 335-52.

Abstract: As part of an International Biological Program study of desert ecosystem convergence this report concerns the structure of *Larrea*-dominated plant communities in Arizona, USA (*L. divaricata*) and in Catamarca, Argentina (*L. cuneifolia*). The two regions are vegetationally and floristically similar, but climatically somewhat different. Twenty-three sites were sampled in Arizona and 21 in Catamarca using a sample area of 1536 ml containing 256 contiguous quadrats. Cover and presence of all perennial species and density, pattern, and height frequency distribution of *Larrea* shrubs were determined for each site. The sites were selected to reflect gradients of moisture and elevation. In both areas total ground cover and species richness generally increased with increasing elevation. Density of *Larrea* shrubs dropped with elevation in Arizona, but peaking in mid-elevations in Catamarca. As rainfall increased (holding elevation, slope and soil texture as constant as possible), so did total ground cover, *Larrea* cover, and *Larrea* shrub density; but species richness could be low at either end of the moisture gradient. Species richness was more influenced by soil texture than by rainfall, high diversity being associated with high percentage of rock and gravel. Comparing sites of equivalent precipitation in both deserts the absolute values of total cover, *Larrea* cover, and *Larrea* shrub density were often roughly similar. Pattern of *Larrea* shrub distribution did not change with elevation, but did change with increasing moisture from random to clumped in Arizona, from regular to either clumped or random in Catamarca. The causes of shrub pattern,

however, remain to be identified. Height frequency diagrams of *Larrea* shrubs (height reflecting age) in both regions tended to become less peaked at any one size and to increase in overall range of sizes as moisture increased. Argentina populations showed many more small shrubs in all sites than did Arizona sites, indicating that establishment occurs far more frequently in Argentina.

Barbour, M. G., D. V. Diaz, and R. W. Breidenbach. 1974. Contributions to the biology of *Larrea* species. *Ecology* 55, no. 6: 1199-215. Abstract: Seeds were collected from three taxa: *L. divaricata* from Arizona in the Sonoran desert of North America (LDNA); and *L. divaricata* and *L. cuneifolia* from northwestern Argentina, in the Monte of South America (LDSA and LC). These three desert shrubs are generally not sympatric, and LDSA appears to occupy the most mesic sites. Seedlings were grown to the age of 3-7 mo in a greenhouse and compared as to root- and shoot-growth rate, photosynthesis and transpiration under high and low water stress, pathway of photosynthesis employed, leaf stomatal density, and leaf anatomy. Herbarium specimens collected from 55 sites along moisture gradients were also analyzed for path of photosynthesis, leaf stomatal density, and leaf anatomy. Under mesic conditions, LDSA had a higher growth rate, yet maintained the lowest biomass fraction in leaves and the highest in roots. There were no differences among taxa in net photosynthesis, though LDSA had a significantly higher transpiration rate. Under xeric conditions (plant pressure potential about -45 atm), the photosynthetic rates of LDSA were depressed the most, but variability within taxa prevented conclusions on differences in rates of photosynthesis and transpiration. Stomatal density was greatest for LDSA and least for LC, and these differences were maintained in the greenhouse. Reduction in stomate number seems to be a major mechanism for transpiration reduction between *Larrea* taxa, but within a taxon there was no relationship between site precipitation and stomatal density. The path of photosynthesis (from $13C/12C$ and enzyme-activity ratios) was consistently C3. Leaf cross-sections appeared to reveal mesophyll differences between LC and the two LD taxa. Two ecotone sites, where LDSA and LC share dominance, were sampled for community structure and the presence of putative hybrids. One site, with a one-to-one ratio of *Larrea* taxa, showed no evidence of biotic interaction between the taxa or between them and associated species, and hybrids accounted for less than 1% of all shrubs. Analysis of mass-collected random leaf samples also showed little evidence of hybridization in leaf shape or stomatal density. A second ecotone site, 600 km to the south, differed in some respects from the above, but, again, hybridization was a rare event. The basis of the mesophytic nature of LDSA might lie with its shrub architecture as well as with its physiological properties.

Barbour, M. G., J. A. MacMahon, S. A. Bamberg, and J. A. Ludwig. 1977. The structure and distribution of *Larrea* communities. In *Creosotebush - Biology and Chemistry of Larrea in New World Desert*. Editors T. J. Mabry, J. H. Hunziker, and D. R. Jr. DiFeo, 227-76. Dowden Hutchinson & Ross Publications. Abstract: Species of *Larrea* so thoroughly dominated the warm deserts of North and South America that if we were truly to discuss *Larrea* communities in this chapter, we would find doing so a lengthy and difficult task. Such a task would also be beyond the basic objectives of this volume. Our purpose in this chapter is to review recent IBP research. Vegetation on IBP study sites is emphasized. The IBP data are supplemented with data from other, earlier studies only in a limited number of instances.

BassiriRad, H., D. C. Tremmel, R. A. Virginia, J. F. Reynolds, A. G. de Soyza, and M. H. Brunell. 1999. Short-term patterns in water and nitrogen acquisition by two desert shrubs following a simulated summer rain. *Plant Ecology* 145: 27-36.

Abstract: A field experiment was conducted to compare the rapidity with which the shrubs *Larrea tridentata* and *Prosopis glandulosa* utilized water, CO₂ and nitrogen (N) following a simulated summer rainfall event. Selected plants growing in a roughly 50-m² area were assigned to treatment and control groups. Xylem water potential (ψ_x) and net assimilation rate (A_{net}) were evaluated one day before and one and three days after watering. To monitor short-term N uptake, soils around each plant were labeled with eight equally distant patches of enriched ¹⁵N before watering. Nitrogen uptake, measured as leaf $\delta^{15}N$, was evaluated at smaller time intervals and for a longer period than those used for $\delta\psi_x$ and A_{net} . Both $\delta\psi_x$ and A_{net} exhibited a significant recovery in watered vs. control *Larrea* plants within 3 days after the imposition of treatment, but no such recovery was observed in *Prosopis* in that period. *Larrea* also exhibited a greater capacity for N uptake following the rain. Leaf $\delta^{15}N$ was 5-fold greater in watered compared to unwatered *Larrea* plants within 2 days after watering, while foliar $\delta^{15}N$ was not significantly different between the watered and unwatered *Prosopis* plants during the same period. Lack of a significant change in root ¹⁵NO₃ uptake kinetics of *Larrea*, even 3 days after watering, indicated that the response of *Larrea* to a wetting pulse may have been due to a greater capacity to produce new roots. The differential ability of these potential competitors in rapidly acquiring pulses of improved soil resources following individual summer rainfall events may have significant implications for the dynamic nature of resource use in desert ecosystems.

Bazzell, Marcia Thyra. 1988. "Postfire recovery of creosote bush scrub in the Mojave desert of Southern California." M. S. Thesis, University of California.

Beatley, Janice C. 1974. Effects of rainfall and temperature on the distribution and behavior of *Larrea tridentata* (creosote-bush) in the Mojave desert of Nevada. *Ecology* 55, no. 4: 245-61.

Abstract: The effects of rainfall and temperature on the distribution and certain behavioral characteristics of *Larrea tridentata* (Creosote-bush) at and near its northern limits in the northern Mojave desert of southern Nevada, were investigated at 39 sites with *Larrea* and 20 sites without *Larrea* in eight drainage basins at elevations of 915-1,770 m over a 2,600-km² area of the Nevada Test Site. Data used were (1) rainfall records for 9 yr (1963-71) for each site; (2) maximum and minimum air temperature records for each site, November 1962-February 1972; (3) percentage cover by all shrubs species and by *Larrea*; (4) height and density data for *Larrea*; and (5) percentage of germinable seeds from 29 of the *Larrea* populations for three seasons (1963-65) in relation to the seasonal rainfall for each site. Total percentage cover by all shrubs species is highly correlated with mean annual rainfall, less well correlated with elevation. Percentage cover by *Larrea* follows two patterns of relationship with rainfall: (1) where mean rainfall is low to intermediate, the same pattern as total shrub cover in relation to rainfall, and (2) on sites of high mean rainfall, consistently low cover, a function of low density of *Larrea* on these sites. In general, in undisturbed communities, the taller the *Larrea* plants the fewer there are of them, but the relationship is not strictly linear. Using height as an index to plant volume, numbers of *Larrea* plants are highly

correlated with total plant volume. Mean height is not strongly correlated with mean annual rainfall or temperature parameters, but is well correlated with the ratio of mean precipitation/mean temperature. Tall plants (>1 m) occur in low density and on sites with high rainfall (mean 160-183 mm). The prevailing low minimum air temperatures and their extremes in the lowlands of enclosed drainage basins are inferred to be the primary cause of the absence of *Larrea* in three discrete vegetation zones (*Atriplex confertifolia*, *Lycium pallidum*, and *L. shockleyi*) in Frenchman Flat, and over most of the basin floor of Yucca Flat, where the communities are *Atriplex* and *Grayia-Lycium andersonii*. The year-round low minima in the lowlands of these basin result from nocturnal cold air drainage phenomena and formation of a cold air layer of variable depth. Average extreme minima on these sites were mostly below 0 F; the extreme minimum was -18 F in one of the *Atriplex* communities of Frenchman Flat. *Larrea* occurs over the bajadas of Frenchman Flat on sites above the lower layers of cold air. In Yucca Flat, at its northern limits, it is restricted to certain upper bajada sites and notably one site on the basin floor. Average extreme minimum air temperatures on all *Larrea* sites were above 1 F; the absolute minimum was -8 F. Upper altitudinal limits of *Larrea* apparently are not determined by minimum temperatures since minima (including the extremes) in *Coleogyne* vegetation, which replaces *Larrea* altitudinally on the slopes, are well within the range of those recorded on *Larrea* sites. There is no pattern of relationship between maximum temperatures and the distribution of *Larrea*, although the highest extreme maxima usually occur on non-*Larrea* sites in the lowlands of Frenchman Flat. Mean annual rainfall on the *Larrea* sites ranged from 118 to 183 mm. Altitudinal and latitudinal limits of *Larrea* coincide with a maximum mean rainfall of 183 mm. Mean altitudinal rainfall of 160-183 mm appears to be critical to the behavior of *Larrea*. Germination trials support the inference of a deleterious effect of high rainfall on *Larrea* populations through time: there were high correlation coefficients (negative or positive, depending on the year) between the rainfall of the effective rainfall season and the percentage of germinable seeds; highest mean germination percentages (20%-60%) occurred with 80-150 mm of seasonal rain, and either lower or higher seasonal rainfall resulted in lower percentages of germinable seeds (0%-20%).

———. 1974. Phenological events and their environmental triggers in Mojave desert ecosystems. *Ecology* 55: 856-63.

Abstract: Phenological events in Mojave desert systems are triggered by heavy rains (>25 mm [1 in]). The most predictable and consequential of these is a regional rain between late September and early December. This rainfall event is usually the precursor of successful vegetative and reproductive growth of shrubs the next spring, and is usually necessary for all growth phenomena of herbaceous perennials and winter annuals during the following winter and spring. For most plant components in most years, the growing season is synchronized within the autumn-winter-spring period, and the relative biological success each spring is dependent upon the occurrence or failure of occurrence of events of the preceding autumn. Under certain conditions rainfall during other seasons may trigger growth and reproduction of the primary producers and permit at least moderate or local successes every season. The relationships are stated in a flow diagram for the rainfall and phenological events, as documented for 13 yr in the Mojave desert of southern Nevada.

Botkin, C. W., and P. C. Duisberg. 1949. The nordihydroguaiaretic acid content of the creosote bush. *New Mexico Agricultural Experiment Station Bulletin* No. 349: 1-18.

Bowers, J. E., and M. A. Dimmitt. 1994. Flowering phenology of six woody plants in the northern Sonoran Desert. *Bulletin of the Torrey Botanical Club* 121: 215-29.

Abstract: Climatic and flowering data from a site in the northern Sonoran Desert of southern Arizona were used to define flowering triggers and developmental requirements for 6 woody plants. These formulations were then used to predict flowering dates at a second northern Sonoran Desert site. It was determined that flowering is triggered by rain in *Larrea tridentata* (DC.) Cov., *Fouquieria splendens* Engelm., *Encelia farinosa* A. Gray, *Ambrosia deltoidea* (A. Gray) Payne and *Acacia constricta* Benth., and that flowering is triggered by photoperiod in *Cercidium microphyllum* (Tort.) Rose & Johnst. The base temperature for floral development in *L. tridentata*, *F. splendens*, *E. farinosa*, *A. deltoidea* and *C. microphyllum* is about 10°C. Their mean degree-day requirements range from 414 to 719. *Acacia constricta* requires 522 degree-days above 15°C. Minimum rainfall triggers varied from 9 mm for *Ambrosia* to 20 mm for *Encelia*. Flowering time in *C. microphyllum* may reflect phylogenetic constraints, while flowering time in *F. splendens* may be strongly influenced by pollinator availability. Flowering times of the remaining species seem constrained more by climate than by biotic considerations such as phylogeny, seed germination and competition for pollinators.

Bowers, Janice E., Robert H Webb, and Renee J. Rondeau. 1995. Longevity, recruitment and mortality of desert plants in Grand Canyon, Arizona, USA. *Journal of Vegetation Science* 6, no. 4: 551-64.

Abstract: The demography of woody desert plants along the Colorado River in Grand Canyon, Arizona, USA, was analyzed using 355 pairs of replicated photographs taken as long ago as 1872. Longevity, recruitment, and mortality were determined for 38 species characteristic of ungrazed desert scrub. Individual plants that survived 100 yr or more included *Acacia greggii*, *Ambrosia dumosa*, *Atriplex canescens*, *A. confertifolia*, *Echinocactus polycephalus*, *Ephedra* spp., *Fouquieria splendens*, *Larrea tridentata*, *Lycium andersonii*, *Opuntia acanthocarpa*, *O. basilaris*, *O. erinacea*, *Pleuraphis rigida*, and *Yucca angustissima*. This is the first evidence of long lifespan for most of these species, particularly the succulents. Most of the long-lived species registered overall increases in population during the past century. Only four species with lifespans ≥ 100 yr had a net loss of individuals between 1889 and the present, and only two decreased between 1923 and the present. It seems likely that climatic fluctuations over the past century are largely responsible for these recruitment and mortality patterns; however, nurse plants, predation refuges and other biotic factors may also play a role.

Boyd, R. S. 1983. Jackrabbit herbivory and creosote bush (*Larrea tridentata*) reproduction. *Madroño* 30: 194-95.

Boyd, R. S., and G. D. Brum. 1983. Postdispersal reproductive biology of a Mojave desert population of *Larrea tridentata* (Zygophyllaceae). *American Midland Naturalist* 110: 25-36.

- . 1983. Predispersal reproductive attrition in a Mojave desert population of *Larrea tridentata* (Zygophyllaceae). *American Midland Naturalist* 110: 14-24.
Abstract: During the 1979 blooming season, 92% of the reproductive potential of a Mojave Desert creosote bush population was destroyed prior to seed dispersal. The losses were partitioned into 12 categories. The largest category was insect predation (19.5%), which primarily occurred during the flower-bud stage. Most of the losses (57%) occurred during or after anthesis. While all pollination modes were equally successful in producing fruits the behaviors of native bees and the flowers combined to favor xenogamy in open-pollinated flowers, substantially boosting seed set. Despite the high rate of attrition, reproductive output was sufficient to allow dispersal of 7.8×10^5 viable seeds per hectare.
- Briones, Oscar, Carlos Montaña, and Exequiel Ezcurra. 1996. Competition between three Chihuahuan desert species: evidence from plant size-distance relations and root distribution. *Journal of Vegetation Science* 7, no. 3: 453-60.
See abstract under *Pleuraphis mutica*
- . 1998. Competition intensity as a function of resource availability in a semiarid ecosystem. *Oecologia* 116, no. 3: 365-72.
See abstract under *Pleuraphis mutica*
- Brisson, J., and J. F. Reynolds. 1994. The effect of neighbors on root distribution in a creosotebush (*Larrea tridentata*) population. *Ecology* 75, no. 6: 1693-702.
Abstract: We excavated and mapped the lateral extension of 32 creosotebush shrubs (*Larrea tridentata*) in the Chihuahuan desert of New Mexico to examine the effect of neighborhood interaction on root distribution. The smallest closed-angle polygon encompassing all roots of an individual was taken as a representation of its root system. Several geometrical characteristics of these polygons were measured and compared to interference vectors based on the location and size of the neighbors. We found that root systems were more developed away from the maximum competitive pressure of neighbors. Relation between root system shape and pressure from neighbors was stronger when the competitive vectors were integrating effect from all neighbors. Size of neighbors did not appear to contribute significantly to the relation. The resulting spatial pattern tended to reduce the overlap between neighboring root systems. Two conceptual models of root growth response to neighbors appear to explain our results. Both models assume that when the root system of neighbors meet, root growth is impaired or ceases at the zone of contact. In the non-overlapping, non-compensatory model, the decrease in root growth between two close neighbors is not compensated elsewhere, possibly affecting the overall plant performance. In the non-overlapping, compensatory model, a plant with a close neighbor responds by investing in root growth away from the competitive pressure or simply in zones free of neighbors. Under this model, two plants can be close to each other and not compete. Competition in the population is for space and only occurs when a plant root system is crowded on all sides.

———. 1997. Effects of compensatory growth on population processes: a simulation study. *Ecology* 78, no. 8: 2378-84.

Abstract: The spatial extent of the canopy or root system of a plant is often used as an index of its potential to acquire resources, such as water and nutrients. This has given rise to the area of influence (AOI) and neighborhood concepts for quantifying competitive interactions between neighboring plants. Both are based on a circle of fixed radius centered on a plant, which presupposes that two plants in close proximity are always strong competitors. There is evidence that this is not always the case. In this paper, we present a simple model of plant population dynamics that extends the concept of AOI by considering "compensatory" growth of root systems. The ability of a plant to grow roots into soil zones free of neighbors in response to competitive pressures is expressed by the value of a single parameter, . Effects on population attributes resulting from competition in plants with compensatory growth are compared with populations with noncompensatory growth.

Simulations show that compensatory plants are better able to utilize available space, have greater biomass, and outcompete noncompensatory plants. The change from a clumped to a regular distribution of individuals due to density-dependent mortality is delayed in noncompensatory plants. These theoretical results suggest that growth plasticity and the resulting asymmetry in space acquisition may play an important role in plant population dynamics.

Brown, David E. 1984. "Fire and changes in creosote bush scrub of the Western Colorado Desert, California." M. S. Thesis, University of California.

Abstract: Heavy growth of native annuals and exotic grasses encouraged by extraordinarily heavy precipitation since 1976 in the western Colorado Desert of southern California has resulted in numerous burns over extensive areas of creosote bush scrub. Analysis of fire effects, shrub response, and germination in several burns near Palm Springs reveals that most species are poorly adapted to fire, even in low intensity burns. As a result of poor sprouting and minimal reproduction, common shrubs including *Larrea tridentata*, *Ambrosia dumosa*, and *Opuntia* spp. have been replaced by an open stand *Encelia farinosa* with a herbaceous understory of European exotics, mostly *Bromus rubens* and *Schismus barbatus*. Successional studies elsewhere indicate many long-lived desert perennials are slow colonizers of disturbed sites.

Recurrent fire supported by a postfire increase of herbaceous cover, may therefore discourage recovery of local creosote bush scrub. Differences in fire response of creosote bush scrub species to those of chaparral and coastal sage scrub, where recurrent fire is important, suggests western and upper elevational limits of some desert species may be related to infrequent fire.

Buffington, Lee Charles. 1964. "Vegetational changes on a semidesert range from 1858 to 1963." M.S. Thesis, New Mexico State University.

Abstract: The purpose of this study was to show the degree of encroachment of brush and also to study the nature of the invasion on the various soil types. Vegetation surveys of 1858, 1915, 1928, and 1963, formed the basis for comparisons. Factors possibly responsible for changes in vegetation were examined. The study was conducted on 144,475 acres of the Jornada Experimental Range, located 23 miles northeast of Las Cruces, New Mexico. Climatic change was not considered a major factor in brush invasion; however,

periodic drought had some effect on brush invasion. Selective grazing by livestock also aided in the establishment of brush. Livestock are important in the dispersion of mesquite seeds. Early-day fires were not considered to be a factor in the maintenance of brush-free range, since no fires were reported by early travelers on the Jornada plain.

Buffington, Lee C., and Carlton H. Herbel. 1965. Vegetational changes on a semidesert grassland range from 1858 to 1963. *Ecological Monographs* 35, no. 2: 139-64.

Abstract: General Land Office Survey notes made in 1858 for the 144,475 acres in the study area on the Jornada Experimental Range were analyzed and compared with vegetation maps on ocular reconnaissance range surveys for the years 1915, 1928, and 1963. Comparisons were also made among the reconnaissance surveys. Acreages covered by mesquite, creosotebush, and tarbush, and their various combinations, were studied on the basis of the soil types on which they occurred.

In 1858 good grass was present on more than 90% of the study area. By 1963 less than 25% of the area had good grass. Mesquite has been present on all soil types. However, the main invasion of mesquite was on sandy soils. As mesquite begins to dominate a sandy site, low dunes form and grass cover is greatly reduced. In 1858 over 6,000 acres had abundant mesquite; by 1963 an area more than ten times as great was dominated by mesquite, with half of that increase occurring after 1928.

In 1858 isolated mesquite stands were present on the western part of the study area. Those areas were not in the immediate vicinity of stock water developments, but the initial spread was from these areas having mesquite in 1858. It was not until later years that mesquite became prevalent in the overgrazed areas around the wells even though the entire study area was heavily stocked from about 1904 to 1925. On the higher areas on the northeastern part of the Range, Indian activity contributed to the early formation of mesquite dunes before domestic livestock grazed on that area. Grazing by livestock occurred earlier there than farther out on the plain because stock water was available from springs in the nearby mountains. Mesquite seed dispersal by livestock was of great importance in the spread of mesquite to adjacent areas. Grass cover was reduced by livestock grazing and the occurrence of periodic droughts. With the introduction of seed, mesquite plants were readily established in sparse grass cover. Once established, the grasses could not compete with the mesquite. Rodent and rabbit activity was a secondary factor in the spread of mesquite.

Only slight mesquite invasion has taken place on soils having gypsum in their profile. Creosotebush was not found on the gypsiferous soils in the study area; however, it has been observed on those soils in other areas. On the Jornada Experimental Range, creosotebush occurred mainly on the relatively shallow, coarser textured soils on slopes; however, it was present on all soil textures in the study area. The area dominated by creosotebush increased from about a section in 1858 to over 12,000 acres in 1963.

On the southeastern part of the study area, creosotebush was present in some areas in 1858; however, a good stand of grass was also present. With selective grazing of grasses by livestock and recurring droughts, the equilibrium on those drier sites between creosotebush and grass was shifted in favor of brush. As creosotebush increased, the soil surface became unstable and soil erosion increased. Since the major grass species in that area, black grama, is sensitive to deposition and erosion of soil, the grass cover was further reduced. With this reduced competition, creosotebush increased rapidly.

Tarbush has been present on all soils where creosotebush is growing, but creosotebush has not been present on all areas where tarbush dominates, while mesquite may or may not be present in these areas. Tarbush appears to move from the mixed grass areas with medium textured soils onto the adjacent lighter soils and grows in conjunction with mesquite. It also moves onto the heavier soils and grows in conjunction with tobosa and burrograss. Tarbush increased in acreage until 1928. Since 1928, creosotebush has invaded the tarbush areas. Livestock grazing is considered to have had little direct effect on the invasion of heavy soils by tarbush. Fires could have been a factor; however, no extensive fires were reported.

The climate has not changed enough to be the major factor responsible for the rapid increase of brush species. However, only a slight change in the climate to warmer, drier conditions, in conjunction with grazing, could have some effect on vegetation changes in the drier portions of the semidesert grassland. Periodic droughts have been a factor in reducing grass competition so that brush species can become established. Fire was not considered to be a factor in the maintenance of brush-free range. Rodent and rabbit activity was a secondary factor in the spread of brush. Seed dispersal, accompanied by heavy grazing and periodic droughts, appeared to be the major factor affecting the rapid increase of shrubs.

Burk, Jack Harlan. 1970. "Comparative production of *Larrea divaricata* Cav. on three geomorphic surfaces in southern New Mexico." Ph.D. Dissertation, New Mexico State University.

Abstract: Net above ground productivity was measured for 3 years on creosotebush (*Larrea divaricata* Cav.) occurring on three geomorphic surfaces which differed in age and profile characteristics. Rates of stem elongation, fruit production, flower production, and accumulation of secondary wood were ascertained for each of the geomorphic surfaces. Growth rates varied among plants of the different surfaces, but when the net production of stands on each surface were compared the surfaces were remarkably similar. Statistically significant differences were present in both growth and net productivity between years. Creosotebush seems to have a great capacity for adjusting to sites of broad ecological amplitude with no apparent effect upon its ability to fix energy.

———. 1977. Sonoran desert. In *Terrestrial vegetation of California*. Editors M. G. Barbour, and J. Major, 869-89. New York: John Wiley and Sons.

Burk, J. H., and W. A. Dick-Peddie. 1973. Comparative production of *Larrea divaricata* Cav. on three geomorphic surfaces in southern New Mexico. *Ecology* 54, no. 5: 1094-102.

Abstract: Net above-ground productivity was measured for 3 years on creosotebush (*Larrea divaricata* Cav.) occurring on three different geomorphic surfaces. Rates of stem elongation, fruit production, flower production, and accumulation of secondary wood were ascertained for each of the geomorphic surfaces. Growth rates varied among plants of the different surfaces, but when the net production of stands were compared, rates for the surfaces were remarkably similar. Statistically significant differences were present in both growth and net productivity between years. Creosotebush seems to have a great capacity for adjusting to sites of broad ecological amplitude with no apparent effect upon its ability to fix energy.

Castellanos-Perez, Edmundo. 2000. "Ecophysiological relationship of creosotebush (*Larrea tridentata*) and bush muhly (*Muhlenbergia porteri*) when growing alone and in common." Ph. D. Dissertation, New Mexico State University.

Abstract: The study was conducted on the Chihuahuan Desert Rangeland Research center, 32 km north of Las Cruces, NM. Physiological responses of creosotebush and bush muhly growing together were quantified from the summer of 1997 to the winter of 1998/99. Large and small plants of creosotebush with or without bush muhly were randomly chosen, as were bush muhly plants growing alone. In the summer of 1997, creosotebush competed with bush muhly for water as shrub plants growing alone had higher integrated photosynthesis than shrubs with bush muhly following a heavy rainfall event. Creosotebush had lower water use efficiency (wue) than bush muhly plants. In the summer of 1998, bush muhly had greater xwp than creosotebush when the soil water potential was above -30 bars. Creosotebush had higher stomatal conductance than bush muhly, with small creosotebush growing alone having the highest stomatal conductance. Defoliation of bush muhly growing under small creosotebush resulted in shrubs having higher photosynthetic activity than when the grass was undefoliated. While differences in net assimilation between shrubs and grasses was not discernible, bush muhly presented a higher wue. While green in the fall season, bush muhly had higher xwp, lower stomatal conductance, and higher wue than creosotebush plants. Net assimilation was similar between shrubs and grass plants. Both species responded to the availability of moisture in this season. Bush muhly growing alone had higher net assimilation than when growing under creosotebush. In the winter season, with bush muhly dry, xwp was influenced by low temperatures. Small creosotebush growing alone had higher photosynthetic activity than small creosotebush with bush muhly ($p < .005$). Creosotebush growing alone, both small and large plants, had higher activity than creosotebush growing with bush muhly ($p < .01$). In the spring, although the stomatal conductance of creosotebush was higher, this was not reflected with a higher net assimilation, as bush muhly had the same net assimilation with less water loss. When soil water potential decrease below of -80 bars, creosotebush still showed net assimilation. Roots of creosotebush and bush muhly were found concentrated closest to the center of the plant, declining with depth and distance from the plant center. Bush muhly had higher root biomass at the soil surface when growing under creosotebush than when growing alone, probably because of the plant age. Creosotebush growing alone had higher amount of root biomass than creosotebush with bush muhly. Creosotebush had greater root biomass in all the horizons.

Chew, Robert M., and Alice Eastlake Chew. 1965. The primary productivity of a desert shrub (*Larrea tridentata*) community. *Ecological Monographs* 35, no. 4: 355-75.

Abstract: 1. The growth and productivity of the creosote bush, *Larrea tridentata*, and associated vegetation was studied in a desert-shrub community in the San Simon Valley of southeastern Arizona in the period June, 1958 through August, 1959. This region has a semiarid mesothermal climate with water deficits in all seasons.

2. Where the soil is shallow (24 cm) over dense caliche, *Larrea* composes 84% of the shrub cover, which overspreads 20.7% of the ground. Where the soil is deeper (60cm), tarbush, *Flourensia cernua*, makes up about 44% of the shrub cover, which equals 8.7% of the ground surface.

3. *Larrea* began to invade the area of shallow soil about 1893, but its population density increased rapidly only relatively recently, apparently at the expense of *Flourensia*. The densities of these two shrubs have a

highly significant correlation of $r = -0.43$. In 1958 the Larrea population had a density of 4460 individuals per hectare, a median age of 17 yrs, and a mean age of 20 yrs. The population had shown little increase in density in the previous 10 yrs, following a period of sigmoid growth. Density is expected to decline to about 2075 Larrea individuals per hectare within 20 yrs, and perhaps eventually to a stable density of 1000 per ha.

4. Shoot volume, that standing dry weight of different plant parts, and the cumulative production of different parts, all increase in a sigmoid fashion from 20 to 50 yrs of age. Annual production of dry matter reaches an asymptotic value of about 900 g per plant at 65 to 70 yrs. Standing biomass asymptotes at about 9500 g dry wt per plant at 80 to 90 yrs.

5. As a plant gets older, leafless stems form a progressively greater proportion of its total weight. Plant composition is relatively constant when considered in terms of cumulative production of different parts.

6. Growth of Larrea in terms of addition of new nodes, occurred only at soil temperatures above 16.9 C in 1958-1959. Growth was largely independent of rainfall and soil moisture.

7. In comparison with Rhododendron, Larrea has a greater production per plant, at least up to 40 yrs, and a greater accumulation of shoot weight, at least up to 32 years. Larrea has more of its production in leaves, and produces more per unit of shoot weight.

8. In comparison with shrubs that have been previously studied, Larrea has; (1) a higher ratio of leaf weight to leaf area, about 23 mg dry wt per cm², than all but a few species; (2) the highest shoot production per unit of leaf area, about 400 g dry wt per m², per year; (3) an average degree of shoot production per unit of leaf weight; (4) a low leaf area index, 0.9 to 1.3

9. In 1958-1959 the creosotebush production was about 74% of the total net annual primary production of the community, estimated as about 6100 megacal per ha.

Chew, Robert M., and W. G. Whitford. 1992. A long-term positive effect of kangaroo rats (*Dipodomys spectabilis*) on creosotebushes (*Larrea tridentata*). *Journal of Arid Environments* 22: 375-86.

Abstract: Several studies have shown the effects of the mounds of the banner-tailed kangaroo rat (*Dipodomys spectabilis* Merriam) on desert annuals. There can be effects on density, biomass and composition of the herbaceous assemblage (Moroka et al., 1982; Mun & Whitford, 1989). As a result of a long-term study of a site in south-eastern Arizona, we observed a positive effect of these mounds on the growth, flowering and fruiting, and survival of creosotebush, which is the dominant woody perennial of the community. This effect became obvious at this site long after the kangaroo rats disappeared from the system, probably as a result of invasion of creosotebushes and other shrubby vegetation into what was previously a desert grassland system. Whereas creosotebushes had a negative effect on the kangaroo rat population, the mounds created by these rodents have had a residual positive effect on the creosotebushes. A number of measurements were made to examine the nature of this unusual, if not unique, relationship, and to provide some basis for speculation as to the cause(s) of the positive effect.

Clark, M. S. 1975. Ecology and management of Southwestern semidesert grass-shrub ranges. *USDA Forest Service Research Paper* RM-156: 1-39.

Cody, M. L. 2000. Slow-motion population dynamics in Mojave desert perennial plants. *Journal of Vegetation Science* 11: 351-58.

Cox, J. R., H. A. Schreiber, and H. L. Morton. 1983. The initial growth of two range grasses on nonfertilized and fertilized soils collected from creosotebush communities in the southwestern United States. *Journal of Range Management* 36: 726-29.

Abstract: A glasshouse study was conducted to determine how nonfertilized and fertilized soils collected in creosotebush [*Larrea tridentata* (DC.) Coy.] communities would influence seedling leaf growth and shoot production of Lehmann lovegrass (*Eragrostis lehmanniana* Nees) and blue panicgrass (*Panicum antidotale* Ritz.). Soils were collected at 3 locations around creosotebush plants: (1) at the crown base (Basal), (2) along the outer canopy edge (Drip), and (3) In areas between plants (Open). Leaf lengths and shoot production were greatest on nonfertilized soils collected at the plant base, intermediate at the canopy edge, and least in open areas. Leaf lengths and shoot production significantly increased on fertilized soils collected in open areas.

Cunningham, G. L., and J. H. Burk. 1973. The effect of carbonate deposition layers (caliche) on the water status of *Larrea divaricata*. *The American Midland Naturalist* 90, no. 2: 474-80.

Abstract: The seasonal pattern of water status of *Larrea divaricata* was measured on three sites in southern New Mexico. One site had no carbonate deposition layer. One site had a carbonate deposition layer at a depth of 15 cm and the third had carbonate deposition at a depth of 25 cm. *Larrea* shrubs on sites with no carbonate deposition layer experienced less water stress during periods of greater precipitation. However, plants on sites with carbonate deposition layers showed less water stress when precipitation was low. These differences may in part account for local variations in size, density and pattern of spatial distribution of *Larrea*.

Cunningham, Gary L., and James F. Reynolds. 1978. A simulation model of primary production and carbon allocation in the creosotebush (*Larrea tridentata* [DC.] Cov.). *Ecology* 59, no. 1: 37-52.

Abstract: A preliminary simulation model of primary productivity and carbon allocation in creosotebush (*Larrea tridentata* [DC] Cov.) is described. The model utilizes a systems approach in which movement of assimilate within the plant is in response to changes in source-sink strengths of leaves, stems, roots, early reproductive buds, maturing reproductive buds, flowers, and fruits. Two distinct compartments are defined per organ or developmental stage to separate assimilate into a pool fraction (labile or translocatable) and a structural fraction (nonlabile). The changes in magnitude (within upper and lower limits) of a pool compartment during the course of a simulation (i.e., growth and development of the plant) are a function of the rates of maintenance respiration and growth as well as a priority scheme governing allocation of assimilates; the increases and decreases in dry weight of a structural compartment are a function of aging and the magnitude of its associated pool (which determines structural growth and physiological death). A 1-yr simulation of a hypothetical *Larrea* plant shows that the model exhibits a reasonable behavior, although no validation is attempted at this stage in its development. The heuristic

value of the model is illustrated in the sensitivity analysis, which shows the need for detailed knowledge of "priority" carbon movement during both vegetative and reproductive growth periods, the importance of substrate controlled respiration rates, and the need for further studies of the dynamics of labile pools in the plant. The model has been an excellent tool in our initial attempt to integrate the voluminous information on *Larrea* into a complete functional description of the autecology of the species. Further refinement of this model, as data from our current research and that of other investigators become available, should lead us to a better understanding of the ecological role of *Larrea* in desert ecosystems.

Cunningham, G. L., J. F. Reynolds, and J. P. Syvertsen. 1979. Modelling net photosynthesis of *Larrea*. *Larrea. Serie del desierto*. 2 ed., E. C. Lopez, T. J. Mabry, and S. F. Tavizon, 165-79. Saltillo, Coah, Mexico: Centro de investigacion en quimica aplicada.

Abstract: A net photosynthesis model for *Larrea tridentata* was constructed using the modeling approach developed by Reed et al. for the temperate deciduous tree *Liriodendron tulipifera* L. The model was constructed using gas exchange data collected on controlled-environment chamber grown plants. Output from the model indicates that previously reported low temperature optima for net photosynthesis in *L. tridentata* were a result of experiments being conducted at very low photon flux densities. Dark respiration continues to be a significant component of the net CO₂ exchange until photon flux densities reach about one-half of full sunlight. The increase in dark CO₂ release with increasing temperature results not only in lower temperature optima but also in lower high temperature CO₂ compensation points at photon flux densities below one-half of full sunlight. These results imply that shrub architecture, through mutual leaf shading, can have a significant effect on productivity.

Cunningham, G. L., and J. P. Syvertsen. 1977. The effect of non-structural carbohydrate levels on dark CO₂ release in creosotebush. *Photosynthetica* 11, no. 3: 291-95.

Abstract: The effect of substrate levels on the rate of dark respiration of shoots of the warm desert evergreen perennial, *Larrea tridentata* DC Cov., was investigated. Rates of dark CO₂ release were compared to both the concentration of total nonstructural carbohydrates (TNC) and the amount of CO₂ accumulated during the light period immediately preceding the dark CO₂ release measurements. Levels of TNC were measured at the beginning of an experiment and estimated during the course of an experiment from CO₂ exchange data. The rate of dark CO₂ release is a function of TNC concentration and not a function of CO₂ accumulated in the preceding light period except when TNC concentrations are extremely low.

Cunningham, G. L., J. P. Syvertsen, and T. V. Feather. 1975. "Primary production and carbon allocation in creosotebush." Research Memorandum 75-9. Utah State University, Logan, Utah.

Cunningham, G. L., J. P. Syvertsen, J. F. Reynolds, and J. M. Willson. 1979. Some effects of soil-moisture availability on above-ground production and reproductive allocation in *Larrea tridentata* (DC) Cov. *Oecologia* 40: 113-23.

Abstract: Data from the US/IBP Desert Biome validation studies indicate that above-ground production and biomass allocated to reproduction in *Larrea tridentata* vary from one year to another depending upon the timing and extent soil-moisture availability. In an attempt to verify these observations and determine to what extent water availability can affect total above-ground production and reproductive allocation in this widely distributed warm desert shrub, a series of soil-moisture augmentation experiments were conducted. High levels of soil moisture had a greater effect on reproductive allocation than on total above-ground production. Enhanced soil moisture during the period of active growth increased total above-ground production and reduced the percentage of biomass allocated to reproduction. Enhanced soil moisture during the normal periods of little or no growth did not increase total above-ground production.

Dalton, Patrick D. Jr. 1961. "Ecology of the creosotebush *Larrea tridentata* (DC.) Cov." Ph.D. Dissertation, University of Arizona.

Abstract: Although more than three hundred references to *Larrea tridentata* (DC.) Cov., (creosotebush), occur in the literature, little is known concerning its ecology, anatomy, and physiology. Creosotebush is reported to have invaded extensive areas once covered with desirable grass. This shrub has no forage value, it is not a good soil builder, nor does it have any economic value and therefore is a noxious weed. This study was designed to investigate various phases of those disciplines where data are vague, incomplete, or entirely lacking. The bicentric distribution of the genus *Larrea* in North and South America, and the general distribution of the species *Larrea tridentata* (DC.) Cov., in North America as affected by climate and edaphic factors, has been discussed. Two maps are presented, one of the general distribution of *Larrea* in the North American southern deserts, and the second of the specific distribution of *Larrea* in Arizona. A community analysis indicates seven distinct *Larrea* community associations. These are, (1) *Larrea* dominant, (2) *Larrea* -desert scrub, (3) *Larrea* Franseria, (4) *Larrea* Opuntia, (5) *Larrea* Fouquieria, (6) *Larrea*-grass, and (7) *Larrea* subordinate. Germination studies indicate that *Larrea tridentata* seed germinates best as follows: (1) In soil that was capable of retaining an adequate moisture supply, (2) at a moderately high optimum temperature of 35°C, (3) in total darkness, (4) in the presence of oxygen, (5) at an optimum neutral pH level, and (6) following an after-ripening period. Rate of germination was decreased by mold infestation and a pre-germination cooling period. The phenology of *Larrea*, based on observations of this investigator and which may not apply elsewhere, indicates: (1) Flowering occurs when daily maximum-minimum temperatures reach 80° and 40° F. respectively, (2) flowering-precedes a resumption of vegetative growth, (3) during periods of moisture stress mature leaves and flowers are shed and immature leaves remain undeveloped, (4) a low rate of flower production, accompanied by accelerated vegetative growth and bright greening-up of leaves, results from an above-normal moisture supply, and (5) *Larrea* initiates renewed flowering and vegetative regrowth with each new supply of available moisture following a sustained dry period, as long as maximum-minimum temperatures remain above 80° and 40° F. Anatomical examination indicates four means by which transpiration may be reduced. These are: (1) Resins coating the outside layers of palisade cells and lining the stomatal cavity, (2) a guard cell ledge or lip which reduces the perimeter of the external aperture of the stomata, (3) matting of epidermal hairs in the cuticular resins to form a leaf coating, and (4) the scarcity of spongy mesophyll and intercellular space and the presence of thick, compact layers of palisade tissue which limit internal gas exchange. *Larrea* leaf moisture is correlated closely with the amount of moisture in the soil root zone. Moisture in the soil is dependent on

both quality and quantity of precipitation and because of the relatively gentle nature of winter storms and the lower temperatures that generally prevail, winter rain exerts a greater influence than summer rain on replenishing soil moisture. Atmospheric temperature exerts a strong secondary influence. Extracts from Larrea leaves and roots do not exhibit a significant inhibiting effect on the germination and early growth of, either Larrea or certain grasses. However, mature Larrea plants possess a marked ability to absorb available soil moisture. Even spacing of creosotebush appears to result from moisture competition. Examination of a Larrea burn area indicated a 13 percent death rate for severely burned creosotebush plants, 69 percent death rate for ones moderately burned, and 63 percent for lightly burned plants. Good seedling establishment occurred on the burn area, probably due to reduced competition for soil moisture, while no seedling establishment was noted on unburned areas.

De la Rosa Ibarra, M., and J. A. Villarreal. 2000. Effect of leaf extract of *Larrea tridentata* Cov. on germination and growth of barley seedlings. *Phyton Buenos Aires* 66: 83-86.

Abstract: This work is part of a program to detect alternative sources of plant growth regulators in some of the plants with wide distribution in the arid lands of Mexico. From a crude extract of leaves of "creosote bush" (*Larrea tridentata* Cav.) five fractions were obtained and tested in a barley seed bioassay in a completely randomised design with four replications. The results showed highly significant differences among the fractions. The chloroformic fraction showed the best response promoting a significant increase in the growth of barley seedlings. These results will serve as a base for subsequent isolation and purification studies of the active principle(s).

de Soyza, A. G., W. G. Whitford, E. Martinez-Meza, and J. W. Van Zee. 1997. Variation in creosotebush (*Larrea tridentata*) canopy morphology in relation to habitat, soil fertility and associated annual plant communities. *American Midland Naturalist* 137: 13-25.

de Soyza, A. G., W. G. Whitford, R. A. Virginia, and J. F. Reynolds. 1996. Effects of summer drought on the water relations, physiology, and growth of large and small plants of *Prosopis glandulosa* and *Larrea tridentata*. In *Proceedings: symposium on shrubland ecosystem dynamics in a changing environment*, Compilers J. R. Barrow, E. D. McArthur, R. E. Sosebee, and R. J. Tausch, 220-223Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station.

Abstract: Large and small plants of creosotebush and mesquite were subjected to drought during summer 1993. Large and small plants responded to drought with lowered xylem water potential and lowered photosynthetic gas exchange. Large plants appear to maintain a reduced but constant photosynthetic rate during drought, and responded to precipitation with increased photosynthesis. However, small plants attempted to maintain a high photosynthetic rate throughout the season, responding less strongly to precipitation events, but probably depleting reserves more and causing photosynthesis to decline more when droughted. Our results suggest that large, established plants are better able to withstand drought than are small, establishing shrubs.

DeGarmo, H. C.Jr. 1966. "Water requirement and production of eight desert plant species under four soil moisture levels." M. S. Thesis, New Mexico State University.

Downum, K. R., J. Dole, and F. Rodriguez. 1988. Nordihydroguaiaretic acid: inter- and intrapopulational variation in the Sonoran desert creosote bush (*Larrea tridentata*, Zygophyllaceae). *Biochemical Systematics and Ecology* 16: 551-55. Abstract: Nordihydroguaiaretic acid (NDGA) is the principle phenolic constituent in the leaf resin of the creosote bush, *Larrea tridentata*, the dominant perennial shrub throughout most of the warmer arid and semi-arid regions of North America. In an effort to determine the quantitative significance of this biologically active lignan catechol in desert ecosystems, we conducted studies of leaf extracts from geographically distinct populations of *Larrea* which occur throughout the Sonoran Desert. Seasonal influences on NDGA concentration as well as on the hexane- and MeOH-soluble leaf constituents were also examined within two populations of *Larrea* growing near Palm Desert, California. Intrapopulational studies revealed that NDGA concentrations declined from northern to southern sampling sites whereas the levels of hexane- or MeOH-soluble leaf components showed little variation. Intrapopulational studies showed that the mean level of both hexane- and MeOH-soluble leaf components increased significantly between mid-April and late June, but these increases slowed down or stopped between June and July. The mean concentration of NDGA decreases significantly in plants between April and July suggesting a possible relationship between the resin concentration of NDGA and seasonal (i.e. climatic) changes. These observations may, in part, explain some of the latitudinal variation in NDGA levels found in Sonoran desert representatives of *Larrea*.

Dugas, William A., Ralph A. Hicks, and Robert P. Gibbens. 1996. Structure and function of C3 and C4 Chihuahuan desert plant communities. Energy balance components. *Journal of Arid Environments* 34, no. 1: 63-79. Abstract: During the past 150 years, the C-3 shrubs creosotebush (*Larrea tridentata* (DC.) Cov.), mesquite (*Prosopis glandulosa* Torr. var. *glandulosa*), and tarbush (*Flourensia cernua* DC.) have invaded extensive areas of former C-4 grasslands in deserts of the south-western United States. We measured energy balance components of these grass and shrub communities in the Chihuahuan Desert. Midday net radiation in the *P. glandulosa* community was about 20% less than that in the others, where it was about equal. Midday soil heat flux was large in all communities and was greater in communities with small leaf areas. Midday and daily latent heat fluxes (or evapotranspiration rates, ET) were about equal in all communities except the *F. cernua* community, where they were about 50% greater due to greater leaf area and water supply. The fraction of ET made up of soil evaporation varied from 0.3 to 0.6 and was greater in *L. tridentata* and *P. glandulosa* communities. Differences of surface energy balance components of plant communities in this desert environment were generally small and were more related to surface characteristics (e.g. leaf area) and water supply than to photosynthetic pathway or vegetation type.

Dwyer, Don D., and Harlan C. DeGarmo. 1970. Greenhouse productivity and water-use efficiency of selected desert shrubs and grasses under four soil-moisture levels. *New Mexico Agricultural Experiment Station Bulletin* No. 570.

Ernest, Kristina A. 1994. Resistance of creosotebush to mammalian herbivory: temporal consistency and browsing-induced changes. *Ecology* 75, no. 6: 1684-92.

Abstract: Interactions between genotype and environment determine the underlying constitutive (background-level) resistance of individual plants to herbivory. Resistance, however, may change in response to herbivory (induced resistance). This study was designed to investigate temporal fluctuations in resistance, and to test the relative influences of constitutive and browsing-induced resistance on patterns of mammalian herbivory. A natural population of creosotebush, *Larrea tridentata*, browsed by black-tailed jackrabbits, *Lepus californicus*, served as the study system. Creosotebushes varied considerably in their resistance to jackrabbit browsing. Some individual plants were fed upon lightly and infrequently, while others had up to 90% of their living branches clipped during a single month, and were browsed several times per year. Resistance levels of individual shrubs were similar between seasons, and over time scales > 2 yr. Shrubs with a history of heavy browsing (low constitutive resistance) were more likely to be browsed again than were individuals with a history of light browsing (high constitutive resistance). In an experiment designed to test jackrabbit response to constitutive resistance and recent browsing damage (artificially clipped vs. unclipped), the importance of both factors was confirmed. Jackrabbits browsed more heavily on plants with low than with high consecutive resistance, but less heavily on clipped shrubs than on controls. The enhanced resistance of clipped shrubs is interpreted as an induced response by individuals to herbivory, and may be responsible for variation in browsing levels of individual shrubs over time scales of 1-2 yr.

Ettershank, George, Jennifer Ettershank, Martha Bryant, and Walter G. Whitford. 1978. Effects of nitrogen fertilization on primary production in a Chihuahuan Desert ecosystem. *Journal of Arid Environments* 1: 135-39.

Abstract: In a Chihuahuan desert ecosystem, the growth responses to nitrogen amendment of a perennial shrub (creosotebush, *Larrea tridentata*) and a perennial grass (fluff grass, *Erioneuron pulchellum*) were made twice during the growing season: first during a period of average rainfall, then during a period of above average rainfall. Fluff grass exhibited a marked increase in biomass to 25 kg ha⁻¹ and 100 kg ha⁻¹ nitrogen fertilization. Creosotebush increased biomass production only at the higher level during both periods. These results suggest that productivity of a Chihuahuan desert system is partially nitrogen limited and that shallow-rooted plants utilized the available nitrogen at the 25 kg ha⁻¹ fertilization level, thus making it unavailable to creosotebush.

Ezcurra, E., S. Arizaga, P. L. Valverde, C. Mourelle, and A. Flores-Martínez. 1992. Foliole movement and canopy architecture of *Larrea tridentata* (D.C.) Cov. in Mexican deserts. *Oecologia* 92: 83-89.

Ezcurra, E., C. Montaña, and S. Arizaga. 1991. Architecture, light interception, and distribution of *Larrea* species in the Monte desert, Argentina. *Ecology* 72, no. 1: 23-34.

Abstract: This paper analyzes the correlation between leaf orientation and the environmental conditions that prevail within the biogeographic range of each of the four South American *Larrea* species (*L. ameghinoi*, *L. cuneifolia*, *L. divaricata*, and *L. nitida*; Zygophyllaceae). Data on the distribution of *Larrea* species were gathered from herbarium specimens. Measurements of leaf orientation were made throughout the Monte Desert, and in more detail in northern Patagonia, where the four species coexist. The direct solar radiation intercepted by the unshaded leaves of each species was estimated through a computer model and plotted as a function of the hourly time for the summer and winter solstices. *L. ameghinoi* presents horizontal leaves and prostrate growth, characters which allow its development on sites that are exposed to the Patagonian westerlies. The species, however, is an inefficient light interceptor in winter and early spring, when moisture conditions are adequate in Patagonia. Its architecture is the result of selection for cushion-type, wind resistant forms, at the expense of light interception. It is restricted to windy, open areas of the Patagonian steppe. *L. cuneifolia* shows erect, east-facing leaves and branches, which maximize interception in the early morning and late afternoon, keeping noon interception at a minimum. It can tolerate very hot environments by physically evading the midday sun and intercepting more early morning and late afternoon light. It colonizes the hotter and drier parts of the Monte Desert. *L. divaricata* has divaricate leaves with folioles uniformly distributed in all azimuthal directions, and showing an inclination of around 70°. Although it never shows maximum light interception efficiencies, it performs relatively well in all seasons and at all hours of the day. Its distribution is wide, not only in the arid Monte, but reaching also the Chaco woodlands and the Pacific coastal deserts. *L. nitida* shows erect, north-facing leaves and branches. Its leaf orientation distribution allows the gradual warming of the leaf surfaces during the morning, with a maximum light interception near winter noons. The species grow in the Patagonian Monte and on the slopes of the Andes. Its general affinity with the colder west side of the Patagonian and Monte Deserts links its distribution with winter-type rains of Pacific origin. The results suggest that the contrasting leaf orientations of the four South American *Larrea* species reflect the prevalent selective conditions endured under long periods in isolation, and that leaf orientation is an adaptive character that influences the habitat specificity of the different species.

Fisher, F. M., J. C. Zak, G. L. Cunningham, and W. G. Whitford. 1988. Water and nitrogen effects on growth and allocation patterns of creosotebush in the northern Chihuahuan Desert. *Journal of Range Management* 41, no. 5: 387-91.

Abstract: A field experiment using 2 patterns of irrigation and 1 level of nitrogen fertilizer (10 g-N m⁻²) was conducted in order to discern water and nitrogen interactions that may control production of creosotebush (*Larrea tridentata* (D.C.) Cov.). The 2 patterns of irrigation simulated precipitation from small, frequent events (6 mm water added weekly) or large, infrequent events (25 mm water added monthly). Understanding the factors controlling the production of this rangeland shrub may aid in the development of strategies for management. Vegetative growth occurred mostly during March-May (spring) and August-October (summer-fall). Fruit production occurred mainly in the spring and root growth occurred mainly in the summer-fall. Irrigation increased vegetative growth and decreased fruit production. Responses to irrigation were greater during summer-fall than in the spring. Small, frequent water

additions caused larger increases in vegetative plus fruit growth than did large, infrequent water additions. Nitrogen fertilization increased the growth of both vegetation and fruit in irrigated and unirrigated plots. Stem mortality and root growth were not significantly affected by irrigation or nitrogen fertilizer. These results suggest that creosotebush production is limited by both soil moisture and nitrogen availability and that temporal patterns of rainfall may be as important as total amounts.

Floyd, Ted. 1996. Top-down impacts on creosotebush herbivores in a spatially and temporally complex environment. *Ecology* 77, no. 5: 1544-55.

Abstract: I studied top-down effects on creosotebush (*Larrea tridentata*) insect herbivores by protecting them from bird and arthropod predation. The purpose of my study was to investigate experimentally the differential and/or interactive effects of two predator guilds on herbivore densities. I performed my experiments on 24 creosotebushes at each of three sites within the Jornada Long-Term Ecological Research Site in the Chihuahuan Desert of southwestern New Mexico, USA. At each site the experiment consisted of: six creosotebushes from which birds were excluded with nylon mesh cages; six creosotebushes from which arthropod predators were removed by hand or aspirator; six creosotebushes from which both birds and arthropod predators were removed; and six control creosotebushes from which neither birds nor arthropod predators were removed. I conducted nondestructive nocturnal visual censuses of herbivores on each creosotebush at the beginning of the experiments in mid-May, 6 wk after the start of the experiment in late June, and 12 wk after the start of the experiment in early August. I conducted these experiments and censuses in 1993 and again in 1994. In both years the herbivore densities became significantly higher in experimental than in control creosotebushes. The effects of bird and arthropod predation on herbivore densities were additive in 1993, but they were compensatory in 1994. In 1994 arthropod predator densities became lower in creosotebushes from which birds had been removed than in creosotebushes from which birds had not been removed, but this result did not obtain in 1993. These results may be due to a combination of factors including: avian and arthropod predation on herbivores, "intraguild" predation of birds on arthropod predators, and competition within the herbivore community. The relative numerical impacts of the predator-removal experiments varied among seasons and among sites within either year, but temporal and spatial variation in predator impacts did not correlate strongly with known gradients of climatic or bottom-up heterogeneity in this system. The results of this study confirm the important direct and cumulative effects of multiple predator guilds, even against a complex background of temporal and spatial heterogeneity.

Franco, A. C., A. G. de Soyza, R. A. Virginia, J. F. Reynolds, and W. G. Whitford. 1994. Effects of plant size and water relations on gas exchange and growth of the desert shrub *Larrea tridentata*. *Oecologia* 97: 171-78.

Abstract: *Larrea tridentata* is a xerophytic evergreen shrub, dominant in the arid regions of the southwestern United States. We examined relationships between gas-exchange characteristics, plant and soil water relations, and growth responses of large versus small shrubs of *L. tridentata* over the course of a summer growing season in the Chihuahuan Desert of southern New Mexico, USA. The soil wetting front did not reach 0.6 m, and soils at depth of 0.6 and 0.9 m remained dry throughout the summer, suggesting that *L. tridentata* extracts water largely from soil near the surface. Surface soil layers (<0.3 m) were drier

under large plants, but pre-dawn xylem water potentials were similar for both plant sizes suggesting some access to deeper soil moisture reserves by large plants. Stem elongation rates were about 40% less in large, reproductively active shrubs than in small, reproductively inactive shrubs. Maximal net photosynthetic rates (P_{max}) occurred in early summer ($21.3 \text{ u mol m}^{-2} \text{ s}^{-1}$), when pre-dawn xylem water potential (XWP) reached ca. -1 MPa . Although both shrub sizes exhibited similar responses to environmental factors, small shrubs recovered faster from short-term drought, when pre-dawn XWP reached about -4.5 MPa and P_{max} decreased to only ca. 20% of unstressed levels. Gas exchange measurements yielded a strong relationship between stomatal conductance and photosynthesis, and the relationship between leaf-to-air vapor pressure deficit and stomatal conductance was found to be influenced by pre-dawn XWP. Our results indicate that stomatal responses to water stress and vapor pressure deficit are important in determining rates of carbon gain and water loss in *L. tridentata*.

Garcia, E., C. Soto, and F. Miranda. 1960. Larrea y clima. *Anales Del Instituto De Biología De La Universidad Nacional Autónoma De México* 31: 133-71.

Abstract: The distribution of *Larrea tridentata* in Mexico coincides with certain climatic characteristics. Following Koppen's climatic classification it covers the zones designated as "BW" and also part of those with "BS" climate in which the ratio, annual precipitation/ mean annual temperature, is smaller than 22.9, and the winter precipitation less than 10.2 per cent of the annual. Its southern boundary seems to be in areas where the annual range of temperature is less than 7°C . Part of its northern boundary in the United States coincides closely with the 3.5°C January isotherm. The related *Larrea divaricata* from South America shows an outstanding symmetry with *Larrea tridentata*; it has the same climatic boundaries except in its eastern limits where it penetrates slightly into the "C" subhumid climates. The long distance migration proposed by Axelrod to explain the distribution of *Larrea* does not seem a plausible hypothesis. The present-day distribution of more macrothermic xeric plants such as *Castela* and *Cercidium* suggests a greater continuity between the dry zones in the past. The bi-zonal distribution of *Larrea* and its climatic adjustment could also indicate that temperatures in the tropical zone were lower in past epochs, facilitating its transtropic spread.

Gardner, J. L. 1951. Vegetation of the creosotebush area of the Rio Grande Valley in New Mexico. *Ecological Monographs* 21: 379-403.

Abstract: The valley of the Rio Grande in New Mexico is bordered by a narrow belt of brush dominated mainly by creosotebush (*Larrea divaricata*) nearly as far north as the mouth of the Rio Puerco. This area is one of sparse vegetation and low rainfall. Par to the precipitation, however, falls as intense storms, resulting in flash floods from arroyos. These flash flows cause appreciable damage to highway and irrigation installations and to crops and agricultural land in the valley. The information presented in the present paper was collected during the course of investigations on arroyo control along the Rio Grande. It is derived from notes and measurements made in the shrub belt from Las Cruces, New Mexico, as far north as creosotebush is prominent in the vegetation, a distance of approximately 170 miles.

Gibbens, R. P., K. M. Havstad, D. D. Billheimer, and C. H. Herbel. 1993. Creosotebush vegetation after 50 years of lagomorph exclusion. *Oecologia* 94, no. 2: 210-217.

Abstract: In 1939, an experiment was established on the Jornada Experimental Range to evaluate the effects of shrub removal, rabbit exclusion, furrowing, and seeding in creosote-bush (*Larrea tridentata* (DC.) Cov) vegetation. Sixteen plots (21.3 times 21.3 m) were laid out in four rows of four plots per row with a buffer zone of 7.6 m between plots and rows. A barbed wire fence excluded cattle and poultry wire fencing excluded lagomorphs. Treatments were factorially applied at two levels. Plant cover in the plots was sampled in 1938 (before treatment), 1947, 1956, 1960, 1967 and 1989 with randomly located, line-intercept transects. Data from all sampling dates were analyzed as a split plot in time and main effects for 1989 tested by analysis of variance for a 2 times 4 factorial experiment. There were significant ($P < 0.10$) year times treatment interactions. Seeding and furrowing treatments were ineffective but lagomorph exclusion and shrub clearing treatments resulted in significant treatment differences for several species. In 1989, basal area of spike dropseed (*Sporobolus contractus* A.S. Hitchc.) was 30-fold greater on the lagomorph excluded than on the lagomorph unexcluded treatment. Canopy cover of honey mesquite (*Prosopis glandulosa* Torr. var. *glandulosa*), tarbush (*Flourensia cernua* DC.) and mariola (*Parthenium incanum* H.B.K.) were affected by lagomorph exclusion. None of the responses were viewed as successional in nature. They principally represented individual species sensitivities to either absence of a primary herbivore or removal of aboveground shrub biomass. Though the physical treatments could be regarded as relatively severe disturbances of the system, the impacts on community vegetation dynamics were relatively insignificant.

Gibbens, Robert P., Ralph A. Hicks, and William A. Dugas. 1996. Structure and function of C3 and C4 Chihuahuan desert plant communities. Standing crop and leaf area index. *Journal of Arid Environments* 34, no. 1: 47-62.

See abstract under *Flourensia cernua*

Gibbens, R. P., and J. M. Lenz. 2001. Root systems of some Chihuahuan desert plants. *Journal of Arid Environments* 49, no. 2: 221-63.

See abstract under *Bouteloua eriopoda*

Gile, L. H., Robert P. Gibbens, and J. M. Lenz. 1998. Soil-induced variability in root systems of creosotebush (*Larrea tridentata*) and tarbush (*Flourensia cernua*) . *Journal of Arid Environments* 39, no. 1: 57-78.

See abstract under *Flourensia cernua*

Gill, Richard A., and Ingrid C. Burke. 1999. Ecosystem consequences of plant life form changes at three sites in the semiarid United States. *Oecologia* 121, no. 4 : 551-63.

Abstract: Many semiarid rangelands have recently experienced changes in dominant plant life form. Both woody plant expansion into grasslands and the invasion of annual grasses into shrublands have potential influence on regional carbon cycling. Soil carbon content, chemistry, and distribution may change following

shifts in dominant plant life form because plant life forms differ in litter chemistry and patterns of detrital input. This study assesses the amount, quality, and distribution of soil C below woody vegetation and grasses at three rangelands in Texas, New Mexico, and Utah. At each of these sites there has been a well-documented shift in dominant plant life form. In Texas and New Mexico, woody plants have increased in grasslands, while grasses have invaded into former shrublands in Utah. We measured total soil carbon, particulate organic matter (POM) C, and the carbon isotopic composition of soil carbon beneath woody plants and grasses at each of these three sites. At the La Copita Research Area in south-central Texas there was significantly more soil C found beneath *Prosopis glandulosa*, the dominant woody plant, than was found beneath grasses. Mean soil C content to 1 m was 7.2 kg C m⁻² beneath *P. glandulosa* and 6.0 kg C m⁻² beneath grasses. There was also significantly more POM C beneath *P. glandulosa* than beneath grasses. Stable carbon isotopic composition indicated that the expansion of *P. glandulosa* in savannas in Texas first influences carbon cycling in surface soils, then deep soil C, and finally throughout the soil profile. At the Sevilleta National Wildlife Refuge in central New Mexico, we found that there was significantly more soil C in the upper 10 cm of the soil profile beneath *Larrea tridentata* than was found beneath *Bouteloua* spp. Stable carbon isotopic composition indicated that the expansion of *L. tridentata* influenced C cycling throughout the soil profile. At Curlew Valley in northern Utah, we found no significant differences in total profile soil C beneath different plant life forms. However, there was significantly more soil C found at the soil surface beneath woody plants than was observed beneath annual grasses. There was significantly less POM C beneath annual grasses than was found beneath woody plants or perennial grasses. Based on stable carbon isotopic analyses, we concluded that the invasion of grasses into shrublands influenced only the upper 30 cm of the soil profile. We determined that following changes in plant life form dominance, the most consistent change in soil C was an alteration in content and distribution of POM C, a slowly cycling pool of soil C. While we failed to find a consistent change in total profile soil C with plant life form across our sites, the change in soil C chemistry may have important implications for long-term soil C storage in semiarid systems where there have been shifts in plant life form.

Goldberg, Deborah E., and Raymond M. Turner. 1986. Vegetation change and plant demography in permanent plots in the Sonoran Desert. *Ecology* 67, no. 3: 695-712.

Abstract: We report on vegetation changes and population dynamics during a 72-yr period within permanent plots in Sonoran Desert vegetation. A set of plots established in 1906 and supplemented in 1928 at Tumamoc Hill, near Tucson, Arizona, USA, have been mapped at irregular intervals through 1978. Data from the four 100-m² and one 800-m² plots censused most frequently (6-8 times since 1906 and 1928) are presented in detail; data from five less frequently censused plots are noted briefly. At each census all woody and succulent plants, including seedlings, were mapped by recording both stem coordinates and canopy outline. There have been no consistent, directional changes in vegetation composition in the Tumamoc Hill plots between 1906 and 1978, despite large fluctuations in absolute cover and density of most species. The relative cover of the dominants was generally similar within a given plot over the entire time sequence. Coverage of most species responded strongly to regimes of extremely wet or extremely dry years; the response of density to climatic extremes was somewhat less strong. Total cover, density, and species diversity have increased more or less continuously in many plots between 1906 and 1978. The

species were divided into five groups based on several population dynamic traits. At one end of continuum are species with long maximum lifespan (often greater than the 72-yr study period), high early and long-term (50-yr) survivorship, large size at maturity, low density, erratic recruitment, and age structure skewed toward older plants. At the other end of the continuum are species with short maximum life-span, low early and long-term survivorship, small size at maturity, high density, some recruitment at most censuses, and age structures strongly skewed toward newest recruits. While some of these traits are necessarily related (e.g., long maximum life-span and high long-term survivorship), others are not (e.g., high early survivorship and erratic recruitment), and the relationships deserve further study.

Grover, H. D., and H. B. Musick. 1990. Shrubland encroachment in southern New Mexico, USA. An analysis of desertification processes in the American Southwest. *Climatic Change* 17, no. 2-3: 305-30.

Abstract: The area dominated by the shrubs creosotebush (*Larrea tridentata*) and mesquite (*Prosopis glandulosa*) in the American southwest has increased several-fold over the last century, with a corresponding decrease in areal coverage of productive grasslands and increased surface soil erosion throughout the region. The factors thought to be responsible for this regional shift in vegetation are: (1) overgrazing by domestic livestock; (2) fire suppression; and (3) historical changes in climate. We examine the evidence concerning each of these factors and develop a synthetic model outlining the principles affecting shrubland encroachment, which focuses on life history characteristics of the dominant shrubs and a number of positive biotic and edaphic feedback mechanisms contributing to their establishment and persistence. We conclude that the expansion of shrub dominance that has occurred over the last century may have been triggered by extreme livestock overgrazing at the end of the nineteenth century, which coincided with rainfall regimes that were unfavorable for perennial grass growth. Hence, the landscape we observe today may be a product of positive feedback mechanisms triggered over a century ago by management practices that were uninformed with regard to the importance of historical climate patterns and the life history characteristics of important rangeland species. Our consideration of these issues also addresses potential land surface-climate interactions that could occur as a result of regional alterations in vegetation dominance and physiognomy.

Gutierrez, Julio R., and Walter G. Whitford. 1989. Effect of eliminating subterranean termites on the growth of creosotebush, *Larrea tridentata*. *The Southwestern Naturalist* 34, no. 4: 549-51.

Abstract: Soils devoid of termites are more compacted (Elkins et al., 1986, *Oecologia* 68: 521-528), and nitrogen concentrations in the soil surface decrease with depth. This should affect the growth of deep-rooted shrubs. We studied the effects of water supplementation and termite removal on shoot growth of the common Chihuahuan Desert shrub *Larrea tridentata* to test the hypothesis that reduced infiltration by removal of termites would reduce growth rates of the shrub.

Gutschick, V. P. 1996. Physiological control of evapotranspiration by shrubs: scaling measurements from leaf to stand with the aid of comprehensive models. In *Proceedings: shrublands ecosystem dynamics in a changing*

environment, Compilers J. R. Barrow, E. D. McArthur, R. E. Sosebee, and R. J. Tausch, 214-19Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station.

Abstract: Plants exert major control over hydrologic budget- and, thus, over their own community stability- by their own transpiration and by their partial control over soil evaporation via soil shading. Furthermore, they exert major control over atmospheric humidity and consequent radiation balance in climate.

Predicting further plant status and future climate will require predicting evapotranspiration (ET) over large regions and under varied climates. Models that are useful for diverse sites and species will require understanding of ET control at the process level, physiologically and micrometeorologically. ET prediction also presents significant challenges in quantifying vegetation and its spatial and physiological heterogeneity. We review how process-level understanding can be gained and tested by scaling down from satellite data and scaling up from leaf gas exchange. We have synthesized a model of leaf conductance and fitted its parameters to data on *Larrea tridentata* and *Prosopis glandulosa*. To scale up to whole-shrub and whole-stand evapotranspiration, we must sum over all leaves, accounting for (1) their different current microclimates and (2) their physiological states of acclimation to long-term histories of temperature and irradiance. We have developed models for each of these phenomena and are fitting them to data on many individual leaves. Our model can be integrated to predict whole-plant and whole-stand ET. We outline tests that will be performed on a 1000 m x 300 m transect of mixed shrubland on the Jornada Experimental Range.

Hallmark, C. T., and B. L. Allen. 1975. The distribution of creosotebush in West Texas and Eastern New Mexico as affected by selected soil properties. *Soil Science Society of America. Proceedings* 39: 120-124.

Abstract: Morphological, physical, chemical, and mineralogical studies were made on 32 pedons from west Texas and southeastern New Mexico to evaluate edaphic factors related to creosotebush [*Larrea tridentata* (D.C.)] distribution. Creosotebush grows on soils with a wide range of properties. The soils studied were well drained and generally moderately developed, as indicated by horizonation and carbonate redistribution. The data indicate that gravel content and depth to free CaCO₃ are the most important soil factors affecting distribution of the shrub in the study area. Soils low in gravel and noncalcareous at the surface tend to be devoid of the shrub. Soils that support creosotebush are generally calcareous throughout the profile and many have significant amounts of gravel. The complex interactions among other edaphic factors such as texture, available water, salinity in deeper horizons, and gypsum content greatly complicate the resolution of properties influencing distribution.

Hamerlynck, Erik P., Joseph R. McAuliffe, Eric V. McDonald, and Stanley D. Smith. 2002. Ecological responses of two Mojave desert shrubs to soil horizon development and soil water dynamics. *Ecology* 83, no. 3: 768–779.

Abstract: In the arid southwestern United States, subtle differences in soil horizon development affect seasonal soil hydrology and consequently influence plant performance and community structure. We measured canopy development, population structure, and seasonal ecophysiology (predawn water potential Ψ_{pd} , and midday net photosynthetic assimilation, A_{net}) of two co-dominant warm-desert shrubs, the evergreen *Larrea tridentata* and drought-deciduous *Ambrosia dumosa*, in five Mojave Desert soils varying in surface and sub-surface soil development, and we used process-based soil hydrology modeling output to

determine longer-term soil water dynamics underlying soil/plant responses. We hypothesized that ecophysiological performance would covary with plant development, which would reflect soil hydrological characteristics. Among three sites on alluvial fan deposits of different geological ages (Young Alluvial, <4000 yr BP; Intermediate Alluvial, 12000 yr BP; Old Alluvial, 40000 yr BP), total canopy volume of *Larrea* (cubic meters per 100 m² ground area) was highest on the Young Alluvial site, in close agreement with soil modeling results showing that these coarse-textured, weakly developed soils permit deeper water infiltration. In older, stronger developed soils, infiltration and persistence of soil water was sharply reduced, which was reflected by lower individual *Larrea* plant volumes. However, during peak spring conditions, Ψ_{pd} and A_{net} were highest in *Larrea* at the Intermediate Alluvial site (-4.2 ± 0.32 MPa and 3.2 ± 0.91 $\mu\text{mol m}^{-2}\text{s}^{-1}$), where soils had substantial surface and subsurface horizons, and at the Pavement site, where soils had strong surface layers but little subsurface development. Concurrent plant performance at the Young Alluvial site was unexpectedly low (-4.8 ± 0.49 MPa and 1.7 ± 0.56 $\mu\text{mol m}^{-2}\text{s}^{-1}$, respectively). During summer drought Ψ_{pd} and A_{net} remained high in Intermediate Alluvial plants, but were extremely low in Pavement site *Larrea* (-8.17 MPa and -0.04 $\mu\text{mol m}^{-2}\text{s}^{-1}$, respectively), due to curtailed infiltration of summer precipitation. These findings suggest that *Larrea* growing in older soils experience greater mortality and reduced growth but are not subject to strong intra-specific competition resulting from the persistence of large individuals apparent in younger, coarser textured soils.

In contrast to *Larrea*, density of *Ambrosia* increased with soil horizon development, but smaller plant sizes resulted in similar canopy volume per area, and identical Ψ_{pd} and A_{net} across all soils where it occurred, suggesting greater plasticity to the transmittal of precipitation. These findings show that a strong geomorphology and soils context is essential for understanding the variation in plant responses and vegetation structure in desert environments.

Herbel, C. H. 1966. Creosotebush (*Larrea tridentata* [DC] Coville). *Chemical control of range weeds*. U. S. Dep. Agric. and U. S. Dep. Interior., 21. Vol. Interagency Rep.

Herbel, C. H., and R. P. Gibbens. 1985. Field water regimes of sandy loam soils on arid rangelands of southern New Mexico. *Proceedings XV International Grassland Congress*, 514-16.

Abstract: There is little information on field measurement of soil water on arid rangelands. Forage production is largely dependent upon adequate water. The soil water potential is characterized for three sandy loam soils during 1957-76 on arid rangelands of southwestern United States. Gypsum-impregnated resistance blocks were placed at soil depths of 10, 25, 41, 61, and 91 cm. The average annual precipitation during the study periods was 244, 265, and 233 mm. At the 10-cm soil depth, the probability of soil water ≥ -1.5 megapascals during December-March was 66, 70, and 68% at the three sites; during July-September, it was 46, 50, and 49%, respectively. Factors affecting soil water were: 1) precipitation amount, 2) surface soil characteristics, 3) topography, 4) soil texture, and 5) vegetation type. This information is useful for modeling the range ecosystem.

Ho, Mengchi, Rachel E. Roisman, and Ross A. Virginia. 1996. Using strontium and rubidium tracers to characterize nutrient uptake patterns in creosotebush and mesquite. *Southwestern Naturalist* 41, no. 3: 239-47.

Abstract: During the past 100 years, large areas of perennial grassland in the Chihuahuan Desert have been replaced by woody plants such as mesquite (*Prosopis glandulosa*) and creosotebush (*Larrea tridentata*). We investigated the short-term pattern of resource acquisition by these two dominant desert shrubs during the summer in the Jornada del Muerto Basin, New Mexico. We hypothesized that for a given size class of shrubs, nutrient uptake favors isolated plants and that larger plants have higher access to soil resources. We applied tracer solutions containing Sr and Rb (0.02 M each) to patches of soil located either beneath or beyond the canopy of isolated creosotebush and mesquite shrubs to examine the ability of these plants to acquire nutrients as a function of distance. Tracer solutions were also applied equidistant between paired shrubs to examine whether neighboring plants had equal access to soil resources. Mature foliage was analyzed for Sr and Rb at day 7, 21, and 35 after tracer application. Strontium and Rb in creosotebush increased steadily at a relative accumulation rate of 0.018 per day. Mesquite accumulation rates were lower, 0.013 per day for Sr and 0.002 per day for Rb. The highest Rb concentrations were found in small creosotebush receiving tracers beneath the canopy. Tracer accumulations by paired plants of both creosotebush and mesquite were not equal and these differences between neighboring shrubs could not be explained by variation in canopy volume. Creosotebush and mesquite had distinct uptake patterns for the two tracers indicating these species differ in surface root distribution and activity. Creosotebush appears to respond more rapidly to short-term increases in the availability of soil moisture and nutrients.

Hochstrasser, Tamara. 2001. "Pattern and process at a desert grassland-shrubland ecotone." Ph. D. Dissertation, Colorado State University.

Abstract: Over the past century, shrub encroachment has occurred in desert grasslands all over the American Southwest. In the Northern Chihuahuan desert, most encroachment was due to creosotebush (*Larrea tridentata* [Sessé & Moc. ex DC.] Coville) expanding into black grama (*Bouteloua eriopoda* [Torr.] Torr.) dominated grasslands. Dominant plants contribute significantly to ecosystem structure and function, and grasses and shrubs differ fundamentally in their role in ecosystems. This dissertation investigated the influence of dominant plants, grasses and shrubs, on pattern and process at a desert grassland-shrubland ecotone. First, small-scale species coexistence patterns in microsites around dominant grasses (*B. eriopoda*) and shrubs (*L. tridentata*) were compared. Second, small-scale patterns were related to landscape scale species richness. Third, a gap-dynamics simulation model (ECOTONE) was used to investigate mechanisms that could create some of the patterns observed.

Contrary to expectations, subdominant species abundance was lower in microsites around grasses than in microsites around shrubs. Different functional groups of subdominant species had a different distribution in microsites. When extrapolating to the landscape, it was found that perennial species richness is related to the distribution of dominant plants across scales from the plant to the landscape, whereas annual species richness seems to be mainly influenced by disturbance. Both biotic and abiotic factors contributed to the patterns observed across scales. Soil texture differences between microsites may explain differences in subdominant species abundance between the canopy area of plants and interspaces. In contrast, differences in subdominant species abundance between canopy areas of grasses and shrubs were most

likely due to biotic factors, namely the morphological differences between the canopies of the dominant lifeforms. The use of the simulation model showed that black grama dominates the vegetation by a combination of intensive exploitation of water resources underneath its canopy and by its capacity to cope with soil disturbances, whereas creosotebush dominates by its long lifespan and low yearly biomass turnover rate. Replacement of black grama by creosotebush under the current disturbance and climatic regime would take a very long time. Similar to field observations, subdominant species abundance was higher in simulated creosotebush dominated landscapes than black grama dominated ones. It was concluded that the shift in the dominant lifeform by itself does not have a negative influence on plant species diversity at the ecotone investigated. On the contrary, the addition of shrubs to the vegetation increases spatial heterogeneity and has a positive effect on the overall diversity of the vegetation in an ecotone situation. Indirect processes induced by creosotebush that likely can be linked to species loss seem to only be important in areas where creosotebush dominates large extents of vegetation. Furthermore, other processes than shrub encroachment, such as human activities and drought, may contribute to species loss during desertification.

Hoefler, William C. 1984. "Response of creosotebush and mesquite communities after applying hexazinone ." M. S. Thesis, New Mexico State University.

Holzman, Barbara Ann. 1988. "Recovery of a disturbed desert creosote (*Larrea tridentata*) community in Joshua Tree National Monument, California." M. A. Thesis, University of California.

Huenneke, L. F., J. P. Anderson, M. Remmenga, and W. H. Schlesinger. 2002. Desertification alters patterns of aboveground net primary production in Chihuahuan ecosystems. *Global Change Biology* 8, no. 3: 247-64. See abstract under *Bouteloua eriopoda*

Huenneke, Laura F., Dennis Clason, and Esteban Muldavin. 2001. Spatial heterogeneity in Chihuahuan desert vegetation: implications for sampling methods in semi-arid ecosystems. *Journal of Arid Environments* 47, no. 3: 257-70. See abstract under *Bouteloua eriopoda*

Humphrey, R. R., and L. A. Mehrhoff. 1958. Vegetation changes on a southern Arizona grassland range. *Ecology* 39: 720-726.

Abstract: Vegetation surveys of the Santa Rita Experimental Range in southern Arizona were made in 1904, 1934 and 1954. The survey data were analyzed to determine changes in area and abundance of the four most common woody plants: creosotebush, burroweed, cholla and mesquite. All of the species increased markedly in area and abundance during the 50-year period 1904 to 1954. Maximum increase had occurred by 1934 but, except for burroweed, continued at a slower rate from 1934 to 1954.

Climate, grazing, rodents and fire were evaluated as factors that may have contributed to the vegetational changes noted. Conclusions were: (a) there have been no apparent changes in climate that would result in the vegetational changes noted; (b) grazing by domestic livestock has affected that composition of the vegetation, in part because of selective grazing and in part because of the removal of grass by grazing that formerly served as fuel for range fires; (c) rodents bury mesquite seeds and transport cholla cactus joints, thus serving to propagate those plants; (d) fires maintained desert grassland as such, prior to the introduction of livestock; (e) shrub invasion of southern Arizona semidesert grassland ranges is due primarily to reduction of range fires.

Hunter, Kimberly L., Julio L. Betancourt, Brett R. Riddle, Thomas R. Van Devender, Kenneth L. Cole, and W. Geoffrey Spaulding. 2001. Ploidy race distributions since the Last Glacial Maximum in the North American desert shrub, *Larrea tridentata*. *Global Ecology and Biogeography* 10, no. 5: 521-33.

Abstract: 1 A classic biogeographic pattern is the alignment of diploid, tetraploid and hexaploid races of creosote bush (*Larrea tridentata*) across the Chihuahuan, Sonoran and Mohave Deserts of western North America. We used statistically robust differences in guard cell size of modern plants and fossil leaves from packrat middens to map current and past distributions of these ploidy races since the Last Glacial Maximum (LGM). 2 Glacial/early Holocene (26-10 14C kyr BP or thousands of radiocarbon years before present) populations included diploids along the lower Rio Grande of west Texas, 650 km removed from sympatric diploids and tetraploids in the lower Colorado River Basin of south-eastern California/south-western Arizona. Diploids migrated slowly from lower Rio Grande refugia with expansion into the northern Chihuahuan Desert sites forestalled until after approx 4.0 14C kyr BP. Tetraploids expanded from the lower Colorado River Basin into the northern limits of the Sonoran Desert in central Arizona by 6.4 14C kyr BP. Hexaploids appeared by 8.5 14C kyr BP in the lower Colorado River Basin, reaching their northernmost limits (approx 37degreeN) in the Mohave Desert between 5.6 and 3.9 14C kyr BP. 3 Modern diploid isolates may have resulted from both vicariant and dispersal events. In central Baja California and the lower Colorado River Basin, modern diploids probably originated from relict populations near glacial refugia. Founder events in the middle and late Holocene established diploid outposts on isolated limestone outcrops in areas of central and southern Arizona dominated by tetraploid populations. 4 Geographic alignment of the three ploidy races along the modern gradient of increasingly drier and hotter summers is clearly a postglacial phenomenon, but evolution of both higher ploidy races must have happened before the Holocene. The exact timing and mechanism of polyploidy evolution in creosote bush remains a matter of conjecture.

Hurd, Paul D. Jr., and E. Gorton Linsley. 1975. *The principal Larrea bees of the southwestern United States (Hymenoptera, Apoidea)*. Washington: Smithsonian Institution Press.

Hyder, Paul W. 2001. "Total phenolics, condensed tannins, and nordihydroguaiaretic acid (NDGA) as potential allelopathic compounds in creosotebush (*Larrea tridentata* (Sess. & Moc. ex DC.) Cov.) and tarbush (*Flourensia cernua* DC) in the northern Chihuahuan Desert ." Ph. D. Dissertation, New Mexico State University.

See abstract under *Flourensia cernua*

Ibarra Flores, F. A. 1984. "Brush control, forage production and tebuthiron residues in soils and plants at four creosotebush (*Larrea tridentata*) sites in the Chihuahuan and Sonoran deserts." M. S. Thesis, University of Arizona.

Johnson, Donald Edward. 1961. "Edaphic factors affecting the distribution of creosotebush, *Larrea tridentata* (DC.) Cov., in desert grassland sites of southeastern Arizona." M. S. Thesis, University of Arizona. Abstract: Edaphic factors that might explain the distribution of *Larrea* in the desert grassland of southeastern Arizona were investigated. The composition, distribution and total cover of the vegetation in several adjoining desert grassland and Chihuahuan desert shrub associations were analyzed, and a permanent line transect established to record any future vegetational changes. Soils of two shrub and three grass communities were mechanically analyzed for textural class, water-holding percent and available moisture; and chemically for calcium carbonate content and pH. Results can be summarized as follows:

1. Soils that supported grasses usually contained a larger percentage of clay and had a higher percent available moisture than soils that grew largely shrubs.
2. *Larrea* was most abundant on sites where shallow, sandy soils with low available moisture, caliche hardpan, or erosion pavement resulted in relatively unfavorable moisture relationships for the growth of other species.
3. The form of calcium carbonate, as affecting permeability and root penetration, was more a factor in determining *Larrea* distribution than was percent of occurrence.
4. Factors that seem most likely to prevent the establishment of *Larrea* in the grass communities studied are: poorly drained heavy soils, competition from better adapted species, or low pH values that prevent seed germination.
5. Soil moisture relationships in the *Bouteloua eriopoda* community, the only community that *Larrea* was invading, resembled those in the shrub associations more closely than in the other grass communities.

Jordan, Gilbert L., and Marshal R. Haferkamp. 1989. Temperature responses and calculated heat units for germination of several range grasses and shrubs. *Journal of Range Management* 42, no. 1: 41-45.

Kemp, Paul R. 1983. Phenological patterns of Chihuahuan desert plants in relation to the timing of water availability. *Journal of Ecology* 71, no. 2: 427-36.

See abstract under *Bouteloua eriopoda*

King, T. J., and S. R. J. Woodell. 1973. The causes of regular pattern in desert perennials. *Journal of Ecology* 61, no. 3: 761-65.

Abstract: The evidence that regular patterns occur in populations of desert shrubs is reviewed. The objections by Anderson (1971) to the hypothesis of Woodell et al. (1969) that regularity in *Larrea divaricata* in California is due to competition for a limiting water resource are discussed and refuted

Knipe, D., and C. H. Herbel. 1966. Germination and growth of some semidesert grassland species treated with aqueous extract from creosotebush. *Ecology* 47, no. 5: 775-81.

Abstract: The effects of aqueous extracts from creosotebush (*Larrea tridentata*) material on germination and initial growth of black grama (*Bouteloua eriopoda*), bush muhly (*Muhlenbergia porteri*), and creosotebush were studied. There was no apparent difference among extracts obtained from the various creosotebush plant parts. An aqueous extract from leaves and twigs significantly reduced germination of black grama caryopses, but the germination of bush muhly caryopses and of creosotebush seeds (removed from the carpels) was not affected. Less concentrated extracts did not significantly reduce germination of the test species. However, radical and plumule growth of black grama and bush muhly were significantly reduced by all extracts. Apparently the relatively low osmotic concentrations or the moderate pH's were not responsible for these reductions in growth.

Knipe, Oren D. 1960. "The effects of aqueous extracts of creosotebush on germination and growth of some desert plains grassland plants." M.S. Thesis, New Mexico State University.

Abstract: The purpose of this study was to determine if the creosotebush contains an inhibitor which may be a contributing factor to the invasion of creosotebush on grassland.

Aqueous extracts from creosotebush plant material, of relatively high concentration, significantly reduced the germination of black grama caryopses, prevented the development of radicles and significantly reduced plumule growth of both black grama and bush muhly. The extract was not inhibitory to germination or seedling growth of creosotebush.

Korzdorfer, Edward Jay. 1968. "Seeding, furrowing, brush removal, and rabbit exclusion effects on creosotebush-infested sites." M.S. Thesis, New Mexico State University.

Abstract: Creosotebush (*Larrea tridentata* (DC) Cov.) dominates much of the formerly productive rangelands of the southwest. A successful and practical method of eradicating this shrub, followed by revegetation of the area by desirable forage plants, would greatly improve these creosotebush-infested areas for livestock use. The purpose of this factorially designed experiment was to study the effects of seeding, furrowing, brush removal, and rabbit exclusion on three creosotebush-infested sites on the Jornada Experimental Range, Las Cruces, New Mexico.

Brush removal consistently decreased the canopy cover of creosotebush and total shrubs, regardless of other treatments. The brush removal alone or the brush removal x rabbit exclusion treatment significantly increased the grass species at the Ragged and Parker Tank sites. The rabbit exclusion fence was present in the treatment applications that significantly increased the grass cover at the Dona Ana site. This treatment was significant in increasing the grass cover due to its soil retaining and soil depositional effects on this site with the steeper slope and the more severe erosion and runoff condition.

Lajtha, K. 1987. Nutrient reabsorption efficiency and the response to phosphorus fertilization in the desert shrub *Larrea tridentata*. *Biogeochemistry* 4: 265-76.

Abstract: A field fertilization experiment demonstrated that growth of *Larrea tridentata* was not limited by phosphorus, even though soils contained high levels of pedogenic carbonates that can potentially fix high amounts of phosphorus. Nutrient reabsorption efficiencies in unfertilized shrubs ranges from 72-86% for P, making nutrient reabsorption a very effective nutrient conservation mechanism. Absolute amounts of N and P reabsorption increased with N and P concentrations in leaves, with reabsorption being greater during drought stress than during rapid leaf growth. However, only N reabsorption efficiency increased with increasing plant N status. A model was developed to explain patterns of nutrient reabsorption efficiencies over large gradients in nutrient availability.

Lajtha, Kate, and Melanie Klein. 1988. The effect of varying nitrogen and phosphorus availability on nutrient use by *Larrea tridentata*, a desert evergreen shrub. *Oecologia* 75: 348-53.

Abstract: In a phytotron study of the effects of nitrogen and phosphorus supply ration on nutrient uptake and use by *Larrea tridentata*, seedlings responded to increases in N and P availability with increases in leaf size, total biomass, and leaf nutrient concentration, and with decreases in root:shoot ratio. N and P use efficiency decreased with increasing N and P availability, respectively, but increased with increasing availability of the other nutrient, suggesting that *Larrea* responds both to the absolute and to the relative availability of limiting nutrients. Absolute amounts of N and P reabsorption, as well as N and P reabsorption efficiencies did not demonstrate a significant trend with nutrient availability, and there was no evidence of significant interactions between the two nutrients. More studies of the effects of nutrient interactions in the cycling and use of nutrients by different plant species are needed before more general conclusions can be drawn.

Lajtha, Kate, and William H. Schlesinger. 1986. Plant response to variations in nitrogen availability in a desert shrubland community. *Biogeochemistry* 2: 29-37.

Abstract: Spatial variations in nitrogen availability were studied in a desert community codominated by *Larrea tridentata* (DC.) Cov. and *Prosopis glandulosa* Torr. Measurements of natural ^{15}N values in tissues suggested that *Prosopis* obtains approximately half of its nitrogen through direct symbiotic fixation. Soils were collected under 1) *Prosopis* shrubs, 2) *Larrea* shrubs < 2 m from *Prosopis* (LP), and 3) *Larrea* < 2 m from other *Larrea* but > 5 m from the nearest *Prosopis* (LL). *Prosopis* soils showed significantly higher rates of nitrogen mineralization than LL soils in both A and B horizons. Rates of mineralization in LP soils were significantly higher than rates in LL soils only in the B horizon and were not significantly different from rates in *Prosopis* soils. Leaf nitrogen concentrations were significantly higher in LP shrubs (2.06%) than in LL shrubs (1.78%), although ^{15}N values did not differ between the two shrub types. Nitrogen concentrations in *Perezia nana* Gray, a perennial herb, were greater in plants under *Prosopis* shrubs (2.09%) than under LP shrubs (1.93%) or LL shrubs (1.67%). Despite apparent differences in nitrogen availability, biomass of *Larrea* and density of *Perezia* did not differ significantly among these sites.

———. 1988. The effect of CaCO₃ on the uptake of phosphorous by two desert shrub species *Larrea tridentata* (D. C.) Cov. and *Parthenium incanum* H.B.K. *Botany Gazette* 149, no. 3: 328-34.

Abstract: In a phytotron growth study, the effects of soil CaCO₃ on the uptake of P by two desert shrub species were species specific. *Larrea tridentata* seedlings responded to soil CaCO₃ with increased root:shoot ratios, increased N:P ratios in tissues, and decreased specific absorption rates of P, indicating that CaCO₃ directly inhibited the uptake or the availability of P to roots. *Parthenium incanum* seedlings responded negatively to CaCO₃, but this response was not specific to P uptake and did not appear to be caused by a reduction in P availability. Pedogenic carbonates, present in many arid-land soils of the world, might greatly affect both P availability and the biogeochemical cycle of P in desert ecosystems.

Lajtha, Kate, John Weishampel, and William H. Schlesinger. 1987. Phosphorous and pH tolerances in the germination of the desert shrub *Larrea tridentata* (Zygophyllaceae). *Madroño* 34, no. 1: 63-68.

Abstract: Seeds of *Larrea tridentata*, a dominant shrub of deserts in the southwestern U.S., were germinated on both a pH and phosphorus (P) gradient to determine if requirements for germination can help explain the field distribution of *Larrea*. Germination decreased significantly above pH 8, which is consistent with the conspicuous absence of *Larrea* from high pH sodic or saline desert soils. Although *Larrea* tends to be absent from noncalcareous soil, seed germination was not inhibited in acidic solutions. Germination showed no response to P or to interactions of pH and P. In contrast, recent literature has suggested that *Larrea* may be restricted to calcareous soils of low phosphorus availability due to toxicity of high concentrations of P to seedlings.

Lajtha, Kate, and Walter G. Whitford. 1989. The effect of water and nitrogen amendments on photosynthesis, leaf demography, and resource-use efficiency in *Larrea tridentata*, a desert evergreen shrub. *Oecologia* 80: 341-48.

Abstract: In the Chihuahuan Desert of southern New Mexico, both water and nitrogen limit the primary productivity of *Larrea tridentata*, a xerophytic evergreen shrub. Net photosynthesis was positively correlated to leaf N, but only in plants that received supplemental water. Nutrient-use efficiency, defined as photosynthetic carbon gain per unit N invested in leaf tissue, declined with increasing leaf N. However, water-use efficiency, defined as the ratio of photosynthesis to transpiration, increased with increasing leaf N, and thus these two measures of resource-use efficiency were inversely correlated. Resorption efficiency was not significantly altered over the nutrient gradient, nor was it affected by irrigation treatments. Leaf longevity decreased significantly with fertilization although the absolute magnitude of this decrease was fairly small, in part due to a large background of insect-induced mortality. Age-specific gas exchange measurements support the hypothesis that leaf aging represents a redistribution of resources, rather than actual deterioration or declining resource-use efficiency.

Lightfoot, David Carleton. 1988. "Relationships between creosotebush productivity and associated foliage arthropod assemblages." Ph.D. Dissertation, New Mexico State University.

Abstract: I conducted field experiments to examine relationships between creosotebush (*Larrea tridentata*)

foliage production and associated foliage arthropods. Chapter One presents the results of an experiment designed to assess the effects of increased nitrogen and water on creosotebush foliage arthropods. Nitrogen fertilizer and irrigation treatments were applied to creosotebush shrubs. Water with nitrogen, and nitrogen alone, increased foliage production, foliar nitrogen contents, and numbers of foliage arthropods. Water alone had less effect on foliage production, and no effect on foliar nitrogen or numbers of arthropods. Sap-sucking insects were the most abundant arthropods responding to increased foliage production and foliar nitrogen contents. The experiment presented in Chapter Two was designed to determine if phytophagous insects on creosotebush increase rates of plant to soil nitrogen flux from nutrient-rich shrubs. Foliage arthropod populations, and nitrogen in canopy throughfall and stemflow, were measured to assess nitrogen flux rates relative to arthropod densities on fertilized and unfertilized shrubs. Foliage arthropod densities and biomasses, and amounts of nitrogen in throughfall, were greater from fertilized shrubs. Nitrogen excreted by foliage arthropods accounted for about 20% of the total nitrogen flux from unfertilized shrubs. I propose a model predicting foliage arthropods to enhance nitrogen availability to creosotebush shrubs. In Chapter Three, I tested the hypothesis that creosotebush shrubs growing in nutrient-rich micro-sites support more insects than shrubs growing in less productive sites. Shrubs from nutrient-rich sites had greater branch growth, flower production, and foliar nitrogen, than shrubs from less productive sites. Shrubs from nutrient-rich sites also supported greater densities of foliage arthropods. Shrub characteristics indicative of productivity covaried positively with foliage arthropod densities, and foliar resin concentrations covaried negatively with arthropod guilds. These findings are inconsistent with the theory that phytophagous insects are more successful on stressed host plants.

Lightfoot, David C., and Walter G. Whitford. 1987. Variation in insect densities on desert creosotebush: is nitrogen a factor? *Ecology* 68: 547-57.

Abstract: A field experiment was conducted to assess the effects of nitrogen and water on the densities and taxonomic and trophic compositions of arthropods on the foliage of desert creosotebush (*Larrea tridentata*). Nitrogen and water were manipulated through a series of fertilizer and irrigation treatments applied to naturally growing creosotebush shrubs at a site in the northern Chihuahuan Desert. Water with nitrogen, and nitrogen fertilization alone, significantly increased creosotebush foliage production and foliar nitrogen contents. Foliage production, foliar nitrogen contents, and numbers of foliage arthropods were all higher in the late spring than in the mid or late summer. Numbers of foliage arthropods increased significantly on fertilized plants in the late spring. Water treatments alone had no effect on numbers of foliage arthropods, but a positive water-fertilizer interaction effect on numbers of foliage arthropods was evident in the late spring. Overall, there were significant positive correlations between foliage production, foliar nitrogen contents, and foliage arthropod densities. Photophagous sap-sucking insects accounted for the majority of arthropods on creosotebush, and their densities varied most in relation to foliage production and foliar nitrogen contents. Results of our study demonstrated that sap-sucking phytophagous insects are more responsive than leaf-chewing insects to increased nitrogen content of creosotebush foliage, and that much of the between-plant variation in densities of phytophagous insects within a stand of creosotebush may be due to sap-sucking insects tracking variable foliar nitrogen.

- . 1989. Interplant variation in creosotebush foliage characteristics and canopy arthropods. *Oecologia* 81: 166-75.

Abstract: We conducted a field study to test the hypothesis that creosotebush (*Larrea tridentata*) shrubs growing in naturally nutrient-rich sites had better quality foliage and supported greater populations of foliage arthropods than shrubs growing in nutrient-poor sites. Nutrient-rich sites had significantly higher concentrations of soil nitrogen than nutrient-poor sites. Multivariate analysis of variance revealed significant differences between high nutrient and low nutrient shrubs based on a number of structural and chemical characteristics measured. High nutrient shrubs were larger, had denser foliage, greater foliage production, higher concentrations of foliar nitrogen and water, and lower concentrations of foliar resin than low nutrient shrubs. Numbers of foliage arthropods, particularly herbivores and predators, were significantly higher on high nutrient shrubs. Shrub characteristics and foliage arthropod abundances varied considerably from shrub to shrub. Shrub characteristics representing shrub size, foliage density, foliage growth, and foliar nitrogen and water concentrations were positively correlated with arthropod abundances. Foliar resin concentrations were negatively correlated with foliage arthropod abundances. The positive relationship between creosotebush productivity and foliage arthropods is contradictory to the tenet that physiologically stressed plants provide better quality foliage to insect herbivores.

- . 1991. Productivity of creosotebush foliage and associated canopy arthropods along a desert roadside. *The American Midland Naturalist* 125: 310-322.

Abstract: A sampling study was designed to test the hypothesis that creosotebush (*Larrea tridentata*) shrubs along a roadside were larger, more vigorous and supported greater populations of foliage arthropods than shrubs growing 20 m away from the road margin. Structural and chemical attributes of shrubs and associated foliage arthropods were measured. Roadside shrubs were larger, had denser foliage, more flowers, higher foliar nitrogen contents and lower foliar resin contents than shrubs growing away from the road. Foliage arthropod densities were significantly higher on roadside shrubs. Sap-feeding herbivores dominated numerically and accounted for most of the differences in arthropod abundances between roadside and nonroadside shrubs. Numbers of foliage arthropods were positively correlated with shrub size, density and foliar nitrogen contents, and negatively correlated with foliar resin contents. These findings, in concordance with other studies, indicate that in arid environments productive, vigorous plants are preferred hosts for herbivorous insects.

- Ludwig, J. A., and P. Flavill. 1979. Productivity patterns of *Larrea tridentata* in the Northern Chihuahuan desert. In *Larrea*. Editors E. C. Lopez, T. J. Mabry, and S. F. Tavizon, 139-51. Saltillo, Coah, Mexico: Centro de investigacion en Quimica Aplicada.

- Ludwig, John A., James F. Reynolds, and Paul D. Whitson. 1975. Size-biomass relations of several Chihuahuan Desert shrubs. *The American Midland Naturalist* 94, no. 2: 451-61.

Abstract: Rapid, nondestructive methods are needed to quantify plant biomass dynamics. Methods known as dimension analysis can be used to establish regression relationships between plant biomass and

estimate the dry weight of foliage, living and dead stems and roots from canopy area and volume for eight desert shrubs. The results show that volume and canopy area are generally suitable estimators.

Regression equations developed for *Larrea tridentata* compare favorably with equations in similar studies in Arizona and Nevada, suggesting that our results might be applicable in other desert regions, at least for shrubs with well-defined growth forms. Other considerations when using these techniques are discussed.

Lunt, O. R., J. Letey, and S. B. Clark. 1973. Oxygen requirements for root growth in three species of desert shrubs. *Ecology* 54, no. 6: 1356-62.

Abstract: Shrubs of *Artemisia tridentata* and *Larrea tridentata* have unusually high oxygen requirements for root growth. Roots of *Franseria dumosa*, like many economic plants, need lesser amounts of oxygen. An oxygen diffusion rate of about $0.30 \text{ mg cm}^{-2} \text{ min}^{-1}$ is required by *Franseria* to achieve a root growth rate that is 50% of maximum at the experimental temperatures. The corresponding figures for *Artemisia* and *Larrea* are about 0.50 and 0.43, respectively. It is concluded that the general exclusion of *Larrea* and *Artemisia* from fine-textured and poorly drained soils in the desert is a reflection of their relatively high oxygen requirements for root growth.

Mabry, T. J., J. H. Hunziker, and D. R. DiFeo, Jr. 1977. *Larrea and its role in desert ecosystems*. Stroudsburg: Dowden, Hutchinson and Ross.

Mahall, B. E., and R. M. Callaway. 1991. Root communication among desert shrubs. *Proceedings of the National Academy of Science of the United States of America* 88: 874-76.

———. 1992. Root communication mechanisms and intracommunity distributions of two Mojave desert shrubs. *Ecology* 73, no. 6: 2145-51.

Abstract: Experimental studies using root observation chambers to observe the effects of encounters between individual roots on root elongation rates have revealed that the interactions among roots of *Ambrosia dumosa* and *Larrea tridentata* are more complex than simple competition for a limiting resource. *Larrea* roots inhibited elongation of either *Larrea* or *Ambrosia* roots in their vicinity, and *Ambrosia* roots inhibited elongation of contacted roots on other *Ambrosia* plants only. The purpose of the study reported here was to test the hypothesized involvement of inhibitory substances released by roots in these interroot encounters by attempting to remove such substances by adsorption to activated carbon. The presence of activity carbon caused a significant decrease in the inhibition of elongation of neighboring roots by *Larrea* roots, but activated carbon had no effect on the intraspecific responses of *Ambrosia* roots. These results support the hypotheses that the interaction mechanism of *Larrea* roots involves the release of a readily diffusible, generally inhibitory substance by *Larrea* roots into the soil, rather than a simple depletion of water or nutrients from around *Larrea* roots, and that the intraspecific, self-nonspecific-recognizing interaction mechanism of *Ambrosia* roots is mediated by contact and is fundamentally different from that of *Larrea*. These findings may enhance our understanding of Mojave desert community structure. The root-mediated allelopathy of *Larrea* may play a role in producing and maintaining the commonly occurring,

regular distributions of *Larrea*. The complex communication mechanism of *Ambrosia* roots appears to constitute a detection and avoidance system that may allow this shrub to grow in clumped intraspecific distributions with little or no intraspecific competition for water. The interspecific interference between *Larrea* and *Ambrosia* in the field may be mechanistically asymmetrical due to their different root communication mechanisms.

Marco, D. E., A. A. Calviño, and S. A. Páez. 2000. Patterns of flowering and fruiting in populations of *Larrea divaricata* in dry Chaco (Argentina). *Journal of Arid Environments* 44: 327-46.

Abstract: We analyzed the pattern of flower, fruit and seed production in three populations of *L. divaricata* occurring in three different habitats of the semi-arid Chaco Forest. Two populations occupied old forest areas replaced by scrublands after severe disturbances. The third population had been located in an undisturbed forest area since the beginning of this century. Both timing and production of flowers, fruits and seeds differed between the populations analysed during the sampling period. The forest population showed earlier reproduction and a fruit production comparable to or higher than the scrubland populations. The wide distribution of *L. divaricata* may be related to its ability to maintain its reproductive output in habitats with contrasting conditions.

Marshall, K. Anna. 1995. Korthuis, Sara Lynn. 1988. *Larrea tridentata*. U.S. Department of Agriculture, Forest Service Rocky Mountain Research Station Fire Sciences Laboratory. 2001. "Fire effects information system." Web page. Available at <http://www.fs.fed.us/database/feis/> .

Martinez-Meza, Ernesto. 1994. "Stemflow, throughfall, and root water channelization by three arid land shrubs in southern New Mexico." M.S. Thesis, New Mexico State University.

See abstract under *Flourensia cernua*

Martinez-Meza, E., and W. G. Whitford. 1996. Stemflow, throughfall and channelization of stemflow by roots in three Chihuahuan desert shrubs. *Journal of Arid Environments* 32: 271-87.

See abstract under *Flourensia cernua*

Martinez Turanzas, Gustavo Angel. 1993. "Effects of irrigation and drought on growth of *Larrea tridentata* [(DC) Cov.] and decomposition process in the northern Chihuahuan desert ." M. S. Thesis, New Mexico State University.

McCraw, D. J. 1985. "A phytogeographic history of *Larrea* in southwestern New Mexico illustrating the historical expansion of the Chihuahuan desert." M. A. Thesis, University of New Mexico.

Abstract: An unprecedented invasion of brush has overtaken the rangelands of the American southwest within the last century. Southwestern New Mexico is no exception as *Prosopis juliflora* (mesquite) and

Larrea divaricata ssp. *tridentata* (the creosotebush) now cover thousands of hectares of former desert grassland. It is considered to be the best Indicator species of the northern Chihuahuan Desert; thus, this research accounts for the historical expansion of the Chihuahuan Desert (via *Larrea*) into southwestern New Mexico. This involves describing both the phytogeographic history of desert scrub here and the causes and patterns (temporal and spatial) of historical *Larrea* invasion. Paleoecological data, obtained from 45 sites in Arizona, New Mexico, Texas, Chihuahua, Coahuila, and Durango, indicate that during the Wisconsinan, southwestern New Mexico was not desert at all, but was covered by mesic pinon-oak-Juniper woodlands. A desert taxa gradient is documented, trending from few to no desert scrub genera in New Mexico to 'pseudo-desert scrub-woodland' in Mexico and west Texas. During the early Holocene, the New Mexican woodlands become more xeric as pinon disappears and desert taxa move northward. Grasslands are established in southeastern Arizona by 11,000 BP and probably in southwestern New Mexico by 8,000 BP. The first major climatic change to arid conditions occurred between 5,000 and 4,000 BP. This coincides with the first arrivals of *Larrea* to the northwestern Chihuahuan Desert. Alternating mesic spells (3,000-2,500 BP and 1,100-500 BP) and xeric spells (4,000-3,300 BP, 2,500-1,100 BP, and present) most likely induced widespread expansions and contractions of desert scrub. The primeval vegetation of southwestern New Mexico is documented in historical journals and territorial survey field notes as widespread expanses of desert grassland with highly restricted nodes of *Larrea* desert scrub found on xeric, gravel-covered slopes. Of the 141 townships analyzed, only 15 report *Larrea* present, with an estimated primeval distribution of 122 km². The historical invasion of *Larrea* began around the turn of the twentieth century. The causes behind invasion are a combination of two primary factors: overgrazing and drought. During the 1890s, the rangelands were seriously overstocked and a drought, documented by both station precipitation data and Palmer Drought Severity Indices, took place during the period 1891-1904. As a result, resurveys from 69 of 101 townships analyzed describe *Larrea* present by 1919, covering an estimated 1,815 km². During the period 1920-1940, as preferred habitat sites (bajada slopes) were covered, *Larrea* began migrating downslope onto basin floors. Its expansion was greatest during this period (from 1,815 km² to an estimated 4,370 km² or 76% of its present distribution) due to a lag time effect. *Larrea* has continued to expand into the grasslands since 1940. This has, in effect, created a desert/desert grassland mosaic, or a transition zone surrounding the Chihuahuan Desert (*Larrea*-dominant communities). The present distribution of *Larrea* in southwestern New Mexico² covers approximately 5,775 km².

McGee, K. P., and D. L. Marshall. 1993. Effects of variable moisture availability on seed germination in three populations of *Larrea tridentata*. *American Midland Naturalist* 130: 75-82.

Abstract: During the past century the area of the southwestern United States dominated by creosote bush (*Larrea tridentata* (DC) Cov.) has increased substantially. Further expansion may be affected by changes in seed germination at the margins of the range due to environmental and population genetic effects. To evaluate this possibility, seeds from three populations (Isleta, Sevilleta, Jornada) on a 350 km North-South gradient, respectively, were planted at a common site in five different watering treatments. Germination differed significantly among both populations and treatments. Seeds receiving intermediate moisture fared best, whereas those receiving the most moisture fared worst. The Isleta seeds had the highest percentage of germination overall, suggesting that germination ability is not reduced at the northern margin of the range of the species in New Mexico. However, since these seeds were collected later than those of the other

populations, a subsequent experiment was performed to ascertain whether seed age influenced germination. For both the Jornada and the Sevilleta populations, freshly collected seeds had higher germination percentages than stored seeds. Thus, the differences among populations may be largely due to seed age. However, there were also significant differences among populations in the pattern of response to moisture, suggesting differentiation among populations along the North-South gradient.

Mead, R. 1966. A relationship between individual plant-spacing and yield. *Annals of Botany* 30: 301-9.

Meinzer, F. C., M. R. Sharifi, E. T. Nilsen, and P. W. Rundel. 1988. Effects of manipulation of water and nitrogen regime on the water relations of the desert shrub *Larrea tridentata*. *Oecologia* 77: 480-486.

Meinzer, F. C., C. S. Wisdom, A. Gonzalez-Coloma, P. W. Rundel, and L. M. Schultz. 1990. Effects of leaf resin on stomatal behaviour and gas exchange of *Larrea tridentata* (DC.) Cov. *Functional Ecology* 4: 579-84.
Abstract: Stomatal response to humidity and total gas exchange of untreated leaves of *Larrea tridentata* (DC.) Cov. were compared with those of leaves treated to remove most of their external resin by washing attached branches in an ethanol-water mixture. The ethanol-water mixture did not infiltrate the stomatal pores and produced no visible symptoms of tissue damage. Partial resin removal enhanced stomatal responsiveness to humidity in illuminated leaves and the responsiveness of leaf conductance to humidity in the dark. Diffusive conductances and transpiration of both illuminated and darkened leaves increased following resin removal. The net effect of resin removal on total gas exchange was to reduce water use efficiency by altering the coupling between assimilation and conductance. These results indicated that the resin behaved as an ideal antitranspirant because it diminished transpiration more than assimilation rates. Possible mechanisms for the responses to resin removal are discussed.

Metcalf, Orrick Baylor. 1904. "A study of the Atriplex and *Larrea* tension line in the Mesilla Valley, New Mexico ." M. S. Thesis, New Mexico State University.

Miller, Richard E., and Laura F. Huenneke. 1996. Size decline in *Larrea tridentata* (creosotebush). *The Southwestern Naturalist* 41, no. 3: 248-50.

Abstract: This study documents a dramatic decline in size of individuals within a *Larrea tridentata* population in southern New Mexico over a decade long period. It is most likely that the decline in size represents individual plants shrinking in size resulting from the death of shoot systems, especially the larger branches within these multi-stemmed shrubs. We suggest that the decline in size observed in our study area may be the initial stages of a more widespread phenomenon, driven by the desertification process that accompanies the conversion of grasslands into shrublands.

- . 2000a. Demographic variation in a desert shrub, *Larrea tridentata*, in response to a thinning treatment. *Journal of Arid Environments* 45: 315-23.

Abstract: We performed a perturbation experiment to determine the relative importance of intra-specific competition on the demographic performance of a population of creosotebush, *Larrea tridentata*. From 1992 to 1995, we following 1000 individuals, half of which were in plots subjected to a thinning treatment, and the other half were in unmanipulated plots. We found no significant response to the thinning treatment for any of the traits studied. The strict interpretation of these results is that intra-specific competition is not important in this *Larrea* population.

- . 2000b. The relationship between density and demographic variation within a population of *Larrea tridentata*. *The Southwestern Naturalist* 45, no. 3: 313-21.

Abstract: *Larrea tridentata* is a dominant desert shrub throughout the warm deserts of North America. We studied *Larrea* population we believed to be in the process of invading adjacent grasslands. To determine whether our hypothesis was correct we developed a set of predictions about characteristics of invading populations and examined the relationship between *Larrea* density and demographic variation. For an invading *Larrea* population we predicted that: 1) individuals in low density areas would exhibit attributes indicating higher intrinsic rates of increase--individuals would have greater fruit production, 2) individuals in high density areas would exhibit the effects of negative density-dependence--plants would have canopies in poor condition (with at least 20% dead branches) and be small in size, and 3) low density areas would be below carrying capacity--plots would have a lower total *Larrea* biomass than high density areas. We measured height, average width, canopy condition, and fruit set for 2,000 plants sampled from 40 plots varying in density. We also estimated the total *Larrea* biomass for each plot. We collected data on two measures of microenvironmental variation, cover of the common grassland species, and cover of gravel on the soil surface. All plant characters were significantly correlated with *Larrea* density and both measures of microenvironmental variation were significantly correlated with density. In contrast, results for total *Larrea* biomass did not conform to our prediction. Although the relationship between *Larrea* density and the plant characters supported our predictions for an invading *Larrea* population, results for total *Larrea* biomass did not. An alternative explanation that the pattern of demographic variation within the study population was determined by microenvironmental variations was more strongly supported.

- Molinero, Hugo Bruno. 1983. "Examination of field techniques for the estimation of above ground biomass on five Chihuahuan Desert shrub species." M.S. Thesis, New Mexico State University.

Abstract: A group of common Chihuahuan Desert shrubs having highly varied growth forms were studied in an attempt to see if standardized field measurement techniques could be used for the prediction of above ground biomass. The most efficient (best estimation for least time expenditure) field measurement was obtained for each species. It was found that the techniques yielded reliable results for plants which were of medium to large size for the species, but biomass predictions were unreliable from measurements made upon plants which were small (reproduction) for the species. It was found that it is not necessary to obtain volume or canopy area values to estimate biomass, but that single field measurements could be used. Formulas were developed for these measurements. The biomass of two species, *Larrea tridentata* and

Acacia constricta, which have growth forms resembling an inverted cone, could be most efficiently estimated using a single field measurement-internal height. In the case of two other species, *Gutierrezia sarothrae* and *Krameria parvifolia*, which tend to be more compact and regularly globose a single measurement-maximum diameter was the most efficient biomass estimator. External height measurements were found to be the best for *Flourensia cernua*.

Monson, R. K., and S. D. Smith. 1982. Seasonal water potential components of Sonoran desert plants. *Ecology* 63, no. 1: 113-23.

Abstract: Seasonal water potential components were measured for seven Sonoran Desert plant species representing a variety of growth forms. Three of the species (*Amsinckia intermedia*, *Erodium cicutarium*, and *Baccharis sarothroides*), which occupy the most mesic microhabitats, possessed the highest osmotic potentials and lowest pressure potentials, with very little seasonal adjustment in either parameter. In contrast, two species (*Larrea tridentata* and *Atriplex polycarpa*), which experienced substantial periods of water stress, had relatively low osmotic potentials and high pressure potentials with seasonal adjustments occurring in both. Two species (*Encelia farinosa* and *Olneya tesota*) exhibited intermediate responses for dawn plant water potential. *Encelia* also exhibited intermediate osmotic and pressure potential values. However, in *Olneya* these latter values were very similar to those for *Larrea* and *Atriplex*. The capacity for osmoregulation was noted in four of the seven species, with fluctuations in the osmotic potential at full turgor ranging from 0.3 to 0.8 MPa. Adjustments in tissue elasticity and pressure potential were also noted in four of the species. In general these adjustments allow the species to maintain higher turgor pressures at most relative water contents during periods of drought stress. The results indicate that a plant's capacity to avoid water stress is reflected in its water potential components.

Montaña, C., B. Cavagnaro, and O. Briones. 1995. Soil water use by co-existing shrubs and grasses in the Southern Chihuahuan Desert, Mexico. *Journal of Arid Environments* 31: 1-13.

See abstract under *Flourensia cernua*

Moorhead, Daryl L., James F. Reynolds, and Walter G. Whitford. 1986. A conceptual model of primary productivity, decomposition, and nitrogen cycling in the Chihuahuan creosotebush desert. *Tree Physiology* 2: 215-22.

Abstract: The conceptual framework for a simulation model of primary productivity, decomposition and nitrogen cycling in a shrub-dominated desert ecosystem in southern New Mexico is presented. This model is based on our previous attempt to simulate carbon allocation patterns in the desert shrub *Larrea tridentata* Cov., which demonstrated that moisture patterns alone are insufficient to predict desert productivity. These results, as well as others, suggest that mineral nutrients, especially nitrogen, may also be an important determinant of productivity in arid environments. Our current research in the Chihuahuan desert is directed towards elucidating the numerous biotic and abiotic interactions that determine the rates and directions of carbon, nitrogen and water fluxes in this ecosystem. The development of this working model will serve as a tool to accomplish three major objectives: (1) to

synthesize the large amounts of existing data on decomposition and nitrogen cycling in deserts, (2) to quantify our present state of knowledge about the structure and function of ecosystem components important in carbon and nitrogen dynamics in deserts, and (3) to address hypotheses concerning the complex mechanisms of interactions and feedbacks among the organisms involved in carbon and nitrogen exchanges in deserts.

Muller, Cornelius H. 1940. Plant succession in the *Larrea-Flourensia* climax. *Ecology* 21, no. 2: 206-12.

Abstract: The *Larrea-Flourensia* Desert Scrub is a widespread and relatively homogeneous community common to the central continental areas of the southwestern United States and northern Mexico. Its significance in the classification of plant communities is vastly different from those of other North American communities. The present paper is intended to present the problem in the light of investigations carried out on a selected site in western Texas. Study was begun in 1931, was continued in 1932 and 1933, and was reviewed in 1939. The successively denuded and covered Tornillo Clay beds were chosen for study because of their extremely unfavorable conditions for plant growth.

The denuding of clay and its subsequent mixture with pervious soil carries an area through the following stages of retrogressive and progressive succession:

1. Original climax *Larrea-Flourensia* Desert Scrub with which are associated many xeric shrub and herb species, occupying unbroken sandy or gravelly soil.
2. Sparse remnants of the more xeric shrubs and shallow-rooted grasses on soil a foot or less in depth above the impervious clay.
3. Last relicts of grasses on shallow remnants of soil on denuded clay.
4. No plant growth at all on bare, impervious clay.
5. Shallow-rooted grasses, the first invaders of weathered clay with a thin cover of washed-in sand and rubble.
6. Sparse shrubs tolerant of soil a foot deep on clay.
7. Dense shrubs of all species on well covered clay of rough topography.
8. Sparse representation of *Larrea-Flourensia* Desert Scrub on the new plain of immature soil at the base level of the erosion system.
9. Typical climax *Larrea-Flourensia* Desert Scrub on base level plains of mature soil.

In the succession described above, this vegetation type is exposed to the more extreme disturbance, but the result is not a succession in the sense of Weaver and Clements. Only species comprising the original desert scrub are found in the disturbed areas, and as soon as the soil is capable of supporting a cover of plants, the original vegetation type appears in scarcely modified form. In the strict sense there is no succession in *Larrea-Flourensia* Desert Scrub. To distinguish between those vegetation types which are relatively unstable climaxes and those, such as *Larrea-Flourensia* Desert Scrub, which are highly stable, it is here proposed that the latter be called *super-climax*. To this class of vegetation types belong all those communities which, upon being profoundly disturbed, are replaced by their original component species and thereby directly form a community ecologically (as well as floristically) equal to the original vegetation.

Musick, Hugh Bradley. 1977. "The physiological basis of calcicolity of *Larrea tridentata*." Ph. D. Dissertation, University of Arizona.

Abstract: The distribution of *Larrea divaricata* Cav. in relation to soil CaCO_3 was examined in a portion of the Walnut Gulch Experimental Watershed, near Tombstone in southeastern Arizona. Although moderately frequent on calcareous soils, *L. divaricata* was extremely rare on soils with non-calcareous,

slightly acid to circumneutral surface horizons. Some mechanisms that might account for the exclusion of *L. divaricata* from non-calcareous soils were investigated. Soil CO₂ concentrations during the summer rainy season tended to be slightly higher in non-calcareous soils than in calcareous soils, but did not exceed 0.41%. In solution culture, 1% CO₂ at pH 6, pH 7, or pH 8 had no significant effect on root length of seedlings seven days old. Root elongation during the first three days appeared to be inhibited by high HCO₃ concentrations, produced either by high pH or by high CO₂ concentrations. Carbon dioxide toxicity cannot account for exclusion of *L. divaricata* from non-calcareous soils. Cotyledon necrosis and seedling mortality occurred after 1-2 wk in solution culture at pH 6, but not at pH 8. The nature of this pH effect in solution culture was investigated in order to predict the likelihood of such an effect in the field. Necrosis was apparently caused by toxic accumulations of P in the cotyledons. At pH 6, P concentrations as low as 10 μM in solution resulted in P toxicity, owing primarily to the extremely high P uptake rate, 52 μmol (g fresh root wt)⁻¹ day⁻¹. Increasing pH to 8 decreased P uptake per unit root weight by 69-86%, and thus increased the solution P level necessary for toxicity. Slow growth and an ample supply of P from the seed contributed to early development of P toxicity when uptake rates were high and also enabled seedlings with no external supply to avoid P deficiency for 3-4 wk after germination.

Nelson, J. T., and C. Vick. 1988. Chemical control of mesquite, creosotebush, and catclaw mimosa with tebuthiuron and subsequent grass production. *Texas Journal of Agriculture and Natural Resources* 2 : 30-32.

See abstract under *Prosopis glandulosa*

Neufeld, Howard S., Frederick C. Meinzer, Charles S. Wisdom, M. Rasoul Sharifi, Philip W. Rundel, Mollie S. Neufeld, Yoram Goldring, and Gary L. Cunningham. 1988. Canopy architecture of *Larrea tridentata* (D. C.) Cov., a desert shrub: foliage orientation and direct beam radiation interception. *Oecologia (Berlin)* 75: 54-60.

Abstract: At sites in the United States, creosote bushes (*Larrea tridentata* (DC.) Cov.) orient foliage clusters predominantly toward the southeast. Foliage of bushes at the southernmost distribution extreme in Mexico shows no predominant orientation. Clusters at all sites are inclined between 33 degrees and 71 degrees from the horizontal. Inclinations are steeper in the drier and hotter Mojave Desert than in the Chihuahuan Desert. Individual leaflets, though not measured, appear more randomly oriented than foliage clusters. In several populations studied, branches were shorter in the southeastern sectors of the crown, reducing self-shading early in the morning. Measurements of direct beam radiation interception by detached branches, using digital image processing, indicated that foliage clusters oriented toward the southeast exhibited less self-shading during spring mornings than clusters oriented northeast. This effect was not apparent at the summer solstice. This type of canopy architecture may tend to minimize self-shading during the morning hours when conditions are more favorable for photosynthesis, resulting in an improved daily water use efficiency.

Oechel, W. C., B. R. Strain, and W. R. Odening. 1972. Tissue water potential, photosynthesis, ^{14}C -labeled photosynthate utilization, and growth in the desert shrub *Larrea divaricata* Cav. *Ecological Monographs* 42, no. 2: 127-41.

Abstract: Tissue water potential is the most important factor throughout the seasons controlling phenological events, photosynthesis, and productivity of *Larrea divaricata* growing in Deep Canyon near Palm Desert, California. Growth of reproductive structures was initiated at the time of highest tissue water potential and ceased as water potential decreased. Percentage foliation correlated strongly with dawn water potential ($r = 0.89$). The elongation rate of stems and the rate of node production were both dependent on tissue water potential. Leaf growth and node growth proceeded at varying rates throughout the year, providing a continuous sink for photosynthates. Photosynthesis rates ranged from 9.02 mg CO_2 incorporated per day per gram dry weight of leaf tissue in September to an estimated 74.7 mg CO_2 in early February. Net photosynthesis and relative productivity correlated very strongly with dawn water potential ($r = 0.93$ and $r = 0.97$, respectively). *Larrea* plants were labeled at 1- to 2-month intervals with photosynthetically incorporated $^{14}\text{CO}_2$ to determine the utilization in growth and storage of photosynthate fractions produced at various times throughout the year. Tissue was subsampled at similar intervals, and the activity in various metabolic compounds (sugar, starch, lipid, organic acid, amino acid, protein, cellulose, and cell-wall materials) was analyzed. The utilization of photosynthates in the various fractions was similar in all seasons. No appreciable mobilization into and out of storage materials was apparent. Never dormant, *Larrea* remains metabolically active and forms new tissue throughout the year. This growth pattern may be an important adaptation allowing *Larrea* to exist in a wide range of geographical and climatic areas, and, perhaps owing to the species' tropical affinities, it might have been a preadaptation to the desert environment.

Parker, J. M. 1982. "Soil and plant characteristics at five creosotebush (*Larrea tridentata* (DC.) Cov.) sites in three North American Deserts." M. S. Thesis, University of Arizona.

Phillips, D. L., and J. A. MacMahon. 1981. Competition and spacing patterns in desert shrubs. *Journal of Ecology* 69: 97-115.

Abstract: (1) Spacing patterns of shrubs were studied on a series of sites in the Mojave and Sonoran Deserts. Both aggregation and regularity in dispersion of individual shrubs were fairly common. Aggregation may result from vegetative reproduction or environmental heterogeneity, and regularity from competition among plants. (2) Small shrubs tend to be clumped, medium-sized ones tend to a random arrangement, and large shrubs tend to a regular pattern. This suggests the increasing importance of competition as the plants grow. (3) Further evidence of interference between plants was provided by the correlations of plant size with the distance to their neighbours. (4) Root systems were extensive enough to abut or overlap each other in the interplant spaces. (5) Most plants tended to have neighbours of the same species rather than other species. (6) None of these results depended on position along the considerable climatic gradients across the Mojave and Sonoran Deserts.

Pockman, W. T., and J. S. Sperry. 1997. Freezing-induced xylem cavitation and the northern limit of *Larrea tridentata*. *Oecologia* 109: 19-27.

Abstract: We investigated the occurrence of freezing-induced cavitation in the evergreen desert shrub *Larrea tridentata* and compared it to co-occurring, winter-deciduous *Prosopis velutina*. Field measurements indicated that xylem sap in *L. tridentata* froze at temperatures below c. -5°C , and that this caused no measurable cavitation for minimum temperatures above -7°C . During the same period *P. velutina* cavitated almost completely. In the laboratory, we cooled stems of *L. tridentata* to temperatures ranging from -5 to -20°C , held them at temperature for 1 or 12 h, thawed the stems at a constant rate and measured cavitation by the decrease in hydraulic conductivity of stem segments. As observed in the field, freezing exotherms occurred at temperatures between -6.5 and -9°C and as long as temperatures were held above -11°C there was no change in hydraulic conductivity after thawing. However, when stems were cooled to between -11°C and -20°C , stem hydraulic conductivity decreased linearly with minimum temperature. Minimum temperatures between -16 and -20°C were sufficient to completely eliminate hydraulic conductance. Record (>20 year) minimum isotherms in this same range of temperatures corresponded closely with the northern limit of *L. tridentata* in the Mojave and Sonoran deserts.

Reynolds, James F. 1986. Adaptive strategies of desert shrubs with special reference to the creosotebush (*Larrea tridentata* [DC] Cov.). In *Pattern and process in desert ecosystems*. Editor W. G. Whitford, 19-49. Albuquerque, New Mexico: University of New Mexico Press.

Abstract: In this paper, my objective is, first, to discuss the biology of the creosotebush in terms of a static definition of its adaptive strategy, and, second, to present an overview of the approach that we're using to model the dynamic features of the adaptive strategy of *Larrea* in the Chihuahuan Desert. The value of the approach for hypothesis testing will be evaluated with regard to its potential as a tool for increasing our understanding of plant adaptations in arid environments.

Reynolds, James F., and Gary L. Cunningham. 1979. Modeling primary production in *Larrea tridentata* (DC.) Cov. In *Larrea. Serie del desierto*. 2 Editors E. C. Lopez, T. J. Mabry, and S. F. Tavizon, 181-215. Saltillo, Coah, Mexico: Centro de investigacion en quimica aplicada.

———. 1981. Validation of primary production model of the desert shrub *Larrea tridentata* using soil-moisture augmentation experiments. *Oecologia* 51: 357-63.

Abstract: In previous papers we have described and verified a primary production model of the desert shrub *Larrea tridentata*. Here we address the validation phase of the evaluation of this model. Two versions of the model which differ in the priority scheme used for allocating carbon to reproductive or vegetative organs were compared on the basis of their usefulness and reliability over a range of soil-moisture conditions. Over an entire growing season when soil-moisture conditions were near "normal" both versions of the model were adequate predictors of total above-ground vegetative growth and one was an adequate predictor of reproductive growth as well. A more detailed analysis revealed that the versions varied in the range of soil-moisture conditions over which they were adequate and that neither was

adequate when soil-moisture had remained high for extended periods. The validation process has revealed some likely areas for model improvement to increase adequacy.

Reynolds, J. F., G. L. Cunningham, and J. P. Syvertsen. 1979. A net CO₂ exchange model for *Larrea tridentata*. *Photosynthetica* 13, no. 3: 279-86.

Abstract: A net CO₂ exchange model for the warm desert evergreen perennial *Larrea tridentata* (DC) Cov. (creosotebush) was developed using the modeling approach of Reed *et al.* (1976) for the temperate deciduous tree *Liriodendron tulipifera* L. The approach was very successful using gas exchange measurements on environment chamber-grown *Larrea tridentata* and hence this approach may have side applicability and versatility for photosynthesis modeling.

Reynolds, J. F., B. R. Strain, G. L. Cunningham, and K. R. Knoerr. 1980. Predicting primary productivity for forest and desert ecosystem models. In *Predicting photosynthesis for ecosystem models*. Editors J. D. Hesketh, and J. W. Jones, 169-207. Vol. II. Boca Raton, Florida: CRC Press, Inc.

Abstract: A major goal of the Analysis of Ecosystems Program of the U.S. International Biological Program (IBP) was to understand how entire ecosystems function so that their behavior, particularly in response to man-made stresses, might be predictable. A significant part of the research was focused on increasing our knowledge of productivity in natural ecosystems. Productivity was broadly defined so as to include not only energy flux within the trophic structure of the ecosystem but also the attendant water and nutrient fluxes. A major component of the research design in each of the various IBP Biome projects (i.e., grassland, desert, tundra, and deciduous and coniferous forests) was the development of ecosystem-level models of energy and material fluxes.

Reynolds, James F., Ross A. Virginia, Paul R. Kemp, Amrita G. De Soyza, and David C. Tremmel. 1999. Impact of drought on desert shrubs: Effects of seasonality and degree of resource island development. *Ecological Monographs* 69, no. 1: 69-106.

Abstract: Large areas of semiarid grasslands in the southwestern United States have been virtually replaced by shrubs during the past century. Understanding the causes and consequences of such vegetation dynamics requires that we elucidate the interplay between external forces of change (e.g., climate, human impacts) and the internal forces within these ecosystems that foster resilience and/or stability. Several conceptual models of arid ecosystems address this interplay by including the potential role of autogenic shrub effects on ecosystem processes, which lead to the formation of "resource islands" and tend to promote shrub persistence. Specifically, during the process of shrub establishment and maturation, the cycling of nutrients is progressively confined to the zones of litter accumulation beneath shrubs, while bare intershrub spaces become increasingly nutrient poor. As shrub resource islands develop, there is increased interception and stemflow by shrub canopies, confining infiltration of nutrient-enriched rainfall directly beneath the shrubs; the barren intershrub spaces generate overland flow, soil erosion by wind and water, and nutrient losses. These islands are preferred sites for the regeneration of shrubs and herbaceous plants and are correlated with spatial variation in soil microbial populations and soil microfauna that promote

nutrient cycling. If further changes in the transition between grassland and shrubland are to be correctly predicted-or if we wish to intervene and redirect transitions-we must develop a greater mechanistic understanding of the structural and functional relationships between shrubs and the resource islands associated with them. We conducted a 3-yr field study in the Jornada Basin of southern New Mexico to explore the relationships between seasonal manipulations of soil water and its impact on soil nutrient dynamics of resource islands and shrub growth and physiology. At our study site, where total annual precipitation is approx 230 mm (approx 65% falls during the summer period), we simulated seasonal drought in summer (1 June-30 September) and winter/spring (1 October-31 May) by constructing large rainfall-exclusion shelters over shrub resource islands at different stages of development. Our experiment tests two principal hypotheses. The first is that the two major shrub species in the Jornada Basin, creosotebush (*Larrea tridentata*) and mesquite (*Prosopis glandulosa*), have different growth phenologies, rooting patterns, and physiological responses to resource availability (primarily water). The second is that different size classes of shrubs ("small" and "large") represent distinct stages of resource island development (i.e., "young" and "mature," respectively) and, hence, different stabilities-that is, as islands develop, their associated shrubs become less coupled to short-term fluctuations in precipitation and more resistant to long-term drought or climate shifts. With regard to the first hypothesis, we conclude that the two species are relatively similar in function despite the different phenological "strategies" of *Larrea* (evergreen) and *Prosopis* (winter deciduous). In the absence of drought, both species exhibited maximal rates of shoot and root growth, as well as high photosynthesis and transpiration, in late spring. This remained as the period for maximal growth and physiological activity for *Prosopis* shrubs that experienced drought in either summer or winter/spring. On the other hand, *Larrea* shrubs that experienced drought in winter/spring had maximal growth and activity shifted to the summer period, and in the absence of drought, *Larrea* shrubs also exhibited high physiological activity during the summer (especially following high rainfall). Thus, *Larrea* appears to have a greater capacity for shifting its activity patterns to alternate periods to take advantage of changes in resource availability. Shrubs of both species appeared well adapted to withstand season-long droughts. Mechanisms for survival include the following capacities: (1) to shift growth and physiological activity to utilize different temporal moisture (*Larrea*); (2) to utilize different levels of soil water (both species); (3) to carry out limited physiological activity and growth during drought (especially *Larrea*); and (4) to compensate for some negative impacts of drought through enhanced physiology (especially *Prosopis*) and growth (especially *Larrea*) in the season following drought. With regard to the second hypothesis, we again found more similarities than differences between the different aged (young vs. mature) islands. The stage of maturity of a resource island complex did not seem to be a significant factor to the growth and physiological activity of the shrub.

Rice, Patricia May. 1993. "Estimating and modelling stemflow and throughfall on creosote (*Larrea tridentata*) in an arid environment." M.S. Thesis, New Mexico State University.

Abstract: Creosote bush (*Larrea tridentata*) is one of the most common plants in the desert southwestern United States. The purpose of this study was to estimate stemflow and throughfall percentages, try to predict stemflow values, observe whether or not dryfall adds significantly to the ionic nutrients in stemflow, and to explore the relationship between branch angle and percentage of stemflow in an arid environment. To address these concerns several methods including calculating percentages, multiple

regression, and paired t-tests were employed. It was found that the average stemflow rate was 16.8 percent while the average throughfall rate was 64.7 percent. The multiple regression produced several important variables in predicting stemflow including mean branch angle, mean branch length, total branch surface area, and canopy area. It seemed obvious during the analysis that several important variables were not included since they were unavailable. It was shown that dryfall does add significantly to the ionic nutrients in stemflow, especially nitrogen which is the most important nutrient for desert plants. No highly significant relationships was found in this study between branch angle and percentage of stemflow.

Rivera, R. L., and E. C. Freeman. 1979. The effects of some alternating temperatures on germination of creosotebush (*Larrea tridentata* [D.C.] Cov.: Zygophyllaceae). *Southwestern Naturalist* 24: 711-14.
Abstract: Creosotebush is the most common shrub in the hot deserts of southwestern North America. Yet despite its great importance, we still have little understanding of factors which control its distribution. Unlike many xerophytic desert perennials, creosotebush appears to reproduce primarily by sexual means. Barbour (Ecology 49:915-923, 1968) found that germination of creosotebush was readily accomplished in the laboratory and he conducted an extensive study to determine how various constant temperatures affected seed germination. He found the optimum to be 23° C and that germination did not occur at 40° C. In addition, he determined that populations did not vary in their germination responses across the range of the species in the United States. His finding gave rise to this study. While germination data in response to constant temperature are interesting, it is obvious that they do not approximate the fluctuating temperatures experienced by seeds in the soil under field conditions. We wanted to determine what effects fluctuating temperatures similar to those experienced during the late summer rainy season of the Chihuahuan Desert would have on creosotebush germination.

Rossi, B. E., G. O. Debandi, I. E. Peralta, and E. Martinez Palle. 1999. Comparative phenology and floral patterns of *Larrea* species (Zygophyllaceae) in the Monte desert (Mendoza, Argentina). *Journal of Arid Environments* 43: 213-26.

Abstract: Phenological patterns and floral stages are described for *Larrea divaricata*, *L. cuneifolia*, and *L. nitida* in the Monte desert. In addition, floral structures and their relation to self-pollination levels are compared. Rainfall events and/or microclimatic conditions resulted in phenological differences between sites and years. Seven floral stages were determined and protogyny was detected in the early stages. *Larrea divaricata*, *L. cuneifolia* and *L. nitida* were observed to have a range of large to small floral structure sizes, respectively. This coincides with an increase of autogamy, while at the same time an increase in the percentage of flowers with protogyny.

Rundel, P. W., and R. M. Sharifi. 1993. Carbon isotope discrimination and resource availability in the desert shrub *Larrea tridentata*. In *Stable isotopes and plant carbon/water relations*. Editors James R. Ehleringer, Anthony E. Hall, and Graham D. Farquhar, 173-85. San Diego: Academic Press.

Abstract: Patterns of distribution of $\delta^{13}\text{C}$ in leaf tissues of *L. tridentata* demonstrate a strong genetic component to the control of gas exchange parameters and thus W in this species. Our analyses of multiple

populations of *L. tridentata* have found a relatively small degree of variation in $\delta^{13}\text{C}$ and thus W despite substantial differences in water availability and, seasonality among these sites (Fig. 11). Values of $\delta^{13}\text{C}$ in leaf tissues range from -21.6 to 25.8‰ in our samples of individual shrubs from these regions in years with normal precipitation. For the Sonoran and Mojave Deserts where our sample sizes are larger, intrapopulation variation in $\delta^{13}\text{C}$ was often as great as interpopulation differences. Roadside shrubs, which grow many times larger because of improved water relations, were not significantly different in $\delta^{13}\text{C}$ from adjacent populations of *Larrea* away from the road (Fig. 11). We have observed no significant change in $\delta^{13}\text{C}$ among *Larrea* shrubs, across substantial environmental gradients of water availability from wash woodland to rocky bajada. There is also an evident phenotypic component of physiological response to short-term changes in water availability brought on by drought or augmented water resources. Under natural conditions of multiyear drought we have observed a phenotypic plasticity in the physiological nature of gas exchange characteristics of *Larrea* sufficient to increase mean $\delta^{13}\text{C}$ value 2-3‰. Similarly, field plants have responded to irrigation over 2 years by decreasing $\delta^{13}\text{C}$ value 2-3‰ in field plants and water-use efficiency declined. Despite the strong linear relationship between assimilation and conductance over substantial changes in environmental condition the relative homeostasis in gas exchange characteristics and W in *L. tridentata* under controlled-growth experiments changed greatly from that in the field. The $\delta^{13}\text{C}$ ratio of drought-stressed greenhouse plants was comparable to that of irrigated plants in the field; while well-watered greenhouse plants had much more negative values of $\delta^{13}\text{C}$ (Fig. 11). Thus the phenotypic plasticity of W and $\delta^{13}\text{C}$ under greenhouse and growth chamber conditions extended far beyond that encountered in the field. These data suggest the importance of understanding of phenotypic components of water-use efficiency in plant species. Despite a relatively conservative response to gradients of water availability under field conditions; *L. tridentata* has a broad potential for phenotypic flexibility in changing W .

Runyon, Ernest H. 1934. The organization of the creosote bush with respect to drought. *Ecology* 15, no. 2: 28-138.

Abstract: 1. The creosote bush, the most successful and conspicuous xerophyte in the desert regions of North America, thrives on abundant water.

2. The reactions to changes in the water supply involve striking changes in the density and color of the foliage, and a peculiar difference in branching.

3. The leaves are distinguished by no extreme xeromorphism, and yet they are in part persistent throughout the driest seasons.

4. Leaves of plants in dry and in moist soil have the same structure.

5. Leaves which successfully endure the most prolonged and severe drought are only partially grown.

6. The dormancy of these leaves is not complete; they show the unique ability of resuming growth and activity after return of favorable conditions.

7. One factor in the drought resistance of *Larrea* leaves may be the hardening of resinous substances which occur on and within the epidermal cells.

Sakakibara, M., D. DiFeo Jr., N. Nakatani, B. N. Timmermann, and T. J. Mabry. 1976. Flavonoid methyl ethers on the external leaf surface of *Larrea tridentata* and *L. divaricata*. *Phytochemistry* 15: 727-31.

Abstract: The external phenolic resin on the leaves of *Larrea tridentata* contains eighteen flavone and flavonol aglycones (mostly as methyl ethers) one dihydroflavonol and two lignans (including nordihydroguaiaretic acid). Except for a few isolated 2n populations which exhibited minor differences, a single chemical type was observed for all three ploidy levels (2n, 4n and 6n) in the North American *L. tridentata* suggesting an autopolyploid origin for the tetraploid and hexaploid races. The resin chemistry of the North American taxon was most similar to that of the Argentinian diploid *L. divaricata*, although the resin of the latter taxon did not contain the three 8-hydroxyflavonols; however, 8-hydroxyflavonol aglycones were detected in Peruvian populations of *L. divaricata*.

Sakakibara, M., and T. J. Mabry. 1975. A new 8-hydroxyflavonol from *Larrea tridentata*. *Phytochemistry* 14: 2097-98.

Sakakibara, M., B. N. Timmermann, N. Nakatani, H. Waldrum, and T. J. Mabry. 1975. New 8-hydroxyflavonols from *Larrea tridentata*. *Phytochemistry* 14: 849-51.

Sammis, T. W., and L. W. Gay. 1979. Evapotranspiration from an arid zone plant community. *Journal of Arid Environments* 2: 313-21.

Abstract: The 1-year water loss from a weighing lysimeter containing a large creosotebush (*Larrea tridentata* (DC) Cav.) was 259 mm at a Sonoran desert site near Tucson, Arizona. The loss from an adjacent stand of creosotebush totalled 242 mm, and that from bare soil plots was 231 mm. The three loss estimates were in good agreement with measured annual precipitation of 234 mm. Transpiration made up only 7 per cent of the loss from the lysimeter according to a simplified diffusion model. There was no deep drainage or runoff, so the remaining losses were by evaporation from the soil surface.

Sanderson, Steven H. 1980. "Creosotebush seed production and viability following herbicide treatment." M.S. Thesis, New Mexico State University.

Abstract: The flower, green and mature schizocarp (fruit) production, and germination responses of creosotebush (*Larrea tridentata* (DC) Cov.) treated with four levels of three different herbicides were evaluated in this study. Additional data analyzed included herbivory on mature schizocarps and from other studies being conducted on the study site creosotebush mortality.

This research was undertaken to assess the effect of low levels of herbicide, 0.28, 0.56 and 0.84 kilogram per hectare on creosotebush seed viability and fruit production. It asserts that if creosotebush were not totally removed, it could increase in density due to herbicide response or reinfest areas where herbicides have been used.

Herbicide levels were found to differ significantly throughout this study, with the exception of the herbivory data. Flower, green and mature schizocarp productions were negatively correlated and creosotebush germination and death were positively correlated to herbicide levels.

In this study, creosotebush demonstrated significantly progressive increases in seed viability for the 0.00, 0.28 and 0.56 kilogram per hectare herbicide level.

Saunier, Richard E. 1967. "Geographic variability of creosotebush (*Larrea tridentata* (D.C.) Cov.) in response to moisture and temperature stress." Ph. D. Dissertation, University of Arizona.

Schlesinger, W. H., A. D. Abrahams, A. J. Parsons, and J. Wainwright. 1999. Nutrient losses in runoff from grassland and shrubland habitats in Southern New Mexico: I. rainfall simulation experiments. *Biogeochemistry* 45: 21-34.

Schlesinger, W. H., P. J. Fonteyn, and G. M. Marion. 1987. Soil moisture content and plant transpiration in the Chihuahuan desert of New Mexico. *Journal of Arid Environments* 12: 119-26.

Schlesinger, William H., Jane A. Raikes, Anne E. Hartley, and Anne F. Cross. 1996. On the spatial pattern of soil nutrients in desert ecosystems. *Ecology* 77, no. 2: 364-74.

Abstract: We examined the spatial distribution of soil nutrients in desert ecosystems of the southwestern United States to test the hypothesis that the invasion of semiarid grasslands by desert shrubs is associated with the development of "islands of fertility" under shrubs. In grasslands of the Chihuahuan Desert of New Mexico, 35-76% of the variation in soil N was found at distances <20 cm, which may be due to local accumulations of soil N under *Bouteloua eriopoda*, a perennial bunchgrass. The remaining variance is found over distances extending to 7 m, which is unlikely to be related to nutrient cycling by grasses. In adjacent shrublands, in which *Larrea tridentata* has replaced these grasses over the last century, soil N is more concentrated under shrubs and autocorrelated over distances extending 1.0-3.0 m, similar to mean shrub size and reflecting local nutrient cycling by shrubs. A similar pattern was seen in the shrublands of the Mojave Desert of California. Soil PO₄, Cl, SO₄, and K also accumulate under desert shrubs, whereas Rb, Na, Li, Ca, Mg, and Sr are usually more concentrated in the intershrub spaces. Changes in the distribution of soil properties may be a useful index of desertification in arid and semiarid grasslands worldwide.

Sharifi, M. Rasoul, Arthur C. Gibson, and Philip W. Rundel. 1999. Phenological and physiological responses of heavily dusted creosote bush (*Larrea tridentata*) to summer irrigation in the Mojave Desert. *Flora Jena* 194, no. 4: 369-78.

Abstract: In the Mojave Desert, numerous human activities damage soil structure, often resulting in increased wind erosion and deposition of dust on plant leaves. Especially susceptible to dust coating are the resinous, evergreen leaves of the dominant creosote bush (*Larrea tridentata*) wherever these shrubs grow along unpaved roads and trails and at the margins of dry playas. A yearlong field study was conducted, begun during summer drought, to investigate effects of summer irrigation on heavily dusted plants of *L. tridentata*. Plant water relations, quantitative phenology, and gas exchange were monitored for sets of five

plants under three conditions: dusted nonirrigated, dusted irrigated, and undusted nonirrigated (control). Following watering, dusted irrigated plants experienced rapid shoot growth and had significantly higher predawn shoot water potentials ($\psi = -2.5$ MPa) than dusted nonirrigated plants (-5.5 MPa), and midday values were -3.1 to -4.1 MPa versus -5.5 to -6.4 MPa, respectively. For dusted plants, irrigation resulted in marked increases of assimilation (14.0 versus 1.24 $\mu\text{mol m}^{-2} \text{s}^{-1}$), stomatal conductance (0.19 versus 0.03 $\text{mol m}^{-2} \text{s}^{-1}$), and linear growth, and accompanying new growth the old, dusted leaves were mostly abscised. All measures of water-use efficiency (WUE) were higher in controls than in dusted plants, and during the summer, dust was associated with a 40-90% reduction in shoot growth. Nonirrigated controls showed much greater water stress than dusted irrigated plants, but when irrigation was discontinued, the formerly irrigated plants rapidly converged on the physiological and phenological characteristics of not watered control plants. Dust deposition may reduce plant carbon gain by decreasing WUE and impairing tolerance of water stress. This experiment demonstrated that creosote bushes can recover rapidly from acute heavy dust deposition if irrigation, simulating heavy summer rainfall, is provided, and these results may be useful in measures to minimize the ecological impact of human activities in desert ecosystems.

Sharifi, M. R., F. C. Meinzer, E. T. Nilsen, P. W. Rundel, R. A. Virginia, W. M. Jarrell, D. J. Herman, and P. C. Clark. 1988. Effect of manipulation of water and nitrogen supplies on the quantitative phenology of *Larrea tridentata* (Creosote bush) in the Sonoran desert of California. *American Journal of Botany* 75: 1163-74. Abstract: Two years of water and nitrogen augmentation experiments on *Larrea tridentata* (creosote bush) were carried out in a southern Californian warm desert wash plant community. Treatments consisted of control (C), water (W), water and soil nitrogen (W + SN), and soil nitrogen (SN). Quantitative phenological data and microclimatic measurements were collected prior to the onset of and during the growth period and treatments. Predawn and midday water potentials were lower in nonirrigated than irrigated individuals. Leaf conductance was higher in irrigated than in nonirrigated shrubs, with a maximum difference of 1 cm s^{-1} observed in July 1984 under relatively low vapor pressure deficit conditions. Leaf production rates were significantly higher in the irrigated (W and W + SN) treatments than in the nonirrigated (C and SN) treatments in 1984. Addition of soil nitrogen caused no increased in vegetative growth rates in 1984. In 1985, a drier year, there was only minimal growth during the spring and summer growth periods in the nonirrigated treatments, while the W and W + SN treatments resulted in significantly higher leaf and shoot growth rates. Growth rates in 1985 were significantly higher in the W + SN treatment than in the W treatment. Reproductive growth was higher in the nonirrigated than the irrigated treatments, with the lowest reproductive activity noted in the W treatment.

Shellhorn, S. J. 1955. "Studies on the seedling anatomy of *Larrea tridentata*." M. S. Thesis, University of Arizona. Abstract: 1. The anatomy of 28-hour seedlings of *Larrea tridentata* was studied in detail and in certain instances their structure was compared to that of older plant material. 2. *Larrea* seed was harvested by shaking the plants and collecting the capsules and foreign material on a canvas. The *Larrea* seed appeared to exhibit little, if any, temporary dormancy. Immediate germination resulted when these seeds were placed in a moist chamber on a hot plate at 37°C . 3. A compact pressure chamber was developed for use in the wax infiltration process of the paraffin method. This pressure chamber can be placed directly in the

oven. 4. A special extended staining schedule was worked out for seedling material. Brilliant stains were obtained, with clear definition of cell structure. 5. A planing method for sectioning mature woody structures of *Larrea* was developed. By this method, both longitudinal and transverse sections of old wood (up to 2 cm. diameter) can be processed from specimen to a finished slide in about one hour. 6. A special abbreviated staining schedule involving a low safranin concentration was developed for *Larrea* mature wood. Brilliant colors and clear definition of structures was obtained. 7. During germination the radicle emerged in 6 to 10 hours. Early development involved mostly root tissue followed by rapid elongation of the hypocotyl after the 30-hour stage. Cotyledon expansion was not completed until about 7 to 8 days. An average 240-hour plant had a 6 cm. root, a 3 cm. hypocotyl, and two cotyledons 1.3 cm. in length. 8. Three groups of initial cells in the root apex gave rise to the central cylinder, the cortex, and the protoderm and root cap. The earliest differentiated structures in the central cylinder were two ducts in the primary phloem next to the pericycle. These ducts were alternate with and parallel to the diarch protoxylem which matured later. Formation of these ducts occurred by the breakdown and dissolution of cell end walls and protoplasts. 9. Hypocotyl development in 28-hour material was root-like up to the basal end of the cotyledons. Root-hypocotyl-cotyledon transition occurred after the 42-hour stage and appeared complete in 240-hour material. 10. Each protoxylem element was completely developed and continuous from a short distance back of the root apex to the edge of expanding cotyledons. Protoxylem points were on the same radii as the cotyledons and consisted of three or four elements. 11. Metaxylem development was exarch in the root and lower hypocotyl and endarch in the cotyledons. It matured after the 28-hour stage. 12. The vascular cylinder did not enlarge appreciably. Cortical cells expanded to many times their original volume and the protoderm formed an extensive zone of root-hairs. The root cap cells covered the protoderm almost to the root-hair zone. 13. The shoot apex appeared between the two cotyledons as a flattened egg-shaped mass of cells. It had no detectable vascular developments at the 28-hour stage. Two distinct layers of tunica occurred with a less discernible third layer. Corpus cells appeared to be in all planes. Leaf buttress primordia were observed. 14. Stomata occurred on both the upper and lower epidermal surfaces of the cotyledons. They consisted of two guard cells and a pore without the formation of accessory cells. Transverse sections showed an upper epidermis, a two storied palisade tissue, a spongy tissue 6 to 12 cells in thickness, and a lower epidermis. 15. Druses were abundant, particularly in the cotyledons and upper hypocotyl, as were particles of stored food. 16. Vascular development in 28-hour material was quite complete and apparently functional.

Sheps, L. O. 1973. Survival of *Larrea tridentata* S. & M. seedlings in Death Valley National Monument, California. *Israel Journal of Botany* 22: 8-17.

Abstract: The fate of *Larrea* seedlings which germinated after a September 1967 rain was followed in several habitats in Death Valley National Monument. Maximum survival after 21 months was 16%. Seedlings which germinated beneath mature *Larrea* plants soon died. Similarly, attempts to plant *Larrea* beneath mature *Larrea* plants failed, whereas some success was obtained if the seedlings were growing sufficiently removed from the mother plants or in a non-*Larrea* area. The addition of fungal infected desert litter improved survival and growth both in the field and the greenhouse. Survival of *Larrea* seedlings grown under conditions nearer optimal in the greenhouse showed mortality rates almost as high as in the field, suggesting that factors other than moisture and nutrients may be involved. These results lend

support to the self inhibition hypothesis and suggest another as yet poorly understood factor in the survival of *Larrea* in nature.

Shmida, A., and R. H. Whittaker. 1981. Pattern and biological microsite effects in two shrub communities, Southern California. *Ecology* 62, no. 1: 234-51.

Abstract: Strip transects of 100 contiguous, aligned quadrats were sampled during the spring blooming in a creosotebush (*Larrea tridentata*) semidesert and a chamise (*Adenostoma fasciculatum*) chaparral, with species covers in quadrats recorded. Techniques of pattern analysis included reciprocal averaging ordination of quadrats, measurements of pattern diversity and pattern periodicity, and species association and contagion. In both communities the first ordination axis expressed a strong pattern of differentiation of the herb flora from shrub centers to openings; second and third axes expressed other responses of herb species to shrub species and shrub cover. The pattern axis represents a principal direction of niche difference to which most species responded and along which several pairs of congeners were separated. Pattern periodicities were 6 m (weakly defined) in the semidesert and 9 m in the chaparral; pattern diversities were 1.4 and 1.8 half-changes. Quadrat species richness was highest in the transitions between shrub clumps and openings in the semidesert, but higher in the openings and lower under the shrubs of the chaparral. Overall alpha diversity resulted from roughly comparable contributions of point or small-quadrat diversity, pattern diversity of more common species, and rare species. The importance of biological modification of microsites for population function and niche relationships is suggested by species responses to the primary pattern axis, the responses of some herb species to particular shrub species, and the indicated allelopathic effects in the chaparral.

Shreve, Forrest, and Arthur L. Hinckley. 1937. Thirty years of change in desert vegetation. *Ecology* 18, no. 4: 463-78.

Abstract: On the grounds of the Desert Laboratory, at Tucson, Arizona, the perennial plants of 7 areas have been mapped and their changes followed for 30 years or less. Five areas 10 m. square were first mapped in 1906. One area of 557 sq. m. was enumerated in 1910, and one area of 800 sq. m. was mapped in 1928. The laboratory grounds have been protected from grazing and other disturbance since 1907. All of the areas established in 1906 have shown increases in plant population, which range from 42 per cent to 851 per cent. The increase in the last 8 years was greater than in the preceding 22 years, due to the slow and cumulative effect of the restoration of favorable conditions for establishment. The total number of large perennials has remained almost unchanged. Of the original large perennials 30 per cent died and were succeeded by nearly the same number of new individuals. The increases of total plant population are due to newly established shrubs and bushes, particularly *Fraseria deltoidea*, *Encelia farinosa*, *Caliandra eriophylla*, *Janusia gracilis* and *Coldenia canescens*. Grasses were a negligible component of the vegetation in 1906 but now cover 2.7 per cent of the 500 sq. m. comprised in the oldest areas. The area of 800 sq. m. first mapped in 1928 has increased in plant population from 163 to 466, but 197 of the 303 new plants are young individuals of the range weed *Aplopappus hartwegi*. The data secured in the enumerations give some indication of the length of life of the plants involved. The diversity which characterized the vegetation of the areas at the outset has been perpetuated in the nature of the changes they have undergone and in

the present composition of the vegetation of the several areas. On the five oldest areas the number of species represented has decreased slightly on two and increased from 29 to 44 on the other three. There is no common trend discoverable in the history of the various areas other than their consistent increase in population.

Shreve, F., and T. D. Mallery. 1933. The relation of caliche to desert plants. *Soil Science* 35: 99-113.

Abstract: In the southwestern United States, layers of calcareous hardpan, or "caliche," are abundant over extensive areas. The formation of caliche is due primarily to the interrupted penetration of rain water under arid conditions. Various modifying factors are involved in the formation of caliche in different situations. It occurs in hard layers and in amorphous masses, in both of which forms it has an important influence on the physical and chemical properties of the soil and on the development of the root system. The maximum water content is very low for the hard layers of caliche (3.2 to 6.5 per cent) but higher for the softer masses (12.9 to 17.3 per cent). Even the thinnest layers of caliche greatly retard the upward or downward movement of water in the soil. Evaporation from caliche which is underlaid by water is less than from an equal surface of a porous cup atmometer. Considerable differences of moisture content may exist in bodies of soil separated by a layer of caliche. Caliche will convey water more rapidly from soil beneath it to soil above it than it will from soil to the atmosphere. Roots are unable to penetrate the silicified hard layers of caliche and their distribution is thereby seriously interfered with. The abundance of caliche in the soil of bajadas appears to be an important condition in determining the low and open character of the vegetation, chiefly restricted in such localities to the creosote bush, *Larrea tridentata* (= *Covillea tridentata*). Cultures of *Larrea* were made in 18 types of soil, varying in texture and percentage of soft caliche. The poorest growth was made in pure caliche; the best growth in soils containing equal amounts of caliche and sand, loam, or clay respectively, or these soils with lower percentages of caliche. The dry weight of the plants decreased with increasing percentages of caliche. The percentages of CaO in the ash of the cultured plants varied from 20.24 to 39.19 and those of MgO from 2.06 to 6.02. The varying amounts of caliche in the soils were without influence on the amounts of CaO and MgO in the ash. This result has been confirmed by data from field material taken on soils with and without surface caliche. The fact that the Ca/Mg ratio of the young cultured plants is consistently higher than that of mature plants growing in their natural habitats is due to the higher CaO, and may indicate greater drought resistance on the part of the young plants. The chemical properties of highly calcareous soils appear to be of less importance than the physical in relation to the growth of *Larrea*.

Shreve, F., and I. L. Wiggins. 1964. *Vegetation and flora of the Sonoran desert*. 1 ed. Stanford, California: Stanford University Press.

Silvertown, J., and J. B. Wilson. 1994. Community structure in a desert perennial community. *Ecology* 75: 409-17.

Singh, Surendra Pratap. 1964. "Cover biomass and root-shoot habit of *Larrea divaricata* on a selected site in southern New Mexico." M.S. Thesis, New Mexico State University.

Abstract: A study of the cover, biomass, and root-shoot habit of creosotebush (*Larrea divaricata*) was conducted on a one-square mile area as the initial step for a comprehensive study of community structure and function from the view point of its metabolism and energy relationships. The random pairs and the line intercept methods were used for obtaining cover and density. Comparisons between these two methods were made and are discussed. The cover, density, and biomass of creosotebush accounted for more than half of the shrub vegetation on the study area. The study was confined to the perennials and the vegetation of the major arroyos was not measured. However, a discussion listing major arroyo species is included. The biomass accumulation and ratio between live and dry weights among green leaves and twigs, stems and branches, and roots of creosotebush were calculated. The root systems of a stand of creosotebush were examined and charted. The uniform distribution of creosotebush appeared to be due to passive "competition" of roots for water on a "first-come, first-served" basis., rather than due to the production of toxic substances.

Smith, S. D., R. K. Monson, and J. E. Anderson. 1997. *Physiological ecology of North American desert plants*. Adaptations of Desert Organisms, ed. J. L. Cloudsley-Thompson. Berlin: Springer.

Contents: 1- North American Deserts: Environments and Vegetation; 2- Plant Processes and Responses to Stress; 3- Evergreen Shrubs; 4- Drought-Deciduous Shrubs; 5- CAM Succulents; 6- Perennial Grasses; 7- Phreatophytes; 8- Desert Annuals; 9- Poikilohydric Plants; 10- Exotic Plants

Spalding, Volney M. 1904. Biological relations of certain desert shrubs. I. The creosote bush (*Covillea tridentata*) in its relation to water supply. *Botanical Gazette* 38: 122-38.

———. 1909. *Distribution and movements of desert plants.*, Vol. 113. Washington, D.C. Carnegie Institution of Washington.

Steinberger, Y., and W. G. Whitford. 1983. The contribution of shrub pruning by jackrabbits to litter input in a Chihuahuan Desert ecosystem. *Journal of Arid Environments* 6: 183-87.

Abstract: Jackrabbits, *Lepus californicus*, prune stems from creosotebushes *Larrea tridentata* during the dry winter months, eating the previous season new woody stems allowing the leaves and old wood to fall the ground. This unconsumed material was 66 kg/ha/year of stem and 35 kg/ha/year of leaves; approximately one-fifth of the quantity of shrub litter input by natural infall. Jackrabbits preferentially pruned stems of shrubs with higher tissue moisture content. Rabbits tend to prune stems from the same shrubs in successive years.

Sternberg, L. 1976. Growth forms of *Larrea tridentata*. *Madroño* 23: 408-17.

Syvertsen, James P., G. L. Cunningham, and T. V. Feather. 1975. Anomalous diurnal patterns of stem xylem water potentials in *Larrea tridentata*. *Ecology* 56, no. 6: 1423-28.

Abstract: Diurnal stem xylem H₂O potentials of *Larrea tridentata* (DC.) Cov. were measured with a pressure chamber during the summers of 1973, 1974. Plants growing in dry soils had minimum stem xylem H₂O potentials at night and maximum values during the daylight hours. Vertical H₂O vapor movements in the soil profile in response to temperature gradients may be implicated although further data are needed to establish their role conclusively. Water vapor apparently moves up our to the rooting zone at night and back down into the rooting zone during the day. The occurrence of this phenomenon probably enhances the ability of *Larrea* shrubs to maintain photosynthetic activity when soil H₂O potentials are low and makes questionable the use of predawn stem xylem H₂O potential measurements to assess seasonal trends in plant H₂O status.

Tipton, J. L. 1984. Evaluation of three growth curve models for germination data analysis. *Journal of the American Society for Horticultural Science* 109: 451-54.

Abstract: Polynomial, monomolecular, logistic, and Gompertz growth curves were evaluated for their suitability as mathematical models for germination data. Germination of hulled or leached creosote bush [*Larrea tridentata* (DC.) Cov.] mericarps were used in the evaluation. The Gompertz model gave the best fit. Germination curves and germination rate curves gave similar patterns of response to results obtained by other methods, which suggests the Gompertz model may have application in germination data analysis. Hulling improved germination over leaching intact mericarps. Nine hours was the optimum leaching duration for intact mericarps.

———. 1985. Light, osmotic stress, and fungicides affect hulled creosotebush mericarp germination. *Journal of the American Society for Horticultural Science* 110: 615-18.

Abstract: Light reduced final percentage of germination, maximum germination rate, and time to maximum germination rate of hulled creosotebush [*Larrea tridentata* (D.C.) Cov.] mericarps. The final percentage of germination declined at an osmotic stress greater than -0.4 MPa, but maximum germination rate increased at a stress greater than -0.6 MPa, and inflection time increased with increasing stress. Twice the recommended level of 3 fungicides tested had a negative impact on germination, and all fungicides delayed the time to maximum germination rate at all levels.

Tromble, J. M. 1988. Water budget for creosotebush-infested rangeland. *Journal of Arid Environments* 15: 71-74.

Abstract: A water budget for creosotebush-infested rangeland was calculated using values determined from a water interception study, runoff from instrumented plots, and precipitation data. Combining data generated from precipitation events received for the study period showed that 20 per cent and 9 per cent of the rainfall contributed to runoff and interception, respectively. Abstraction of approximately 30 per cent of the precipitation by these two variables impacts the onsite water availability.

———. 1988. Water interception by two arid land shrubs. *Journal of Arid Environments* 15: 65-70.

See abstract under *Flourensia cernua*.

Turner, Raymond M. 1990. Long-term vegetation change at a fully protected Sonoran desert site. *Ecology* 71, no. 2: 464-77.

Abstract: To investigate desert vegetation dynamics, I undertook an open-ended study of a site that offers a combination of multiple observations through time with continuous protection from domestic livestock and other human impacts. The site is MacDougal Crater in the Sierra del Pinacate Reserve, Sonora, Mexico. Three sources of data have been used: a series of exactly matched photographs, begun in 1907; detailed permanent-plot maps, dating from 1959-1960; and an age-distribution analysis of a 170-yr-old population of *Carnegiea gigantea*. The crater vegetation is dominated by the woody perennials *Cercidium microphyllum*, *Encelia farinosa*, *Prosopis* sp., and *Larrea tridentata*, and the columnar cactus *Carnegiea gigantea*. Various populations of *Larrea tridentata* declined 50-90%, and *Cercidium* declined 60%, during the first half of this century with little or no recruitment since. *Carnegiea* numbers increased fourfold over the same period. A 200-fold increase in *Prosopis* in the playa-like crater center occurred in the early 1970s. Elsewhere on the crater floor, *Encelia* density increased markedly during the same period from insignificant levels in the early 1960s. Age distribution analysis for the *Carnegiea* population reveals three major establishment peaks during the 1790 period. Recruitment and mortality records from the three sources of data are compared with regional climate records. The high mortality for some of the species was probably the result of the prolonged drought during 1936-1964. Establishment surges for some appear related to periods of unusually heavy precipitation during certain seasons. Clearly, desert communities are highly responsive to changes in the climate regime under which they grow.

Turner, R. M., J. E. Bowers, and T. L. Burgess. 1995. *Sonoran desert plants. An ecological atlas*. Tucson: University of Arizona Press.

Valentine, K. A. 1970. Creosotebush control with phenoxy herbicides, picloram, and fuel oil in southern New Mexico. *New Mexico Agricultural Experiment Station Bulletin* No. 554.

Abstract: Creosotebush was sprayed with various formulations of 2, 4-D and 2,4,5-T, and with picloram and fuel oil, using ground spray equipment, on the University's Agricultural Experiment Station ranch, from 1962 to 1966.

Results of spraying regrowth of mowed creosotebush at different seasons varied with herbicide used. With 2,4,5-T ester, highest kills were obtained in late summer, and lowest kills were obtained in spring and fall. Early summer results were not significantly different from those of the other seasons. Picloram gave lowest kills in spring, highest kills in fall. The intermediate-level early and late summer kills did not differ significantly from either spring or fall kills. Fuel oil gave lowest kills in spring, highest kills in fall, and intermediate-level kills in early and late summer.

Valentine, K. A., and J. J. Norris. 1964. A comparative study of soils of selected creosotebush sites in southern New Mexico. *Journal of Range Management* 17: 23-32.

Abstract: This paper presents the results of a study of physical and chemical properties of soils of four selected creosotebush sites in southern New Mexico. The soils remain capable of supporting establishment and growth of the climax dominant grasses, although deterioration through erosion, and in one case loss of structure, has occurred. One site appeared to have lost soil to the extent that production capacity for the test species had been significantly reduced. At the same site, continuing erosion threatened to further reduce soil productivity by exposure of an underlying high gypsum substratum. Range management practices consisting of proper grazing management and control of creosotebush to preserve and improve these range areas were strongly indicated.

Valentine, K. A., and J. B. Gerard. 1969. Life-history characteristics of the creosotebush, *Larrea tridentata*. *New Mexico Agricultural Experiment Station Bulletin* No. 526: 1-32.

Vasek, F. C. 1980. Creosote bush: long-lived clones in the Mojave desert. *American Journal of Botany* 67: 246-55.

Abstract: Creosote bush clones in the Mojave Desert develop by irregular radial growth, stem segmentation and the production of new stems at the outer edge of stem segments. The resulting circular clone encloses a central bare area as the central dead wood rots away. Old clones become elliptical and may exceed 20 m in length. Modern growth rates estimated from annual increments in stem wood of seedlings (0.73 mm/yr) and young clones (0.82 mm/yr) approximate those estimated for radiocarbon-dated wood samples (0.66 mm/yr). Assuming comparable growth rates through time, the extrapolated age of the largest known clone (average radius = 7.8 m) may approach 11,700 years. If growth rates have changed, that clone's age may be somewhat less.

———. 1979-1980. Early successional stages in Mojave desert scrub vegetation. *Israel Journal of Botany* 28: 133-48.

Abstract: A creosote bush scrub community was destroyed by excavation of a borrow pit in 1970-71, and replaced by a community of small gray shrubs. *Larrea tridentata* (312m³ per hectare), *Opuntia bigelovii* (165m³) and *Krameria grayi* (34m³) dominate the neighboring undisturbed vegetation. *Encelia frutescens* (164m³ per ha in 1979), *Ambrosia dumosa* (28m³), *Stephanomeria pauciflora* (24m³) and *Opuntia bigelovii* (19m³) dominate the vegetation of the deeply disturbed borrow pit bottom. Several strategies are apparent: (I) *Larrea tridentata* and other very long-lived shrubs are eliminated by heavy disturbance. New seedlings are slowly recruited after several years delay. (II) Opportunistic shrubs of intermediate long-life spans normally recycle within the community given certain opportunities of open surface. They are eliminated by heavy disturbance, but rapidly establish new populations from stem joints (*Opuntia*) or from seeds (*Ambrosia*). (III) Short-lived perennials (pioneers) invade by seed from occasional plants scattered in small washes and other natural slightly disturbed sites in the region (*Encelia*, *Stephanomeria*). Plant succession occurs in desert ecosystems and appears comparable to that in other ecosystems.

———. 1983. Plant succession in the Mojave desert. *Crossosoma* 9: 1-23.

Abstract: Three studies are described showing that plant succession does occur in desert vegetation, that perennial herbs and short-lived shrubs are prominent pioneers, and that some annuals may be members of stable old communities. I. A mature creosote bush scrub community destroyed by excavation of a borrow pit was replaced by populations of short lived perennials. Three reproductive strategies were identified: large populations of pioneer perennials establish from seed (*Euphorbia polycarpa*, *Encelia frutescens*, *Stephanomeria pauciflora*); long-lived opportunists establish from seed but persist by continued reproduction via seeds (*Ambrosia dumosa*) or stem joints (*Opuntia bigelovii*); very long-lived perennials establish slowly and eventually attain extreme ages (*Larrea*) perhaps on the order of several millenia. II. On Rabbit Dry Lake, *Kochia californica* and *Suaeda torreyana* seedlings establish in mud cracks on the open playa. Small soil mounds accumulate around the pioneer plants. *Atriplex torreyi* invades small mounds and accumulates larger volumes of organic debris and wind blown soil. Eventually, large mounds coalesce forming giant confluent mounds on which *Atriplex confertifolia*, *Haplopappus acradenius*, etc. become established. Erosion reduces giant mounds and fills intervening areas with soil forming a "degradation" zone with a more or less continuously distributed xerophytic salt bush scrub vegetation raised above original playa level. III. Upper Johnson Valley has a creosote bush scrub vegetation characterized by low ground cover, few shrub species and large, ancient creosote clones. Open ground between clones is occupied by numerous annuals. The correlation of a stable, old, shrub community of low species diversity with a rich annual flora and dense annual vegetation suggests that some annuals may comprise adapted components of very old communities. The successional time span in desert vegetation may involve several millenia.

Vasek, F. C., and M. G. Barbour. 1977. Mojave desert scrub vegetation. *Terrestrial vegetation of California*. M. G. Barbour, and J. Major, 835-67. New York: John Wiley and Sons.

Wainwright, John, Anthony J. Parsons, and Athol D. Abrahams. 1999. Rainfall energy under creosotebush. *Journal of Arid Environments* 43: 111-20.

Abstract: Simulated rainstorms of 15 min duration and average intensity 148 mm h⁻¹ were applied to seven creosotebushes. Intensity of the sub-canopy rainfall was reduced to 90% of the rain falling out with the canopy, whereas the kinetic energy was reduced to 70%. Although leafdrip makes up 28.9% of the sub-canopy rainfall, it contributes only 10% of the sub-canopy kinetic energy. Comparison of the effective kinetic energy (that possessed by raindrops with sufficient energy to detach sediment) beneath the canopy with that outside the canopy shows that the former is 55% of the latter. These results quantify the process of differential splash that contributes to the build-up of mounds beneath desert shrubs, and improves the understanding of the development of islands of fertility in desert ecosystems.

Wallace, A., E. M. Romney, and R. T. Ashcroft. 1970. Soil temperature effects on growth of seedlings of some shrub species which grow in the transitional area between the Mojave and Great Basin deserts. *BioScience* 20: 1158-59.

Walters, J. P., and E. C. Freeman. 1983. Growth rates and root:shoot ratios in seedlings of the desert shrub *Larrea tridentata*. *Southwestern Naturalist* 28: 357-63.

Welsh, Richard G. 1972. "Some ecological relationships between creosotebush (*Larrea tridentata* DC.) and bush muhly (*Muhlenbergia porteri* Scribn)." M.S. Thesis, New Mexico State University.

Abstract: Bush muhly appears to dominate creosotebush and is perhaps responsible for the death of the creosotebush. A study in 1972 was conducted on New Mexico State University's Agricultural Experiment Station Ranch in Dona Ana County, New Mexico, to determine if the above statement is true, and if so, which factors may be responsible.

Welsh, Richard G., and Reldon F. Beck. 1976. Some ecological relationships between creosotebush and bush muhly. *Journal of Range Management* 29, no. 6: 427-75.

Abstract: Some ecological relations between creosotebush and bush muhly were observed and measured to determine the influence of bush muhly on creosotebush environment and vigor when the bush muhly is growing within the creosotebush canopy. Bush muhly growing within the creosotebush canopy significantly reduced the light intensity reaching the lower limbs of creosotebush. Shade screens used for simulating bush muhly shading did not significantly reduce the light reaching the creosotebushes but still appeared to influence the new growth of creosotebush leaves. Evidently, surface reflection under the screens still permitted sufficient light for some plant growth. No new basal stem growth was observed in creosotebushes where bush muhly was removed after occupying more than half of the aerial space of the creosotebush. There were more dead stems (50%) in creosotebushes growing with bush muhly present than in those without (20%). The amount of moisture in leaves and stems of creosotebush was significantly less when bush muhly was present.

Went, F. W. 1948. Ecology of desert plants. I. Observations on germination in the Joshua Tree National Monument, California. *Ecology* 29, no. 3: 242-53.

Abstract: Observations on the germination of desert plants in the Joshua Tree National Monument and surroundings have shown that plants can be divided into 5 groups as far as their germination and growth are concerned: 1. Summer annuals (*Amaranthus fimbriatus*, *Boerhaavia spicata*, *Bouteloua aristoides*, *Bouteloua barbata*, *Euphorbia micromera*, *Euphorbia setiloba*, *Mollugo Cerviana*, *Pectis papposa*, *Portulaca oleracea*), which only germinate after heavy summer rains. 2. Winter germinating spring annuals (*Cryptantha*, *Eriophyllum Wallacei*, *Filago*, *Gilia* species, *Nemacladus*, *Pectocarya*, *Plantago*, etc.), most of them of diminutive size, germinating almost exclusively after late fall and winter rains. 3. Summer germinating spring annuals (*Abronia*, *Erodium cicutarium*, *Oenothera deltoides*, *Salvia Columbariae*, etc.) to which most of the larger-sized spring annuals belong. 4. Plants unrestricted in germination conditions (*Cucurbitaceae*, *Datura*, *Palafoxia linearis*) which can be found as seedlings at almost any time of the year after rains. 5. Shrubs. These are almost all summer germinators (*Acacia*, *Chilopsis*, *Dalea*, *Fouquieria*, *Hymenoclea*, *Hyptis*, *Larrea*, *Lycium*, etc.) with the exception of *Eriogonum* which germinates only in

winter. These observations explain in general the distribution in time and space of the desert plants in the Joshua Tree National Monument.

Went, F. W., and M. Westergaard. 1949. Ecology of desert plants. III. Development of plants in the Death Valley National Monument, California. *Ecology* 30: 26-38.

Abstract: Observations on germination and growth of plants in the Death Valley region (California) show a correlation between amount of rainfall and the temperatures immediately following the rain, and the species of plants germinating and developing. A rain followed by 30°C minimal temperatures resulted in no germination (there is no summer annual vegetation) ; followed by 15-16°C minimal temperatures a rain caused only germination of *Larrea*, but followed by 8-10°C minimal temperatures full germination of winter annuals occurred, with no *Larrea*. Some differences in the floristic composition of the winter-annual flora were found, especially according to salinity of soil and altitude. In general the Valley Bottom had the smallest number of plants growing, and this number increased with increased altitude. In a few greenhouse experiments it was found that best germination of the seeds in Death Valley soil occurred at 18° phototemperature and 13° nyctotemperature.

Whitford, W. G., J. Anderson, and P. M. Rice. 1997. Stemflow contribution to the 'fertile island' effect in creosotebush, *Larrea tridentata*. *Journal of Arid Environments* 35: 451-57.

Abstract: Stemflow, throughfall and bulk precipitation were collected on six creosotebushes (*Larrea tridentata*) during 18 events in the northern Chihuahuan Desert. The average stemflow was 16.8±1.9%; throughfall averaged 64.7±3.2%. The concentration of all ions measured were significantly higher in stemflow than in the bulk precipitation. Total nitrogen, sulfate, and calcium concentrations were more than an order of magnitude higher in the stemflow than in the bulk precipitation. Concentration of ions in the upper 10 cm of soils were generally higher in soils under shrubs than in soils between shrubs. Measured quantities of ions in dry-fall were of sufficient magnitude to account for the increased concentration in stemflow water of most ions. Increases in nitrogen in stemflow water may be due to biological activity of stem crust micro-organisms in addition to dry-fall. Dry-fall that collects on the leaves and stems of this desert shrub may contribute to the 'fertile island' effect on the soils under the canopies of creosotebushes.

Whitford, W. G., E. Martinez-Meza, and A. de Soyza. 1996. Morphological variation in creosotebush, *Larrea tridentata*: effects on ecosystem properties. In *Proceedings: symposium on shrubland ecosystem dynamics in a changing environment*, Compilers J. R. Barrow, E. D. McArthur, R. E. Sosebee, and R. J. Tausch, 195-98Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station.

Abstract: Morphological characteristics of creosotebush canopies (angle of exterior stems), size of litter layer and sub-canopy soil chemistry were measured on several sites on the Jornada Experimental Range. Soils under canopies of inverted cone shaped shrubs had little or no litter layer and significantly lower total soil nitrogen and soil carbon than soils under canopies of hemispherically shaped shrubs. In Death Valley, creosotebushes growing in braided washes were predominantly inverted cone shaped. The morphological

characteristics of creosotebushes appear to vary with soil type and with mean annual rainfall. The proportional distribution of different morphotypes of creosotebush affects the heterogeneity of creosotebush dominated ecosystems.

Whitford, Walter G., Turanzas Gustavo Martinez, and Meza Ernesto Martinez. 1995. Persistence of desertified ecosystems: explanations and implications. *Environmental Monitoring and Assessment* 37, no. 1-3: 319-32. Abstract: Studies of rainfall partitioning by shrubs, responses of shrub-dominated ecosystems to herbicide treatment, and experiments using drought and supplemental rainfall were conducted to test the hypothesis that the shrub-dominated ecosystems that have replaced desert grasslands are resistant and resilient to disturbance. Between 16 and 25% of the intercepted rainfall is channelized to deep soil storage by stemflow and root channelization. Stemflow water is nutrient enriched and contributes to the "islands of fertility" that develop under desert shrubs. Drought and rainfall augmentation experiments during the growing season after 5 consecutive years of summer drought found that (1) growth of creosotebushes, *Larrea tridentata*, was not significantly affected, (2) perennial grasses and forbs disappeared on droughted plots, (3) nitrogen mineralization increased in the short term, and (4) densities and biomass of spring annual plants increased on the droughted plots. Doubling summer rainfall for 5 consecutive years had less-significant effects. Coppice dunes treated with herbicide in 1979 to kill mesquite (*Prosopis glandulosa*) had the same frequency of occurrence of the shrub as the untreated dunes when remeasured in 1993. These data indicate that the shrub-dominated ecosystems persist because they are resistant and resilient to climatic and anthropogenic stresses.

Whitford, Walter G., Ronald Nielson, and Amrita de Soyza. 2001. Establishment and effects of establishment of creosotebush, *Larrea tridentata*, on a Chihuahuan Desert watershed. *Journal of Arid Environments* 47, no. 1: 1-10. Abstract: Creosotebush (*Larrea tridentata*) seedlings were planted in plots that were irrigated, plots that were irrigated and fertilized with ammonium nitrate, and plots that were not amended in three plant communities on a Chihuahuan Desert watershed: ungrazed black grama (*Bouteloua eriopoda*) grassland, creosotebush shrubland, and overgrazed grassland. No seedlings were planted in one-half of the area of each plot. No seedlings survived in the black grama grassland or the creosotebush shrubland 2 years after planting. Growth of established creosotebush shrubs was highest in plots with the lowest grass cover. Fifteen years after the seedlings were planted in the overgrazed grassland, the area under the shrubs was nearly devoid of perennial grasses and forbs. The aggregate stability of the soils under the established creosotebush shrubs was significantly lower than the soils in the unplanted split-half of the plots. Electrical conductivity, calcium, and nitrate were significantly lower in soils under shrubs than soils in the unplanted split-half of the plots. There were also significant reductions in densities of annual plants growing under the shrubs than in the unplanted split-half of the plots. Successful establishment of creosotebush in desert grasslands is dependent upon the presence of large patches of soil with no perennial plant cover. Intense grazing by domestic livestock creates microsites and landscape characteristics favourable for seed dispersal, germination and establishment of creosotebush. Soil changes resulting from

shrub establishment reduce the probability of re-establishing perennial grasses in creosotebush-dominated shrubland.

Wondzell, Steven M., and John A. Ludwig. 1995. Community dynamics of desert grasslands: Influence of climate, landforms, and soils. *Journal of Vegetation Science* 6, no. 3: 377-90.

See abstract under *Flourensia cernua*

Wood, K. M., E. L. Garcia, and J. M. Tromble. 1991. Runoff and erosion following mechanical and chemical control of creosotebush. *Weed Technology* 5: 48-53.

Abstract: Runoff and sediment yield were monitored from 1983 through 1986 on a range site dominated by creosotebush. The site was rootplowed and seeded, treated with tebuthiuron at 36 kg ai ha⁻¹, or left untreated. Runoff from rootplowed and herbicide-treated plots was no different from untreated plots for 1 yr, but sediment yield from treated plots was lower than that from the untreated plots. Rootplowing and seeding increased sediment yield in the second year (1984), whereas treating with herbicide decreased sediment yield. Runoff and sediment yield during 1985 and 1986 were greatest from the untreated areas and least from the rootplowed and herbicide-treated areas. Total cover was nearly the same for each treatment. The untreated plots had 13% shrub cover; the others had none. Between shrubs in untreated plots, bare ground occupied large interconnected areas that contributed to the higher runoff and erosion rates.

Woodell, S. R. J., H. A. Mooney, and A. J. Hill. 1969. The behaviour of *Larrea divaricata* (creosote bush) in response to rainfall in California. *Journal of Ecology* 57: 37-44.

Wright, R. A. 1970. The distribution of *Larrea tridentata* (D.C.) Coville in the Avra valley, Arizona. *Journal of the Arizona-Nevada Academy of Science* 6: 58-63.

Abstract: The distribution of *Larrea tridentata* was investigated at eight sites in the Avra Valley, Arizona. Excavations of *Larrea* mounds showed that individual *Larrea* plants are dumped into mounds thus, there is a small-scale contagious distribution. Statistical analysis indicated that the mounds themselves are contagiously distributed on a larger scale. It is proposed that the small-scale pattern is due to: (1) root sprouting of buried branches, (2) crown splitting, and (3) a type of mutual facilitation due to modification of the microenvironment.

Yang, Tien Wei. 1950. "Distribution of *Larrea tridentata* in the Tucson area as determined by certain physical and chemical factors." M. S. Thesis, University of Arizona.

———. 1970. Major chromosome races of *Larrea divaricata* in North America. *Journal of Arizona Academy of Science* 6: 41-45.

Yeaton, R. I., J. Travis, and E. Gilinsky. 1977. Competition and spacing in plant communities: the Arizona upland association. *Journal of Ecology* 65, no. 2: 587-95.

Abstract: Spacing and competition were studied within and between species of the 'Arizona upland association' in Organ Pipe Cactus National Monument. *Larrea tridentata*, *Franseria deltoidea*, *Opuntia fulgida*, *Carnegiea gigantea*, and *Fouquieria splendens* comprise 95% of the individuals and 94% of the plant cover in the area studied. All intraspecific nearest-neighbour comparisons show that competition is occurring. *Larrea tridentata* competes with all species studied except *Carnegiea gigantea*, *Franseria deltoidea* competes only with *Larrea tridentata*, while there is no evidence of *Carnegiea gigantea* competing with other species (its interaction with *Opuntia fulgida* could not be determined). The root system of *Larrea tridentata* occupies a position intermediate between and overlapping those of *Franseria deltoidea* and *Opuntia fulgida* and as a result competes with both. *Opuntia* and *Franseria* do not compete as their root systems are segregated vertically from each other in the soil. It is suggested that vertical separation of root systems is the mechanism through which interspecific competition is reduced and co-existence maintained between these associated species of plants.

Yoder, C. K., and R. S. Nowak. 1999. Soil moisture extraction by evergreen and drought-deciduous shrubs in the Mojave desert during wet and dry years. *Journal of Arid Environments* 42: 81-96.

Abstract: Annual and seasonal evapo-transpiration (ET) were compared among Mojave Desert shrubs with different leaf phenologies over a 3-year period during which annual precipitation varied from well below average to more than twice average. During the wet year, soil wetting fronts reached maximum depths of 0.75 m to > 1.95 m, depending on soil texture at the study sites. The evergreen shrubs *Larrea tridentata* and *Ephedra nevadensis*, and the drought-deciduous shrub *Ambrosia dumosa*, were able to extract soil water in a uniform manner to depths > 1 m. For stands of the deciduous shrub *Lycium pallidum*, a soil texture change at c. 0.75 m impeded percolation of water below that depth. There were no significant differences ($p < 0.05$) in annual ET between the evergreen shrubs *Larrea* and *Ephedra* relative to the drought-deciduous shrubs *Ambrosia* and *Lycium* during the 3 years of the study. Early in the growing season, extraction of soil water from beneath plant canopies was slightly greater than from shrub interspaces for *Ambrosia*, *Ephedra*, and *Lycium*, but not for *Larrea*. For all species, annual soil water extraction from beneath plant canopies was not significantly different than that from shrub interspaces. The lower limit of soil water extraction (L_e) for the study sites varied from 4 to 10 volumetric per cent, depending on soil texture, and did not differ significantly among species. For all species, L_e was reached within 6 to 12 months following twice average precipitation during the period of November 1994 to March 1995. We conclude that ET in the Mojave Desert is dependent largely on winter precipitation and the amount of soil water available during the growing season rather than on species composition.

6 *Prosopis glandulosa* Torr. (Honey mesquite)



Mesquite is a deciduous, thorny, C3 woody plant of various growth forms ranging from small shrubs to trees (Steinberger 2001). In the northern Chihuahuan desert it mostly occurs as shrubs. It gathers sand in its crown and can form coppice dunes or nabkhas several meters in height (Langford 2000). This species comprises several recognized varieties (Steinberger 2001). Mesquite is a facultative phreatophyte and can develop very deep roots (Smith, Monson, and Anderson 1997). Since mesquite is a legume, it can host N₂-fixing bacteria in nodules on its roots, and obtain about half of its nitrogen from these bacteria (Jarrell and Virginia 1990). It is very widespread throughout the North American warm deserts, and even occurs in the subtropical savannahs of north-central Texas (Steinberger 2001). Mesquite plants can live up to two hundred years. They flower in spring when leaves are produced (Simpson 1977). Seed production is often greatly reduced by insect predation (Simpson 1977). Seeds are encased in indehiscent fruit, and passage through the digestive tracts of animals greatly enhances germination. Therefore, the introduction of livestock to southwestern grasslands not only contributed to the dispersal of mesquite seeds, but also enhanced their germinability, which led to great expansion of mesquite dominated areas (Archer 1978; Brown and Archer 1987).



El mezquite. 1955. *El Campo* 22, no. 766 : 54-55.

Al Humaid, A. I., and M. O. A. Warrag. 1998. Allelopathic effects of mesquite (*Prosopis juliflora*) foliage on seed germination and seedling growth of bermudagrass (*Cynodon dactylon*). *Journal of Arid Environments* 38, no. 2: 237-43.

Abstract: Allelopathic effects of aqueous extracts of 10, 20, 30, 40, 50 and 60g dry mesquite (*Prosopis juliflora*) leaves in a litre of distilled water on seed germination and early growth of bermudagrass (*Cynodon dactylon* 'Common Bermuda') at 30degreeC were investigated. The final germination percentage and the germination rate, as judged by corrected germination rate index (CGRI) and to a lesser extent by the time to 50% of the final germination (GT50), were significantly reduced by the extracts in comparison with the distilled water control. This reduction increased with increasing extract concentration, until germination was totally inhibited with the most concentrated extract. Both radicle and plumule lengths were also significantly retarded. The radicles, which did not elongate at all in the most concentrated extract, were more affected. Polyethylene glycol 2000 solutions, with the same pH and osmotic potentials as the extracts, resulted in a significantly higher germination percentage, CGRI and radicle growth rate than their corresponding extracts. A similar trend was exhibited by the plumules at the three highest concentrations only. These results indicate that the mesquite foliage contains water-soluble allelochemicals which could inhibit seed germination and significantly retard the rate of germination and seedling growth of bermudagrass.

Andrews, Scott Alan. 1988. "Volume estimation and multi-purpose management of *Prosopis velutina* in southern Arizona ." M. S. Thesis, University of Arizona.

Ansley, R. J., S. L. Dowhower, and D. H. Carlson. 1992. Seasonal trends in leaf area of honey mesquite trees: determination using image analysis. *Journal of Range Management* 45, no. 4 : 339-44.

Abstract: Black-and-white photographs were used to estimate seasonal trends in whole plant leaf area of honey mesquite (*Prosopis glandulosa* var. *glandulosa* Torr.) trees occurring on a site with limited subsurface water. Height and canopy width of the trees ranged from 1 to 5 m and 1 to 7 m, respectively.

Images consisted of profile-view angles of trees occurring on flat terrain. Four image variables, height, width, canopy profile perimeter length, and canopy profile area were obtained from the photographs and used to predict leaf area of unharvested trees. Predictive equations were based on adjacent trees which were photographed and harvested for actual leaf area determination. Canopy profile area was evaluated as the most accurate image variable for predicting leaf area. Whole plant leaf area of unharvested trees varied within and between growing seasons and was dependent on precipitation patterns. During the 1987 growing season, leaf area declined significantly by 14.6% from 17.1 m² (1 leaf surface) in May to 14.6 m² in August, in conjunction with a mid-summer dry period. Leaf area increased in September 1987 in response to late-summer precipitation. Leaf area was less in the spring of 1988 than the spring of 1987 because of lower precipitation during the winter prior to the 1988 than the 1987 growing season. Leaf area did not decline significantly from spring to mid-summer in 1988 as it did the previous year because of atypically high precipitation in July 1988. Leaf area did not increase in September of 1988 as it did in 1987 because of lack of late-season rains in 1988. These results suggest mesquite on this study site used partial leaf shedding to augment drought resistance.

Ansley, R. J., W. A. Dugas, M. L. Heuer, and B. A. Trevino. 1994. Stem flow and porometer measurements of transpiration from honey mesquite (*Prosopis glandulosa*). *Journal of Experimental Botany* 45, no. 275: 847-56.

Abstract: The objective of this study was to compare stem flow and porometer methods of measuring transpiration of honey mesquite (*Prosopis glandulosa*) trees on a semi-arid site. Stem flow was measured using heat balance stem flow gauges. Porometer measurements of leaf stomatal conductance (g-s) were made within foliage layers of each stem and scaled to transpiration values for the entire stem (E-stem) using stem leaf area. Simultaneous measurements using both methods were made diurnally and under artificially imposed stem shading or defoliation in June and October 1990. Stem flow and E-stem had similar diurnal patterns except on 2 d in June when E-stem increased during the afternoon while stem flow declined relative to midday values. During October, E-stem was greater than stem flow throughout the day. This was attributed to sampling error in which only undamaged leaves were used for porometer measurements yet, by this time in the growing season, many leaves on each stem were damaged from insects or wind and likely had lower transpiration rates. A regression coefficient between E-stem and stem flow of 0.79 in June and 0.91 in October suggested the two methods were comparable, but there was considerable variation between methods during peak transpiration rates. Both techniques detected that artificial shading or defoliation caused similar relative declines in transpiration. Results imply that estimates of stem transpiration can be obtained by scaling porometer measurements of leaves but accuracy declines at higher transpiration rates.

Ansley, R. J., P. W. Jacoby, and G. J. Cuomo. 1990. Water relations of honey mesquite following severing of lateral roots: influence of location and amount of subsurface water. *Journal of Range Management* 43, no. 5 : 436-42.

Abstract: Location and amount of subsurface water may influence the degree of dependence of honey mesquite (*Prosopis glandulosa* Torr.) on shallow lateral roots to supply water. The objective of this study

was to determine influence of lateral roots on water relations of honey mesquite on 2 sites which differed in location and amount of subsurface water. Lateral roots were severed with barriers placed to 1.5 m depth and completely surrounding individual trees in February 1985, during mesquite winter dormancy. Stomatal conductance and predawn leaf water potential were significantly reduced in root-severed trees during the following growing season (May-September) at both sites, but reduction was greater on the site with less subsurface water. Daytime leaf water potential was higher in root-severed than control trees on the site with less subsurface water, but not on the other site. By mid-summer 1986, no difference in stomatal conductance between treatments were detected at either site, yet daytime leaf water potential remained higher in root-severed than control trees at the site with: less subsurface water. Predawn leaf water potential was greater in root-severed than control trees in 1986, which was a reversal of 1985 trends. Leaf abscission was not observed in either treatment during: either growing season. These results suggest that: (1) when less subsurface water was available, trees were more dependent on lateral roots to supply water, (2) treatment effects were minimized by the second growing season following root severing, possibly from new root growth within or below the root barrier region, and (3) the lateral root system may play a significant role in regulating leaf water relations on sites with limited subsurface water.

Ansley, R. J., P. W. Jacoby, and R. A. Hicks. 1991. Leaf and whole plant transpiration in honey mesquite following severing of lateral roots. *Journal of Range Management* 44, no. 6 : 577-83.

Abstract: This study examined water loss by fully grown honey mesquite (*Prosopis glandulosa* var. *glandulosa* Torr.) trees at 2 levels of resolution, the whole plant (canopy) and the individual leaf. Trees were manipulated by severing lateral roots during winter dormancy. Leaf transpiration and photosynthesis were measured in root-severed and unsevered (control) trees for 2 growing seasons following treatment. An empirical model which integrated leaf transpiration, whole plant leaf area, and influence of shading within the canopy on leaf transpiration was used to calculate daily water loss from individual trees. During the first growing season leaf abscission occurred on root-severed, but not control trees, in early July, resulting in a 50% reduction in whole plant leaf area. Following abscission, transpiration and photosynthesis of remaining leaves on root-severed trees were significantly greater than on control trees from July through September. Because of increased transpiration of remaining leaves on root-severed trees, daily water loss per tree was not significantly different between root-severed and similar-size control trees before or after leaf abscission. No differences in leaf or canopy transpiration were found between root-severed or unsevered honey mesquite during the second growing season. Daily water loss per tree ranged from 30 to 75 liters during the study. These responses illustrate that water loss from mesquite may be regulated by various combinations of stomatal control and adjustment of transpirational surface area.

Ansley, R. J., P. W. Jacoby, and B. K. Lawrence. 1989. Influence of stress history on water use patterns of honey mesquite. 75-82. General Technical Report INT - U.S, 256 Department of Agriculture, Forest Service, Intermountain Research Station.

Ansley, R. J., P. W. Jacoby, C. H. Meadors, and B. K. Lawrence. 1992. Soil and leaf water relations of differentially moisture-stressed honey mesquite (*Prosopis glandulosa* Torr). *Journal of Arid Environments* 22, no. 2 : 147-59.

Abstract: The objective of this study was to determine plant/soil water relations of honey mesquite (*Prosopis glandulosa* Torr.) following preconditioning to different levels of moisture stress. Moisture stress of 12 naturally occurring trees (mean height 3-2 m) located in north Texas, was manipulated through the use of drip irrigation and sub-canopy rain shelters. Pre-dawn leaf water potential and average daily stomatal conductance were greatest in irrigated trees and least in rain-sheltered trees on 27 June and 28 July 1986 after 1 and 2 months of stress preconditioning, respectively. Following a common irrigation of all trees (equivalent to 35-40 mm precipitation) on 28 June and 29 July, pre-dawn leaf water potential increased to similar levels in all trees within 1 day. Increase to maximum average daily stomatal conductance was delayed in moisture-stressed trees following the July watering, suggesting that moisture stress inhibited ability to respond to moisture availability. A positive relationship was found between soil moisture content and pre-dawn leaf water potential, and between soil moisture and average daily stomatal conductance. However, average daytime leaf water potential was unaffected by soil moisture content.

Ansley, R. J., D. L. Jones, T. R. Tunnell, B. A. Kramp, and P. W. Jacoby. 1998. Honey mesquite canopy responses to single winter fires: Relation to herbaceous fuel, weather and fire temperature. *International Journal of Wildland Fire* 8, no. 4: 241-52.

Abstract: Honey mesquite (*Prosopis glandulosa* Torr.) canopy responses to fire were measured following 20 single winter fires conducted in north Texas. Weather conditions during the fires, understory herbaceous fine fuel (fine fuel) amount and moisture content, fire temperature at 0 cm, 10-30 cm and 1-3 m above ground, and canopy responses were compared. Ten fires occurred on a site where fine fuel was a mixture of cool and warm season grasses (mixed site). The other 10 fires occurred on a site dominated by warm season grasses (warm site). When both sites were included in regressions, peak fire temperature at all heights was positively related to fine fuel amount. Fine fuel amount, fine fuel moisture content, air temperature (AT) and relative humidity (RH) affected fire temperature duration in seconds over 100degreeC (FTD 100) at 1-3 m height, but not at ground level. Mesquite percent above-ground mortality (topkill) increased with increasing fine fuel amount, decreasing fuel moisture content, increasing AT, and decreasing RH. Percent foliage remaining on non-topkilled (NTK) trees was inversely related to fine fuel amount and AT, and positively related to fine fuel moisture content. Effect of fire on mesquite topkill and foliage remaining of NTK trees was strongly affected by RH at the warm site ($r^2 = 0.92$ and 0.82 , respectively), but not at the mixed site. This difference was due to RH affecting fuel moisture content (and subsequently fire behavior) to a greater degree at the warm than at the mixed site, because of the lower green tissue content in warm site grasses at the time of burning. Under adequate fine fuel amounts to carry a fire, mesquite canopy responses to fire (i.e., topkill vs. partial canopy defoliation) were largely determined by AT and RH conditions during the fire. This has implications if the management goal is to preserve the mesquite overstory for a savanna result instead of topkilling all trees. Two substudies were conducted during 3 of the fires. Substudy 1 determined mesquite response to fire in 2 plots with different understory herbaceous fuel loads (5,759 vs. 2,547 kg/ha) that were burned under similar weather conditions. Mesquite topkill was 81% and 11% in the high and low fuel fires, respectively. Under similar weather conditions, fine fuel was an

important factor in affecting mesquite responses to fire. However, as demonstrated in the main study, under a variety of weather conditions, AT and RH influenced mesquite response to fire as much or more than did fine fuel. Substudy 2 compared response of mesquite plants with abundant and dry subcanopy fine fuel (3252 kg/ha; fuel moisture 10.4%), or sparse and green subcanopy fuel (1155 kg/ha; fuel moisture 25.9%) to a high intensity fire. All trees were topkilled, including those with low subcanopy fuel, probably from convection heat generated from herbaceous fuel in interspaces between trees. In support of this conclusion, thermocouple data from all 20 fires indicated that canopy responses were more related to fire temperature at 1-3 m than at lower heights. This suggests that the topkill mechanism was due to convective heat within the canopy rather than a girdling effect of fire at stem bases.

Ansley, R. J., B. A. Trevino, and P. W. Jacoby. 1998. Intraspecific competition in honey mesquite: leaf and whole plant responses. *Journal of Range Management* 51, no. 3 : 345-52.

Abstract: Leaf and whole plant responses of honey mesquite (*Prosopis glandulosa* Torr.) to intraspecific competition were compared under low (LD) or high (HD) stand density in a semi-arid region of north Texas. The HD trees occurred within a stand of 300 trees ha⁻¹. The LD trees occurred in areas of the dense stand that were thinned to 80 trees ha⁻¹ with no neighbors within 10 m of study trees. Tree size was similar in each treatment at study initiation. Five years after thinning, tree height, canopy volume, basal stem diameter, leaf area, and leaf area index were significantly greater in LD than HD trees. No differences in leaf predawn water potential, stomatal conductance, and photosynthesis were found between LD and HD trees during growing seasons 4 or 6 years after study initiation. Results indicate resources necessary for growth of individual mesquite plants were limiting under increased stand density and suggest the occurrence of intraspecific competition. Limitations were manifest at the whole plant level via modification of tree size and leaf area per tree, and not through adjustment of leaf physiological processes. The limiting factor appeared to be soil water. Daily water loss tree⁻¹ was 2.5 to 4 times greater in LD than HD trees, and ranged from 119 to 205 kg and 46 to 59 kg in LD and HD trees, respectively. Projected daily water loss by mesquite at the stand level was similar between treatments, however, and ranged from 9,500 to 17,700 kg ha⁻¹.

Ansley, R. J., X. B. Wu, and B. A. Kramp. 2001. Observation: long-term increases in mesquite canopy cover in a north Texas savanna. *Journal of Range Management* 54, no. 2 : 171-76.

Abstract: It is necessary to quantify rates of woody plant encroachment on southwestern USA rangelands to determine the economic feasibility of treatments designed to manage these plants. This study observed changes in honey mesquite (*Prosopis glandulosa* Torr.) canopy cover over a 20-year period (1976-1995) in 2 treatments: an untreated area that initially had a moderately dense mesquite stand (14.6% cover), and an area cleared of mesquite with root-plowing in 1974. Canopy cover of mesquite was estimated from scanned color-infrared aerial photograph images by manually delineating mesquite canopies with a computer using ArcView software. During the 20 years, mesquite cover in the untreated area increased (P less than or equal to 0.05) from 14.6 to 58.7%, averaging 2.2 percentage units per year. Cover in the root-plow treatment also significantly increased during the same period from 0 to 21.9% (1.1 percentage units per year), but the rate of increase was significantly lower than in the untreated area because mesquite growth

was from new seedlings instead of established plants and/or new seedlings as occurred in the untreated area. Rate of increase was significantly lower from 1976 to 1990 (1.6 and 0.2 percentage units per year) than from 1990 to 1995 (4.1 and 3.7 percentage units per year) in the untreated and root-plow treatment, respectively. These differences were attributed to precipitation which was near normal from 1976 to 1990 but 25% above normal from 1991 to 1995.

Archer, Steve 1990. Development and stability of grass/woody mosaics in a subtropical savanna parkland, Texas, U.S.A. *Journal of Biogeography* 17: 453-62.

———. 1995. Tree-grass dynamics in a *Prosopis*-thornscrub savanna parkland: Reconstructing the past and predicting the future. *Ecoscience* 2, no. 1: 83-99.

Abstract: Although trends toward increased woody plant abundance in grasslands and savannas in recent history have been reported worldwide, our understanding of the processes involved is limited. Here I review and integrate a series of studies which quantify the rates, dynamics, spatial patterns and successional processes involved in tree patch and woody plant community development at a savanna parkland site in southern Texas, U.S.A. Stable carbon isotope ratios of soil organic carbon indicate C-3 woody plants currently occupy sites once dominated by C-4 grasses. Historical aerial photographs (1941-1990), tree ring analysis and plant growth models all indicate this displacement has occurred over the past 100 to 200 years. Succession from grass-to woody plant-domination occurs when the N-2-fixing arborescent, honey mesquite (*Prosopis glandulosa* (Torr.) var. *glandulosa*), invades and establishes in herbaceous patches. Over time, this plant modifies soils and microclimate to facilitate the ingress and establishment of additional woody species. The result is a landscape comprised of shrub clusters of varying ages organized around a *Prosopis* nucleus. As new clusters form and existing clusters enlarge, coalescence occurs. This process appears to be in progress on upland portions of the landscape and has progressed to completion on lowlands. Rates of cluster development and patterns of distribution appear regulated by subsurface variations in clay content and by variations in annual rainfall. Simulation models based on reconstructions and forward projections indicate succession from grassland to woodland steady states would require 400-500 years, with the most dramatic changes occurring over a 200-year period. The shrubs initially facilitated by *Prosopis* appear to contribute to its demise and prevent its re-establishment. Structure and function of future communities may therefore depend on how remaining woody plants react to changes in microclimate and nitrogen cycling that occur after *Prosopis* is gone.

Archer, Steve, Charles Scifres, C. R. Bassham, and Robert Maggio. 1988. Autogenic succession in a subtropical savanna: conversion of grassland to thorn woodland. *Ecological Monographs* 58, no. 2: 111-27.

Abstract: Dense thorn woodlands occupy what are thought to have been grasslands and savannas prior to settlement of the Rio Grande Plains of Texas. However, the tenet that grasslands have been converted to shrublands and woodlands in recent history is controversial and based largely upon conflicting historical accounts. Our objective was to determine how the presumed physiognomic conversion from grassland or savanna to woodlands might have occurred. Some upland landscapes are dominated by closed-canopy

woodlands in southern Texas, whereas others have a two-phase pattern of discrete shrub clusters scattered throughout a grassland. More mesic sites are dominated by closed-canopy woodlands. We hypothesized the two-phase landscapes represented an intermediate stage in the conversion of grassland to woodland. As new shrub clusters were initiated and existing clusters expanded and coalesced, a gradual shift from grassland to savanna to woodland would occur. To address this hypothesis, we inventoried herbaceous interspaces for woody colonizers, quantified the composition and distribution of shrub clusters on upland sites, and compared the structure of clusters to that of adjacent, more mesic areas with continuous woody plant cover. To assess the physiognomic stability of the two-phase landscapes, cluster size, density, and cover were quantified for 1941, 1960, and 1983 from aerial photographs. A lone mesquite (*Prosopis glandulosa*) plant occurred in >80% of the upland clusters, where it was typically the largest individual in terms of basal area, height, and canopy area. The number of woody species per cluster ranged from 1 to 15 and was strongly related to mesquite basal diameter ($R^2 = 0.86$). Cluster diversity, evenness, and size were also significantly correlated with mesquite size. The data suggest that mesquite plants invaded grasslands and served as recruitment foci for bird-disseminated seeds of other woody species previously restricted to other habitats. The result was a landscape composed of discrete chronosequences of woody plant assemblages organized about a mesquite nucleus. Within the two-phase portion of the landscape, 50% of the clusters were within 5 m of another and 95% were within 15 m of another. Analysis of the size class distribution of clusters suggested that most had yet to realize their growth potential. Moreover, the herbaceous clearings between clusters contained high densities of woody seedlings, mostly (>70%) mesquite, which occurred in 85% of the clearings, with a mean density of 350 plants/ha. Coalescence will become increasingly probable if new clusters are initiated and existing clusters expand. This phenomenon appeared to be in progress on one portion of the landscape and had apparently already occurred on others. As clusters developed on the two-phase portion of the landscape, their species composition, dominance, and size class structure became increasingly similar to that of adjacent closed-canopy woodlands on more mesic. Mean cluster size increased from 494 m² in 1941 to 717 m² in 1983. Growth rates of clusters were a function of cluster size and precipitation. During the 1941-1960 period characterized by severe drought, there was a slight decrease in total woody plant cover resulting primarily from the formation of gaps among clusters on the periphery of the site and a 35% decrease in density of clusters <5 m². These cover losses offset the areal expansion of small (<100 m²) clusters which had an average relative growth rate (RGR) of 0.10 m²/ (m²*yr). Post-drought woody plant cover increased from 8% in 1960 to 36% in 1983 as new clusters were initiated density increased from 16 to 26 clusters/ha), and the RGR of small clusters increased to 0.16 m²/ (m²*yr). Numerous clusters coalesced during this period. RGRs of clusters >100 m² were an order of magnitude lower than those of clusters <100 m² in each time period. The RGR of large clusters following the drought was not significantly increased, except in the largest size class (clusters >1,000 m²). Our results indicate (1) mesquite invaded grasslands and served as the nucleus of cluster organization on upland sites; (2) woody plant community development has been highly punctuated by variations in precipitation; (3) clusters >5 m² in area are persistent features of the landscape; and (4) the present two-phase pattern is moving toward a monophasic woodland as new clusters are initiated and existing clusters expand and coalesce. As a result, (5) shrub clusters on uplands represent an intermediate stage in the conversion of grassland to woodland, and (6) closed-canopy woodlands on more mesic sites appear to represent portions of the landscape where this has already occurred. Because the conversion of

grasslands and savannas to woodlands in the Rio Grande Plains is initiated by mesquite, factors regulating its dispersal, establishment, and role as a facilitator of woody community development are emphasized.

Asner, G. P., C. A. Wessman, and S. Archer. 1998. Scale dependence of absorption of photosynthetically active radiation in terrestrial ecosystems. *Ecological Applications* 8, no. 4: 1003-21.

Asner, G. P., C. A. Wessman, and D. S. Schimel. 1998. Heterogeneity of savanna canopy structure and function from imaging spectrometry and inverse modeling. *Ecological Applications* 8, no. 4 : 1022-36.

Atchley, Michael C., Amrita G. de Soyza, and Walter G. Whitford. 1999. Arroyo water storage and soil nutrients and their effects on gas-exchange of shrub species in the northern Chihuahuan Desert. *Journal of Arid Environments* 43, no. 1: 21-33.

Abstract: A variable fraction of the rain falling on desert landscapes runs off and accumulates in ephemeral channels (arroyos), where some of the water is transported downslope. Relatively large amounts of water are stored in arroyo sediments. This water may support high rates of gas-exchange in some riparian species. We examined differences in the timing of flow events, soil water storage, and soil nutrients on gas-exchange rates of shrubs growing on arroyo margins and in adjacent piedmont areas in the Chihuahuan Desert of southern New Mexico, USA. The semi-riparian shrub, *Fallugia paradoxa* (Apache plume), had very different photosynthetic rates between two arroyos, but transpiration rates did not differ. This may result from nutrient limitation differences between arroyos. At one site, the semi-riparian shrub, *Prosopis glandulosa* (mesquite), on arroyo margins had access to more water and showed higher rates of gas-exchange compared with non-arroyo mesquite located on nearby piedmont areas. The obligate riparian shrub, *Chilopsis linearis* (desert willow), had intermediate gas-exchange rates when compared with Apache plume and mesquite, and neither soil water nor nutrient concentrations appeared to affect photosynthesis during the growing season. Variation between and within arroyos was high; however, our data suggest that stored water enabled mesquite of arroyo margins to maintain relatively high rates of gas-exchange. When water was relatively abundant, nutrient availability appeared to limit photosynthetic rates of Apache plume.

Bahre, C. J., and M. L. Shelton. 1993. Historic vegetation change, mesquite increases, and climate in southeastern Arizona. *Journal of Biogeography* 20, no. 5: 489-504.

Abstract: Long-term directional vegetation change in the wild landscape of southeastern Arizona since the advent of major Anglo-American settlement in the 1870s are identified and their relation to climate variations is examined. Particular emphasis is placed on verifying the purported changes in the distribution of major vegetation types and the link between velvet mesquite (*Prosopis velutina* Woot.) increases and precipitation trends since the turn of the century. While there is little doubt that climatic oscillations have resulted in short-term fluctuations in vegetation, precipitation variations do not appear to be connected to any major directional vegetation change since 1870 in southeastern Arizona. In fact, no single trend is evident in regional precipitation during this period. Furthermore, there is no clear evidence

for the upward displacement along a xeric-to-mesic gradient of any major vegetation type, and except possibly for increases in woody xerophytes such as mesquite, all of the identified long-term vegetation changes appear to be of anthropogenic origin. Mesquite increases, however are irregular, show no clear relation to precipitation variations, and are most likely the result of livestock grazing and/or fire exclusion.

Barnes, Paul W., and Steve Archer. 1996. Influence of an overstorey tree (*Prosopis glandulosa*) on associated shrubs in a savanna parkland: Implications for patch dynamics. *Oecologia* 105, no. 4: 493-500.

Abstract: The arborescent legume, honey mesquite (*Prosopis glandulosa*), appears to play a central role in patch dynamics of southern Texas savannas by modifying soils and microclimate and by facilitating the ingress, establishment and/or growth of shrubs in its understorey. As an indirect test for the occurrence and persistence of facilitation in mature shrub clusters (patches), we examined the gas exchange, water relations and production of associated shrubs growing in patches where a *Prosopis* overstorey was present and in patches where *Prosopis* had succumbed to natural mortality. Surface (0-10 cm) soils associated with shrub patches were enriched in total (N) and (C) compared to soils of neighboring herbaceous zones. However, there were no detectable differences in soil (N) or (C) in patches with and without *Prosopis*. Foliar (N) and biomass of various shrub species were also statistically comparable for patches with and without *Prosopis*. These results are in accordance with other studies that indicate the nutrient legacy associated with *Prosopis* occupation of a patch may persist for decades after its demise. In comparison to plants growing in the absence of *Prosopis*, leaf water potentials (predawn and midday), and net photosynthesis and water vapor conductance (morning and midday) of outer-canopy sunlit leaves over an annual growth cycle were comparable for two common evergreen shrubs, *Zanthoxylum fagara* and *Berberis trifoliolata*, growing in patches with a live *Prosopis*. These findings indicate that the presence of *Prosopis* was not enhancing the growth or activity of mature understorey shrubs; facilitation may, therefore, be important only during early stages of cluster development. In addition, we found no indication that the loss of *Prosopis* has initiated a downward phase in a cyclic succession of patch initiation, growth and death. Rather, the understorey shrubs appear to be able to maintain growth and productivity in the absence of a *Prosopis* overstorey, and may, therefore, represent persistent components of woody patches on these savanna landscapes.

Barth, Richard Charles. 1975. "Spatial distribution of carbon and nitrogen in some desert shrub ecosystems." Ph. D. Dissertation, University of Arizona.

Barth, R. C., and J. O. Klemmedson. 1982. Amount and distribution of dry matter, nitrogen, and organic carbon in soilplant systems of mesquite and palo verde. *Journal of Range Management* 35: 412-18.

———. 1986. Seasonal and annual changes in biomass nitrogen and carbon of mesquite and palo verde ecosystems. *Journal of Range Management* 39: 108-12.

BassiriRad, H., D. C. Tremmel, R. A. Virginia, J. F. Reynolds, A. G. de Soyza, and M. H. Brunell. 1999. Short-term patterns in water and nitrogen acquisition by two desert shrubs following a simulated summer rain. *Plant Ecology* 145: 27-36.

See abstract under *Larrea tridentata*

Bedunah, D. J., and R. E. Sosebee. 1986. Influence of mesquite control on soil erosion on a depleted range site. *Journal of Soil and Water Conservation* 41, no. 2 : 131-35.

Abstract: A 3-year study on the influence of some common brush control techniques on soil erosion was conducted on a clay loam site in low to fair range condition. Mesquite (*Prosopis glandulosa*) control by shredding, mechanical grubbing, vibratilling, and foliar spraying with 2, 4, 5-T + picloram reduced erosion. Plowing, disking, and seeding to kleingrass (*Panicum coloratum*) did not reduce erosion compared to the check. Brush control treatments removed mesquite competition, thus increasing the standing crop and cover of herbaceous plants. On the kleingrass, shred, foliar spray, mechanical grub, and check treatments, the amount of plant material protecting the soil surface was the most important variable controlling soil loss. Plant cover, standing crop, organic carbon, and total porosity all related positively to each other. As plant cover and biomass increased, organic carbon and porosity increased and erosion decreased. The absence of grazing for 3 years did not change site condition sufficiently to reduce erosion on the check.

Blanton, Rosa A. 1947. *The mesquite*. New York, N. Y: The Hobson Book Press.

Blydenstein, John. 1957. "The survival of velvet mesquite (*Prosopis juliflora* var. *velutina*) after fire." Ph. D. Dissertation, University of Arizona.

Bock, J. H., and C. E. Bock. 1992. Vegetation responses to wildfire in native versus exotic Arizona grassland. *Journal of Vegetation Science* 3, no. 4: 439-46.

Abstract: Grass and herb cover, and woody plant densities were measured on 25 native and 25 exotic grasslands plots in southeastern Arizona between 1984 and 1990. At least 40 yr previously, the exotic plots had been seeded with two species of lovegrasses (*Eragrostis* spp.) native to southern Africa. A 1987 wildfire burned 11 native and 11 exotic plots. The fire reduced cover of both native and African grasses for two post-fire growing seasons. Herb cover as a whole increased after the fire for 2 yr, although there were important differences among species. One of two dominant shrubs (*Haplopappus tenuisectus*) was killed by the fire, while the other (*Baccharis pteronioides*) was little affected. Mesquite trees (*Prosopis juliflora*) were killed to the ground by the fire, but 62 of 66 trees had re-sprouted to an average 48% of pre-burn height by 1990. Native and exotic grasses appeared equally tolerant of fire, probably because both evolved in fire-type ecosystems. There was no evidence that fire can be used to permanently restore the diverse native flora to species-poor plantations of the South African exotics.

Bogusch, Edwin R. 1950. A bibliography on mesquite. *Texas Journal of Science* 4: 528-38.

- Brock, John H. 1986. Velvet mesquite seedling development in three Southwestern soils. *Journal of Range Management* 39, no. 4 : 331-34.
- Brown, Joel R., and Steven Archer. 1987. Woody plant seed dispersal and gap formation in a North American subtropical savanna woodland: the role of domestic herbivores. *Vegetatio* 73: 73-80.
- . 1988. Establishment of mesquite in grasslands: effects of herbaceous plant density, standing crop, and soil moisture enhancement. *PR - Texas Agricultural Experiment Station CPR-4592* : 6.
- . 1989. Woody plant invasion of grasslands: establishment of honey mesquite (*Prosopis glandulosa* var. *glandulosa*) on sites differing in herbaceous biomass and grazing history. *Oecologia* 80, no. 1: 19-26.
Abstract: Emergence and survival of honey mesquite (*Prosopis glandulosa* var. *glandulosa* Torr.) seedlings was quantified on sites with contrasting grazing histories: long-term continuous grazing (LTG) and long-term protection (LTP) from grazing by cattle. On each site, different levels of herbaceous defoliation were imposed at monthly intervals (no defoliation=ND, moderate=MD and heavy=HD). The two weeks following seed dissemination appeared to be the most critical to *Prosopis* establishment on LTP-ND plots. Openings in the herbaceous layer created by moderate defoliation of grasses on the LTP site increased germination and/or survival 7- to 8-fold during this period. However, increasing the degree of defoliation from moderate to heavy did not stimulate additional emergence on either the LTP or LTG site. Emergence from scarified seed placed in cattle dung (17 to 30%) was lower than that of bare seed placements in various microhabitats (43-60%). However, deposition of scarified *Prosopis* seed in dung in conjunction with graminoid defoliation may be the most likely combination of events when livestock are present. Emergence from seeds transported into grasslands by other fauna likely would be low, unless seeds were deposited in areas where grasses had been defoliated. *Prosopis* survival was comparably high in dung and bare seed placements after one growing season. Survival of seedlings present two weeks after seed dissemination ranged from 74 to 97% at the end of the second growing season. Seedling survival and shoot development (biomass, leaf area and height) were similar on LTP and LTG sites, regardless of the level of herbaceous defoliation or seed placement. In addition, the magnitude and patterns of net photosynthesis, stomatal conductance and xylem water potential were comparable among one-year-old seedlings on ND, MD and HD plots, even though differences in herbaceous species composition and above- and belowground biomass between these treatments were substantial. Such data suggest competition for soil resources between grasses and *Prosopis* may be minimal early in the life cycle of *Prosopis*. High rates of *Prosopis* emergence and establishment on LTP-MD plots are counter to the widespread assumption that long-term and/or heavy grazing is requisite for *Prosopis* encroachment into grasslands. Results are discussed with regard to factors contributing to the recent, widespread invasion of this woody legume into grasslands of southwestern North America.
- . 1990. Water relations of a perennial grass and seedling vs adult woody plants in a subtropical savanna, Texas. *Oikos* 57: 366-74.

———. 1999. Shrub invasion of grassland: Recruitment is continuous and not regulated by herbaceous biomass or density. *Ecology* 80, no. 7: 2385-96.

Abstract: Proliferation of woody plants in grasslands and savannas since the 1800s has been widely documented. In the southwestern United States, increased abundance of honey mesquite (*Prosopis glandulosa* var. *glandulosa*) has been attributed to heavy grazing by livestock. Here, we test the hypothesis that *P. glandulosa* invasion of grasslands requires, first, reductions in herbaceous biomass and density such as those that accompany livestock grazing and, second, episodes of high soil moisture availability. No combination of grass density (nonmanipulated or reduced 50%) or defoliation (none, moderate, heavy) significantly affected *P. glandulosa* seedling emergence within a watering regime (natural and supplemented) at our field site in semiarid southern Texas. Seedling emergence on plots receiving only natural rainfall was high (42%), despite the fact that precipitation was substantially below normal. Supplemental watering, to generate moisture levels approximating years of unusually high annual rainfall, increased emergence to 59%. Seedling survival after 2 yr was high (62-77%) and statistically comparable across the density, defoliation, and watering treatments. Net photosynthesis (A_n) of 1-yr-old seedlings was enhanced by supplemental watering, but reductions in grass density or biomass had little effect on seedling A_n or xylem water potential. Height, aboveground biomass, and leaf area were comparable among 1- and 2-yr-old seedlings across all density, defoliation, and watering combinations. High seedling emergence and survival on unwatered plots, even during a "drought year," suggests that *Prosopis* recruitment is not contingent upon unusual or episodic rainfall. Reductions in biomass and density of herbaceous vegetation had no influence on seedling emergence, growth, or survival, suggesting that *Prosopis* invasion is minimally influenced by grass competition. Historic grazing at this site appears to have altered herbaceous composition and reduced above- and belowground biomass production below the threshold level required for competitive exclusion of woody vegetation. Such data suggest that rates and patterns of seed dispersal may be the primary determinants of *P. glandulosa* encroachment on present-day landscapes in semiarid regions. Minimizing livestock dispersal of seed (in the case of leguminous shrubs) and maintenance of an effective fire regime (through production of fine fuels) may be crucial for sustaining herbaceous composition and production in grazed systems prone to invasion by unpalatable woody plants.

Brownlee, Evelyn A, and National Agricultural Library (U.S.). 1987. *Mesquite : recent research, 1979-May 1987 : 246 citations*. Quick Bibliography Series, 88-02. Beltsville, Md. : U.S. Dept. of Agriculture, National Agricultural Library.

Buffington, Lee Charles. 1964. "Vegetational changes on a semidesert range from 1858 to 1963." M.S. Thesis, New Mexico State University.

See abstract under *Larrea tridentata*

Buffington, Lee C., and Carlton H. Herbel. 1965. Vegetational changes on a semidesert grassland range from 1858 to 1963. *Ecological Monographs* 35, no. 2: 139-64.

See abstract under *Larrea tridentata*

Bush, J. K., and O. W. Van Auken. 1990. Growth and survival of *Prosopis glandulosa* seedlings associated with shade and herbaceous competition. *Botanical Gazette* 151, no. 2: 234-39.

Abstract: Both shade and herbaceous competition reduced the germination and growth of *Prosopis glandulosa* Torr. (honey mesquite). Natural and artificial shade was used and herbaceous competition was manipulated by clipping and herbicide. Greatest growth of *P. glandulosa* seedling was in full sunlight when there were no competitors. Plants in shade without competitors or in full sunlight with competitors had intermediate growth, while those in shade with competitors were the smallest. Natural shading by *P. glandulosa* trees caused similar trends, although significant differences were not always found. *Prosopis glandulosa* germination in the laboratory was 93 ± 5% versus 2%-19% in the field. No *P. glandulosa* seedlings survived after one growing season in two grassland plots with high biomass, compared with 8% in the herbicide plot. Lack of *P. glandulosa* seedling germination and growth under mature *P. glandulosa* trees appears to be the result of reduced light levels and herbaceous plant competition. These factors also result in low numbers of seedlings in grasslands and, coupled with herbivory or fire, could account for their absence.

———. 1991. Importance of time of germination and soil depth on growth of *Prosopis glandulosa* (*Leguminosae*) seedlings in the presence of a C4 grass. *American Journal of Botany* 78: 1732-39.

Abstract: In an investigation of the causes of the invasion of woody plants into grasslands, competition between seedlings of *Prosopis glandulosa* and *Bouteloua curtipendula* was examined. Data suggest that *P. glandulosa* and other shade-intolerant woody species that establish in grasslands do so in disturbances or vegetation gaps

———. 1995. Woody plant growth related to planting time and clipping of a C-4 grass. *Ecology* 76, no. 5: 1603-9.

Abstract: The density of woody plants has increased in grasslands throughout the world, but the cause has been elusive, although changes in herbivory seem central. In this study, the importance of relative time of planting and clipping of *Bouteloua curtipendula*, a C-4 grass, on *Prosopis glandulosa*, a woody seedling, was evaluated in a 2-yr field study in central Texas, USA. Secondly, effects of planting date, presence of the woody seedling, and clipping of the grass on the growth of the grass were evaluated. Relative growth rates (RGRs) of *Prosopis glandulosa* (honey mesquite) seedlings grown alone were seasonal, generally high in spring and decreasing as summer progressed. When *P. glandulosa* was planted earlier than *Bouteloua curtipendula* (side-oats grama), the grass had little or no effect on the woody seedling RGRs. However, the dry mass of *P. glandulosa* increased 2.3 times when the grass was clipped but was reduced 54% when the grass was unclipped. When the two species were started at the same time and the grass was not clipped, *P. glandulosa* RGRs decreased and remained zero over the 2 yr, dry mass was reduced 99.8%, and mortality was 80%. If both species were started at the same time and the grass was clipped, 1st- and 2nd-yr growth of *P. glandulosa* was comparable to that of seedlings grown no increase when the grass was planted late. Evidence suggests that woody seedling growth in undisturbed C-4 grasslands would be very limited, and establishment requires gap formation.

Cable, Dwight R. 1965. Damage to mesquite, Lehmann lovegrass, and black grama by a hot June fire. *Journal of Range Management* 18: 326-29.

See abstract under *Bouteloua eriopoda*

———. 1967. Fire effects on semidesert grasses and shrubs. *Journal of Range Management* 20: 170-176.

Abstract: Immediate effects of fire on perennial grasses lasted only 1 or 2 years. Burroweed was easily killed, but came back quickly with adequate cool-season moisture. Fire was relatively ineffective against mesquite, fair against cactus.

———. 1967. Fire effects on southwestern semidesert grass-shrub communities. *Proceedings of the tall timbers fire ecology conference*, 109-27.

Cable, Dwight R., and Samuel Clark Martin. 1975. Vegetation responses to grazing, rainfall, site condition, and mesquite control on semidesert range . Rocky Mountain Forest and Range Experiment Station. 24 p. : ill., map ; 27 cm . USDA Forest Service Research Paper RM, 149. Fort Collins, CO: U.S. Department of Agriculture, Forest Service.

Cable, Dwight R., and F. H. Tschirley. 1961. Responses of native and introduced grasses following aerial spraying of Velvet Mesquite in Southern Arizona. *Journal of Range Management* 14: 155-59.

Abstract: Velvet mesquite (*Prosopis juliflora* var. *velutina* (Wont.) Sarg.)³ covers large acreages in the Southwest, has greatly thickened during the past 60 to 75 years, and has been responsible for sizable losses in perennial grass forage. These facts are well known and well documented (Parker and Martin, 1952; Glendening, 1952). The need for information on methods of control and on the benefits to be expected are obvious.

Velvet mesquite can be controlled best by mechanical or chemical methods. Aerial application of herbicides is the most feasible control method where velvet mesquite exceeds 200 trees per acre (Reynolds and Tschirley, 1957). But before aerial spraying is widely adopted as a control measure, there should be some assurance that increased grass production will pay for the cost of control. To help answer this question, data from an area on the Santa Rita Experimental Range about 30 miles southeast of Tucson, Arizona, showing the response of native and introduced perennial grasses following aerial spraying of velvet mesquite are presented here.

Campbell, R. S. 1929. Vegetative succession in the *Prosopis* sand dunes of southern New Mexico. *Ecology* 10, no. 4: 392-98.

Abstract: The Jornada Range Reserve, on which this study was made, was established in 1912, and has been conducted by the U.S. Forest Service as a range experiment station since 1915. It is typical semi-desert range, adjacent to the Rio Grande valley in Dona Ana County, New Mexico, about 50 miles north of the Mexican boundary. There are about 145,000 acres (58,000 hectares) in the mesa portion, of which

approximately one-fourth is covered by the *Prosopis* sand dune type, consisting of low, evenly distributed dunes occupied principally by mesquite (*Prosopis glandulosa* Torr.), with "blow outs" (wind formed hollows) in between the dunes.

The soils of the mesa are mostly Quaternary alluvium with older sands and gravels (Darton, '22), and the *Prosopis* type is always found in the loose, wind-blown phase of the more sandy soils. The community, as shown in Plate XII, 1, is rather extensive in southern New Mexico, although it is not mentioned by Watson ('21) in his description of the northern part of the state.

Cantu Ayala, Cesar M. 1990. Fenologia de la floracion y fructificacion del mezquite *Prosopis laevigata* (Humb. & Bonpl. ex Willd.) M.C. Johnst. en nuevo leon y el efecto de las cabras sobre la dispersion de sus semillas. 38 p. : ill., map ; 23 cm. Reporte Cientifico, no. 18. Linares, N.L., Mexico : Facultad de Ciencias Forestales, Universidad Autonoma de Nuevo Leon.

———. 1991. Zur Biologie, Ökologie und Schadwirkung der Blüten- und Fruchtschadlinge an der Mesquitepflanze *Prosopis laevigata* (Humb. & Bonpl. ex Willd.) M.C. Johnst. in Nuevo Leon, Mexico, unter besonderer Berücksichtigung der Samenkäfer (Bruchidae). 119 p. : ill., map ; 21 cm. Göttinger Beiträge zur Land- und Forstwirtschaft in den Tropen und Subtropen , Heft 64. Göttingen : E. Goltze.

Carlson, D. H., T. L. Thurow, R. W. Knight, and R. K. Heitschmidt. 1990. Effect of honey mesquite on the water balance of Texas Rolling Plains rangeland. *Journal of Range Management* 43, no. 6 : 491-96.

Carpenter, Brent D., Don E. Ethridge, and R. E. Sosebee. 1990. Economic losses from broom snakeweed poisoning in cattle. *Rangelands* 12, no. 4: 206-8.

Carter, M. G. 1964. Effects of drought on mesquite. *Journal of Range Management* 17: 275-76.

Chojnacky, David C. 1988. Juniper, pinyon, oak, and mesquite volume equations for Arizona . 15 p. ill., maps . Research Paper INT, 391. Ogden, UT : U.S. Department of Agriculture, Forest Service, Intermountain Research Station.

Claveran Alonso, Ramon. 1967. "Desert grassland mesquite and fire." Ph. D. Dissertation, University of Arizona.

Connin, S. L., R. A. Virginia, and C. P. Chamberlain. 1997. Isotopic study of environmental change from disseminated carbonate in polygenetic soils. *Soil Science Society of America Journal* 61, no. 6 : 1710-1722. Abstract: We evaluated the extent to which delta13C and delta18O values of disseminated carbonate preserve a signal of Holocene and modern vegetation changes in polygenetic soils of the Jornada Basin,

New Mexico. Factors and processes influencing carbonate chemistry were constrained in a relict grassland community and recent mesquite [*Prosopis glandulosa* var. *torreyana* (L. Benson) M. Johnston] dunes, using ^{14}C dates and $\delta^{13}\text{C}$ data of soil organic matter (SOM) as independent measures of site history. Total-profile carbonate contents ranged from 39 to 451 kg m⁻² due to local patterns of soil water infiltration and erosion. In grassland soils, ^{14}C ages and $\delta^{13}\text{C}$ values of disseminated carbonate in A and B horizons were influenced by the presence of older detrital carbonate, reworked from surrounding surfaces. As a result, carbonate isotopes did not record mid-Holocene climate and vegetation changes, which were inferred from $\delta^{13}\text{C}$ values of coexisting SOM. Shrub expansion during the past century was recorded by changes in the $\delta^{13}\text{C}$ values of disseminated carbonate and SOM from mesquite dunes. Carbon-14 data and mass balance estimates indicated that at least 80% of the dune carbonate (in C horizons) has been isotopically altered by dissolution and recrystallization processes in <100 yr. The modern carbonate is apparently forming from soil waters composed of nearly equal amounts of summer and winter rainfall, as evidenced by carbonate $\delta^{18}\text{O}$ values. Our analyses indicate that disseminated carbonate can provide a meaningful environmental signal in polygenetic soils, when pedogenic contributions to isotopic variability are constrained.

Cornejo-Oviedo, E., S. Gronski, and P. Felker. 1992. Mature mesquite (*Prosopis glandulosa* var. *glandulosa*) stand description and preliminary effects of understory removal and fertilization on growth. *Journal of Arid Environments* 22, no. 4 : 339-51.

Abstract: The growth of a mature stand of *Prosopis glandulosa* was measured following understory removal, thinning, and phosphorus fertilization. Many of the 193 trees ha⁻¹ were multi-stemmed at the base, with the result that there were 356 stems ha⁻¹. The basal diameters ranged from 5.7 to 40.7cm, with a mean of 16.4 cm. The trees were examined over three growing seasons using permanently mounted bands inscribed with a vernier scale capable of reading 0.25 mm increments. Regressions were used to convert basal area increases to volume and weight increases. Understory removal stimulated the greatest growth. Thinning multi-stemmed trees to a single stem with best form resulted in 33 m³ of firewood ha⁻¹. The understory removal, plus herbicide resprout treatment, plus thinned, plus fertilizer had the greatest growth of; 0.86 m³ ha⁻¹ in volume, 1890 kg/ha in green weight, and 0.61 cm in basal diameter over three growing seasons. Significant treatment differences (p = 0.05) were found between the growth of the control treatment and the (1) treatment with understory removal plus thinning and (2) the treatment with understory removal plus thinning plus fertilization.

Cox, J. R., A. de Alba-Avila, R. W. Rice, and J. N. Cox. 1993. Biological and physical factors influencing *Acacia constricta* and *Prosopis velutina* establishment in the Sonoran Desert. *Journal of Range Management* 46, no. 1 : 43-48.

Abstract: Over the past century woody plants have increased in abundance on sites formerly occupied by grasslands in the Sonoran Desert. Woody plant invasion has been associated with a multitude of biological and physical factors. This study was conducted to determine temperature, soil, fire, rodent, and livestock effects on the germination and establishment of whitethorn acacia (*Acacia constricta* Benth.) and velvet mesquite (*Prosopis velutina* (Woot.) Sarg.). Optimum termination temperatures for both shrubs ranged

from 26 to 31 degrees C, and seedling emergence was greatest from seed sown at 1 to 2 cm depths in sandy loam soil. Merriam's kangaroo rats (*Dipodomys merriami*) fed seeds in the laboratory removed seed coats and planted embryos at 2 to 4 cm depths in a sandy loam soil. Prescribed fire killed 100% of seed placed on the soil surface but had no measurable effect on the germination of seed planted at 2 cm. After passage by sheep, about 6% of the *A. constricta* and 13% of the *P. velutina* seeds germinated while after passage by cattle, only 1% of the *A. constricta* and 3% of the *P. velutina* seed terminated. Embryo planting by rodents may improve survival efficiencies for these leguminous shrub seedlings, but seed consumption and passage by sheep and cattle appear to adversely affect seed germination. *Dipodomys merriami*, rather than domestic livestock, may be responsible for the spread of these shrubs in the Sonoran Desert.

Cuomo, C. J., R. J. Ansley, P. W. Jacoby, and R. E. Sosebee. 1992. Honey mesquite transpiration along a vertical site gradient. *Journal of Range Management* 45, no. 4: 334-38.

Abstract: Honey mesquite (*Prosopis glandulosa* Torr.) occurs on a variety of sites varying in soil depth and moisture availability. The objective of this study was to compare water use by honey mesquite on upland, lowland, and riparian sites which were assumed to represent increasing levels of available soil moisture within a single watershed. Effects of the upland and lowland sites were evaluated in 1985. The riparian site was evaluated with the other 2 sites in 1986. Soil moisture and average daily transpiration were greater ($P < 0.05$) on the upland than on the lowland site from mid-May to July in both years, and from mid-August through September 1986. These differences were attributed mainly to soil surface characteristics which created greater infiltration on the upland site. The riparian site was near an ephemeral stream and had a water table as shallow as 1.5 m. Soil water content was much greater for this site compared to the other 2 sites throughout 1986. Mesquite transpiration was greater on the riparian site than on the other sites during July 1986, when seasonal vapor pressure deficit was at maximum. However, transpiration was less on the riparian site than on the upland site during May and June 1986. Soil temperature was significantly lower on the riparian than on the upland site and potentially inhibited transpiration on the riparian site in May and June. The study demonstrated a positive relationship between water availability and transpiration by mesquite but did not support the hypothesis that water availability or transpiration was lowest on upland sites.

de Soyza, Amrita, Augusto C. Franco, Ross A. Virginia, James F. Reynolds, and Walter G. Whitford. 1996. Effects of plant size on photosynthesis and water relations in the desert shrub *Prosopis glandulosa* (Fabaceae). *American Journal of Botany* 83, no. 1: 99-105.

Abstract: The Jornada del Muerto basin of the Chihuahuan Desert of southern New Mexico, USA, has undergone a marked transition of plant communities. Shrubs such as mesquite (*Prosopis glandulosa*) have greatly increased or now dominate in areas that were previously dominated by perennial grasses. The replacement of grasses by shrubs requires an establishment phase where small shrubs must compete directly with similar-sized grass plants. This is followed by a phase in which large, established shrubs sequester nutrients and water within their biomass and alter soil resources directly under their canopy, creating "islands" of fertility. We hypothesized that these two phases were associated with shrubs having different physiological response capacities related to their age or size and the resource structure of the

environment. As a corollary, we hypothesized that responses of small shrubs would be more tightly coupled to variation in soil moisture availability compared to large shrubs. To test these hypotheses, we studied gas exchange and water relations of small (establishing) and large (established) shrubs growing in the Jornada del Muerto as a function of varying soil moisture during the season. The small shrubs had greater net assimilation, stomatal conductance, transpiration, and xylem water potential than large shrubs following high summer rainfall in July, and highest seasonal soil moisture at 0.3 m. High rates of carbon assimilation and water use would be an advantage for small shrubs competing with grasses when shallow soil moisture was plentiful. Large shrubs had greater net assimilation and water-use efficiency, and lower xylem water potential than small shrubs following a dry period in September, when soil moisture at 0.3 m was lowest. Low xylem water potentials and high water-use efficiency would allow large shrubs to continue acquiring and conserving water as soil moisture is depleted. Although the study provides evidence of differences in physiological responses of different-sized shrubs, there was not support for the hypothesis that small shrubs are more closely coupled to variation in soil moisture availability than large shrubs. Small shrubs may actually be less coupled to soil moisture than large shrubs, and thus avoid conditions when continued transpiration could not be matched by equivalent water uptake.

de Soyza, A. G., W. G. Whitford, R. A. Virginia, and J. F. Reynolds. 1996. Effects of summer drought on the water relations, physiology, and growth of large and small plants of *Prosopis glandulosa* and *Larrea tridentata*. In *Proceedings: symposium on shrubland ecosystem dynamics in a changing environment*, Compilers J. R. Barrow, E. D. McArthur, R. E. Sosebee, and R. J. Tausch, 220-223 Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station.

See abstract under *Larrea tridentata*

DeBano, L. F., G. J. Gottfried, J. Villanueva-Diaz, P. F. Ffolliott, and D. Valdez-Zamudio. 1996. Initial assessment of fire-damaged mesquite trees following an illegal burn. In *Effects of fire on Madrean Province ecosystems: a symposium proceedings*, Technical coordinators P. F. Ffolliott, L. F. DeBano, M. B. Baker Jr., G. J. Gottfried, G. Solis-Garza, C. B. Edminster, D. G. Neary, L. S. Allen, and R. H. Hamre. General Technical Report RM-289. Fort Collins, Colorado: USDA Forest Service, Rocky Mountain Experiment Station.

DeGarmo, H. C. Jr. 1966. "Water requirement and production of eight desert plant species under four soil moisture levels." M. S. Thesis, New Mexico State University.

DeLoach, C. J. Conflicts of interest over beneficial and undesirable aspects of mesquite (*Prosopis* spp.) in the United States as related to biological control. In *Proceedings of the VI International Symposium on Biological Control of Weeds*, Editor Ernest S. Delfosse.

Drewa, Paul B., Debra P. C. Peters, and Kris M. Havstad. 2001. Fire, grazing, and honey mesquite invasion in black grama-dominated grasslands of the Chihuahuan desert: a synthesis. in *Proceedings of the invasive*

species workshop: the role of fire in the control and spread of invasive species. Fire conference 2000: the first national congress on fire ecology, prevention, and management. Editors K. E. M. Galley, and T. P. Wilson, 31-39. Tallahassee, Florida: Tall Timbers Research Station.

Abstract: Prior to European settlement, the Chihuahuan Desert was comprised, in part, of grasslands dominated by the perennial grass, black grama (*Bouteloua eriopoda*) as well as by other species of herbaceous vegetation. 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 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. However, 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.

Dugas, W. A., M. L. Heuer, and H. S. Mayeux. 1992. Diurnal measurements of honey mesquite transpiration using stem flow gauges. *Journal of Range Management* 45, no. 1 : 99-102.

Abstract: Honey mesquite (*Prosopis glandulosa* Torr. var. *glandulosa*) stem flow was measured on days with contrasting environmental conditions during the 1989 growing season in Texas. Midday stem flow varied from near 10 to about 300 g hour⁻¹ and daily totals varied from about 1,000 to 2,000 g day⁻¹. On days with low potential evaporation, regardless of precipitation totals for the previous 20 days, stem flow mirrored potential evaporation. On a day with high potential evaporation and high precipitation totals for the previous 20 days, stem flow was greatest and the diurnal pattern was similar to that of potential evaporation. On a day with high potential evaporation and little precipitation for the previous 20 days, stem flow mirrored potential evaporation until about 1030 and decreased throughout the day, while potential evaporation remained high. Variability of stem flow between stems was large, with a C.V. of about 30% for midday rates and a seasonal average C.V. of 37% for daily rates. Stem flow gauges provide continuous and accurate measurements of honey mesquite transpiration. They respond to changing environmental conditions and are useful for evaluating short-term responses of stem flow to physiological and environmental factors in the field and glasshouse.

Dugas, William A., Ralph A. Hicks, and Robert P. Gibbens. 1996. Structure and function of C3 and C4

Chihuahuan desert plant communities. Energy balance components. *Journal of Arid Environments* 34, no. 1: 63-79.

See abstract under *Larrea tridentata*

Dugas, W. A., and H. S. Mayeux Jr. 1991. Evaporation from rangeland with and without honey mesquite. *Journal of Range Management* 44, no. 2 : 161-70.

Abstract: The Bowen ratio/energy balance technique was used to estimate evaporation (E) from honey mesquite (*Prosopis glandulosa* Torr. var. *glandulosa*) as the difference in total E (plant and soil) between that of adjacent mesquite-dominated and mesquite-free rangeland areas near Throckmorton, Tex. After treatment with diesel in July 1988 to defoliate the honey mesquite, E from the treated area decreased to a minimum value of about 40% of that from the untreated area. In 1989, seasonal E totals from the untreated and treated areas were, respectively, 190 and 176 mm-a 7% reduction in E due to mesquite defoliation. Total E for the herbaceous and honey mesquite vegetation in 1989 in the untreated area was 117 and 73 mm, respectively. Honey mesquite foliar cover was 15% in the untreated area, but it accounted for 38% of the total E. These honey mesquite E data were supported by independent measurements of sap flow. While honey mesquite used substantial amounts of water, E from the rangeland from which it was removed was just slightly lower due to increased herbaceous evaporation associated with increases in standing crop. Under the circumstances of low grazing intensity and low runoff potential, honey mesquite removal would provide little if any additional water for off-site uses in the short-term and, therefore, the removal of this species for purely hydrological purposes would not be justified. Increases in off-site water availability may, however, result from honey mesquite control under grazing regimes which preclude accumulation of additional herbaceous standing crop or at site with greater runoff potential.

Dutton, Roderic W. 1989. *Prosopis* species. Aspects of their value, research and development: Proceedings of the *Prosopis* Symposium held by CORD, University of Durham. 320Durham Centre for Overseas Research and Development.

Abstract: This book summarizes the proceedings of a conference on species of the genus *Prosopis*. The 44 species of *Prosopis* trees and shrubs grow mainly in arid and semi-arid areas and although sometimes perceived as an invasive weed, the book argues that with careful management, *Prosopis* species could yield social, economic and ecological benefits in less developed areas. *Prosopis* species possess valuable properties: they can tolerate low rainfall, poor and saline soils and in some species such as *P. cineraria*, vast temperature ranges. They increase soil moisture in the environs of the tree or shrub, fix nitrogen in the soil, produce protein-rich leaves and beans and provide fodder for animals. Investigating the actual and potential properties of different *Prosopis* species, and how these might be developed for more extensive use was thus an important theme of the book.

After an initial section on a possible research programme, the book is divided into five sections: the first focuses on the current and potential value of *Prosopis* species in different countries. Its importance as a forage crop is everywhere evident and improving the quantity and quality of trees and bushes for livestock feed is a recurrent theme. The second section examines the possibilities of improving genetic resources and

section three on ecophysical research discusses methods of improving nitrogen fixation, and the effects of soil salinity and sodicity on *Prosopis* species. Section four investigates the potential of *Prosopis* for enhancing animal and human nutrition, and section five, on management systems considers the role of *Prosopis* species in rangeland improvement and also the value of technological aids such as remote sensing for mapping the distribution of the species.

The book skillfully brings together a wide range of material on the genus *Prosopis*, all of it relevant to the development debate. Although much of the material is highly technical, discussions and summaries are quite comprehensible to the lay reader. However, two related questions emerge unanswered. First, what are the possible disadvantages of increasing the spread of *Prosopis* species? There must be some but these have received scant attention. Other 'super species' such as *Leucaena* in parts of South East Asia and the neem tree in West Africa have often been far from the successes predicted. And second, what are the views of local people on the incorporation of *Prosopis* species into indigenous land-use systems? Were the trees and bushes to become invasive, as they have done in parts of the southern USA, this could create severe problems in areas where access to labour and technology is limited.

Nevertheless, the book makes a convincing argument for further research into species of the genus *Prosopis* and will be of interest to anyone concerned with the problems of arid and semi-arid lands.

Dwyer, Don D., and Harlan C. DeGarmo. 1970. Greenhouse productivity and water-use efficiency of selected desert shrubs and grasses under four soil-moisture levels. *New Mexico Agricultural Experiment Station Bulletin* No. 570.

Ehleringer, J. R., H. A. Mooney, P. W. Rundel, R. D. Evans, B. Palma, and J. Delatorre. 1992. Lack of nitrogen cycling in the Atacama Desert. *Nature* 359, no. 6393 : 316-18.

Abstract: Mesquite (*Prosopis*) trees growing in the rainless region of the Atacama Desert produce leaves that abscise and accumulate on a concrete-like carbonate surface, often attaining litter depths of 45 cm. The virtual lack of surface moisture inhibits leaf decomposition, and prevents cycling of nitrogen, the mineral most often limiting plant growth. Leaves in the midpoint of a litter profile were aged to pre-bomb dates (older than 1950) and had both high nitrogen concentrations and a carbon to nitrogen ratio comparable to that of live leaves. The thick carbonate layer prevents root growth into the litter. *Prosopis* appear to persist by having roots that fix nitrogen in moist subsurface layers and by extracting water and other nutrients from ground water, allowing plants to persist in an ecosystem in which there is no nitrogen cycling.

El Youssoufi, M., and S. Archer. 1988. Population biology of mesquite in the South Texas Plains. *PR - Texas Agricultural Experiment Station* CPR-4592 : 9.

Felker, P. 1998. The value of mesquite for the rural Southwest: fine lumber and soil improvement. *Journal of Forestry* 96, no. 3 : 16-20.

Figueiredo, A. A. 1990. Mesquite: History, composition, and food uses. *Food Technology* 44, no. 11 : 118-28.

Abstract: Once thought useless, this pod-bearing tree provides a new seed gum for potential application in a variety of food products.

Flinn, R. C., S. Archer, T. W. Boutton, and T. Harlan. 1994. Identification of annual rings in an arid-land woody plant, *Prosopis glandulosa*. *Ecology* 75, no. 3: 850-853.

Abstract: The utilization of woody plants for dendroecology requires species that produce distinguishable rings in most years, that possess ring features that can be dated dendrochronologically, and that attain sufficient age to provide that time control required for a particular investigation. Our survey suggests that *P. glandulosa* plants from a range of climatic regimes produce true annual rings and that the surface preparation technique described here was effective in highlighting these rings for analysis. Models of *P. glandulosa* size/age relationships based on plant growth rate analysis suggest stems of some trees may exceed 200 yr in age. Thus, tree ring analysis of *P. glandulosa*, which is sufficiently long live to be a canopy dominant in the vegetation over much of its range, appears to be a promising tool for reconstructing climatic events, disturbance, stand development, and successional history in many arid and semiarid ecosystems of the southwestern United States and Mexico.

Frias, Hernandez J. T., Ledezma A. L. Aguilar, Portugal V. Olalde, J. A. Balderas Lopez, Juarez G. Gutierrez, Gil J. J. Alvarado, J. J. Castro, H. Vargas, A. Albores, L. Dendooven, and L. C. M. Miranda. 1999. Soil characteristics in semiarid highlands of Central Mexico as affected by mesquite trees (*Prosopis laevigata*). *Arid Soil Research and Rehabilitation* 13, no. 3: 305-12.

Abstract: In the semiarid highlands of central Mexico the mesquite tree (*Prosopis laevigata*) is often removed for agricultural and forestry purposes. Clearing of land for agricultural purposes has a significant impact on soil processes and nutrient dynamics and, ultimately, on crop production. We have studied the effect of the mesquite tree on soil respiration, amounts of bacteria, fungi, and actinomycetes, and soil characteristics. Soil was sampled from three distinct locations: under the canopy of the mesquite tree, in the area surrounding the mesquite tree but not covered by its canopy, and in adjacent cultivated land. It was found that the mesquite tree plays an important role in nutrient cycling in arid and semiarid regions. Soil microorganisms and nutrients (N, P, and Fe) were more abundant under the canopy of the mesquite tree than in the surrounding area and in the adjacent arable soil.

Fulbright, T. E., J. O. Kuti, and A. R. Tipton. 1997. Effects of nurse-plant canopy light intensity on shrub seedling growth. *Journal of Range Management* 50, no. 6 : 607-10.

Abstract: Spiny hackberry (*Celtis pallida* Torr.) occurs almost exclusively beneath honey mesquite (*Prosopis glandulosa* Torr.) canopies. We hypothesized that maximum early seedling growth of spiny hackberry occurs at light intensities similar to those beneath honey mesquite, whereas maximum growth of huisache (*Acacia smallii* Isely), a plant characteristic of nonshaded habitats, occurs at light intensities near full sunlight. Photosynthetic photon flux densities (PPFD) under 4 honey mesquite canopies and in adjacent interspaces were recorded during July 1990 to July 1992. Seedling growth indices of spiny

hackberry and huisache were determined at PPFs characteristic of those found under honey mesquite canopies and in herbaceous interspaces. In contrast to our prediction, relative growth rate (Kw), net assimilation rate (NAR), and seedling mass of spiny hackberry were greater in sunlight than in shade characteristic of honey mesquite canopies. Huisache also had greater Kw, NAR, and total seedling mass in sunlight. Aggregation of spiny hackberry beneath honey mesquite canopies does not result from an ability to maintain maximum seedling growth at low light intensities.

Gadzia, Jimi S. Graham, and John A. Ludwig. 1983. Mesquite age and size in relation to dunes and artifacts. *The Southwestern Naturalist* 28, no. 1: 89-94.

Abstract: In a duneland dominated by mesquite (*Prosopis glandulosa* var. *torreyana*) twelve mesquite-dune complexes were analyzed in order to determine relationships between plant age, plant canopy size, and dune size. In addition, surface Indian artifacts were measured along the study transect which centered through remnants of an Indian campsite. These data were collected in an attempt to investigate the theory that mesquite is at least partially responsible for the initiation and continuation of the dune building process in the Jornada Plains.

Plant age was significantly related to the volume of the plant canopy, and to the volume of the dune. Surface artifact densities tended to be highest in areas of greater dune formation, which suggests that artifacts are more visible in areas of greater soil erosion. The ring numbers, taken from these samples do support earlier observations that there has been a recent and rapid increase of mesquite on the Jornada Plains.

Geesing, D., P. Felker, and R. L. Bingham. 2000. Influence of mesquite (*Prosopis glandulosa*) on soil nitrogen and carbon development: implications for global carbon sequestration. *Journal of Arid Environments* 46, no. 2: 157-80.

Abstract: The genus *Prosopis* contains many N-fixing species throughout the world's semi-arid regions. Previous work with *Prosopis glandulosa* found that small young trees obtained most of their N from N-fixation, while mature trees that had accumulated 1.3 Mg N ha⁻¹ in the soil beneath their canopy derived a much smaller percentage of their N from N-fixation. This work examined the percentage of nitrogen derived from nitrogen-fixation (%Ndfa) and soil development as a function of tree size on seven Texas sites. The tree basal diameters ranged from 3.2 cm to 76.4 cm. Leaf and trunk core samples were taken from trees to determine N, P, and natural abundance ratios of ¹⁵N/¹⁴N. Soil samples were taken 75 cm from the trunk and outside the influence of the tree canopy. Soil values for organic C, available P, pH, NO₃, NH₄ and ¹⁵N/¹⁴N were measured. A comparison of ¹⁵N/¹⁴N from background soil parent material and the leaves or trunk was used to estimate the percentage of N derived from N fixation. Increases under canopy over background in soil C, N, and P were significantly correlated with trunk diameter and had maximum values of 17.7 Mg ha⁻¹ for C, 4.4 Mg ha⁻¹ for N and 13 kg ha⁻¹ for available P. The soil C/N ratio was negatively correlated with trunk diameter. Leaf concentrations of N and P increased with trunk diameter. The soil N was significantly correlated with leaf N and P, the soil P was significantly correlated with leaf P. The ¹⁵N/¹⁴N ratios of the soil were highly correlated with the ¹⁵N/¹⁴N of the leaves, but were not correlated with the ¹⁵N/¹⁴N ratios of trunk wood. The trunk wood had a much higher % Ndfa (75%) than the leaves (25%). This difference was to be

expected, since the trunk represents the oldest tissues (when the trees obtained most of its N from fixation) while the leaves represent the current years growth and is coupled with soil¹⁵N/¹⁴N values. The %Nd_f of the leaves declined significantly with soil nitrate levels as would be expected since the N-fixation process is strongly inhibited by available N. If an increase of 2 Mg ha⁻¹ soil C could be achieved on the subtropical, semi-arid areas to which *Prosopis* and *Acacia* are adapted, 6.2×10⁹Mg of carbon would be sequestered. As projected 2010 carbon emissions are 8.5×10⁹Mg of carbon, management of tree legumes in arid regions has significant potential to positively impact global C sequestration.

Gibbens, Robert P., Reldon F. Beck, Robert P. McNeely, and Carlton H. Herbel. 1992. Recent rates of mesquite establishment in the northern Chihuahuan desert. *Journal of Range Management* 45, no. 6: 585-88.
Abstract: Honey mesquite (*Prosopis glandulosa* Torr. var. *glandulosa*) populations continue to expand and become more dense, even on areas once "successfully" treated either with herbicides or by bulldozing in southern New Mexico. Areas treated from 1958-1964 for mesquite control on the USDA-ARS Jornada Experimental Range and the New Mexico State University College Ranch were sampled to determine mesquite density changes. On herbicide treated areas sampled in 1976 and again in 1988, mesquite densities increased 10% to 128% and had densities from 67 to 494 plants/ha. Two areas treated by either bulldozing or fenuron in 1959-60, and with original kills near 100%, had an average density of 377 plants/ha by 1988, with an establishment rate of 13.5 plant/ha/year. On the College Ranch, mesquite densities increased 11%, from 130 (1982) to 147 (1988) plants/ha. Only 19% of a cohort of mesquite seedlings which germinated in 1989 were still alive in May 1990. Even though only a small percentage of the mesquite that germinated survived into the second year, this is enough to change former grasslands into mesquite-dominated rangelands.

Gibbens, R. P., K. M. Havstad, D. D. Billheimer, and C. H. Herbel. 1993. Creosotebush vegetation after 50 years of lagomorph exclusion. *Oecologia* 94, no. 2: 210-217.
See abstract under *Larrea tridentata*

Gibbens, R. P., C. H. Herbel, H. L. Morton, W. C. Lindemann, J. A. Richman D. B. Ryder-White, E. W. Huddleston, W. H. Conley, C. A. Davis, J. A. Reitzel, D. M. Anderson, and A. Guiao. 1986. Some impacts of 2,4,5-T on a mesquite duneland ecosystem in southern New Mexico: a synthesis. *Journal of Range Management* 39, no. 4: 320-326.
Abstract: Two aerial applications of 2,4,5-T [(2,4,5-trichlorophenoxy) acetic acid] were applied to 3,634 ha of mesquite (*Prosopis glandulosa* Toff. var. *glandulosa*) dunelands in southern New Mexico. Herbicide residuals; herbaceous plant production; soil microorganisms; insect, small mammal, and bird populations; cattle weights; travel; time budgets; and diets were studied on the treated area and an adjacent, untreated area. Stem kill of mesquite ranged from 17 to 66%. Herbicide residuals in soils and plant tissue on the treated area dissipated within a single season. Herbaceous plant production was measured for 5 years on a small area sprayed in 3 consecutive years and on untreated rangeland. Production was greater on the sprayed than the unsprayed area for the first 3 years and was about the same on both areas for the next 2

years. Microbial populations were not numerically different between treatments but dehydrogenase activity and CO₂ evolution were greater in dunal than interdunal soils. Numbers of tenebrionid beetles (*Coleoptera: Tenebrionidae*) did not differ between treatments. More mesquite leaf tiers (*Tetralopha euphemella*) were found on the sprayed area than on the untreated area. Population statistics for small mammals were similar on both treatments. More bird species were found on untreated than on sprayed areas. Cattle weights, travel, and time budgets did not differ between treatments and there were only minor differences between treatments in cattle diet quality. The sprayed area supported over twice as many AUM's of grazing as the untreated area in the first 3 post-treatment years. In the second post-treatment year, cattle liveweight produced was 2.9 and 1.5 kg/ha on the sprayed and untreated areas, respectively. Overall, the 2,4,5-T treatment caused relatively minor perturbations in measured ecosystem components.

Gibbens, Robert P., Ralph A. Hicks, and William A. Dugas. 1996. Structure and function of C3 and C4 Chihuahuan desert plant communities. Standing crop and leaf area index. *Journal of Arid Environments* 34, no. 1: 47-62.

See abstract under *Flourensia cernua*

Gibbens, R. P., and J. M. Lenz. 2001. Root systems of some Chihuahuan desert plants. *Journal of Arid Environments* 49, no. 2: 221-63.

See abstract under *Bouteloua eriopoda*

Gibbens, Robert P., J. M. Tromble, J. T. Hennessy, and M. Cardenas. 1983. Soil movement in mesquite dunelands and former grasslands of Southern New Mexico from 1933 to 1980. *Journal of Range Management* 36, no. 2: 145-48.

Abstract: Soil levels were marked on grid and transect stakes in mesquite duneland and grassland areas at 3 sites on the Jornada Experimental Range in 1933 and 1935. Soil levels on one set of transect stakes were remeasured in 1950 and 1955. Remeasurement of soil levels at both transect and grid stakes in 1980 revealed that extensive soil movement had occurred during the intervening years. On a 259-ha site containing large mesquite dunes in 1935, maximum deposition and deflation was 86.9 and 64.6 cm, respectively, in 1980. There was a net gain of 1.9 cm in soil depth over the entire area. On a 259-ha site only partially occupied by mesquite dunes in 1933, there was a net loss of 4.6 cm in soil depth and mesquite dunes had completely occupied the site by 1980. On a transect established across a mesquite duneland-grassland ecotone in 1935, there was a net loss in soil depth of 3.4 cm. Mesquite dunes had completely occupied the former grassland and dune intercept increased from 34.9 m in 1935 to 149.6 m in 1980. Gross erosion rates on wind deflated areas were equivalent to 69 tonnes/ha/yr on the area of large mesquite dunes. On the area partially occupied by mesquite in 1935 the gross erosion rate was 52 tonnes/ha/yr. At the ecotone transect gross erosion rates were 45, 101, and 40 tonnes/ha/yr for 1935-1950, 1950-55, and 1955-80 periods, respectively.

Gile, L. H., R. P. Gibbens, and J. M. Lenz. 1997. The near-ubiquitous pedogenic world of mesquite roots in an arid basin floor. *Journal of Arid Environments* 35, no. 1: 39-58.

Abstract: A major invasion of grassland by shrubs began about 1850 A.D. in many desert areas of southern New Mexico. Mesquite (*Prosopis glandulosa*) is the most numerous of these invading shrubs in a studied basin floor. Mesquite roots readily penetrated all soil horizons except for continuously indurated petrocalcic horizons. However, roots grew along the top of petrocalcic horizons and in places found locations for penetration, such as cracks and pipes, with numerous, often upward-growing roots enroute to utilize the sparse precipitation. At another site, mesquite roots descended to a depth of at least 5.5 m. Although the spread of mesquite seed by cattle was a major factor in the spread of mesquite, its successful establishment over large areas is apparently due to the ability of mesquite roots to adapt to a wide variety of soils and soil conditions to take advantage of the sparse precipitation; to their ability to greatly proliferate while spreading laterally over long distances; to grow upward and take advantage of small precipitation events that only wet the soil to depths of a few centimeters; and to descend to great depths along cracks and other openings in the soil, down which soil water also penetrates, and thus to their ability to utilize available water at all depths.

Glendening, George Elmo. 1952. Some quantitative data on the increase of mesquite and cactus on a desert grassland range in southern Arizona. *Ecology* 33, no. 3: 319-28.

Abstract: Recent remapping of two sample plots established on the Santa Rita Experimental Range in 1932 has yielded quantitative data on changes in abundance of velvet mesquite and four species of cactus and in density of perennial grasses under three grazing treatments during the period 1932 to 1949. Results show that mesquite more than doubled in number and crown area while perennial grass density decreased more than 95 percent under all grazing treatments. The data indicated that the mesquite stand may attain a crown canopy cover of about 30 percent on the site studied; and that such a stand will largely prevent the growth of perennial grasses. Rapid encroachment of several species of cactus which are adapted to the use of temporarily available surface moisture accompanied the increase in mesquite. In conclusion, mesquite, once seed trees are present, may rapidly increase in abundance regardless of grazing treatment. At the same time, where moderate stands of mesquites (50-80 per acre) are left to increase on grazed areas, the perennial grass cover will become less dense, less productive, and under some conditions, may go out almost completely. (2) It is improbable that moderation in livestock grazing will prevent the loss of grass cover within mesquite stands where the trees have gained sufficient size and density to completely utilize or materially reduce that moisture supply, and where the population of seed planting rodents is high. (3) On many similar deteriorated semi-desert grasslands now occupied by mesquite, artificial control of mesquite may be the only practical means of rehabilitating the desirable grass cover. Such control to be most effective should be initiated while the plants are too small to produce seed, and while they can be easily grubbed out. If this is not done the present trend toward mesquite and cactus may ultimately convert large areas of semi-desert grassland to a desert shrub type of much lower grazing value.

Glendening, G. E., and D. E. Brown. 1982. Mesquite (*Prosopis juliflora*) response to severe freezing in southern Arizona. *Journal of the Arizona-Nevada Academy of Science* 17: 15-18.

Glendening, George Elmo, and Harold A. Paulsen. 1955. Reproduction and establishment of velvet mesquite as related to invasion of semidesert grasslands. 50 p. United States Department of Agriculture Technical Bulletin no. 1127., Washington.

Goen, J. P., and B. E. Dahl. 1982. Factors affecting budbreak in honey mesquite in west Texas. *Journal of Range Management* 35, no. 4: 533-34.

Golubov, J., L. E. Eguiarte, M. C. Mandujano, J. Lopez-Portillo, and Carlos Montaña. 1999. Why be a honeyless honey mesquite? Reproduction and mating system of nectarful and nectarless individuals. *American Journal of Botany* 86, no. 7: 955-63.

Abstract: Populations of *Prosopis glandulosa* var. *torreyana* in the Chihuahuan desert have a fixed dimorphic system of nectar production in which half the individuals produce nectar (are nectarful) and the other half are nectarless. We analyzed the impact of nectar production on different estimates of fitness, comparing nectarful against nectarless individuals in size, mating system, seed traits, and fruit set in a 1-ha scrubland. Of the reproductive individuals (358), 46% were nectarful and 54% were nectarless. Neither tree size nor flowering phenology differed between nectar morphs. Fixation indices (F) for both progeny (F = -0.2) and adults (F = -0.45) were negative, and high heterozygosities were found in adults and progeny (H = 0.45). No differences were found between nectar morphs for F, H, and single (t(s) = 1.1) and multilocus (t(m) = 1.03) outcrossing rates. Controlled pollinations showed differences between selfing and control treatments with no differences between nectar morphs. Nectarless individuals produced significantly more pollen grains than did nectar producers, but all other measured floral traits showed no differences. Nectarful trees were visited by pollinators 21 times more often and had a significantly higher overall fruit set than did nectarless trees. No differences between nectar morphs in seed mass or in percentage seed germination were found, but heavier seeds tended to have higher heterozygosities. Both morphs had similar success as females, but nectarless trees had approximately 7% higher male function. We discuss three possible scenarios for the evolution of the fixed dimorphism in nectar production, two involving unstable phases (substitution of one morph by the other, and evolution towards dioecy) and one stable scenario (maintenance of the dimorphic system).

Golubov, Jordan, Maria Del Carmen Mandujano, Miguel Franco, Carlos Montana, Luis E. Eguiarte, and Portillo Jorge Lopez. 1999. Demography of the invasive woody perennial *Prosopis glandulosa* (honey mesquite). *Journal of Ecology* 87, no. 6: 955-62.

Abstract: To assess the effect of annual environmental variability on the long-term population dynamics of the invasive woody perennial *Prosopis glandulosa* var. *torreyana* (honey mesquite), we employed elasticity analyses of annual, mean and periodic matrix models. Growth, survival and reproduction were recorded for 1306 individuals in a 1-ha plot over a 4-year period. The volume of each individual was estimated, and transition matrices with nine size classes were constructed. Standard matrix analysis was performed, and the relative importance of individual life-cycle components to changes in the finite rate of population increase (λ) was determined. 2 Periodic matrix analysis projected a 29% annual increase in

population size ($\lambda = 1.29$), while annual projection λ -values varied between 0.99 and 1.44. For both methods, elasticity of seedling recruitment was always very low in all 4 years, and the highest elasticities were generally associated with permanence in the same size class. 3 Periodic and annual projections predicted similar elasticity patterns, with the relative contribution to a change in λ of different demographic processes changing between 'good' and 'bad' years. However, annual matrices identified two bad years, with fecundity and growth elasticity decreasing relative to survival, whereas periodic analysis identified only one such year, and elasticity changes were seen only in fecundity and survival.

Gould, Walter L. 1982. Wind erosion curtailed by controlling mesquite. *Journal of Range Management* 35, no. 5: 563-66.

Abstract: A sand-dune mesquite area with very little interdunal vegetation was treated aially one to three times with 2,4,5-T at 0.56 kg/ha in an oil:water emulsion. Four and five years after the initial treatment, the amount of blowing soil was evaluated using sandtraps located at various distances from the boundary between sprayed and unsprayed mesquite. The amount of wind-blown particles was greatly reduced on the area chemically treated to control mesquite. During the windy season the amount of blowing soil in the unsprayed area was more than 15-fold greater than at 180 m into the sprayed area. Intermediate amounts were measured between the boundary and 180 m into the treated area.

Grover, H. D., and H. B. Musick. 1990. Shrubland encroachment in southern New Mexico, USA. An analysis of desertification processes in the American Southwest. *Climatic Change* 17, no. 2-3: 305-30.

See abstract under *Larrea tridentata*

Gutschick, V. P. 1996. Physiological control of evapotranspiration by shrubs: scaling measurements from leaf to stand with the aid of comprehensive models. In *Proceedings: shrublands ecosystem dynamics in a changing environment*, Compilers J. R. Barrow, E. D. McArthur, R. E. Sosebee, and R. J. Tausch, 214-19Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station.

See abstract under *Larrea tridentata*

Haas, R. H., and J. D. Dodd. 1970. Seasonal water stress pattern in honey mesquite. *PR - Texas Agricultural Experiment Station* 2801/2828 : 59-62.

———. 1972. Water-stress patterns in honey mesquite. *Ecology* 53, no. 4: 674-80.

Abstract: Water stress (LWP) was measured in honey mesquite, *Prosopis glandulosa* var. *glandulosa* [Torr.], trees by using pressure-chamber method to detect negative hydrostatic pressure in the xylem of leaf petioles. The method was sufficiently sensitive to measure short-term changes of ± 1 bar LWP throughout the diurnal period. Mean differences between sun-exposed and shaded leaves averaged 4.7 bars LWP on a clear day in May. Although the mean LWP for five trees ranged from 15.8 to 18.1 bars LWP, the interaction

of exposure and tree was relatively minor in comparison with the large diurnal differences in LWP. Diurnal changes in LWP, often greater than 20 bars, were associated with changes in the evaporative potential of the atmosphere. Total daily water stress (ΣL) and net daily water stress ($\Sigma L - \Sigma L_0$) were calculated by integrating the area under a curve formed by the periodic measurements of LWP during the diurnal period. Net daily water stress was more sensitive to changes in environmental variables than other daily summaries. Throughout the range of available soil moisture there was a close relationship between net daily water stress and the integrated evaporative potential on a daily basis.

Haque, Zahoorul. 1986. "Changes in vegetation following herbicidal control of honey mesquite (*Prosopis juliflora* (Swartz) DC. Var. *glandulosa* (Torrey) Cockerell) in southern New Mexico ." Ph. D. Dissertation, New Mexico State University.

Abstract: Herbaceous and shrubby vegetation on New Mexico State University College Ranch was studied to find out changes resulting from herbicidal control of honey mesquite (*Prosopis juliflora* var. *glandulosa*). The soil of the study area belongs to Berino-Dona Ana Association. Density of all species, aerial cover of shrubs, and basal cover of herbaceous species were measured in summers of 1985 and 1986. Density and basal cover of cool season annual forbs were recorded in spring 1986. Vegetational patterns around honey mesquite shrubs were also studied and light intensity measured in different zones, beneath and outside the mesquite canopy. The herbicides aerially applied in June 1984 and June 1985 were picloram + clopyralid at 0.14 + 0.14 kg ai/ha (Treatment 1 = low p + c), picloram + clopyralid at 0.28 + 0.28 kg ai/ha (Treatment 2 = high p + c), triclopyr at 0.28 kg ai/ha (Treatment 3 = low triclopyr), and triclopyr at 0.56 kg ai/ha (Treatment 4 = high triclopyr). Treatment 5 was untreated control. The study was conducted and analyzed as a randomized complete block design. The herbicide treatments resulted in defoliation of most mesquite and fourwing saltbush (*Atriplex canescens*) plants within 8 weeks of application. There was gradual reduction in the number of completely defoliated shrubs from 1984 to 1986, probably due to resprouting of defoliated shrubs. Shrub cover and density decreased slightly in all treatments from 1985 to 1986. Grasses increased in density and cover in the high herbicide treatments. Forbs positively responded to all herbicide treatments. Total plant cover increased in all treatments from 1985 to 1986, probably in response to higher rainfall in 1986. Cool season annual forb density increased only in the high herbicide treatments. Correlation analysis revealed negative relationship between density as well as cover of total grasses and total forbs (dependent variables) with respect to total shrub cover and total mesquite cover (independent variables). Bush muhly (*Muhlenbergia porteri*) occupied the center zone beneath mesquite canopy but gradually reduced in density in the interspaces. Black grama (*Bouteloua eriopoda*) occurred rarely near mesquite and gradually increased toward the interspaces. Mesa dropseed (*Sporobolus flexuosus*) was observed only in the open. Light intensity in the center zone of mesquite canopy was reduced to one-fifth that of the interspace area

Haque, Zahoorul, Amade Younga, Kirk C. McDaniel, and Rex D. Pieper. 1991. Two-phase pattern in mesquite-herbland vegetation in southern New Mexico. *The Southwestern Naturalist* 36, no. 1: 54-59.

Abstract: Vegetation on upland sites in southern New Mexico is represented by a mosaic pattern composed of scattered mesquite (*Prosopis glandulosa*) plants and associated understory plants, interspersed in open

herbland composed of various grasses and forbs. Bush muhly (*Muhlenbergia porteri*) was the main grass species occurring under mesquite canopies. Purslane portulaca (*Portulaca oleracea*) was the only forb species showing a positive correlation with mesquite canopy cover. Abundance of other grass and forb species was greater at the mesquite periphery or in the open areas than under the mesquite canopies. Black grama (*Bouteloua eriopoda*) was distributed in open herbland between trees.

Heitschmidt, R. K., R. J. Ansley, S. L. Dowhower, P. W. Jacoby, and D. L. Price. 1988. Some observations from the excavation of honey mesquite root systems. *Journal of Range Management* 41, no. 3: 227-31.

Hennessy, John Thomas. 1981. "Soil movement and vegetational changes over a forty-five year period in south-central New Mexico." M.S. Thesis, New Mexico State University.

Abstract: The purpose of this study was to evaluate the vegetational changes and soil movement which accompanied the processes of mesquite (*Prosopis glandulosa*) spread and dune building on the Jornada Experimental Range in southwestern New Mexico. Two 259 ha grid systems and two belt transects were established in the mid-1930's. Both grid systems and transects were referenced to soil surface levels at that time and the transects were mapped in detail showing perennial plant species present and dune profiles and lateral extent. Using this early data for comparison, soil surface levels, plant species, and mesquite dune data were gathered in 1980. The results showed that a substantial amount of soil movement had occurred on all areas. While one area gained soil over the 45-year period, all other sites lost soil. An equation developed to determine the constitution of the loss showed that it was mostly in the fine sand and silt fractions.

———. 1982. "Mesquite (*Prosopis glandulosa* Terr.) dunes and interdunes in southern New Mexico: a study of water relations and plant production ." Ph. D. Dissertation, New Mexico State University.

Abstract: This study, conducted on a southern New Mexico mesquite-grassland range, was initiated to explain, through the measurement and analysis of soil properties, water relations, and other environmental factors, why mesquite sand dunes appeared to be a better environment for the establishment of fourwing saltbush (*Atriplex canescens*) than did interdunal areas. Particle size, bulk density, organic matter content, electrical conductivity, pH, and temperature of dunal and interdunal soils were measured. Except for particle size and temperature, dunal and interdunal soils did not differ greatly. Dune soils had greater sand and less silt and clay content than did soils on the interdune. Interdune soil temperatures were found to be higher than temperatures of dune soils from the surface to a depth of 152.0 cm. Although dune soils had greater infiltration and more rapid hydraulic conductivity, interdune soils retained more soil water above -15 bars. Root penetration was often limited by the presence of a caliche layer in soils on the study site, especially on interdunes where the layer was often near the surface. Caliche can absorb water rapidly, holding nearly 25% water by volume, and can retain a high percentage of water at -15 bars. Fourwing saltbush produced more on dunes than interdunes though seasonal growth increments on individual plants were similar on dunes and interdunes. Production of mesa dropseed (*Sporobolus flexuosus*) was similar on dunes and interdunes. In the drier of the two years (1980), overall

plant production (exclusive of mesquite) was greater on interdune areas with broom snakeweed (*Xanthocephalum sarothrae*) accounting for much of the difference. In 1981, a year with greater than average precipitation, dunes had greater production, mostly due to a large annual forb crop. The greater density and production of fourwing saltbush on dunes as opposed to interdunes was attributed to the greater depth to caliche on dunes and to lower soil temperatures resulting from the shade provided by mesquite plants on dunes. It is probable that though the interdune areas had more available water at all times than did dunes, the high soil temperatures of interdune areas limited the establishment of fourwing saltbush.

Hennessy, J. T., R. P. Gibbens, J. M. Tromble, and M. Cardenas. 1985. Mesquite (*Prosopis glandulosa* Torr.) dunes and interdunes in southern New Mexico: a study of soil properties and soil water relations. *Journal of Arid Environments* 9, no. 1 : 27-38.

Abstract: Soil properties and soil water relations were compared between soils of mesquite (*Prosopis glandulosa* Torr.) dunes and soils of adjacent interdune areas in southern New Mexico. Particle size, bulk density, organic matter content, electrical conductivity, pH, and temperature of dunal and interdunal soils were measured. Except for particle size and temperature, dunal and interdunal soils did not differ greatly. Soils of dunes had more sand and less silt and clay than did soils of interdunes. Soil temperatures were higher in interdunes than in vegetated dunes. Soil temperatures were similar in dunes with plant cover removed and in interdunes. Infiltration and runoff, hydraulic conductivity, and water retention measurements showed that although dune soils had greater infiltration and more rapid hydraulic conductivity, interdune soils retained more water above -P5 MPa matric potential. Evaporative losses, as measured with atmometers 3 cm from the soil surfaces, were greater from interdunes than from vegetated dunes. Through two growing seasons, measured total soil water content at a depth of 30.5 cm was always greater for interdunes than for either vegetated or bare dunes. The dune soils stored water less efficiently than interdune soils and reached -1 -5 MPa matric potential with much greater frequency.

———. 1983. Vegetation changes from 1935 to 1980 in mesquite dunelands and former grasslands of southern New Mexico. *Journal of Range Management* 36, no. 3: 370-374.

Abstract: On the Jornada Experimental Range in southern New Mexico, 2 belt transects, 30.5 cm in width and totaling 2,188 m in length, were established in 1935 on 2 areas where honey mesquite (*Prosopis glandulosa* Torr.) was spreading into black grama [*Bouteloua eriopoda* (Torr.) Torr.] grassland. Maps were made of the transects which portrayed the vegetation occurring in each of the 76,189 contiguous, 0.09-m² plots along the transect. The vegetation on the transects in 1980 was compared to that portrayed by the transect maps made in 1935. One transect had been read in 1950 and 1955. During the 45-year period mesquite attained complete dominance and many new mesquite dunes formed. Black grama had a relatively high frequency in 1935 but had completely disappeared by 1980, both on an area grazed by livestock and on an area protected from grazing. Mesa dropseed [*Sporobolus flexuosus* (Thurb.) Rydb.], fluffgrass [*Erioneuron pulchellum* (H.B.K.) Tateoka] and broom snakeweed [*Xanthocephalum sarothrae* (Pursh) Shinners] increased in abundance, even during the drought period between 1950 and 1955. Only 25% of the perennial forb species encountered in 1935-55 were found in 1980.

Hennessy, J. T., B. Kies, Robert P. Gibbens, and J. M. Tromble. 1986. Soil sorting by forty-five years of wind erosion on a southern New Mexico range. *Soil Science Society of America Journal* 50, no. 2: 391-94.

Abstract: This paper presents the fractional composition of soil lost from wind erosion for a 45-yr period on mesquite sand dune rangeland in south-central New Mexico. In addition, an equation was developed for defining the soil loss by particle size. Three arbitrarily chosen groups (deposition, noneroded, and eroded) were used to categorize the sampling locations. Net soil loss was in excess of 4.6 cm/ha. Maximum deposition was 78.6 cm and maximum erosion was in excess of 61.9 cm. The sand fraction was divided into three particle size classes. There was a significantly greater amount of the 0.5- to 0.05-mm sand fraction in the deposition site than in either the eroded or non-eroded sites. No net loss of sand from the experimental site was measured. The silt fraction was significantly greater in the non-eroded and eroded sites than in the deposition site, indicating removal of the silt fraction by wind erosion. Wind erosion occurring on the site is resulting in a more sandy textured soil.

Herbel, C. H. 1966. Mesquite (*Prosopis juliflora* [Sw] DC). *Chemical control of range weeds*. U. S. Dep. Agric. and U. S. Dep. Interior., 26. Vol. Interagency Rep.

Herbel, Carlton H., Fred Ares, and Joe Bridges. 1958. Hand-grubbing mesquite in the semidesert grassland. *Journal of Range Management* 11: 267-70.

Abstract: A large scale mesquite control program was initiated on the Jornada Experimental Range early in 1958 to make information available to ranchers in the area on the costs and techniques of control measures. The area hand-grubbed was 4,265 acres located in three different pastures.

Herbel, Carlton H., and Robert P. Gibbens. 1987. Soil water regimes of loamy sands and sandy loams on arid rangelands in southern New Mexico. *Journal of Soil and Water Conservation* 42, no. 6: 442-47.

Abstract: The matric potential of soil water is presented for five loamy sand and six sandy loam sites on arid rangelands. Gypsum-impregnated resistance blocks were placed at five soil depths to 91 cm. If caliche was encountered before the 91-cm depth, blocks were placed to that level. The average annual precipitation during the approximate 20-year study period was 237 mm, slightly above the long-term mean. At the 10-cm depth, the probability of soil matric potential ≥ 1.5 MPa during December-April was 69 % at the 11 sites; 83 % of the probability was ≥ -0.1 MPa. During July-September, the probability of soil matric potential at the 10-cm depth was 53 %; 73 % was > -0.1 MPa. Factors affecting soil matric potential were precipitation amount, surface soil characteristics, topography, subsurface conditions, and season of the year.

———. 1996. Post-drought vegetation dynamics on arid rangelands in southern New Mexico. *New Mexico Agricultural Experiment Station Bulletin* No. 776.

See abstract under *Bouteloua eriopoda*

Herbel, Carlton H., and Walter L. Gould. 1970. Control of mesquite, creosotebush, and tarbush on arid rangelands of the southwestern United States. In *XI International Grassland Congress*, 38-41.

Abstract: Sparse stands, up to 200 plants per ha, of mesquite, creosote bush, and tarbush may be economically controlled with an individual plant treatment of fenuron pellets or other dry herbicides. Aerial spraying with 2,4,5-T is also an economical method of reclaiming mesquite-infested areas. The treatment also affords an excellent method of increasing production of perennial grasses.

Herbel, Carlton H., Walter L. Gould, William F. Leifeste, and Robert P. Gibbens. 1983. Herbicide treatment and vegetation response to treatment of mesquites in southern New Mexico. *Journal of Range Management* 36, no. 2: 149-51.

Abstract: Mesquite (*Prosopis juliflora*) is a major unwanted plant in the Southwest. This study evaluated the herbage responses obtained from various aerial applications of 2,4,5-T on mesquites in southern New Mexico. The dead plants on the various areas ranged from 7-64% of the mesquite. Yields of perennial grasses ranged from 3-1931 kg/ha on the untreated controls and 11-2696 kg/ha on the areas sprayed with 2,4,5-T. In dense stands of mesquite, about 30% of the mesquites must be killed before grass yields are significantly increased.

Hibbard, K. A., S. Archer, D. S. Schimel, and D. W. Valentine. 2001. Biogeochemical changes accompanying woody plant encroachment in a subtropical savanna. *Ecology* 82, no. 7: 1999-2011.

Abstract: Ecosystem properties of surficial (0–10 cm) soils in remnant herbaceous patches were compared to those of contrasting woody plant patch types (upland discrete cluster, upland grove, and lowland woodland) where shifting land cover is known to have occurred over the past 50–77 yr. The purpose of this study was to evaluate and quantify the biogeochemical consequences and subsequent developmental rates of woody plant formation on sites formerly dominated by grasses.

Clay and water content of woodland soil patches was higher than that of soils associated with upland discrete cluster and grove patches. Even so, lowland woody patches were generally comparable to upland grove and discrete shrub cluster patches with respect to soil organic carbon (SOC), soil N, the ratio of annual N mineralization:total N, annual litterfall, and root biomass. The fact that finer soil texture, enhanced soil moisture, and the more advanced age of lowland woody patches did not translate into greater accumulations of SOC and N relative to upland grove and discrete cluster patches suggests that C and N losses might be higher in recently developed lowland woodland communities. Fluctuations in monthly root biomass standing crop (0The estimated annual mean rates of soil C accretion in the Woody plant proliferation in grasslands and savannas in recent history has been widely reported around the world. The causes for this shift in vegetation are controversial and center around changes in livestock grazing, fire, climate, and atmospheric CO₂. Our data, which are conservative in that they examine only the upper 10 cm of the soil profile, indicate that the rate and extent of soil C and N accumulation associated with this phenomenon can be rapid, substantial, and accompanied by increased N turnover. This geographically extensive vegetation change thus has important implications for understanding how the global carbon and nitrogen cycles may have been altered since Anglo-European settlement of arid and semiarid regions.

Ho, Mengchi, Rachel E. Roisman, and Ross A. Virginia. 1996. Using strontium and rubidium tracers to characterize nutrient uptake patterns in creosotebush and mesquite. *Southwestern Naturalist* 41, no. 3: 239-47.

See abstract under *Larrea tridentata*

Hoefler, William C. 1984. "Response of creosotebush and mesquite communities after applying hexazinone ." M. S. Thesis, New Mexico State University.

Huenneke, L. F., J. P. Anderson, M. Remmenga, and W. H. Schlesinger. 2002. Desertification alters patterns of aboveground net primary production in Chihuahuan ecosystems. *Global Change Biology* 8, no. 3: 247-64.

See abstract under *Bouteloua eriopoda*

Huenneke, Laura F., Dennis Clason, and Esteban Muldavin. 2001. Spatial heterogeneity in Chihuahuan desert vegetation: implications for sampling methods in semi-arid ecosystems. *Journal of Arid Environments* 47, no. 3: 257-70.

See abstract under *Bouteloua eriopoda*

Hultine, K. R. 2000. The evolutionary relationship between drought tolerance and distribution of mesquites. *ARIDUS* 12, no. 1: 1-4.

Imo, M., and V. R. Timer. 1992. Nitrogen uptake of mesquite seedlings at conventional and exponential fertilization schedules. *Soil Science Society of America Journal* 56, no. 3 : 927-34.

Abstract: Exponential nutrient additions have been shown to induce steady-state nutrition in plants and enhance seedling growth and nutrient status, which suggests improved nutrient efficiencies during the growing season. The objective of this study was to compare periodic growth, plant nutrient status, and N uptake of desert mesquite (*Prosopis chilensis* Mol.) seedlings that received 200 mg N seedling⁻¹ as complete fertilizer delivered either conventionally (as single dose or constant top dressing) or exponentially (as pure or modified exponentially increasing additions) during a 12-wk rotation. Steady-state nutrition (characterized by a stable tissue nutrient concentration) was induced for the cultural period in the modified-exponential fertility regime. The nutrients were supplied exponentially except for higher initial amounts that compensated for the incomplete accessibility of growing medium to the small root systems. These seedlings showed consistently higher N accumulation that matched dry-matter production, reflecting higher fertilizer-N uptake efficiency throughout the growing season. During the same growing season, pure exponential nutrient-addition rates appeared to achieve steady-state conditions 4 wk later because of incomplete interception of applied nutrients by small root systems during establishment. Conventional fertility regimes caused nutrient dilution in plants with time. Nutrient uptake did not match growth in these seedlings, resulting in nutrient stress at varying stages of seedling development.

———. 1992. Growth, nutrient allocation and water relations of mesquite (*Prosopis chilensis*) seedlings at differing fertilization schedules. *Forest Ecology and Management* 55, no. 1-4: 279-94.

Abstract: Effects of contrasting fertilization schedules on biomass and nutrient partitioning between different plant organs, and the water relations of *Prosopis* (mesquite) seedlings were studied in the greenhouse over a 13 week rotation to assess nutritional preconditioning to short term drought. The seedlings received 200 mg N per plant as complete nutrient solution during the growing season supplied either conventionally (as single dose or repeated top dressings) or exponentially (as pure or modified exponentially increasing additions). Although mode of fertilization did not influence total dry matter production of the seedlings, biomass and nutrient distribution between different plant organs were affected. Proportionally more biomass was allocated to the leaf components in exponentially than conventionally fertilized plants. This trend was reversed, however, in root growth as relatively more dry matter was distributed to the roots in conventional than exponential fertilization schedules. Despite stems accounting for about half of the total plant dry mass, relative macronutrient contents in the stems were lower as most nutrients were allocated to the leaves. On the other hand, phosphorus concentration in the roots was higher than in leaves of conventionally fertilized seedlings. At the end of the rotation, exponentially fertilized and well-irrigated seedlings exhibited higher stomatal conductance and transpiration throughout the course of a single day. Induced drought, however, decreased both diurnal stomatal conductance and transpiration. On the same day, drought also altered diurnal patterns as all the treatments were the same except for the single dose fertilized plants which maintained higher stomatal opening and transpiration.

Jacoby, P. W., R. J. Ansley, C. H. Meadors, and A. H. Huffman. 1990. Epicuticular wax in honey mesquite: seasonal accumulation and intraspecific variation. *Journal of Range Management* 43, no. 4 : 347-50.

Abstract: Epicuticular wax on the leaves of honey mesquite (*Prosopis glandulosa*) increased rapidly from May to July and stabilized or decreased by late summer. Pattern of accumulation best fit a second order polynomial regression equation using day of year as the independent variable. Considerable variation in wax accumulation was found among individual trees within populations and appeared to be consistent from year to year. Wax generally increased from about 0.35 g m⁻² to more than 1.00 g m⁻² during the growing season. A difference in maximum wax accumulation was detected between the 2 years of study and was attributed to differing environmental conditions. These findings may partially explain resistance of honey mesquite to foliar-applied herbicides.

Jacoby, P. W. Jr., and R. J. Ansley. 1991. Mesquite: classification, distribution, ecology, and control. *Noxious range weeds*. Lynn F. James, 364-76. Boulder, Colorado: Westview Press.

Jarrell, W. M., and R. A. Virginia. 1990. Soil cation accumulation in a mesquite woodland sustained production and long-term estimates of water use and nitrogen fixation. *Journal of Arid Environments* 18, no. 1: 51-58.

Abstract: Historical records indicate sustained production in a stand of phreatophytic mesquite (*Prosopis glandulosa* var *torreyana*) in the Sonoran Desert of California for 200 to 500 years. The plants are

primarily utilizing moderately saline groundwater (electrical conductivity c. 3.0 dS/m) at 5 m depth. Most of the major cations entering the ecosystem in the groundwater remain in the deep root zone, since root uptake of cations removes only a small proportion of the total input. Under these conditions prolonged root activity could result in excessive salt (cation) accumulation which could limit growth and potentially kill the plant. We measured total Ca, Na, Mg, and K accumulations in the capillary fringe above the water table to determine the pattern and degree of salt accumulation in the active root zone. Possible mechanisms for sustained production by this system include (1) a fluctuating water table which regularly flushes salts out of the root zone; (2) high salt tolerance of the mesquite which prolongs production, but not indefinitely; (3) seasonal fluctuation in water use which allows inverse leaching, capillary rise carrying salts above the most active portion of the root zone during the dormant season. In addition, estimates of total stand water use and symbiotic N-fixation over the total life of the stand may be derived from measurements of total cation accumulation in the plant root zone.

Jenkins, Michael B., Ross A. Virginia, and Wesley M. Jarrell. 1988. Depth distribution and seasonal populations of mesquite-nodulating rhizobia in warm desert ecosystems. *Soil Science Society of America Journal* 52, no. 6: 1644-50.

Abstract: Deeply rooted woody legumes are common in desert ecosystems yet little is known about the distribution of their rhizobial symbionts in relation to their roots and soil properties of the systems. The distribution of mesquite (*Prosopis glandulosa* Torr.)- nodulating rhizobia was investigated to depths of 13 m in warm desert eco systems. Soils were collected under mesquite from sand dune and playa ecosystems in the California Sonoran Desert, and from sand dune, playa, arroyo, and grassland ecosystems in Ten Chihuahuan Desert of southern New Mexico. A *Larrea tridentata* (DC.) Coville (creosote bush) ecosystem in New Mexico, containing no mesquite, was sampled as a reference. Three intact soil cores from each ecosystem were removed during the winter, spring, and fall from the New Mexico sites, and the winter from the California sites. Significant rhizobial population densities were measured in soil from 1- to 4-m depths at the sand due, arroyo, and the playa ecosystems. Tat the playa ecosystem in New Mexico population densities $>10^5$ cells kg^{-1} were measured in soils from 8-m depth, and root nodules containing rhizobia were recovered in soil samples from 3-, 4-, and 7-m depths. Multiple-regression analysis of rhizobial concentration against soil $\text{NH}_4\text{-N}$, $\text{PO}_4\text{-P}$, electrical conductivity, and gravimetric water content indicated that no single soil factor was related significantly to rhizobial concentration across the ecosystems. Rhizobial densities varied with season in the dune and arroyo ecosystems. In these desert ecosystems significant rhizobial populations, root nodules, and presumable symbiotic N_2 fixation occur at soil depths rarely studied.

———. 1989. Ecology of fast-growing and slow-growing mesquite nodulating rhizobia in Chihuahuan and Sonoran desert ecosystems. *Soil Science Society of America Journal* 53, no. 2: 543-49.

Abstract: *Prosopis glandulosa* (mesquite) is effectively nodulated by both fast-growing (FG) and slow-growing (SG) rhizobia. The distribution of indigenous, free-living, FG and SG rhizobia, and their morphological and symbiotic characteristics associated with the rooting systems of mesquite were investigated. The three warm desert ecosystems studied were an arroyo, a sand dune, and a playa in the

Chihuahuan Desert of New Mexico, and a sand dune and playa in the Sonoran Desert of southern California. The FG rhizobia dominated free-living rhizobial population from 0- to 8-m depth, at the New Mexico playa. In contrast to the New Mexico playa, the surface 1 m soil under mesquite at the California playa was dominated by SG rhizobia, otherwise FG rhizobia dominated to 9-m depth. Slow-growing rhizobia dominated the lowest depths of the mesquite rooting system in both playas. Slow-growing rhizobia dominated the entire rooting zone of both sand dune ecosystems. Fast-growing rhizobia dominated the upper 2 m and SG rhizobia dominated below 2 m in the mesquite rooting zone at the New Mexico arroyo. Regression analysis indicated that the distribution of FG and SG rhizobia was related to the concentration of total soil salts (electrical conductivity) ($r^2 = 0.20$). Chi-square analysis of the distribution of colony morphologies indicated distinct rhizobial populations in each ecosystem. The FG rhizobial population at the New Mexico playa was highly effective and had a high frequency of Hup+ phenotypes. The FG rhizobia isolated from the arroyo were, in contrast, less effective and had a low frequency of Hup+ phenotypes. The SG rhizobial population at the New Mexico dune system was, in contrast, mainly ineffective and had a low frequency of Hup+ phenotypes. The relationship between the variable distribution of FG and SG rhizobia and environmental factors associated with the ecosystems is discussed.

Johnson, H. B., and H. S. Mayeux, Jr. 1990. *Prosopis glandulosa* and the nitrogen balance of rangelands: extent and occurrence of nodulation. *Oecologia* 84, no. 2: 176-85.

Abstract: We report the recovery of root nodules from *P. glandulosa* var. *glandulosa* in the eastern portion of its range, where the species reached its greatest vegetational development. Single cores 4.7 cm in diameter and up to 250 cm deep yielded 0 to over 250 nodules. Nodules were found at all depths below 10 cm, with the highest concentration often around 100 cm. Detailed studies of the three trees revealed relatively small volume densities of about 0.02 nodules cm⁻³ high surface area densities of 2-4 nodules cm⁻², and high nodule biomass of 8-23 g m⁻², when compared to cultivated legumes. Nodules are small, weakly attached to roots that are seldom over 0.5 mm in diameter, and not easily observed under field conditions. No nodules were recovered from cores from the more arid western portion of *P. glandulosa*'s range, although seedlings nodulated readily in these soils in the glasshouse as well as in most unamended soils from throughout mesquite's geographical range. Local differences in nodulating potential of soils included a negative association with mesquite canopies and a positive association with mesquite canopies and a positive association with depth. These results suggest a significant role for biological fixation in the nitrogen regime and vegetation dynamics of *Prosopis*-dominated ecosystems.

Jordan, Gilbert L., and Marshal R. Haferkamp. 1989. Temperature responses and calculated heat units for germination of several range grasses and shrubs. *Journal of Range Management* 42, no. 1: 41-45.

Karpiscak, Martin M. 1973. "Aspects of thorn development on *Prosopis juliflora* (Swartz) DC. var. *velutina* (Woot.) Sarg. and *Cercidium australe* I. M. Johnson." M. S. Thesis, University of Arizona.

Kemp, Paul R. 1983. Phenological patterns of Chihuahuan desert plants in relation to the timing of water availability. *Journal of Ecology* 71, no. 2: 427-36.

See abstract under *Bouteloua eriopoda*

Kistler, R. A. 1995. Influence of temperature on populations within a guild of mesquite bruchids (Coleoptera: *Bruchidae*). *Environmental Entomology* 24, no. 3 : 663-72.

Abstract: The effect that harsh, variable desert temperatures might have on the structure and population dynamics of a guild of *Bruchidae* (Coleoptera) that feed in the seeds of mesquite, *Prosopis velutina* Wooten, was examined in a 3-yr field and laboratory study. Metabolic rate, fecundity, longevity, developmental times, survivorship, and body size were measured across the temperature spectrum in which the species normally live. The 4 species that compose the guild-*Algarobius prosopis* (LeConte), *Mimosestes amicus* (Horn), *Mimosestes protractus* (Horn), and *Neltumius arizonensis* (Schaeffer) divide the use of the resource temporally. The first 2 species dominate resource use and overlap entirely in time, whereas the 2 latter minor species utilize opposite ends of the temporal resource spectrum. Of the two dominants, *M. amicus* functions as a physiological generalist, apparently sacrificing resource adaptation for greater temperature adaptation and very high reproductive output. In contrast, *A. prosopis* is well adapted to both the use of mesquite as a resource and also to the desert thermal environment. The 2 minor species seem to be less well adapted to both the resource and the environment. Temperature clearly plays a strong role in determining the structure of this guild of bruchids.

Klemmedson, J. O., and A. R. Tiedemann. 1986. Long-term effects of mesquite removal on soil characteristics. II. Nutrient availability. *Soil Science Society of America Journal* 50, no. 2 : 476-80.

Abstract: Previously we reported differences in nutrient availability of desert grassland soils under mesquite [*Prosopis juliflora* (Schwartz) DC] trees and adjacent open areas. In a related study conducted at that same time (1967), several mesquite trees were removed to measure shading effects. Since then about half of the harvested trees have sprouted and regrown. Now after 13 yr, we report the long-term effects of mesquite removal on nutrient availability of these soils. In a greenhouse pot test, dry weight yield of shoots plus roots of Arizona cottontop [*Digitaria californica* (Heath.) Chase] and barley (*Hordeum vulgare* L var. *gustoe*) was used to measure availability of nutrients. Variables in the pot test were mesquite history (mesquite intact, mesquite removed-sprouted, mesquite removed), location (canopy, open), and nutrients (N, P, S, K). In the analysis of variance, the main effects and all interactions were significant. Yield responses confirmed results of our earlier study that nutrient availability of mesquite canopy soils was significantly greater than that of adjacent open areas. Removal of mesquite resulted in a significant decline in nutrient availability. For sites where mesquite had been removed but then sprouted and regrew, nutrient availability of soils was intermediate between that of mesquite-intact and mesquite-removed sites. Removal of mesquite resulted in a large decline in available soil N; smaller losses of available P, K, and S were noted.

Klemmedson, James O., and Edwin L. Smith, Project leaders. 1972. Distribution and balance of biomass and nutrient in desert shrub ecosystems . Research Memorandum, U.S. International Biological Program, Desert Biome, RM 72-14.

Kneuper, Charles Lloyd. 2000. "Survival of mesquite seeds after consumption by three species of livestock (*Prosopis glandulosa*) ." M. S. Thesis, Angelo State University.

Abstract: Consumption of mesquite (*Prosopis glandulosa* Torr.) fruit by livestock appears to be an important component of seed dispersal. Three trials were conducted to determine preference for mesquite fruit by different species of livestock, intake in relation to fruit maturity, and seed survival. In the first study, cattle, sheep, and goats were offered immature (IM), mature off the tree (MT), or mature off the ground (MG) fruit to quantify intake of each stage. The second study assessed seed survival of digestion from different stages of development. Livestock consumed more mature fruit than immature. Sheep and goats consumed more fruit than cattle. As fruit matured, seed survival increased. Germination of seeds surviving digestion was not greater ($P > 0.05$) than seeds that experienced natural weathering. Cattle seed survival was greater ($P \leq 0.05$) than sheep or goats. Cattle appear to serve as dispersal agents of mesquite while sheep and goats can act as predators

Kramp, B. A., R. J. Ansley, and T. R. Tunnell. 1998. Survival of mesquite seedlings emerging from cattle and wildlife feces in a semi-arid grassland. *Southwestern Naturalist* 43, no. 3: 300-312.

Abstract: This study examined the potential of animals as vectors for mesquite seedling establishment via fecal deposition. Cattle, deer, and coyote fecal material containing emerging mesquite was located in May 1994 on a clay loam site in north Texas and assigned to two grass competition treatments (clipped to 3-cm height, or unclipped) and three moisture treatments (rainfall, rainfall + four 1.25-cm irrigations, or rainfall + one 10-cm irrigation). Except for a 2-week period in August 1993 when feces were deposited, cattle grazing was excluded from the site during the study and for several years prior to study initiation. Seedling emergence and survival were quantified throughout 1994, a dry year, and 1995, which had precipitation well above normal. By spring 1995, survival of 1994 seedlings (all treatments pooled) was 16.6, 9.3, and 1.3% at deer, cattle, and coyote fecal sites, respectively. Survival of 1994 seedlings was not affected by moisture or clipping treatments. New cohorts of emerging seedlings occurred from the same fecal sites during 1995. High rainfall during summer 1995 increased percent survival of 1995 seedlings when compared to survival of 1994 seedlings, even though grass growth was much greater in 1995 than in 1994. A strong trend emerged in which survival of 1995 seedlings appeared to be greater when surrounding perennial grasses were clipped (37.0% in clipped plots vs. 9.4% in unclipped plots), but this was not statistically significant ($P \geq 0.14$). By spring 1996, average number of seedlings emerged per site (1994 and 1995 cohorts combined) was 7.8, 5.2, and 4.5; number of established seedlings per site was 0.8, 0.6, and 0.3; and percent survival was 12.1, 13.5, and 6.5% at cattle, deer, and coyote sites, respectively. Mesquite seedlings were capable of establishing from feces of all three animal vectors within dense, ungrazed stands of perennial grass.

Kustas, William P., John H. Prueger, Jerry L. Hatfield, Kali Ramalingam, and Lawrence E. Hipps. 2000.

Variability in soil heat flux from a mesquite dune site. *Agricultural and Forest Meteorology* 103, no. 3: 249-64.

Abstract: For many natural and agricultural landscapes, vegetation partially covers the ground surface, resulting in significant variations in soil heat flux between interspace areas and underneath vegetation. This is particularly apparent in arid and semiarid regions where vegetation cover is low and clustered or 'clumped' with large areas of exposed soil. Surface heterogeneity presents significant challenges to the use of standard micro-meteorological measurement techniques for estimating surface energy balance components. The objective of this study was to use an array of 20 soil heat flux plates and soil temperature sensors to characterize the spatial and temporal variability in soil heat flux as affected by vegetation and micro-topographic effects of mesquite dunes in the Jornada Experimental Range in southern New Mexico. Maximum differences in soil heat flux among sensors were nearly 300 W m⁻². Maximum differences among individual sensors under similar cover conditions (i.e. no cover or interdune, partial or open canopy cover and full canopy cover) were significant, reaching values of 200-250 W m⁻². The 'area-average' soil heat flux from the array was compared with an estimate using three sensors from a nearby micro-meteorological station. These sensors were positioned to obtain soil heat flux estimates representative of the three main cover conditions: namely, no cover or interdune, partial or open canopy cover, and full canopy cover. Comparisons between the array-average soil heat flux and the three-sensor system indicate that maximum differences on the order of 50 to nearly 100 W m⁻² are obtained in the early morning and mid-afternoon periods, respectively. These discrepancies are caused by shading from the vegetation and micro-topography. The array-derived soil heat flux also produced a significantly higher temporal varying soil heat flux/net radiation ratio than what has been observed in other studies under more uniform cover conditions. Results from this study suggest that, to determine the number and location of sensors needed for estimating area-average soil heat flux in this type of landscape, one needs to account not only for the clustering of the vegetation cover but also micro-topography.

Lajtha, K., and W. H. Schlesinger. 1986. Plant response to variations in nitrogen availability in a desert shrubland community. *Biogeochemistry* 2: 29-37.

See abstract under *Larrea tridentata*.

Langford, R. P. 2000. Nabkha (coppice dune) fields of south-central New Mexico, U.S.A. *Journal of Arid Environments* 46, no. 1: 25-41.

Laxson, J. D., W. H. Schacht, and M. K. Owens. 1997. Above-ground biomass yields at different densities of honey mesquite. *Journal of Range Management* 50, no. 5 : 550-554.

Abstract: Dense stands of honey mesquite (*Prosopis glandulosa* Torr. var. *glandulosa*) negatively impact livestock handling and herbaceous forage production; however, very little information is available on the effect of stand density on biomass production of herbage and wood. Our study compared above-ground yields of herbage and wood in undisturbed, cleared, and 3 levels of thinned (100, 300, and 900 stems ha⁻¹)

stands of mesquite. Total removal of the mesquite canopy resulted in a 45% increase in herbaceous standing crop compared to the control in the first 2 years post-clearing. Herbage yields for the thinning treatments were intermediate although herbage yields for the 900 stems ha⁻¹ (2,017 kg ha⁻¹) treatment was similar ($P>0.1$) to the control (1,849 kg ha⁻¹) and lower ($P<0.1$) than the cleared treatment (2,684 kg ha⁻¹). Total wood production was significantly ($P<0.1$) lower for the 3 thinned treatments (481 to 1,214 kg ha⁻¹ yr⁻¹) than the control (8,128 kg ha⁻¹ yr⁻¹) because of the higher stem density for the control ($>7,500$ stems ha⁻¹). Growth rates of individual mesquite stems were 2- to 3-fold greater ($P<0.1$) for the 100 and 300 stem ha⁻¹ stands than for the higher- density stands during the relatively wet growing season of 1992. Under the drier 1993 conditions, however, growth rates were similar ($P>0.1$) for all treatments. Results indicated that severe thinning to less than 900 stems ha⁻¹ increased the amount of available forage and positively influenced the potential growth rates of the remaining mesquite stems.

Lee, S. G., and P. Felker. 1992. Influence of water/heat stress on flowering and fruiting of mesquite (*Prosopis glandulosa* var. *glandulosa*). *Journal of Arid Environments* 23, no. 3 : 309-19.

Abstract: The relationships between water stress, inflorescence production, nectar secretion, bee activity and pod production were examined in a self-incompatible, xerophytic tree legume *Prosopis glandulosa* var. *glandulosa*. Mature *Prosopis* trees were examined in five study sites located in a 450 to 700mm annual rainfall gradient over a 2-year period. A drought year produced greater water stress (1 - 3 MPa) than a wet year (1 - 0 MPa), had significantly greater inflorescence production and 3-3 times greater pod production. In contrast greater inflorescence lengths and nectar per inflorescence were produced in the wetter year. Inflorescence length was negatively correlated with water stress. Bee visitation was not associated with greater nectar production but it was associated with greater pod production.

Loomis, L. E., S. Archer, and C. J. Scifers. 1988. Relationships between soils and mesquite-dominated shrub clusters. *PR - Texas Agricultural Experiment Station* CPR-4592 : 7.

López-Portillo, Jorge, and Carlos Montaña. 1999. Spatial distribution of *Prosopis glandulosa* var. *torreyana* in vegetation stripes of the southern Chihuahuan Desert. *Acta Oecologica* 20, no. 3: 197-208.

Abstract: Mosaics consisting of vegetation stripes surrounded by bare areas have been described in several arid and semiarid ecosystems. The dynamics of the system depends on the redistribution of rainwater which is preferentially stored and evapotranspired in the vegetated stripes. A process of plant 'colonization' in the upslope fringe of the stripes has been described in some cases and a consequent upslope migration of the stripes has been inferred, but not confirmed in all cases quoted in the literature. In this paper, we studied the spatial distribution of mesquite (*Prosopis glandulosa* var. *torreyana*) and the soil parameters in three vegetation stripes and their associated bare areas in the southern Chihuahuan Desert. The spatial distribution of mesquites of different sizes do not coincide with that expected under the hypothesis of an uniform upslope stripe migration, but soil data suggest that current bare areas had been vegetated some time ago. Dispersion and establishment abilities enhanced by overgrazing may explain the observed mesquite distribution, but the presence of trees with high basal diameters in any part of the stripes

suggests stripe permanence at the same site and no upslope migration. These results point to the conflicting evidence on stripe migration that has been already found in other areas. The most probable scenario in our study area is that of a general long-term change of form of the stripes taking place at very variable speeds in different stripes, including the possibility that some of them remain stationary for prolonged periods, and showing different histories of colonization according to the life-history of the different species concerned. The speed and regularity of the process would show a very high temporal and spatial variability due to the interaction of climatic, geomorphologic and biotic interactions.

López-Portillo, Jorge, Carlos Montaña, and E. Ezcurra. 1996. Stem demography of *Prosopis glandulosa* var. *torreyana* in vegetation arcs and associated bare areas. *Journal of Vegetation Science* 7, no. 6: 901-10.
Abstract: Vegetation arcs are characterized by dense patches of up to 100% plant cover surrounded by bare areas where cover is around 5%. These patterns of contracted vegetation have been reported mainly in alluvial fans of arid and semiarid zones (known as bajadas) with gentle slopes (0.2-2%), summer rainfall, and heavy showers that run as sheet-flow. It has been suggested that run-off water from bare areas is stopped at the front of the arcs and, depending on the amount of rainfall, may advance superficially into the arc, reaching the downslope limit less often. These dynamics would imply a gradient of water availability inside the arc, higher at the upper edge. We termed this the moisture gradient hypothesis. We indirectly tested this hypothesis by following the demography of a cohort of stems of the honey mesquite *Prosopis glandulosa* var. *torreyana* in three vegetation arcs and their corresponding bare areas during a yearly cycle at the Bolson de Mapimi in the Chihuahuan Desert. We selectively removed different plant life-forms (trees, shrubs and herbs) in three positions within the arcs; no manipulation was possible in the bare areas due to low plant cover. The results suggested that removal of other plant life-forms, mainly grasses, affected growth and survival of mesquite low (but not high) stems, making them accessible to medium-sized mammal browsers (jackrabbits and packrats). These results suggest that, at least for the honey mesquite, water availability in vegetation arcs was not the most strongly limiting factor for shoot performance and demography, and that browsing damage, a biotic constraint, took precedence over resource limitation.

Loqa, Harith Jabbouri. 1972. "Influence of mesquite, palo verde, and saguaro on soil chemical properties." Ph. D. Dissertation, University of Arizona.

Ludwig, John A., James F. Reynolds, and Paul D. Whitson. 1975. Size-biomass relations of several Chihuahuan Desert shrubs. *The American Midland Naturalist* 94, no. 2: 451-61.
See abstract under *Larrea tridentata*

Martin, Richard Christopher. 1976. "Soil moisture use by velvet mesquite (*Prosopis juliflora*)." M. S. Thesis, University of Arizona.

Martin, Samuel Clark. 1948. Mesquite seeds remain viable after 44 years. *Ecology* 29, no. 3: 393.

Abstract: Seeds from herbarium specimens were germinated and they were found to be mostly viable after 44 years.

———. 1974. "The effect of mesquite control on the soil moisture content of mesquite-infested range land in Southern Arizona." M. S. Thesis, University of Arizona.

———. 1975. Ecology and management of Southwestern semidesert grass-shrub ranges. *USDA Forest Service Research Paper* RM-156: 1-39.

———. 1986. Values and uses for mesquite. 91-96. General Technical Report RM, 135 Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station.

Martin, S. C., and H. L. Morton. 1993. Mesquite control increases grass density and reduces soil loss in southern Arizona. *Journal of Range Management* 46, no. 2 : 170-175.

Abstract: In 1974 we selected 8 pairs of gully headcuts on the Santa Rita Experimental Range. Mesquite (*Prosopis velutina* Woot.) on the watershed of 1 headcut of each pair was killed with diesel oil. Densities of perennial grasses and shrubs, shrub cover, surface erosion, headcut advance, and gully depth were recorded at 3-year intervals, 1974-1986. Four of the watershed pairs were in pastures grazed yearlong: 4 were in Santa Rita rotations. Each grazing schedule included 2 watershed pairs that were about 200 m higher in elevation than the other 2. In 1974, before mesquite was killed, perennial grass densities were low with little difference between assigned conditions. By 1977 perennial grass density was greater where mesquite was killed than on untreated watersheds and was greater at upper elevations. Lehmann lovegrass (*Eragrostis Lehmanniana* Nees.) made up almost all of the grass density increase at the upper elevation. Native perennial grasses, which were largely replaced by Lehmann lovegrass at the upper elevation, accounted for almost all of the gain at the lower elevation. Lower density (P less than or equal to 0.05) on low elevation rotation grazed watersheds in 1986 was the result of summer drought in 1985 and 1986 that coincided with March-October grazing in 1986. Soil loss (mm) during each 3-year period was lower at headcut-soil surface grids where mesquite was dead. Advances in headcuts and changes in gully depth showed similar trends. On the 4 pairs of watersheds that were equipped to measure runoff, there was more total runoff per millimeter of rainfall where mesquite was alive than where mesquite was killed.

Martinez-Meza, Ernesto. 1994. "Stemflow, throughfall, and root water channelization by three arid land shrubs in southern New Mexico." M.S. Thesis, New Mexico State University.

See abstract under *Flourensia cernua*

Martinez-Meza, E., and W. G. Whitford. 1996. Stemflow, throughfall and channelization of stemflow by roots in three Chihuahuan desert shrubs. *Journal of Arid Environments* 32: 271-87.

See abstract under *Flourensia cernua*

Maynard, Michael Lee. 1970. "Some effects of heat on the physiology of mesquite (*Prosopis juliflora*)."
Dissertation, University of Arizona.

McNeely, Robert P. 1983. "Influence of mesquite on vegetational changes under two grazing strategies in southern New Mexico." M.S. Thesis, New Mexico State University.

Abstract: Seasonal suitability and continuous yearlong grazing systems were initiated in 1967 on desert rangeland on the College Ranch in southern New Mexico. Cover, composition and production were measured on 220 permanent transects in 1968 and 1982. Herbicide was applied to mesquite (*Prosopis glandulosa*) between 1958 and 1964 on extensive areas of the study pastures. Mesquite cover and density were significantly lower ($P < .10$) in the herbicide-treated areas than in the nontreated areas in 1982. Between herbicide treatments and years black grama (*Bouteloua eriopoda*) and dropseed (*Sporobolus* spp.) cover did not increase significantly ($P > .10$). Threeawn (*Aristida* spp.) cover increased ($P < .10$) between 1968 and 1982 in nontreated areas.

The principle of the seasonal suitability system is to provide a grazing system for areas in which different vegetation types and range condition classes are found. Data indicated that the seasonal suitability system did not prove superior to yearlong grazing in areas of varied vegetation and range condition.

McPherson, G. R., and H. A. Wright. 1986. Threshold requirements for burning downed honey mesquite. *Journal of Range Management* 39, no. 4 : 327-30.

Abstract: Forty-one headfires were burned on 0.1-ha test plots on 2 west Texas study sites in the spring of 1984. The purpose of these burns was to develop a prescription for predicting whether downed honey mesquite will be consumed by a prescribed fire. It was found, using regression analysis and discriminant analysis techniques, that critical variables for predicting ignition and combustion of downed honey mesquite are: (1) windspeed, (2) stem moisture content, (3) stem diameter, and (4) proportion of green fuel in the fuel bed. Threshold values for ignition were 6 km/hr windspeed, 6% stem surface moisture content, 5 cm stem diameter, and 15% green:total fine fuel. Threshold values for sustained combustion were 15 km/hr windspeed, 6 cm stem diameter, and 6% stem moisture content at 1.25 cm below the stem surface. A prescription for burning downed honey mesquite was developed.

Meyer, R. E., and R. W. Bovey. 1985. Response of honey mesquite (*Prosopis glandulosa*) and understory vegetation to herbicides. *Weed Science* 33, no. 4 : 537-43.

Abstract: Honey mesquite [*Prosopis glandulosa* (Torr.) =³ PRCJG] was treated with several herbicides and herbicide combinations primarily on the Texas Post Oak Savannah over a 4-yr period. Sprays of glyphosate [N-(phosphonomethyl)glycine], picloram (4-amino-3,5,6-trichloropicolinic acid), 2,4,5-T [(2,4,5-

trichlorophenoxy)acetic acid], and triclopyr {[3,5,6-trichloro-2-pyridinyl)oxy]acetic acid} generally caused a high degree of canopy reduction in the fall of the year the spraying was done. However, sprays of clopyralid (3,6-dichloro-2-pyridinecarboxylic acid) and picloram were the most effective herbicides for killing honey mesquite 1 yr after application. At 1.1 kg ai/ha, clopyralid killed 70 to 95% and picloram killed 20 to 65% of plants 3 yr or older, Picloram plus 2,4,5-T was intermediate in effectiveness. Sprays of 2,4,5-T and triclopyr killed some plants. Picloram and tebuthiuron {N-[5-(1,1-dimethylethyl)-1,3,4-thiadiazol-2-yl]-N,N'-dimethylurea} pellets killed few if any honey mesquite. Hexazinone [3-cyclohexyl-6-(dimethylamino)-1-methyl-1,3,5-triazine-2,4(1H,3H)-dione] boluses killed no more than 37% of the honey mesquite at rates up to 4.5 kg ai/ha. Herbicides sometimes killed more honey mesquite with sprouts 2 or 3 yr old than at 1 yr old.

Meyer, R. E., R. H. Haas, and C. W. Wendt. 1973. Interaction of environmental variables on growth and development of honey mesquite. *Botanical Gazette* 134, no. 3: 173-78.

Miller, D., Steven R. Archer, S. F. Zitzer, and M. T. Longnecker. 2001. Annual rainfall, topographic heterogeneity and growth of an arid land tree (*Prosopis glandulosa*). *Journal of Arid Environments* 48, no. 1: 23-33. Abstract: Basal area growth rates for *Prosopis glandulosa* were quantified for contrasting landscape elements in a subtropical savanna. We hypothesized that growth rates of *P. glandulosa* plants (1) are a function of seasonal or annual rainfall; and (2) vary with patch type and in the rank order observed for large trees. *Prosopis glandulosa* growth was responsive to changes in rainfall ($-0.974 \text{ cm}^2\text{year}^{-1}$ in a dry year; 9.108 in a wet year), but correlations with rainfall were low. Growth of trees in contrasting patches was not consistently different, suggesting that contrasts in tree sizes across the landscape reflect differences in establishment dates rather than differences in growth rates.

Miller, R. E., and L. F. Huenneke. unpublished manuscript. Establishment of mesquite (*Prosopis glandulosa*) seedlings in semi-arid grasslands.

Abstract: In many arid and semi-arid regions throughout the world shrubs have invaded grasslands to then dominate the landscape. Livestock grazing has been suggested to be an important factor promoting shrub seedling establishment in grasslands. This study reports the results of an experiment examining the impact of livestock grazing, artificial grazing (clipping), and fertilizer amendment on shrub seedling establishment. The study was carried out in southern New Mexico, USA, in the Jornada del Muerto basin. In two grasslands, *Prosopis glandulosa* seeds and seedlings were planted into quadrats within areas that were open to livestock grazing and also within livestock exclosures. Quadrats received different pretreatments: (1) clipping the existing vegetation to 7 cm (artificial grazing), (2) two fertilizer amendments at a rate of 10 g/m^2 of nitrogen, (3) combined clipping and fertilizer, and (4) a control. In one grassland, *Prosopis* seedling survival in quadrats that experienced livestock grazing was greater than in quadrats within an exclosure. In addition, seedling survival was consistently greater in quadrats that received the clipping pretreatment. These results suggest grazing increases the likelihood of *Prosopis* establishment in grasslands. An intriguing interaction was detected between the clipping pretreatment

and the fertilizer amendments, where seedlings in quadrats that received both treatments had the poorest survival. A possible explanation for this result is grasses in the clipped and fertilized quadrats were growing vigorously, and therefore *Prosopis* seedling survival was reduced due to competition. Alternatively, lagomorphs may have been attracted to these quadrats and in the process of feeding also clipped many of the *Prosopis* seedlings.

Molinar-Holguin, Francisco. 1999. "Effect of honey mesquite (*Prosopis glandulosa* Torr) cover and soil depth on forage production in the Chihuahuan desert ." Ph. D. Dissertation, New Mexico State University.

See abstract under *Bouteloua eriopoda*

Montaña, C., B. Cavagnaro, and O. Briones. 1995. Soil water use by co-existing shrubs and grasses in the Southern Chihuahuan Desert, Mexico. *Journal of Arid Environments* 31: 1-13.

See abstract under *Flourensia cernua*

Montaña, C., J. Lopez-Portillo, and A. Mauchamp. 1990. The response of two woody species to the conditions created by a shifting ecotone in an arid ecosystem. *Journal of Ecology* 78: 789-98.

See abstract under *Flourensia cernua*

Nelson, J. T., and C. Vick. 1988. Chemical control of mesquite, creosotebush, and catclaw mimosa with tebuthiuron and subsequent grass production. *Texas Journal of Agriculture and Natural Resources* 2 : 30-32.

Abstract: Mortality of mesquite, catclaw mimosa and creosotebush treated with 1.5 lbs. ai/ac of tebuthiuron in April of 1984, and resulting grass production was determined on a draw site and a gravelly site in south Brewster County, Texas. Brush mortality 3 years post-treatment on the draw site was 10% for mesquite, 55% for creosotebush (*Larrea tridentata* DC.) and 75% for catclaw mimosa (*Mimosa biuncifera* Benth.). Mortality on the gravelly site was 0% for mesquite (*Prosopis glandulosa* Torr.), 94% for creosotebush and 100% for catclaw mimosa. Grass production was increased more on the gravelly site (960 lbs/ac on the treated area vs. 161 lbs/ac on the untreated) than on the draw site (509 lbs/ac on the treated area vs. 133 lbs/ac on the untreated control). Forb production was decreased on both treated sites. The lesser degree of grass response on the draw site was attributed to lack of mesquite control on that site.

Neuenschwander, L. H., and H. A. Wright. 1984. Edaphic and microclimate factors affecting tobosagrass regrowth after fire. *Journal of Range Management* 37, no. 2: 116-22.

See abstract under *Pleuraphis mutica*

Nilsen, E. T., P. W. Rundel, and M. R. Sharifi. 1984. Productivity in native stands of *Prosopis glandulosa*, mesquite, in the Sonoran Desert of southern California and some management implications. *California*

riparian systems : ecology, conservation, and productive management. Editors Richard E. Warner, and Kathleen M. Hendrix, 722-27. Berkeley: University of California Press.

Nilsen, Erik Tallak, M. R. Sharifi, and P. W. Rundel. 1984. Comparative water relations of phreatophytes in the Sonoran desert of California. *Ecology* 65, no. 3: 767-78.

Abstract: The seasonal and diurnal water relations were compared among six desert phreatophytes, two evergreen shrubs, and one deciduous shrub. All species were located in one wash woodland in the Sonoran Desert of southern California. There are several mechanisms by which these Phaeocarpa have adapted to the desert environment. One group of winter-deciduous phreatophytes (*Olneya tesota*, *Prosopis glandulosa*, and *Acacia greggii*) experienced summer midday leaf water potentials below -4.0 MPa. These phreatophytes had a series of physiological mechanisms for tolerating summer water stress, including seasonal and diurnal osmotic adjustment and the maintenance of high leaf conductance at low leaf water potential. Osmotic adjustment of these three phreatophytes was similar to or greater than that of two evergreen species (*Larrea tridentata* and *Simmondsia chinensis*). *Dalea spinosa*, a stem-photosynthetic phreatophyte, avoided water stress by maintaining a very small leaf area. The summer-deciduous phreatophytes (*Hyptis emoryi*, and *Chilopsis linearis*) demonstrated mechanisms of drought avoidance such as change in leaf biomass and low summer leaf conductance. Little osmotic adjustment occurred in the summer-deciduous phreatophytes. The phreatophytic species studied in this investigation have evolved adaptations to water stress that are similar to those of deciduous and evergreen shrubs of the Sonoran Desert. Desert phreatophytes are a complex group of species with varied adaptive mechanisms to tolerate or avoid drought and should not be considered simply as a group of species that avoid desert water stress by utilizing deep ground water unavailable to other desert species of drought tolerance and avoidance.

Nilsen, E. T., M. R. Sharifi, R. A. Virginia, and P. W. Rundel. 1987. Phenology of warm desert phreatophytes: seasonal growth and herbivory in *Prosopis glandulosa* var. *torreyana* (honey mesquite). *Journal of Arid Environments* 13, no. 3 : 217-29.

Abstract: Quantitative phenological measurements were collected on *Prosopis glandulosa* var. *torreyana* from 1980 to 1983 in the Sonoran Desert of California. Leaf production and shoot elongation were rapid (up to 28 leaves/week) and of short duration (1-3 weeks). Conversely, shoot diameter increment was gradual and continued from February to December. Two leaf cohorts were produced per year and the second leaf cohort was only a small proportion of the first cohort. Most leaf production, 80-90%, occurred on nodes older than one year (brachyplasts). Developmentally, leaves remained juvenile for a very short period and subsequently remained mature for about 5 months. Leaf survivorship of second cohort leaves was significantly shorter than of first cohort leaves. Leaf herbivores removed about 40% of the leaf production before the leaves matured. Following leaf maturation few leaves were eaten. Insects also ate new shoot meristems, halting shoot elongation in 100% of new shoots during 1981 and 1982. Significant losses (35% of shoots) were the result of herbivory by rodents and rabbits. Such herbivory occurred later in the year than leaf herbivory. The rapid leaf production and new shoot elongation may be an adaptation to minimise losses to leaf herbivores. Generally, the seasonal progression of growth in *Prosopis glandulosa* was uncoupled from the influences of precipitation or temperature. Also, the phenological state of the leaves in

combination with their physiology controlled xylem pressure potential, rather than the reverse. Only very few statistical correlations could be made between phenology and climatic conditions.

Parker, Kenneth W, and S. Clark Martin. 1952. *The mesquite problem on southern Arizona ranges*. Circular / United States Department of Agriculture, no. 908. Washington, D. C. U.S. Govt. Print. Off.

Paulsen, Harold A. Jr., and Fred N. Ares. 1962. *Grazing values and management of black grama and tobosa grasslands and associated shrub ranges of the Southwest*. Technical Bulletin , no. 1270. Washington : U.S. Dept. of Agriculture, Forest Service.
See abstract under *Bouteloua eriopoda*

Pennington, Rodney E., Charles R. Tischler, Hyrum B. Johnson, and H. Wayne Polley. 1999. Genetic variation for carbon isotope composition in honey mesquite (*Prosopis glandulosa*). *Tree Physiology* 19, no. 9: 583-89.
Abstract: Carbon isotope composition ($\delta^{13}\text{C}$) is a useful surrogate for integrated, plant water-use efficiency (WUE) when measured on plants grown in a common environment. In a variety of species, genetic variation in $\delta^{13}\text{C}$ has been linked to the distribution of genotypes across gradients in atmospheric and soil water. We examined genetic variation for $\delta^{13}\text{C}$ in seedlings of honey mesquite (*Prosopis glandulosa* Torr.), an invasive grassland shrub that thrives in the southwestern USA. Fifteen maternal families, representing progeny of 15 adult trees, were studied in three common garden experiments in a greenhouse. The 990-km east-west transect along which the adult trees were located encompasses a wide precipitation gradient, and includes mesic grassland, semiarid grassland, and Chihuahuan desert ecosystems. Genetic variation for $\delta^{13}\text{C}$ in mesquite was substantial, with the rank order of half-sib families based on $\delta^{13}\text{C}$ relatively stable across experiments, which were conducted under different environmental conditions. Conversely, rankings of families by mean seedling height (an index of growth rate) varied markedly among experiments. Seedlings derived from Chihuahuan desert adults emerged more quickly and had more negative $\delta^{13}\text{C}$ (indicative of lower WUE) than seedlings derived from the other regions. Although $\delta^{13}\text{C}$ and seedling height were not correlated, these results suggest that mesquite genotypes at the drier, western extreme of the species' range are adapted for quicker emergence and possibly faster growth than genotypes from mesic areas. Together, these traits may facilitate exploitation of infrequent precipitation events.

Phillips, Walter S. 1963. Depth of roots in soil. *Ecology* 44, no. 2: 424.

Abstract: Presumed mesquite roots have been found in a road ditch near Tucson, Arizona at a depth of 175 feet.

Polley, H. W., H. B. Johnson, H. S. Mayeux, C. R. Tischler, and D. A. Brown. 1996. Carbon dioxide enrichment improves growth, water relations and survival of droughted honey mesquite (*Prosopis glandulosa*) seedlings. *Tree Physiology* 16, no. 10 : 817-23.

Abstract: Low water availability reduces the establishment of the invasive shrub *Prosopis* on some grasslands. Water deficit survival and traits that may contribute to the postponement or tolerance of plant dehydration were measured on seedlings of *P. glandulosa* Torr. var. *glandulosa* (honey mesquite) grown at CO₂ concentrations of 370 (ambient), 710, and 1050 micromole mol⁻¹. Because elevated CO₂ decreases stomatal conductance, the number of seedlings per container in the elevated CO₂ treatments was increased to ensure that soil water content was depleted at similar rates in all treatments. Seedlings grown at elevated CO₂ had a greater root biomass and a higher ratio of lateral root to total root biomass than those grown at ambient CO₂ concentration; however, these seedlings also shed more leaves and retained smaller leaves. These changes, together with a reduced transpiration/leaf area ratio at elevated CO₂, may have contributed to a slight increase in xylem pressure potentials of seedlings in the 1050 micromole mol⁻¹ CO₂ treatment during the first 37 days of growth (0.26 to 0.40 MPa). Osmotic potential was not affected by CO₂ treatment. Increasing the CO₂ concentration to 710 and 1050 micromole mol⁻¹ more than doubled the percentage survival of seedlings from which water was withheld for 65 days. Carbon dioxide enrichment significantly increased survival from 0% to about 40% among seedlings that experienced the lowest soil water content. By increasing seedling survival of drought, rising atmospheric CO₂ concentration may increase abundance of *P. glandulosa* on grasslands where low water availability limits its establishment.

Polley, H. Wayne, Hyrum B. Johnson, and Herman S. Mayeux. 1994. Increasing CO₂: Comparative responses of the C-4 grass *Schizachyrium* and grassland invader *Prosopis*. *Ecology* 75, no. 4: 976-88.

Abstract: The woody C-3 *Prosopis glandulosa* (honey mesquite) and C-4 perennial grass *Schizachyrium scoparium* (little bluestem) were grown along a gradient of daytime carbon dioxide concentrations from near 340 to 200 $\mu\text{mol/mol}$ air in a 38 m long controlled environment chamber. We sought to determine effects of historical and prehistorical increases in atmospheric CO₂ concentration on growth, resource use, and competitive interactions of a species representative of C-4-dominated grasslands in the southwestern United States and the invasive legume *P. glandulosa*. Increasing CO₂ concentration stimulated N-2 fixation by individually grown *P. glandulosa* and elicited in C-3 seedlings a similar relative increase in leaf intercellular CO₂ concentration, net assimilation rate, and intrinsic water use efficiency (leaf net assimilation rate/stomatal conductance). Aboveground biomass of *P. glandulosa* was not altered by CO₂ concentration, but belowground biomass and whole-plant water and nitrogen use efficiencies increased linearly with CO₂ concentration in seedlings that were grown alone. Biomass produced by *P. glandulosa* that was grown with *S. scoparium* was not affected by CO₂ concentration. Stomatal conductance declined and leaf assimilation rates of *S. scoparium* at near maximum incident light increased at higher CO₂ concentration, but there was no effect of CO₂ concentration on biomass production or whole-plant water use efficiency of the C-4 grass. Rising CO₂ concentration, especially the 27% increase since the beginning of the 19th century, may have contributed to more abundant *P. glandulosa* on C-4 grasslands by stimulating the shrub's growth or reducing the amount of resources that the C-3 required. Much of the potential response of *P. glandulosa* to CO₂ concentration, however, appears to be contingent on the shrub's escaping competition with neighboring grasses.

Polley, H. Wayne, Charles R. Tischler, Hyrum B. Johnson, and Rodney E. Pennington. 1999. Growth, water relations, and survival of drought-exposed seedlings from six maternal families of honey mesquite (*Prosopis glandulosa*): Responses to CO₂ enrichment. *Tree Physiology* 19, no. 6: 359-66.

Abstract: Low water availability is a leading contributor to mortality of woody seedlings on grasslands, including those of the invasive shrub *Prosopis*. Increasing atmospheric CO₂ concentration could favor some genotypes of this species over others if there exists intraspecific variation in the responsiveness of survivorship to CO₂. To investigate such variation, we studied effects of CO₂ enrichment on seedling survival in response to uniform rates of soil water depletion in six maternal families of honey mesquite (*P. glandulosa* Torr. var. *glandulosa*). Three families each from the arid and mesic extremes of the species' distribution in the southwestern United States were studied in environmentally controlled glasshouses. Relative water content at turgor loss and osmotic potential were not affected by CO₂ treatment. Increased atmospheric CO₂ concentration, however, increased growth, leaf production and area, and midday xylem pressure potential, and apparently reduced transpiration per unit leaf area of seedlings as soil dried. Consequently, CO₂ enrichment about doubled the fraction of seedlings that survived soil water depletion. Maternal families of honey mesquite differed in percentage survival of drought and in several other characteristics, but differences were of similar or of smaller magnitude compared with differences between CO₂ treatments. There was no evidence for genetic variation in the responsiveness of survivorship to CO₂. By increasing seedling survival of drought, increasing atmospheric CO₂ concentration could increase the abundance of honey mesquite where establishment is limited by water availability. Genetic types with superior ability to survive drought today, however, apparently will maintain that advantage in the future.

Raizada, M. B., and R. N. Chatterji. 1954. A diagnostic key to the various forms of introduced mesquite (*Prosopis juliflora* DC.). *The Indian Forester* 80 : 675-80.

Reitzel, James Aron. 1982. "The effects of brush control on bird populations in a mesquite community." M.S. Thesis, New Mexico State University.

Abstract: This study dealt with the effects that brush control, by aerial applications of 2,4,5-T (2,4,5-Trichlorophenoxy acetic acid) had on indigenous bird populations in a mesquite community in southern New Mexico. Vegetation comparisons indicate that the mesquite was killed more completely in the dune areas than in the flat areas. Treatment effects on bird populations were examined via the parameters of species richness, dominance composition, diversity, activity, and total numbers. Species richness was greater in the unsprayed area in the dune subtype, but was approximately equal in sprayed and unsprayed areas in the flats. Dominance composition differed little between treatment areas. In 1979, three species were restricted to the dune subtype, but only one species was restricted to the unsprayed portion of this subtype. In 1980, only one species was restricted to the dune subtype. The evidence for an effect on bird diversity was weak, but may indicate a lower diversity in the sprayed dune mesquite. Activity was lower in the sprayed dune and the sprayed flat mesquite areas as compared to their respective unsprayed areas in 1979, but only in the sprayed dune area in 1980. Based on total numbers observed for each species, the mesquite control had a detrimental effect on eight species; however, five species may have benefited by mesquite control. In conclusion, it appears that mesquite control has a detrimental effect on populations of

some bird species. These differences are more pronounced in the first year of study, possibly because of the mesquite regrowth which occurred the following year.

Reynolds, H. G., and G. E. Glendening. 1949. Merriam kangaroo rat a factor in mesquite propagation in southern Arizona range lands. *Journal of Range Management* 4, no. 2: 193-97.

Abstract: Merriam kangaroo rats collect mesquite seeds as a preferred food item. Not all the harvested seed is consumed, and a large portion is buried in shallow caches. Mesquite seed stored in such caches, if not rediscovered by rats, germinates during favorable climatic years, resulting in the emergence of seedlings at some distance from the parent tree. As mesquite increases, perennial grass decreases, and greater numbers of Merriam rats occupy the habitat. Hence, once the grass density on range lands is reduced so that the habitat is favorable for rats, and mesquite becomes established, the mesquite seeds may continue to be further spread by rats, as well as by livestock and other agencies. Consequently, on such areas any attempts to stop or retard the invasion of mesquite through a reduction in livestock should also consider control of the Merriam kangaroo rat.

Reynolds, James F., Ross A. Virginia, Paul R. Kemp, Amrita G. De Soyza, and David C. Tremmel. 1999. Impact of drought on desert shrubs: Effects of seasonality and degree of resource island development. *Ecological Monographs* 69, no. 1: 69-106.

See abstract under *Larrea tridentata*

Rogers, Ken E. 2000. The magnificent mesquite. 1 ed. 159 p. : ill. (some col.), maps ; 24 cm. The Corrie Herring Hooks Series, no. 46. Austin : University of Texas Press.

Sappington, N. 1998. *Prosopis* sp.- mesquite. *Arbor Age* 18, no. 4 : 30-31.

Schuster, Joseph L., Editor. 1969. Literature on the mesquite (*Prosopis* L.) of North America; an annotated bibliography. Special Report , ed. International Center for Arid and Semi-arid Land Studies, no 26. Lubbock, Texas: Texas Tech University.

Scifres, C. J., and J. H. Brock. 1970. Growth and development of honey mesquite seedlings in the field and greenhouse as related to time of planting, planting depth, soil temperature and top removal. *PR - Texas Agricultural Experiment Station* 2801/2828 : 65-71.

———. 1970. Moisture-temperature interrelations in germination and early seedling development of honey mesquite. *PR - Texas Agricultural Experiment Station* 2801/2828 : 63-65. ill.

Shoushtari, Nastaran Hakim. 1984. "Rhizobiology of the mesquite tree (*Prosopis juliflora*)." Ph. D. Dissertation, University of Arizona.

Simpson, B. B. 1977. *Mesquite, its biology in two desert scrub ecosystems*. US/IBP Synthesis Series, 4. Stroudsburg, Pa. :, New York : Dowden, Hutchinson & Ross ; exclusive distributed, Halsted Press.

Smith, S. D., R. K. Monson, and J. E. Anderson. 1997. *Physiological ecology of North American desert plants*. Adaptations of Desert Organisms, ed. J. L. Cloudsley-Thompson. Berlin: Springer.
Contents: 1- North American Deserts: Environments and Vegetation; 2- Plant Processes and Responses to Stress; 3- Evergreen Shrubs; 4- Drought-Deciduous Shrubs; 5- CAM Succulents; 6- Perennial Grasses; 7- Phreatophytes; 8- Desert Annuals; 9- Poikilohydric Plants; 10- Exotic Plants

Sosebee, R. E., and C. Wan. 1989. Plant ecophysiology: a case study of honey mesquite. 103-18. General Technical Report INT, 256 Department of Agriculture, Forest Service, Intermountain Research Station.

Spalding, Volney M. 1909. *Distribution and movements of desert plants*., Vol. 113. Washington, D.C. Carnegie Institution of Washington.

Steinberg, P. 2001. *Prosopis glandulosa*. U.S. Department of Agriculture, Forest Service Rocky Mountain Research Station Fire Sciences Laboratory. 2001. "Fire effects information system." Web page. Available at <http://www.fs.fed.us/database/feis/> .

Teaschner, Terri Beth. 2001. "Influence of soil depth and texture on mesquite (*Prosopis glandulosa*) density and canopy cover in the northern Chihuahuan Desert, New Mexico ." M. S. Thesis, New Mexico State University.

Tejada Velez, Einstein Henry. 1990. "Brush control and grazing behavior of goats on semidesert mesquite brush dominated rangeland." M.S. Thesis, New Mexico State University.

Texas Agricultural Experiment Station. 1973. *Mesquite: growth and development, management, economics, control, uses*. Research Monograph , no. 1. College Station, Texas: Texas Agricultural Experiment Station.

Tiedeman, J. A., R. Beck, and R. V. Ecret. 1991. Dependence of standing crop on range condition rating in New Mexico. *Journal of Range Management* 44, no. 6: 602-5.

Abstract: The Sandy Ridge Site of southern New Mexico was studied to determine the dependence of total

standing crop and components of standing crop on range condition rating. Total standing crop which included mesquite (*Prosopis glandulosa* Torr.) decreased, but total standing crop minus mesquite increased as range condition rating increased. These relationships were found to be highly significant (P less than or equal to 0.01) by regression analysis. Very low R-square values for these models indicate that the often assumed positive linear relationship of standing crop to range condition rating is not reliable. Prediction of standing crop from range condition ratings using linear or quadratic models was found to be unreliable for the Sandy Range Site in southern New Mexico.

Tiedemann, Arthur R. 1970. "Effect of mesquite (*Prosopis juliflora*) trees on herbaceous vegetation and soils in the desert grassland." Ph. D. Dissertation, University of Arizona.

Tiedemann, A. R., and J. O. Klemmedson. 1977. Effect of Mesquite trees on vegetation and soils in the desert grassland. *Journal of Range Management* 30: 361-67.

———. 1986. Long-term effects of a mesquite removal on soil characteristics. I. Nutrients and bulk density. *Soil Science Society of America Journal* 50, no. 2: 472-75.

Tromble, John M. 1977. Water requirements for mesquite (*Prosopis juliflora*). *Journal of Hydrology* 34: 171-79.
Abstract: Evapotranspiration (ET) determined by different investigators, compared with values determined by the White and Troxell methods, showed that their values provided reasonable estimates and that utilizing diurnal water table fluctuations furnishes a method of computing ET with less than 100% vegetation density. Average daily maximum ET rates for June were calculated, and ratios were compared with values from other independent studies. Since ET rates, determined by White and Troxell methods, indicated plausible values of water use when compared to other independent studies, they could be considered index values useful as guidelines for water abstracted by mesquite.

Turner, Raymond M. 1990. Long-term vegetation change at a fully protected Sonoran desert site. *Ecology* 71, no. 2: 464-77.

See abstract under *Larrea tridentata*.

Ueckert, D. M., T. L. Whigham, and B. M. Spears. 1978. Effect of burning on infiltration, sediment, and other soil properties in a mesquite-tobosagrass community. *Journal of Range Management* 31, no. 6: 420-425.

Abstract: Burning had a minimal effect on rainfall infiltration and sediment load in runoff from a mesquite-tobosagrass community on slopes less than 1%. Most soil physical properties that affect infiltration on these heavy clay soils were not altered significantly by burning. Potential soil loss in runoff can be minimized by burning under relatively moist conditions. Larger soil aggregates were broken down by burning and had not returned to equilibrium on 5-year-old burns. Trends in levels of soil organic carbon,

salinity, sodium, and potassium following burning varied with degree of soil cracking, which is a function of soil moisture.

Valentine, Kenneth Alva. 1941. "Soil conditions of the Jornada red loamy sand of southern New Mexico; as related to the degree of invasion by mesquite, *Prosopis glandulosa*." M. S. Thesis, University of Arizona.

Valone, Thomas J., and Daniel J. Thornhill. 2001. Mesquite establishment in arid grasslands: an experimental investigation of the role of kangaroo rats. *Journal of Arid Environments* 48: 281-88.

Abstract: Kangaroo rats are thought to play a role in promoting the establishment of woody shrubs in arid grasslands by caching mesquite seeds. We examined this hypothesis experimentally by comparing mesquite establishment of plots from which kangaroo rates have been continuously removed for either 10 or 21 years to control plots with kangaroo rats present. Contrary to the above hypothesis, mesquite establishment was lowest on plots that contained kangaroo rats and highest on plots from which kangaroo rats have been absent for 21 years. We suggest that herbivory, either by kangaroo rats or lagomorphs, who were found to be more active on plots with kangaroo rats, more negatively affects mesquite seedling establishment than the potential positive effects of kangaroo rat seed-caching behavior in arid grasslands.

Van Auken, O. W., and J. K. Bush. 1987. Interspecific competition between *Prosopis glandulosa* Torr. (honey mesquite) and *Diospyros texana* Scheele (Texas persimmon). *American Midland Naturalist* 118, no. 2: 385-92.

Abstract: Short-term growth experiments were carried out in a greenhouse with seedlings of *Prosopis glandulosa* Torr (Honey mesquite) and *Diospyros texana* Scheele (Texas persimmon). The species were grown together in various proportions using the experimental design of de Wit. When they were grown separately at the same density, there was no significant difference in dry mass between the two species. When grown together, *P. glandulosa* had a greater mean stem length, basal diameter, leaf dry mass stem dry mass, and total dry mass compared to *D. texana*. Dry mass and other growth parameters of *P. glandulosa* were greater when it was grown with *D. texana* compared to when grown at the same density by itself. Growth parameters of *D. texana* were lower when grown with *P. glandulosa* than grown alone. *Prosopis glandulosa* was the better competitor of the two species tested. Apparently *P. glandulosa*, a colonizer of disturbed sites, is capable of out-competing species of mature communities such as *D. texana* when grown together in low fertility soils.

———. 1990. Importance of grass density and time of planting on *Prosopis glandulosa* seedling growth. *Southwestern Naturalist* 35, no. 4: 411-15.

Abstract: Growth experiments were conducted in a greenhouse with seedlings of *Prosopis glandulosa* Torr. (honey mesquite) and *Cynodon dactylon* (L.) Pers. (bermuda grass). Effects of density and time of planting of *C. dactylon* on growth of *P. glandulosa* were examined. When one seedling of *P. glandulosa* was grown with two or more *C. dactylon* in an additive experiment, aboveground, belowground, and total dry weight of *P. glandulosa* decreased 84, 71, and 79% respectively. Root:shoot ratios for *P. glandulosa* increased almost

four times from lowest to highest density of *C. dactylon*. Conversely, *P. glandulosa* caused a significant reduction in dry weight of *C. dactylon* but mainly in the lowest grass densities. When *P. glandulosa* was planted with *C. dactylon* at the same time, dry weight of *P. glandulosa* was reduced 83%. If *P. glandulosa* was planted 2 months after *C. dactylon* was planted, dry weight of *P. glandulosa* was reduced 96%. Although *P. glandulosa* had a negative effect on *C. dactylon*, the negative effect only occurred when the density of *C. dactylon* was low or they were planted at the same time. Greenhouse studies suggest that *P. glandulosa* competes almost equally with *C. dactylon*, unless there is a large difference in density or a temporal difference in planting. In the field, early growth and establishment of *P. glandulosa* may require reduced herbaceous plant density or vegetation gaps.

———. 1997. Growth of *Prosopis glandulosa* in response to changes in aboveground and belowground interference. *Ecology* 78, no. 4: 1222-29.

Abstract: Recent increases in woody plant density have occurred in grasslands worldwide, but both the cause and mechanisms involved in these changes have been elusive. Changes in grass biomass mediated by high levels of constant herbivory seem to be the pivotal reason. In this field study in central Texas, USA, effects of aboveground and belowground interference on the growth of seedlings of a deep-rooted, woody heliophyte, *Prosopis glandulosa*, were tested. The effects of two positions (gap or *Bouteloua curtipendula* grassland), two levels of aboveground interference (high or low light), and three levels of grass root interference (2, 20, and 40 cm deep root excluders) on *P. glandulosa* aboveground, belowground, and total dry mass were measured. The exclusion of belowground interference significantly increased aboveground, belowground, and total *P. glandulosa* dry mass, with the reduction of belowground interference to a depth of 20 cm maximizing *P. glandulosa* dry mass. Aboveground, belowground, and total dry mass of *P. glandulosa* were not significantly different when grown in gaps compared to grasslands, nor were there any significant differences when aboveground interference (shade) was imposed. However, the trend was for greater dry mass in gaps and high light. Data indicate that belowground interference from grass roots significantly reduces the dry mass of *P. glandulosa*, while aboveground interference has a lesser effect

Vilela, A. E., and D. A. Ravetta. 2001. The effect of seed scarification and soil-media on germination, growth, storage, and survival of seedlings of five species of *Prosopis* L. (Mimosaceae) . *Journal of Arid Environments* 48, no. 2: 171-84 .

Abstract: *Prosopis* L. (Mimosaceae) species are important vegetation elements in arid and semi-arid environments where they offer shade, firewood, timber and food for man, wildlife and livestock. Many species, specially South-American ones, have been included in afforestation programmes and agroforestry-silvopastoral systems. Within this scope, there is a need of information on eco-physiological responses related to growth and development. The objective of this study was to assess the influence of seed scarification method and growing media on germination, seedling growth, survival and some physiological variables of three *Prosopis* species native to South America: *P. alba*, *P. chilensis* and *P. flexuosa*, and two native to North America: *P. velutina* and *P. pubescens*. All scarification methods can be used to promote germination in the species evaluated in this study, except for the chemical treatment for *P. chilensis* and the thermal treatment for the North American species. Nursery soil mix should be preferred to the soil under

the canopy of *Prosopis* trees, since germination, plant size, and plant survival were higher in this growth media. An increase in biomass partition to above ground structures was an important mechanism that allowed for the superior response of plants in nursery mix. The addition of nutrients to *Prosopis* soil did not improve the rate of leaf appearance or biomass, or changed the shoot:root ratio. Both reserve carbohydrates and C:N ratio were lower in fertilized plants. *Prosopis flexuosa* showed a significant increase in plant biomass with the addition of nutrients to the growth media.

Villanueva Díaz, José. 1993. Distribución actual y características ecológicas del mezquite (*Prosopis laevigata* H. & B. Johnst), en el estado de San Luis Potosí. 36 p. Boletín Divulgativo, no. 74. México, D.F. Secretaría de Agricultura y Recursos Hidráulicos, Instituto Nacional de Investigaciones Forestales y Agropecuarias, División Forestal.

Virginia, Ross A. 1986. Soil development under legume tree canopies. *Forest Ecology and Management* 16: 69-79. Abstract: Tree legumes influence soil development by altering the physical and chemical properties of the soil beneath the plant canopy. The accumulation of extractable NO₃ and PO₄ in soil beneath the Sonoran Desert woody legumes *Prosopis glandulosa* and *Dalea spinosa* was compared to soil from the tree interspaces. Measurements of natural ¹⁵N abundance indicate both these plants symbiotically fix N₂ at the sites studied. Nutrient accumulation was related to the water regime of the site. High concentrations of symbiotically fixed N and P as NO₃ and PO₄ were found in the surface 60 cm of soil beneath a *Prosopis* stand utilizing groundwater. Relatively little NO₃ or PO₄ accumulated in the moist soil above the water table at 5 m. In contrast, NO₃ and PO₄ did not accumulate in the surface soil beneath *Dalea* growing in a sandy wash. Soil NO₃ concentrations were lower beneath *Dalea* canopies than in the nonvegetated wash. The mechanisms by which tree legumes alter soil properties are reviewed. The direction and potential magnitude of soil changes in managed tree legume systems may be inferred from an understanding of the function of native plant-soil systems.

Virginia, R. A., and W. M. Jarrell. 1983. Soil properties in a mesquite-dominated Sonoran desert ecosystem. *Soil Science Society of America Journal* 47: 138-44.

Virginia, R. A., W. M. Jarrell, W. G. Whitford, and D. W. Freckman. 1992. Soil biota and soil properties in the surface rooting zone of mesquite (*Prosopis glandulosa*) in historical and recently desertified Chihuahuan Desert habitats. *Biology and Fertility of Soils* 14, no. 2: 90-98. Abstract: The woody legume, mesquite (*Prosopis glandulosa*), has expanded from its historical habitats (playas and arroyos) to recently occupied grassland and dune habitats during the desertification of perennial grasslands in the Chihuahuan Desert. We studied historical and recently occupied sites, having hypothesized that the trophic structure and population density of soil microarthropods and nematodes associated with the surface root system of mesquite would differ in sites representing historical and recent habitats, and that the N mineralization potential would be lower in the recent habitats. Our results showed that the net N mineralization potential did not differ significantly among the sites, even though soil

nutrient concentrations and texture varied widely. Concentrations of organic C, N, and P were lowest in the recent dune habitat and highest at the playa. Very low concentrations of P in the dune and grassland soils implicated P as a limiting factor in these systems. The bacterial-feeding and omnivore-predator functional groups made up the largest fraction of the nematode community at most of the sites. The highest density of plant-feeding nematodes at the playa indicated that herbivory is potentially most important at this site. Total microarthropod densities did not vary significantly among habitats, with Collembola densities highest in the mesquite dunes. Grazers were the dominant microarthropod functional group. While both C and N pool sizes were higher in the historical habitats, a higher substrate lability in the recent habitats appeared to support biota populations and N mineralization rates equivalent to those in the playa and arroyo. Differences in soil properties and biota among historical and recent mesquite habitats may be important for understanding the changes that have occurred in Chihuahuan Desert ecosystems during desertification.

Wan, C., and R. E. Sosebee. 1990. Characteristics of photosynthesis and conductance in early and late leaves of honey mesquite. *Botanical Gazette* 151, no. 1: 14-20.

Abstract: Photosynthetic rates of early and late leaves of honey mesquite (*Prosopis glandulosa*) were measured on native rangeland with an air-flow open system. Daily maximum photosynthetic rates of early leaves were significantly greater than those of late leaves. Greater photosynthetic rates in early leaves were associated with higher nitrogen content per unit leaf area and a thicker leaf blade. Lack of well-developed photosynthetic apparatus (functional complex leading to CO₂ fixation) in the late leaves is suggested as a cause for lower photosynthesis. Photosynthetic rates of early leaves were generally higher in the morning than late leaves, and they became lower in the afternoon than late leaves. Stomatal conductance was negatively correlated with leaf-air vapor pressure difference (VPD) ($R > .8$) in early leaves, but a low correlation was found between conductance and VPD ($R < .1$ in some samples). Higher photosynthetic rates of late leaves in the afternoon were accompanied by greater leaf conductance and leaf wilting, which suggested that turgor potential is not a sole transducer of water stress.

———. 1990. Relationship of photosynthetic rate and edaphic factors to root carbohydrate trends in honey mesquite. *Journal of Range Management* 43, no. 2: 171-76.

Abstract: Total nonstructural carbohydrate (TNC) concentration in honey mesquite (*Prosopis glandulosa* var. *glandulosa*) roots and its relation to current photosynthetic rate and selected soil parameters were examined on 2 upland soils. Root carbohydrate recharge rates were generally greater in trees on a sandy loam site than those on a clay loam site during the spring rainy season because of higher photosynthetic rates and more apparent root growth. Recharge rate was greater on the clay loam site during midsummer, which was related to higher soil water potential. Root carbohydrate recharge was less sensitive to a moderate water stress (dawn xylem water potential ranged from -1 to -1.6 Mpa) than was photosynthesis; but it was more sensitive to severe water stress (dawn xylem water potential ranged from -1.9 to 2.4 MPa) than was photosynthesis. Effective control of honey mesquite with foliar-applied herbicides is determined by photosynthetic rates and TNC trends as they are influenced by both soil temperature and soil water

content. Higher photosynthetic rates and greater amounts of root TNC are related to higher soil temperature and higher soil water content.

- . 1991. Water relations and transpiration of honey mesquite on 2 sites in west Texas. *Journal of Range Management* 44, no. 2: 156-60.

Abstract: Transpiration rates and internal water relationships of honey mesquite (*Prosopis glandulosa*) were investigated weekly during May through September 1986 on sandy loam and clay loam, both upland sites in west Texas. Average transpiration rates peaked at approximately 7 mmol m⁻² s⁻¹ at 1100 hr during wet periods and reached a plateau between 4 and 5 mmol m⁻² s⁻¹ between 1200 and 1400 hr. During dry periods, the average transpiration rates reached their maximum plateau of 2 mmol m⁻² s⁻¹ at 1000 hr and declined between 1200 and 1600 hr. The transpiration rates ranged from an average of 3.28 +/- 2.05 mmol m⁻² s⁻¹ for trees on a sandy loam site to an average of 3.85 +/- 1.94 mmol m⁻² s⁻¹ for those on a clay loam site. Stomatal closure in midsummer caused a substantial increase in leaf temperature. Mesquite has developed other means, such as leaf orientation, wax accumulation, and reduction in canopy development, to avoid drought. Stomatal conductance of mesquite is very responsive to soil water availability and dryness of the air, and is less responsive to internal water status. This research further substantiates that mesquite behaves like a facultative phreatophyte in west Texas.

- Warrag, M. O. A. 1994. Autotoxicity of mesquite (*Prosopis juliflora*) pericarps on seed germination and seedling growth. *Journal of Arid Environments* 27, no. 1: 79-84.

Abstract: Autotoxicity, expressed as the inhibitory effects, of the pericarp on seed germination and seedling growth of mesquite, was investigated. The final germination of fresh mesquite seeds at 25 +/- 2 degree C in a distilled water control and four pericarp aqueous extracts, prepared by the extraction of 5, 20, 40 and 60 g dry pericarp in a litre of distilled water, revealed that more than 95% of the seeds had germinated in the distilled water control and in the least concentrated extract, whereas 100% germination inhibition was exhibited by the most concentrated extract. Likewise, both radicle and hypocotyl lengths were retarded significantly by the extracts. These lengths decreased with an increase in the extract concentration to be severely affected in the most concentrated extract. Using four NaCl-citric acid solutions, with the same pH and osmotic potentials as the extracts, resulted in more than 95% final seed germination. This was significantly higher than in their corresponding extracts, with the exception of the least concentrated one. As with the extracts, the radicles and hypocotyls decreased in length with an increase in the NaCl-citric acid concentration, but they were still significantly longer than in the corresponding extracts. These results clearly indicate that mesquite pericarp contains allelochemicals which inhibit seed germination and seedling growth of that species. The characterization and identification of these allelochemicals will add to the understanding of their allelopathic mechanism and, hence, could make it possible to use the mesquite pod segments as propagules instead of the seeds which are difficult to extract.

———. 1995. Autotoxic potential of foliage on seed germination and early growth of mesquite (*Prosopis juliflora*). *Journal of Arid Environments* 31, no. 4: 415-21.

Abstract: Aqueous extracts of 10, 20, 40 and 60 g dry leaves of mesquite (*Prosopis juliflora*), in a litre of distilled water, were tested for their autotoxic effects on seed germination and early seedling growth. With the exception of the effect of the least concentrated extract on the final seed germination, all extracts reduced seed germination percentage, and radicle and hypocotyl lengths considerably, in comparison with the distilled water control. This reduction increased with the increase of extract concentration throughout the germination period. The radicles, which did not elongate at all in the highest concentrated extract, were more affected than the hypocotyls. Using ground leaves mixed with sand in the ratios of 1:15, 1:10 and 1:5, (leaves: sand, by volume) compared to sand as a control, resulted in similar findings. The pH and the osmotic potentials of the extracts were not low enough to bring about such effects, so it could be concluded that the mesquite foliage contains water-soluble allelochemicals which could inhibit seed germination and seedling growth of the same species.

Warren, Alan Alden. 1993. "Longterm mesquite control influences on Chihuahuan Desert vegetation." M. S. Thesis, New Mexico State University.

Warren, A., J. Holechek, and M. Cardenas. 1996. Honey mesquite influences on Chihuahuan Desert vegetation. *Journal of Range Management* 49: 46-52.

Weltz, M. A., and W. H. Blackburn. 1993. Modeling water balance with the ERHYM model on south Texas rangelands. *Water Resources Bulletin* 29, no. 3: 461-74.

Abstract: Understanding the hydrologic processes of rangeland plant communities is essential to determine if water augmentation through shrub management is feasible. Vegetation manipulation studies are costly, difficult to accurately replicate, and often require more than 10 years to determine treatment effect on the water budget. If properly applied, hydrologic simulation models are an attractive alternative for assessing vegetation manipulation practices. The ERHYM-II model was evaluated to determine if it was capable of simulating the water balance for honey mesquite shrub clusters, grass interspaces, and bare soil in south Texas. The simulated water budget was within 2 percent of the measured evapotranspiration for the shrub clusters and grass interspaces. The model underestimated the number of runoff events and overestimated runoff volume for the grass interspace and shrub clusters. Simulated runoff was overestimated by approximately twofold for the grass interspace and threefold for the shrub clusters. Although simulated runoff was substantially overestimated, observed and simulated runoff only accounted for 3 to 6 percent of annual rainfall for the grass and shrub dominated areas, respectively. Simulated evapotranspiration was underestimated by 18 percent and soil water content was overestimated by 82 percent for the bare soil. The model underestimated evapotranspiration for the bare soil as a result of restricting evaporative losses to the first soil layer. Based on our analysis, the ERHYM-II model has the potential for simulating the annual water balance for semiarid rangeland plant communities where runoff and deep drainage are limited components of the water balance.

———. 1995. Water budget for south Texas rangelands. *Journal of Range Management* 48, no. 1 : 45-52.

Abstract: Understanding hydrologic processes is essential to determine if water yield augmentation is possible through vegetation manipulation. Nine large non-weighing lysimeters, each 35 m², were installed on the La Copita Research Area, 20 km south of Alice, in the eastern Rio Grande Plain of Texas. The non-weighing lysimeters were used to test the hypothesis that honey mesquite (*Prosopis glandulosa* var *glandulosa* Torr.) shrub clusters have greater evapotranspiration rates than grass interspaces. Annual evapotranspiration rates of shrub clusters and grass interspaces were found to be similar, and both were significantly greater than evaporative losses from bare soil. Surface runoff and deep drainage of water (> 2 m) from the bare soil were significantly greater than from the grass interspaces and shrub clusters. There was no drainage of water below 2 m from the shrub clusters. A total of 22 mm of water percolated below 2 m from the grass interspace during the 18 month study period. These results indicate that no net change in the water budget would occur if shrub clusters were replaced with grasses in years with below average or normal rainfall. Increasing water yield from converting shrub-dominated rangelands to grass-dominated rangelands in south Texas is marginal in this area and limited to years when winter and spring rainfall exceeds potential evapotranspiration. There is little evidence to suggest that the minimal (non-significant difference) increase in percolation and surface runoff from the grass interspaces could be reliably captured and dependably made available off-site.

Whitford, W. G., R. K. Johnson, and D. J. DePree. 1975. "Studies on wood borers, girdlers, and seed predators of mesquite." *Report of 1974 Progress, Research Memorandum 75-26*. Utah State University, Logan, Utah.

Whitford, Walter G., Dirk J. DePree, and Richard K. Johnson Jr. 1978. The effects of twig girdlers (Cerambycidae) and node borers (Bostrichidae) on primary production in mesquite (*Prosopis glandulosa*). *Journal of Arid Environments* 1: 345-50.

Abstract: Production of leaves and shoots on branches of mesquite shrubs which had been girdled by the mesquite twig girdler (*Oncideres rhodisticta*) was compared with the production of unaffected branches on girdled and ungriddled shrubs. We made similar comparisons on mesquite which had been subjected to simulated girdling or terminal node destruction of 40-80 per cent of the branches. There was no significant difference in shoot and leaf growth in either natural or simulated damaged plants compared to controls. These studies suggest that the timing of the activity of stem-destroying insects may be important in minimizing damage to the plant.

Whitford, Walter G., Turanzas Gustavo Martinez, and Meza Ernesto Martinez. 1995. Persistence of desertified ecosystems: explanations and implications. *Environmental Monitoring and Assessment* 37, no. 1-3: 319-32. See abstract under *Larrea tridentata*

Williams, Christopher Paul. 1964. "Lehmann lovegrass; velvet mesquite invasion relationships in the desert grassland." M. S. Thesis, University of Arizona.

Wilson, Steven Allen. 1973. "Endomycorrhizae on desert plants with primary emphasis on *Prosopis juliflora*." M.S. Thesis, New Mexico State University.

Abstract: Roots of thirteen different species of desert plants were examined for the presence of mycorrhizae. Eleven of the thirteen plants contained endomycorrhizae, while none of the plants were found to possess ectomycorrhizae. *Prosopis juliflora*, *Yucca elata*, *Opuntia* sp., and *Larrea tridentata* contained sufficient endomycorrhizae in the root tissue to augment or assist the plants absorptive system. A more extensive study was performed on *P. juliflora* roots from greenhouse and field grown plants of approximately the same size and age to determine the distribution of endomycorrhizae within these roots. Endomycorrhizae were found in all the major branches from the mesquite taproot along with secondaries and tertiaries located in the top 25 cm of soil, but were never found in the taproot itself or the stem. Mycorrhizal spore distribution around *P. juliflora* was also determined. Two different spores were found in the soil around the mesquite roots. The distribution of *Glomus fasciculatus* spores in the soil followed closely the concentration and distribution of the mycorrhizae in the root. The results obtained to establish this relationship are diagrammatically summarized. Distribution of *Glomus macrocarpus* spores appeared to indicate no relationship of this spore with the concentration and distribution of mesquite roots.

Wilson, Thomas Bachman. 2001. "Nutrient dynamics and fire history in mesquite (*Prosopis* spp.)-dominated desert grasslands of the southwestern United States ." Ph. D. Dissertation, University of Arizona.

Abstract: In desert grasslands of the southwestern United States, *Prosopis velutina* (mesquite), an N-fixing legume, has proliferated from historic drainage locations into more xeric grassland plains. This expansion is forming a more heterogenous soil nutrient topography in grasslands, N-pools are becoming localized under mesquite canopies, yet the rate and extent of this sequestration remains relatively unknown. Repeated prescribed burning has been used to control *Prosopis* distribution, but effects of fires on grassland soil nutrient distribution and aboveground plant biomass are also largely unknown. I examined recent research concerning *P. velutina* natural history, emphasizing characteristics that contribute to range expansion. I also evaluated *Prosopis* management practices - which include herbicide treatment, prescribed burning, grazing reduction, and mechanical removal - and management goals - which involve complete removal, no removal, and limited removal. Of these, limited removal is the most beneficial, using an herbicide application followed by periodic prescribed burning. In 1997 I established a study area at Fort Huachuca Military Reservation in southeastern Arizona, selecting two adjacent sites with similar soil composition and topography but different fire histories. I examined spatial and seasonal changes in composition and distribution of available soil N and litterfall. My results indicated these were more spatially and temporally heterogenous on sites with low fire frequency and high *P. velutina* stand development. In 1998 I selected nine sites at Fort Huachuca on two upland surfaces located < 1 km apart, with similar soil physical characteristics and fire frequencies ranging from 0 to 5 fires/decade. I evaluated relationships between fire frequency, soil nutrient status (pH, available P, organic C, total N, and available N), and aboveground plant biomass, including that of the non-native *Eragrostis lehmanniana* (Lehmann lovegrass). Soil pH and ammonium significantly decreased with increased fire frequency on one surface, and available P significantly decreased with increased fire frequency on the other surface. Available P and pH were significantly different between the 2 surfaces, but aboveground biomass was similar. Soil nutrient status and biomass were not related, suggesting plant-available soil nutrients may not control plant

distribution or recovery following fire. *E. lehmanniana* biomass was negatively correlated with native grass and forb biomass, and tended to increase with increasing fire frequency. Surface litter and *E. lehmanniana* biomass were correlated, and may increase fire frequency, an important consideration when implementing grassland fire management practices.

Wilson, Thomas B., Robert H. Webb, and Thomas L. Thompson. 2001. Mechanisms of range expansion and removal of mesquite in desert grasslands of the southwestern United States. 23 p. : ill., map ; 28 cm. General Technical Report RMRS . Ogden, UT : U.S. Dept. of Agriculture, Forest Service, Rocky Mountain Research Station.

Wolters, G. L., S. R. Loftin, and R. Aguilar. 1995. Changes in species composition along Chihuahuan Desert scrub/desert grassland transition zone in central New Mexico. *Fifth International Rangeland Congress*: 614-15.

Wright, Henri A., Stephen C. Bunting, and Leon F. Neuenschwander. 1976. Effect of fire on honey mesquite. *Journal of Range Management* 29, no. 6: 467-71.

Abstract: Based on this research and other work that has been reported, honey mesquite is very difficult to kill with fire on the High Plains and along river bottoms in the Rolling Plains. On upland sites in the Rolling Plains, 27% of the mesquite trees were killed following single fires. Using repeated fires on upland sites at 5 to 10 year intervals, the potential exists to kill 50% of the older mesquite trees. Seedlings of honey mesquite were easy to kill with moderate fires until they reached 1.5 years of age, severely harmed at 2.5 years of age, and very tolerant of intense fires after 3.5 years of age.

Wright, Robert Anderson. 1960. "Increase of mesquite on a southern New Mexico desert grassland range." M.S. Thesis, New Mexico State University.

Abstract: The encroachment of mesquite onto the desert grasslands of the Southwest has reduced the carrying capacity of a considerable portion of these grasslands. The purpose of the present study is to supply some of the information that will supplement studies concerned with the improvement of mesquite-infested ranges.

Grazing by domestic livestock, climatic change, and suppression of grassland fires are each considered as a possible primary cause of the increase of mesquite on the Jornada Plains. The author concludes that grazing by domestic livestock, and the associated mesquite seed dissemination, was the most likely of the three factors to have disrupted the balance and allowed mesquite to extensively invade this area.

Wright, R. A., and J. H. Honea. 1986. Aspects of desertification in southern New Mexico, U.S.A.: soil properties of a mesquite duneland and a former grassland. *Journal of Arid Environments* 11, no. 2 : 139-45.

Abstract: Surface soil samples from beneath perennial plants and the nonvegetated areas between plants along a permanent transect in southern New Mexico were evaluated for total nitrogen, soluble salts, cation

exchange capacity, particle size distribution, pH and moisture retention. Also, three mesquite (*Prosopis glandulosa* (L. Bens.) M. C. Johnst.) dunes were intensively sampled to evaluate spatial patterns of total N. The only differences found in the paired surface samples were for soluble salts and total N. The patterns of total N in the surface and dune samples suggest that mesquite shrubs concentrate N in the soil beneath their canopies. It seems as if the entire set of changes in the soil environment, of which these patterns are a part, ensure that mesquite will occupy those sites for long periods of time.

Yavitt, J. B., and E. L. Smith Jr. 1983. Spatial patterns of mesquite and associated herbaceous species in an Arizona desert grassland. *The American Midland Naturalist* 109: 89-93.

7 *Flourensia cernua* DC. (Tarbush)



Tarbush is a deciduous, C3 perennial shrub. It has a tar-like odor because of the secondary compounds in its leaves {Estell, Fredrickson, et al. 1996 #2147}. Tarbush is characteristic of the Chihuahuan Desert, and also occurs in parts of Arizona and California at elevations ranging from 1,068 m - 1,981 m (Korthuis 1988). It reaches its best development in clay loam soils, which receive some run-on water. New growth of leaves occurs in summer. Flowers can be observed in fall, if there is sufficient water available {Montaña, Lopez-Portillo, et al. 1990 #122}. Tarbush has an extensive root system {Gibbens & Lenz 2001 #1295}. Seeds are wind or water dispersed. This shrub has encroached on grasslands over the past century {Buffington & Herbel 1965 #71}.



Buffington, Lee Charles. 1964. "Vegetational changes on a semidesert range from 1858 to 1963." M.S. Thesis, New Mexico State University.

See abstract under *Larrea tridentata*

Buffington, Lee C., and Carlton H. Herbel. 1965. Vegetational changes on a semidesert grassland range from 1858 to 1963. *Ecological Monographs* 35, no. 2: 139-64.

See abstract under *Larrea tridentata*

Dillon, Michael O. 1984. *A systematic study of Flourensia (Asteraceae, Heliantheae)*. Field Museum of Natural History : Chicago, Ill.

Dugas, William A., Ralph A. Hicks, and Robert P. Gibbens. 1996. Structure and function of C3 and C4 Chihuahuan desert plant communities. Energy balance components. *Journal of Arid Environments* 34, no. 1: 63-79.

See abstract under *Larrea tridentata*

Estell, R. E., E. L. Fredrickson, D. M. Anderson, K. M. Havstad, and M. D. Remmenga. 1996. Tarbush leaf surface terpene profile in relation to mammalian herbivory. *Proceedings: symposium on shrubland ecosystem dynamics in a changing climate; 1995 May 23-25; Las Cruces, NM.* (comps.) J. R. Barrow, E. D. McArthur, R. E. Sosebee, and R. J. Tausch Vol. Gen. Tech. Rep. INT-GTR-338. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station.

Abstract: Cattle, sheep and goats were densely stocked in paddocks containing tarbush (*Flourensia cernua* DC) for six to nine days and defoliation of 160 plants was recorded daily during two years. Plants were separated into high, moderate or low defoliation categories. Leaves were collected from plants during the same stage of maturity during the third year. Leaf surface compounds were extracted with ethanol and mono- and sesquiterpenes were analyzed using gas chromatography/ion trap mass spectrometry. A set of 11 variables was identified that appeared most closely related to plant defoliation categories: dry matter, ash, limonene, camphor, borneol, α copaene, β caryophyllene, α pinene, p-cymene, cis-jasmone and caryophyllene oxide concentrations. This group distinguished among all three defoliation categories ($P < 0.03$) when subjected to multivariate analysis. These data support the hypothesis that leaf surface chemistry is related to degree of defoliation of individual tarbush plants by livestock.

Estell, R. E., E. L. Fredrickson, and K. M. Havstad. 1996. Chemical composition of *Flourensia cernua* at four growth stages. *Grass Forage Sci.* 51

Gibbens, R. P. 1994. Root systems of desert plants. *Sonorensis* 14, no. 1

Gibbens, R. P., K. M. Havstad, D. D. Billheimer, and C. H. Herbel. 1993. Creosotebush vegetation after 50 years of lagomorph exclusion. *Oecologia* 94, no. 2: 210-217.

See abstract under *Larrea tridentata*

Gibbens, Robert P., Ralph A. Hicks, and William A. Dugas. 1996. Structure and function of C3 and C4 Chihuahuan desert plant communities. Standing crop and leaf area index. *Journal of Arid Environments* 34, no. 1: 47-62.

Abstract: During the past 150 years, native C-3 shrubs have invaded and dominated extensive areas of former C-4 grasslands in deserts of the south-western United States. This vegetation shift has caused large changes in several aspects of the structure and function of these plant communities. To examine structural changes, we measured the standing crop of green herbaceous plants and live shrubs, leaf area index (LAI), and canopy cover and shrub density in grass and shrub plant communities that exist on sandy and clay

soils in the Chihuahuan Desert. Standing crop ranged from 800 to 1800 kg ha⁻¹ for grass communities and from 2800 to 3500 kg ha⁻¹ for shrub communities. The LAI in grass communities was typically 0.1 to 0.2 and in shrub communities was 0.3 to 0.4. Averaged over the 2 years, the greatest LAI was in the shrub community on a clay soil that also had a herbaceous understory. Shrub canopy cover varied from 17% (*Flourensia cernua*, tarbush) to 33% (*Prosopis glandulosa*, honey mesquite). On sandy soils, this vegetation shift has resulted in a replacement of herbaceous vegetation with shrubs and a large reduction in species diversity, while on clay soils, due to greater soil fertility and soil water availability, there was only a slight decrease in herbaceous vegetation and little change in species diversity. This vegetation shift of desert grasslands has dramatically changed plant community structure

Gibbens, R. P., and J. M. Lenz. 2001. Root systems of some Chihuahuan desert plants. *Journal of Arid Environments* 49, no. 2: 221-63.

See abstract under *Bouteloua eriopoda*

Gile, L. H., Robert P. Gibbens, and J. M. Lenz. 1998. Soil-induced variability in root systems of creosotebush (*Larrea tridentata*) and tarbush (*Flourensia cernua*). *Journal of Arid Environments* 39, no. 1: 57-78.

Abstract: Creosotebush (*Larrea tridentata*) and tarbush (*Flourensia cernua*) are two of the major shrub invaders of grassland in many desert areas of southern New Mexico. Soils and root systems associated with these two shrubs were studied at three sites on an alluvial fan piedmont. The soils have formed in alluvium derived from monzonite, rhyolite, and andesite, in deposits ranging in age from late Holocene to middle Pleistocene. Soil age, carbonate morphology, particle size, and landscape position were found to be major factors associated with root variability. The stage I carbonate that occurs in youngest soils has relatively little influence on root distribution because the carbonate consists only of thin coatings on sand grains and pebbles. But the increasing carbonate that occurs in stages II, III, and IV results in denser zones of carbonate that control the routes for movement of both soil water and roots. Not only do individual nodules and cemented pebbly zones grow and eventually merge, they also represent zones of restricted hydraulic conductivity, funneling soil water and roots to as yet uncemented parts of the horizon. Continued carbonate accumulation leads to a plugged horizon and an overlying stage IV laminar horizon that is a barrier to roots. Particle size controls the time and amount of carbonate required for formation of these horizons. Calciargids of late Pleistocene age that averaged 4% and 32% by volume of gravel and contained 415 and 317 kg m⁻² of pedogenic carbonate had only stage III horizons. In contrast, a Petrocalcic of the same age and averaging 63% by volume of gravel required only 205 kg m⁻² of carbonate to form the stage IV horizon. Roots penetrated occasional openings in the stage IV horizon. Runoff from soils sloping 2% reduces the number of days with available soil water at various depths as compared to 1% slopes below. At the 2% slope, roots did not extend below 2 m depth, whereas at the 1% slope roots extended to as much as 5 m depth.

Herbel, C. H. 1966. Tarbush (*Flourensia cernua* [DC]). *Chemical control of range weeds*. U. S. Dep. Agric. and U. S. Dep. Interior., 38. Vol. Interagency Rep.

Huenneke, L. F., J. P. Anderson, M. Remmenga, and W. H. Schlesinger. 2002. Desertification alters patterns of aboveground net primary production in Chihuahuan ecosystems. *Global Change Biology* 8, no. 3: 247-64. See abstract under *Bouteloua eriopoda*

Hyder, Paul W. 2001. "Total phenolics, condensed tannins, and nordihydroguaiaretic acid (NDGA) as potential allelopathic compounds in creosotebush (*Larrea tridentata* (Sess. & Moc. ex DC.) Cov.) and tarbush (*Flourensia cernua* DC) in the northern Chihuahuan Desert ." Ph. D. Dissertation, New Mexico State University.

Abstract: Shrubs have replaced arid grasslands over large parts of the American southwest. Multiple mechanisms are proposed to explain this shift. One hypothesis invokes allelopathy as a mechanism for maintenance of shrub dominance in arid grasslands. This paper focuses on secondary compounds found within creosotebush and tarbush, their distribution, and possible losses from plant tissues through precipitation and leaf decay.

Total phenolics, condensed tannins and nordihydroguaiaretic acid (NDGA) were measured in nine categories of tissue. Total phenolic and condensed tannin concentrations were determined using colorimetric methods, NDGA content was determined with high performance liquid chromatography. Total phenolics were present throughout the plant with highest concentrations in leaves (36.2 mg/g), green stems (40.8 mg/g) and roots (mean for all root categories = 28.6 mg/g). Condensed tannins were in all tissues except larger stems (5 to 12 mm in diameter), with highest concentrations in flowers (1.7 mg/g), seeds (1.1 mg/g), and roots less than 5 mm in diameter (1.1 mg/g). Flowers, leaves, green stems, and small stems (<5 mm in diameter) all contained NDGA, with highest concentrations in leaves (38.3 mg/g).

Stemflow, throughfall, and interspace precipitation collections were analyzed for total phenolics and nordihydroguaiaretic acid. Phenolics were found in throughfall and stemflow; 0.088 and 0.086 mg/ml for stemflow and 0.022 and 0.014 mg/ml for throughfall in two creosotebush morphotypes; 0.044 and 0.005 mg/ml for stemflow and throughfall, respectively, in tarbush. Nordihydroguaiaretic acid was not found in any precipitation samples.

Bags containing leaf litter were placed under shrubs. One set was placed on the surface, one set buried at 5 cm. They were then collected at intervals from 0 to 90 days. Sets 1 and 2 (creosotebush and tarbush, respectively) were in place from February to April. Set 3, creosotebush, was in place from April to July. Percent organic matter loss was 1.99 % and 3.23 % for Set 1 surface and buried samples, respectively, 2.31% and 2.49% for Set 2 surface and buried and 34.10% and 75.27% for Set 3 surface and buried, respectively. Set 1 lost total phenolics (surface 6 %), NDGA (19 % surface, 11 % buried), and condensed tannins (53 % surface and 44 % buried). Set 2 had losses in total phenolics (27 % surface, 38 % buried) but concentration of condensed tannins increased slightly (1.41 % surface, 1.47 % buried). Set 3, spring creosote, lost total phenolics (13 % surface, 48 % buried), nordihydroguaiaretic acid (52 % surface, 82 % buried), and condensed tannins (55 % surface, 68 % buried).

This paper demonstrates the presence and distribution of secondary phenolic compounds in creosotebush and the movement of these compounds from production sites in creosotebush and tarbush to sites of possible allelopathic activity in soil. Phenolic compounds, other than NDGA, are moved from plant surfaces to soil through precipitation. Phenolic compounds are lost from leaf litter as the leaf decays. Within the duration of this study, this process is most effective from April through July. The fate of these compounds

once in the soil, and their interactions with other plants, needs to be examined before a complete picture of possible allelopathic activity in creosotebush dominated systems in the northern Chihuahuan Desert can be presented.

Korthuis, S. L. 1988. *Flourensia cernua*. U.S. Department of Agriculture, Forest Service Rocky Mountain Research Station Fire Sciences Laboratory. 2001. "Fire effects information system." Web page. Available at <http://www.fs.fed.us/database/feis/> .

Martinez-Meza, Ernesto. 1994. "Stemflow, throughfall, and root water channelization by three arid land shrubs in southern New Mexico." M.S. Thesis, New Mexico State University.

Abstract: Three experiments were conducted to examine how precipitation-vegetation relationships for the shrubs *Larrea tridentata*, *Prosopis glandulosa*, and *Flourensia cernua* affect the interception, redistribution, and storage of water in desert ecosystem. The first experiment was designed to determine the percentage of rainfall partitioned as stemflow and throughfall, and also to evaluate the effect of some plant canopy parameters on stemflow and throughfall. The second examined the effect of stem-angles on stemflow. The third assessed the effect of varying canopy areas and volumes as well as root allocation on redistribution of stemflow into the soil profile... .

Analysis of rhodamine-B dye distribution under shrubs indicated that root channels are preferential pathways for movement of stemflow water into soil, and that this water is potentially the source of soil moisture which allows shrubs to persist and even prosper under drought conditions.

Martinez-Meza, E., and W. G. Whitford. 1996. Stemflow, throughfall and channelization of stemflow by roots in three Chihuahuan desert shrubs. *Journal of Arid Environments* 32: 271-87.

Abstract: Three studies were conducted to examine precipitation-vegetation relationships in the multi-stemmed shrubs *Larrea tridentata*, *Prosopis glandulosa* and *Flourensia cernua* in a desert ecosystem. We measured stemflow and throughfall as affected by bulk precipitation, canopy architecture and stem-angles. Using fluorescent dye, we traced root channelization of stemflow water. Stepwise regression analysis showed that the best one-variable model for stemflow in *L. tridentata* was canopy volume, which accounted for 87% of variation. The best one-variable model for stemflow in *P. glandulosa* and *F. cernua* was canopy area, which accounted for 82% of variation in both species. Stemflow data from winter and summer months were statistically compared to determine the influence of leaves on stemflow generation in *P. glandulosa* and *F. cernua*. Stemflow amounts collected during winter months do not differ significantly from those of summer months demonstrating that in these winter deciduous species the absence of leaves during winter months does not affect generation of stemflow. Analysis of variance showed that the percentage of throughfall was different among species suggesting that variations in canopy characteristics could explain, in part, these interspecific throughfall differences. Both stem-angle and stem-length had a significant effect on stemflow generation in *F. cernua* and *L. tridentata*, whereas there was only a significant relationship between stem-angle and stemflow in *P. glandulosa*. Analysis of rhodamine-B dye distribution under shrubs indicated that root channels are preferential pathways for movement of stemflow water into soil, and that

this water is potentially the source of soil moisture which allows shrubs to remain physiologically active under drought conditions

Mauchamp, A., and J. L. Janeau. 1993. Water funneling by the crown of *Flourensia cernua*, a Chihuahuan Desert shrub. *Journal of Arid Environments* 25, no. 3: 299-306.

Abstract: In arid climates, plant growth and survival depend primarily upon the amount of soil water available at the roots. Variation in soil water content at the individual plant level must then be taken into account to analyse the production and dynamics of vegetation cover. The plant itself modifies local water availability through rainfall interception and stemflow. Rainfall interception and stemflow was studied for a shrub, *Flourensia cernua*, a dominant species of vegetation stripes in the Chihuahuan Desert, Mexico, in order to determine to what extent it could influence soil water recharge. Simulated rainfalls were applied at two intensities on six 1 m-2 plots centered around each shrub. Shrub cover was determined from vertical photographs. Experimental clipping from three shrubs allowed observations on the decrease in stemflow according to cover and measurement of the dry biomass of leaves and twigs. An experimental design enabled measurements to be made on throughfall, runoff from the base of the shrub, and to deduce stemflow and infiltration. Stemflow accounted for 4-45 per cent of the rainfall in our study plots and was significantly correlated with shrub cover. It was higher for the lower rainfall intensity. Stemflow, together with a high soil permeability, resulted in a greater soil water recharge under the shrub.

Mauchamp, A., C. Montaña, J. Lepart, and S. Rambal. 1993. Ecotone dependent recruitment of a desert shrub, *Flourensia cernua*, in vegetation stripes. *Oikos* 68, no. 1: 107-16.

Abstract: In tropical semi-arid areas, a local concentration of water on sheet wash surfaces allows the persistence of densely vegetated stripes parallel to the contour lines alternating with almost bare soil stripes. The boundaries of the vegetated stripes are upslope, a colonization ecotone and downslope, a regressive ecotone thus inducing a slow upwards displacement. This formation recently described in the Chihuahuan Desert (Mexico), is known from Africa and Australia. *Flourensia cernua* is a dominant shrub species of the stripes whose distribution suggests that its population dynamics is strongly dependent on the upslope ecotone. The spatial restrictions to recruitment were determined analyzing the location of seedlings, young individuals, and adults, and the grass cover (*Hilaria mutica*), in 10 two-meter-wide belts perpendicular to 5 stripes. The seed spatial distribution was studied in 3 other stripes. The survival of seedlings during the winter and spring dry season was observed in naturally open, experimentally clipped and grass-covered plots, as well as under *Flourensia cernua* adults. We compared the root depths, root/shoot ratios, leaf weight per unit area, and predawn water potentials of shaded and sun-grown seedlings. Seeds and seedlings were present throughout the stripes, but they only survived in the upslope ecotones. Vegetation cover, whether grass or shrub, and its corresponding light interception, was associated to the total mortality of seedlings grown under cover. These seedlings were shallowly rooted, had a low leaf weight per unit area, and low water potentials. Two main patterns were observed in the relative distribution of the grass and the shrub cover, some stripes starting with a dense shrub cover, others with 5 to 10m wide grass belt. We suggest that these patterns are related to different recruitment histories and

that, at a landscape scale, *Flourensia cernua* populations can only persist in vegetation stripes through metapopulational dynamics (characterized by successive local extinctions and colonizations).

Molinero, Hugo Bruno. 1983. "Examination of field techniques for the estimation of above ground biomass on five Chihuahuan Desert shrub species." M.S. Thesis, New Mexico State University.

See abstract under *Larrea tridentata*

Montaña, C., B. Cavagnaro, and O. Briones. 1995. Soil water use by co-existing shrubs and grasses in the Southern Chihuahuan Desert, Mexico. *Journal of Arid Environments* 31: 1-13.

Abstract: Soil water use by shrubs and grasses of vegetation patches (vegetation arcs) occurring in two-phase mosaics of the Southern Chihuahuan Desert (Mexico) was investigated after an experimental irrigation equivalent to a 75 mm rainfall. Three shrubs (*Flourensia cernua*, *Larrea tridentata* and *Prosopis glandulosa*) and one grass (*Hilaria mutica*) were studied. Irrigation water did not percolate deeper than 40 cm. This soil layer contained more than 75% of the roots in all species, except *P. glandulosa* where a less developed, deeper root system was detected (but not quantified). Root distribution indicates that the water stored in the 0-40-cm soil layer after the experimental irrigation was available for the four species. However, predawn xylem water potential (XWP) of *F. cernua* and *H. mutica* were strongly influenced by soil water present in the 0-40-cm layer, whereas those of *L. tridentata* and *P. glandulosa* were not. Differences in predawn XWP between watered and unwatered individuals were greatest in *F. cernua* and *H. mutica*, and smallest in *P. glandulosa*. Changes in tissue osmotic potential (TOP) values as a consequence of watering were sharply marked in all species except *P. glandulosa*. *H. mutica* XWP approached zero for a few days in response to small rain events. The results indicate that adult individuals of grasses and shrubs are potential competitors for soil resources (to a variable degree according to the shrub species). Their co-existence in the arcs is probably favoured by a process of slow competitive displacement as long as the recruitment of new shrubs takes place mainly by colonization of the upslope fringe of the arcs where grass biomass is low. As development of the vegetation progresses in the colonization front and the grass canopy is almost closed, the chances of a shrub being suppressed by water competition diminishes in the following order: *F. cernua*, *L. tridentata*, *P. glandulosa*. A drastic reduction in grass biomass because of grazing would depress the competitive ability of the grasses and may preferentially facilitate the establishment of livestock dispersed species like *P. glandulosa*. A consequent shift to a more shrubby community seems unavoidable since the recovery of the grass strata will probably not suppress the newly-established shrubs tapping water from deep water sources

Montaña, C., J. Lopez-Portillo, and A. Mauchamp. 1990. The response of two woody species to the conditions created by a shifting ecotone in an arid ecosystem. *Journal of Ecology* 78: 789-98.

Abstract: Vegetation stripes alternating with bare areas appear in some arid lands as a consequence of the redistribution of rainwater by sheet flow. The borders between stripes and bare areas are ecotones (one upslope and one down-slope of each arc) between a very open scrub and a density vegetated patch. The upslope migration of stripes has been observed or inferred in most of the cases quoted in the literature, but

there is no information on the dynamics of the woody vegetation. Here the hypothesis of arc migration is tested by investigating the distribution of seedlings and adults of woody species and their cover within the arcs. The species studied were *Prosopis glandulosa* and *Flourensia cernua*. The distribution of seedlings and adults was recorded in a 600-m .times. 2-m transect belt perpendicular to the stripes. Cover variation inside the arcs was measured by intercept lines arranged in a design including three arcs, two zones (up-slope and down-slope) inside the arcs and two species. The results show a clear difference in the functioning of the up-slope and down-slope ecotones of the arcs. Seedlings of both species establish in the up-slope ecotone, *F. cernua* almost exclusively and *P. glandulosa* with a marked preference. No seedlings of *F. cernua* were recorded more than 5 m away from the nearest adult whereas seedlings of *P. glandulosa* were recorded more than 30 m away from the nearest adult. *Prosopis glandulosa* was present in all the arcs and in the bare areas between arcs, whereas *F. cernua* was absent in the bare areas and in some of the arcs. Differences in cover value were found between zones and species but not between arcs. There is no evidence upon which to reject the hypothesis of arc-migration, and some hypotheses about the temporal and spatial variability of this process are considered. In the process of migration a central role is played by the up-slope ecotone which functions as the main colonizing area for the woody species

O'Laughlin, Thomas Connor. 1975. "The distribution and productivity of *Flourensia cernua* D.C. (tarbush) in southern New Mexico." M.S. Thesis, New Mexico State University.

Abstract: The absolute cover and productivity pre new growth shoot of *Flourensia cernua* D.C. were looked at with respect to 16 selected soil variables and xylem sap potential along a 1400 m belt transect traversing 5 different plant communities near an enclosed basin in southern New Mexico....

Productivity per new growth shoot, xylem sap potentials, and soil water potentials were observed to be their highest in a *Hilaria* community with the lowest absolute cover value of *Flourensia* . The low absolute cover of *Flourensia* in this community was attributed primarily to the large absolute cover of *Hilaria* for it had been found by others that *Flourensia* will increase in disturbed *Hilaria* communities.

Schowalter, T. D. 1996. Arthropod associates and herbivory on tarbush in southern New Mexico. *Southwestern Naturalist* 41, no. 2: 140-144.

Abstract: Arthropod abundances, seasonality, and defoliation were measured on tarbush (*Flourensia cernua*) in southern New Mexico during 1990 and 1991. The arthropod assemblage on this desert shrub was dominated by five species of sap-sucking herbivores, four species of chewing herbivores, two ants, parasitic Hymenoptera, and two spider families. Species richness and abundances were highest during late summer. Several taxa present in substantial numbers at budburst in spring may overwinter on, or rapidly discover, this resource. Defoliation was caused primarily by a chrysomelid beetle (*Zygogramma tortuosa*) and amounted to about 30% by late summer. The arthropod functional group organization (e.g., proportions of chewing and sap-sucking herbivores, predators and detritivores) on tarbush is similar to that measured on other shrub species using comparable techniques

Tellez, M. R., R. E. Estell, E. L. Fredrickson, and K. M. Havstad. 1997. Essential oil of *Flourensia cernua* DC. *J. Essential Oil Res.* 9: 619-24.

Tromble, John M. 1983. Interception of rainfall by tarbush. *Journal of Range Management* 36, no. 4: 525-26.

Abstract: The objective of this study was to determine the interception by tarbush of artificially applied rainfall. Twelve tarbush shrubs were collected near Las Cruces in southern New Mexico to obtain a representative sample of shrub size classes. Simulated rainfall was applied at the rate of 6 cm/hr for 30 min. Canopy cover of the tarbush community was determined from 10 line intercept transects 30.48 m long. A stepwise regression analysis using the minimum R2 improvement technique was used to examine the effects of plant parameters on interception. The "best" one variable model was shrub green weight, which accounted for 75% of the variability of the intercepted rainfall. Extrapolating the calculated interception of artificially applied rainfall to the native stand of tarbush with 15.2% canopy cover indicated that 0.5 mm of rainfall would be intercepted from a 30 mm rainfall event. Disregarding rainfall events of less than 3.0 mm, an average of 8.5 mm of rainfall would be intercepted by the tarbush community or 6.7% of the average rainfall from May through October.

———. 1988. Water interception by two arid land shrubs. *Journal of Arid Environments* 15: 65-70.

Abstract: The objective of this study was to examine the interception of artificially applied rainfall by creosotebush and tarbush plants for improved understanding of this phenomenon in hydrologic processes.... Because a high percentage of precipitation from small storms is intercepted by the shrub canopy and subsequently evaporated back into the atmosphere, interception by desert shrubs is of significant importance.

Wondzell, Steven M., and John A. Ludwig. 1995. Community dynamics of desert grasslands: Influence of climate, landforms, and soils. *Journal of Vegetation Science* 6, no. 3: 377-90.

Abstract: Permanently marked vegetation transects in Big Bend National Park, Texas, USA were monitored to follow temporal dynamics of desert grassland communities on a variety of landforms and soil types over a 26-yr period after the removal of domestic livestock. Historic records indicate that the park area was severely overgrazed prior to its establishment, and our results show that the species present increased in both cover and density after the removal of livestock. However, the timing of recovery corresponded to multi-year periods of above-average precipitation. Little change was observed in between 1955 and 1960, a period dominated by several consecutive years of drought. The cover of two large shrubs common to the Chihuahuan Desert. *Larrea tridentata* and *Flourensia cernua*, increased from 1960 to 1967, a period dominated by summer drought and frequent wet winters. The cover and density of forbs, perennial grasses. and most shrubs increased on nearly all landforms between 1967 and 1981. when summers were wetter than average. In contrast, the cover of *Larrea tridentata* decreased during this period. Comparisons among the plant communities on each landform showed that they diverged through time after domestic livestock were removed. Presumably, differences in topographic position and soil texture influence water availability which was reflected in the species composition on each soil series. Unfortunately, we cannot

isolate the effects of recovery from grazing from the effects of climate because the study design did not include control plots located within grazed pastures. Certainly, the directional trajectory of change and the regrowth of grasses into inter-shrub spaces. must, at least in part, be the result of recovery from grazing. However, our data also indicate that the desert grassland communities are sensitive to multi-year periods of above- or below-average precipitation. Clearly, the dynamics between shrubs and grasses cannot be explained by a simple successional paradigm that views increased shrub dominance as retrogression from a climax grassland. Many alternate hypotheses have been forwarded to explain the dynamics that control the vegetation composition in the desert and desert grassland region of North America. Experimental tests of these hypotheses are needed to identify the interactions between biotic and abiotic factors that control dominance by shrubs or grasses.

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8 *Gutierrezia sarothrae* (Pursh) Britt. & Rusby (Broom snakeweed)



Broom snakeweed is a relatively short-lived, perennial C3 half-shrub. Because it establishes relatively easily its stands are particularly dense on disturbed areas, where it is one of the first colonizers (Tirmenstein, 1999). *Xanthocephalum sarothrae* is another accepted scientific name for broom snakeweed. It is widespread throughout the western Great Plains and the warm deserts of North America. It is usually dormant during the winter, except in the southern parts of its range where it can remain green over the winter (Sosebee 1990). Flowering occurs in the fall and maturation of seeds over the winter (McDaniel 1984). Germination can usually be observed in the spring. Seedlings grow a deep tap root in the first year and mature plants can have an extensive root systems (Campbell and Bomberger 1934; Gibbens and Lenz 2001). Broom snakeweed is toxic to livestock, particularly when consumed in large quantities (Carpenter, Ethridge, and Sosebee 1990). Broom snakeweed has a large ecological amplitude as it is one of the most important subdominant plant species in many plant communities ranging from sagebrush, piñon-juniper and shortgrass steppe to desert grasslands and shrublands (Tirmenstein 1999).



Berry, Philip Nathan. 1992. "Influence of soil moisture on propagation and survival of broom snakeweed, *Gutierrezia sarothrae* (Pursh) Britt. and Rusby ." M. S. Thesis, New Mexico State University.

Briedé, Jan-Willem. 1990. "The physiological ecology of *Gutierrezia sarothrae* (pursh) rusby in the Chihuahuan desert of southern New Mexico ." Ph. D. Dissertation, New Mexico State University.

Abstract: A descriptive eco-physiological investigation was conducted on *Gutierrezia sarothrae*, a competitive and poisonous half shrub, to describe the species' position in the ecosystem of southern New Mexico, in the northern regions of the Chihuahuan Desert. Little rudimentary physiological knowledge was available on *G. sarothrae* growing in southern New Mexico. This research fills this discrepancy by reporting on plant data collected over more than two years. Data were collected on (1) phenological development of *G. sarothrae*, (2) photosynthetic capacity and carbon gain of the plant, (3) plant-water relations in comparison with *Atriplex canescens*, and (4) canopy architecture. The highest growth rates and photosynthetic activity in plants was seen in spring, which coincides with early spring regrowth after winter dormancy. Photosynthesis rates approached $13 \mu\text{moles m}^{-2}\text{s}^{-1}$ in April, which was determined to be high enough to compensate for spring regrowth, within 14 days. Due to this high photosynthetic activity, plants attain rapid seasonal physiological maturity, allowing *G. sarothrae* to out-compete associated species during this period, monopolizing the already scarce resources such as soil water and nutrients. Because of its rather shallow, but extensive root system, *G. sarothrae* is able to use relatively small rainfall events, as evidenced by its highly fluctuating xylem water potential (pre-dawn ψ ranged from -0.5 to -3.5 MPa), compared to *A. canescens* which had a more stable xylem water potential (pre-dawn ψ ranged from -0.6 to -2.0 MPa). In order to determine if allelopathy may play a role in *G. sarothrae*'s dominance in many communities, a greenhouse trial was set up to test for phytotoxic properties of fresh leaves, dead leaves from *G. sarothrae*, and soil from underneath *G. sarothrae* plants. These residues were added to mature grass plants to determine any growth altering effects before and after clipping (simulated grazing). Grass species used were *Sporobolus airoides*, *Bouteloua gracilis* and *Bouteloua curtipendula*. Residues from *G. sarothrae* did not have detectable effects on *S. airoides*, but significantly altered the growth characteristics

of the two *Bouteloua* species. This research offers some insight into the characteristics that allow *Gutierrezia sarothrae* to dominate some undisturbed native conditions.

Campbell, R. S., and E. H. Bomberger. 1934. The occurrence of *Gutierrezia sarothrae* on *Bouteloua eriopoda* ranges. *Ecology* 15, no. 1: 49-61.

Abstract: *Bouteloua eriopoda* Torr. (black grama) is characteristic of the desert plains association described by Weaver and Clements ('29), and extends from southwestern Texas through southern New Mexico, Arizona and northern Mexico. This grass, if not depleted, is the most abundant and valuable forage species on the well-drained sandy or gravelly soils of dry mesas in the region, especially in southern New Mexico. Jardine and Forsling ('22) have shown that continued overgrazing of *Bouteloua eriopoda* range leads to deterioration of the valuable grasses and the establishment of *Gutierrezia* spp. (snakeweed or broomweed), accompanied by reductions in grazing capacity and loss of soil stability. The ultimate result of continued injudicious grazing may be a transformation of the *Bouteloua* range to the *Prosopis* (mesquite) sand dune scrub association. Periodic drought is partly responsible for the deterioration, because of the wide spacing of plants resulting from low rainfall, and the facility with which the range is overgrazed when inadequate precipitation causes poor forage production.

Many ranchmen believe that *Gutierrezia* will crowd out the valuable forage grasses on the range. This opinion results from failure to recognize over-utilization and ignoring the fact that on grass ranges, the unpalatable *Gutierrezia* plants are subject to little foliage removal by cattle, while the palatable grasses, when overutilized, sometimes are eaten within a half inch of the soil surface.

In order to determine the trend of *Gutierrezia* occurrence in the *Bouteloua eriopoda* association, and to establish its significance in plant succession, a study of the problem was initiated.

The work upon which this paper is based was done near Las Cruces, New Mexico, on the Jornada Experimental Range, a branch of the Southwestern Forest and Range Experimental Station, Forest Service, U.S. Department of Agriculture.

Carroll, Donald Bret. 1994. "Broom snakeweed [*Gutierrezia sarothrae* (Pursh) Britt. & Rusby] seedling response to spring and summer burning in central New Mexico ." M. S. Thesis, New Mexico State University.

DeGarmo, H. C.Jr. 1966. "Water requirement and production of eight desert plant species under four soil moisture levels." M. S. Thesis, New Mexico State University.

Dwyer, Don D., and Harlan C. DeGarmo. 1970. Greenhouse productivity and water-use efficiency of selected desert shrubs and grasses under four soil-moisture levels . *New Mexico Agricultural Experiment Station Bulletin* No. 570.

Gibbens, R. P., and J. M. Lenz. 2001. Root systems of some Chihuahuan desert plants. *Journal of Arid Environments* 49, no. 2: 221-63.

See abstract under *Bouteloua eriopoda*

Hart, Charles Randall. 1992. "Broom snakeweed, *Gutierrezia sarothrae* (Pursh) Britt. & Rusby, and associated herbage response to seasonal burning in New Mexico ." Ph. D. Dissertation, New Mexico State University. Abstract: Prescribed burns were conducted in 1990 and 1991 on a shortgrass prairie in central New Mexico. One experiment evaluated broom snakeweed (*Gutierrezia sarothrae* (Pursh) Britt. & Rusby) control and response of associated grasses to seasonal (March, June, October) fire. A second experiment evaluated fire characteristics in order to develop a burning prescription. Snakeweed mortality averaged 67% after spring (March) burning, 86% after summer (June) burning, and 10% on untreated areas. Fires ignited during October would not carry due to high plant moisture. Snakeweed mortality on plots sprayed with picloram (4-amino-3,5,6-trichloropicolinic acid) at 0.42 kg/ha averaged 94%. In spring, snakeweed had little green foliage (bud break) when burned and canopy destruction was minor (8%) compared to summer fires (66%) when plants were actively growing (stem elongation). Regrowth from basal axillary buds was greater on spring-burned (33%) than summer-burned plants (1%). Herbaceous production decreased the first growing season after summer burning (x = 603 kg/ha), increased after picloram applications (x = 836 kg/ha), and was not statistically different from untreated areas (x = 686 kg/ha) after spring burning (x = 674 kg/ha). Herbaceous production the second growing season averaged 1,198, 1,004, 940, and 962 kg/ha after picloram, spring burning, control, and summer burning treatments, respectively. Grass composition increased after picloram applications, and was not statistically different from untreated areas after spring and summer burning. Fire temperatures 10cm above the soil surface ranged from 147° to 361°C in spring, and 106° to 519°C during summer fires. Air temperature and grass yield accounted for 63% of the variation in spring fire temperatures. Summer fire temperatures were largely explained (86%) by air temperature and total vegetation yield. Duration of heat above 60°C decreased with high grass moisture and percent bareground during spring (collectively accounting for 49% of the variation), and increased with high air temperature, total vegetation yield, and percent litter during summer fires (collectively accounting for 83% of the variation). Preliminary prescriptions were developed for maximum broom snakeweed control and optimal herbaceous response from fire in the shortgrass prairie of New Mexico. During spring, air temperature should be 20° to 30°C, relative humidity 10 to 20%, grass yield >300 kg/ha, wind from the southwest at 2 to 8 m/sec., soil moisture 2 to 7%, and fine-fuel moisture 6 to 9%. Conditions during summer burning are air temperature 20° to 33°C, relative humidity 10 to 20%, grass yield >300 kg/ha, total vegetation yield >1000 kg/ha, wind from the southwest 2 to 8 m/s, soil moisture 1 to 10%, and grass moisture 8 to 15%.

Huddleston, Ellis W. Pieper Rex D. 1989. *Snakeweed, problems and perspectives. Proceedings.* Bulletin, no. 751. Las Cruces: Agricultural Experiment Station, New Mexico State University.

Jeffcoat, B. Lowell. 1980. "Factors affecting seed germination and seedling establishment of broom snakeweed ." M. S. Thesis, New Mexico State University.

Ludwig, John A., James F. Reynolds, and Paul D. Whitson. 1975. Size-biomass relations of several Chihuahuan Desert shrubs. *The American Midland Naturalist* 94, no. 2: 451-61.
See abstract under *Larrea tridentata*

Mayeux, H. S., Jr., and Laura Leotta. 1981. Germination of broom snakeweed (*Gutierrezia sarothrae*) and threadleaf snakeweed (*G. microcephalum*) seed. *Weed Science* 29: 530-534.

McDaniel, Kirk C. 1984. Snakeweed control with herbicides. *New Mexico Agricultural Experiment Station Bulletin* No. 706: 1-34.

McDaniel, Kirk C., and Charles Hart. 1993. *A bibliography of perennial snakeweeds and related genera* , Agricultural Experiment Station, New Mexico State University, Las Cruces, NM.

Molinero, Hugo Bruno. 1983. "Examination of field techniques for the estimation of above ground biomass on five Chihuahuan Desert shrub species." M.S. Thesis, New Mexico State University.
See abstract under *Larrea tridentata*

Muldavin, Deborah. 1989. "Differential biomass allocations of *Gutierrezia sarothrae* and *Gutierrezia microcephala* on a Chihuahuan Desert site." M. S. Thesis, New Mexico State University.

Nadabo, Samu Ibrahim. 1978. "Growth patterns of broom snakeweed (*Xanthocephalum sarothrae* (Pursh) Shinnery) in southern New Mexico." M. S. Thesis, New Mexico State University.

Nadabo, S., R. D. Pieper, and R. F. Beck. 1980. Growth patterns and biomass relations of *Xanthocephalum sarothrae* (Pursh) Shinnery on sandy soils in Southern New Mexico. *Journal of Range Management* 33: 394-97.

Abstract: Growth patterns of broom snakeweed were studied on three areas of sandy range sites in southern New Mexico by measuring plant canopy biweekly during the growing season and calculating canopy volume. Canopy volume increased during the summer of 1977 on all three study areas. In 1978, canopy volume declined throughout much of the growing season because effective rainfall came late in the season. More than 60% of the canopy biomass was contributed by brown stems and leaves, about 30% by green leaves and stems, and less than 10% by inflorescences on most dates. Coefficients of determination

relating canopy volume to canopy biomass were less than 0.70. Growth forms and patterns were quite variable among the populations studied.

Osman, Abdelgader Ahmed. 1982. "Establishment of broom snakeweed (*Xanthocephalum sarothrae* (Pursh) Shinnery) and other species on semidesert grasslands of southern New Mexico ." M. S. Thesis, New Mexico State University.

Abstract: Six individual experiments were conducted at New Mexico State University College Ranch and in a greenhouse. The objectives of these studies were to determine emergence of snakeweed and other species under greenhouse conditions and under field conditions as influenced by snakeweed density, burning, mowing and burning, mowing alone, and protection and grazing. Another objective was to obtain information about vegetational patterns around individual snakeweed plants. The total emergence of grasses and forbs from soils collected from heavy, moderate and light densities of broom snakeweed showed significant differences ($P < .05$) in the greenhouse. In the field, the three densities of broom snakeweed also showed significant differences ($P < .05$). Total emergence of grasses and forbs showed significant differences ($P < .05$) between ungrazed and grazed areas in a 5-year-old enclosure. However, in a 20-year-old enclosure, total emergence of grasses and forbs showed no significant difference ($P > .05$) between ungrazed and grazed treatments in the greenhouse. In the burned and nonburned treatments, total emergence of grasses and forbs showed no significant difference ($P > .05$) between burned and nonburned plots in the greenhouse. More plant species emerged from soil collected from nonburned plots than from the burned plot in the greenhouse. In the field, 4 times as many forbs occurred in the burned plot as occurred in the nonburned plots. The large root/shoot ratios of broom snakeweed occurred at ages of 13 and 17 weeks (May and June). Thinning broom snakeweed by 0,25,50,75 and 100% from its original density in ungrazed and grazed areas resulted in an increase of perennial grass production. Total basal cover of perennial grasses did not differ significantly ($P > .05$) among treatments in the ungrazed area and in both growing seasons. Total emergence of grasses and forbs showed significant differences ($P < .05$) among 20-, 30- and 50-cm distances from snakeweed plants. Grass seed tended to accumulate around individual broom snakeweed plants in the field.

Osman, Abdelgader, Rex D. Pieper, and Kirk C. McDaniel. 1987. Soil seed banks associated with individual broom snakeweed plants. *Journal of Range Management* 40, no. 5: 441-43.

Sosebee, Ronald E. 1990. Broom snakeweed--ecology and management. In *Research highlights: Noxious brush and weed control*. Editors David B. Webster, and Harold L. Schramm Jr., 1-3. Lubbock, TX: Texas Tech University, College of Agricultural Sciences.

Sterling, Tracy M., and David C. Thompson. 1993. Snakeweed research : updates and highlights . *Research report* .Cooperative Extension Service Agricultural Experiment Station. Las Cruces: Agricultural Experiment Station, New Mexico State University.

- Tirmenstein, D. 1999. *Gutierrezia sarothrae*. U.S. Department of Agriculture, Forest Service Rocky Mountain Research Station Fire Sciences Laboratory. 2001. "Fire effects information system." Web page. Available at <http://www.fs.fed.us/database/feis/> .
- Wan, Changgu, Ronald E. Sosebee, and Bobby L. McMichael. 1993. Does hydraulic lift exist in shallow-rooted species? A quantitative examination with a half-shrub *Gutierrezia sarothrae*. *Plant and Soil* 153: 11-17.
- . 1993. Broom snakeweed responses to drought. I. Photosynthesis, conductance, and water-use efficiency. *Journal of Range Management* 46, no. 4: 355-59.
- . 1993. Broom snakeweed responses to drought. II. Root growth, carbon allocation, and mortality. *Journal of Range Management* 46, no. 4: 360-363.
- Wood, Ballard Lee. 1994. "Dispersal, viability, and germination of *Gutierrezia sarothrae* seed ." M. S. Thesis, New Mexico State University.
- Wood, M. K., T. L. Jones, and M. T. Vera-Cruz. 1998. Rainfall interception by selected plants in the Chihuahuan Desert. *Journal of Range Management* 51: 91-96.
See abstract under *Bouteloua eriopoda*

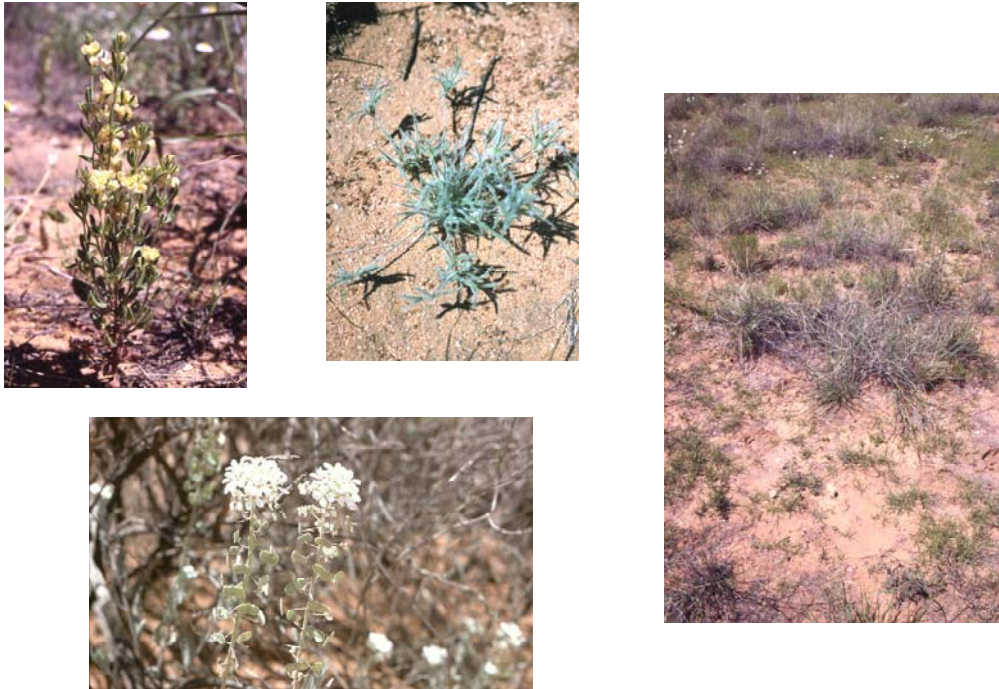
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9 Annual species



Bachelet, D., S. M. Wondzell, and J. F. Reynolds. 1988. A simulation model using environmental cues to predict phenomenologies of winter and summer annuals in the northern Chihuahuan Desert. In *Advances in environmental modelling*. Editor A. Marani, 235-60. Amsterdam: Elsevier.

Abstract: The goal of this study was to quantify the controls of environmental cues on the phenological patterns of northern Chihuahuan Desert annuals. Our specific objectives were to: 1) identify primary environmental cues which result in the germination of summer and winter annuals, 2) quantify the required periods of adequate temperature and soil moisture following germination which insure successful seed set, and 3) incorporate these data into a phenology model (PHENANN) in order to examine life history patterns of Chihuahuan Desert annuals in response to long-term climate records. This work is an extension of Freas and Kemp (1983) and Kemp (1983). Data from Kemp (1983) were used to develop the model which was validated using an independent data set from the Long Term Ecological Research (LTER) Jornada site. Results of the validation indicate that annual plant phenologies in this region can be reasonably predicted based on cues of rainfall, soil moisture, and temperature. In a long-term simulation based on climatic records from 1892 - 1981, summer annuals germinated 8 out of 10 years and successfully completed their life cycles 91% of the time; winter annuals germinated 6 out of 10 years and successfully completed their life cycles about 71% of the time. Limitations of the model are discussed.



Bowers, M. A. 1987. Precipitation and the relative abundances of desert winter annuals: a 6-year study in the northern Mojave desert. *Journal of Arid Environments* 12: 141-50.

Cabin, Robert J., Ann S. Evans, and Randall J. Mitchell. 1997. Do plants derived from seeds that readily germinate differ from plants derived from seeds that require forcing to germinate? A case study of the desert mustard *Lesquerella fendleri*. *American Midland Naturalist* 138, no. 1: 121-33.

Abstract: We compared the performance of plants of the desert mustard *Lesquerella fendleri* derived from seeds that readily germinated ("natural" plants) with plants originating from seeds forced to germinate by the application of gibberellic acid which required an extended germination period ("induced" plants). Before transplanting from the greenhouse, induced plants were significantly larger in diameter but had significantly fewer leaves than natural plants. There were also significant differences between seed source populations, as well as seed source by germination treatment interactions, for both plant diameter and number of leaves. After transplantation to a desert shrubland site, there were highly significant differences in survivorship of natural and induced plants. Five months after transplantation, survival of natural plants (43.3%) was twice that of induced plants (21.3%). Natural plants transplanted beneath creosote bush shrubs were also larger in diameter than induced plants, while the converse was true for plants transplanted in the open intershrub areas. We argue that these results may be, at least partially, the result of genetic differences between seeds that readily germinate and seeds that remain dormant but viable under the same environmental conditions.

Cabin, Robert J., and Diane L. Marshall. 2000. The demographic role of soil seed banks. I. Spatial and temporal comparisons of below- and above-ground populations of the desert mustard *Lesquerella fendleri*. *Journal of Ecology* 88, no. 2: 283-92.

Abstract: Although seed banks may often affect the colonization, succession and structure of surface plant communities, few studies have investigated the demographic relationship between seeds in the soil and above-ground plant populations over space and time. We examined this relationship in the perennial mustard *Lesquerella fendleri* between 1991 and 1994 within a New Mexico desert ecosystem characterized by open patches of soil (intershrub areas) interspersed with dominant creosote (*Larrea tridentata*) shrubs (subshrub areas). 2 For the first 2 years of the study, *Lesquerella* soil seed, surface plant and seed production densities were greater in subshrub vs. intershrub areas. Within the subshrub areas, there were more *Lesquerella* soil seeds and surface plants in the northern and central microsites, compared with the southern and perimeter microsites, respectively. The mean density of the subshrub seed bank did not increase following large inputs of new seeds (2400 seeds m⁻²) in the summer of 1992. In contrast, virtually all of the relatively modest *Lesquerella* intershrub seed production at this time (169 seeds m⁻²) appeared to survive, so that for the remainder of the study most soil seeds were found in the intershrub sites. This spatial reversal of seed bank densities preceded a similar switch in the relative densities of the *Lesquerella* sub- and intershrub surface plant populations in the last 2 years of the study. 3 This study supports the hypothesis that desert seed bank patchiness contributes to surface plant patchiness, but does not support the idea that seed banks are comprised primarily of seeds produced during favourable reproductive periods. Because there was a closer spatial match between *Lesquerella* soil seeds and surface plants than between soil seeds and seed production, the above-ground population may be limited to sites favourable for soil seed persistence.

Cabin, Robert J., Diane L. Marshall, and Randall J. Mitchell. 2000. The demographic role of soil seed banks. II. Investigations of the fate of experimental seeds of the desert mustard *Lesquerella fendleri*. *Journal of Ecology* 88, no. 2: 293-302.

Abstract: Although poorly studied and understood, the post-dispersal movements and fates of seeds may affect critically the subsequent structure of plant communities, particularly in desert ecosystems where seeds can be the most abundant or only viable form of many plant species. We investigated the fate of experimental seeds of the desert mustard *Lesquerella fendleri* by examining seed dispersal and predation, and by quantifying the proportion of seeds that germinated and survived as seedlings in three different microsites within a New Mexico desert shrubland. 2 We found very limited seed dispersal but strong density-dependent seed predation by rodents. There was a significant and consistent microsite effect in the proportion of soil seeds germinating and seedlings surviving to the end of the experiments. We did not find a consistent microsite effect for soil seed persistence, but did find a positive correlation between soil seed persistence and soil seed germination. Overall, these results indicate that seed predation may strongly affect the distribution of the seed bank, and that the abiotic environment may largely determine the extent to which soil seed populations in turn affect the distribution of emerging surface plants. 3 We present a seed fate model that synthesizes the results of the present and previous empirical investigations of the *Lesquerella* study system. This diagram illustrates how interactions among the abiotic environment, microsite variation and seed genotypes can determine which soil seeds successfully germinate and

establish into the surface plant population. We suggest that the demography of desert surface plant populations may depend more on the time between seed inputs and the longevity of these seeds in the soil than on the amount of seeds produced at any one point in time and space.

Dwyer, Don D., and Edmundo V. Aguirre. 1978. Plants emerging from soils under three range condition classes of desert grassland. *Journal of Range Management* 31, no. 3: 209-12.

Abstract: This research was conducted to determine emergence of seedlings from surface soil collected on black grama (*Bouteloua eriopoda*) grassland sites in good, fair, and poor condition classes. The species that emerged and their numbers were compared to the species actually found on the field locations. The following conclusions were drawn: (1) The fair condition site had more seedlings emerge than the other two and of these seedlings by far the most were grasses; (2) Mesa dropseed (*Sporobolus flexuosus*) was the most abundant grass species emerging from collected soil for all three condition classes, but it was much more abundant from fair condition soil; (3) Though black grama dominated the good condition range, emergence of black grama seedlings in the greenhouse from collected soil was much below expectations; (4) More plant species occurred in the field than emerged from collected soils; (5) Secondary successional patterns cannot be predicted accurately from techniques used in this study; (6) Mesa dropseed appears to be a key mid-successional species, filling a broad niche from low good to low fair range condition.

Freas, K. E., and P. R. Kemp. 1983. Some relationships between environmental reliability and seed dormancy in desert annual plants. *Journal of Ecology* 71: 211-17.

Abstract: (1) There are two groups of annual species that grow in the northern Chihuahuan Desert of North America. Plants in one group germinate and complete their life cycle in late summer. Those in the other germinate in winter or early spring and complete their life cycle in the spring. The late summer season is characterized by abundant and reliable rain, while the winter-spring season has less abundant and less reliable rain. (2) Several theoretical models have been suggested which predict that annual plants from uncertain environments may or may not have evolved innate dormancy to offset the possibility of population extinction due to complete germination followed by complete mortality under severely unfavourable conditions. (3) We have tested these models with a comparative experiment examining the germination responses of seeds collected from an annual species which grows during the more reliable summer season and two annual species which grow during the less reliable winter-spring season. (4) The summer annual species does not have a genetically fixed innate dormancy, but the two winter annual species apparently have evolved a genetically controlled innate dormancy. (5) All three annual species exhibited environmentally-controlled seed dormancy with respect to amount of rainfall. Seeds germinated only when the equivalent of more than 10 mm of rain fell. Above 15 mm of simulated rain, germination was positively correlated with increasing amount of rain in all three species. (6) The importance of innate dormancy, water-controlled dormancy, and seed dispersal to the long-term survival of these species is discussed.

Gibbens, R. P., and J. M. Lenz. 2001. Root systems of some Chihuahuan desert plants. *Journal of Arid Environments* 49, no. 2: 221-63.

See abstract under *Bouteloua eriopoda*

Guo, Q., and J. H. Brown. 1997. Interactions between winter and summer annuals in the Chihuahuan desert. *Oecologia* 111: 123-28.

Abstract: Using 18 years of census data from permanent quadrats, we examined the interactions between spatially coexisting but temporally segregated winter and summer ephemeral plant communities in the Chihuahuan Desert. The ability of winter and summer annuals to achieve nearly complete temporal segregation by partitioning the bimodal annual rainfall permits the coexistence of a diverse flora of annual (and perennial) plants in this unproductive arid environment. Despite the differences in their biogeographical affinities and temporal segregation, long-term data indicated that at the scales of both the entire 20-ha study site and small 0.25-m² sample quadrats, abundances of plants were never high in two successive growing seasons, suggesting a negative interaction between winter and summer annuals. We evaluate alternative hypotheses for this phenomenon.

Guo, Q., J. H. Brown, and T. J. Valone. 2000. Abundance and distribution of desert annuals: are spatial and temporal patterns related? *Journal of Ecology* 88: 1-11.

Guo, Qinfeng, James H. Brown, Thomas J. Valone, and Stephen D. Kachman. 2000. Constraints of seed size on plant distribution and abundance. *Ecology* 81, no. 8: 2149–2155.

Abstract: We examined the correlation between seed size (mass) and spatial and temporal distribution and abundance of plants, using both published data from northern England and 18 years of census data from permanent quadrats in the Chihuahuan Desert, Arizona, USA. In both systems, there were many small-seeded species and few large-seeded ones. Spatial patterns of distribution and abundance were constrained by seed size within triangle envelopes, i.e., small-seeded species had a greater range of abundance and a greater number of sites occupied than did large-seeded species. Temporal patterns of abundance and distribution from the Chihuahuan Desert site were similarly correlated with seed size, i.e., small-seeded species were, in general, more abundant and present in more years than were large-seeded species. These patterns probably result because small-seeded species produce more seeds, are more vagile, and persist longer in seed banks than do large-seeded species. The results are consistent with recent findings from seed bank studies, suggesting the generality of the correlation between seed size and plant abundance and distribution.

Gutierrez, J. R., and W. G. Whitford. 1987. Responses of Chihuahuan desert herbaceous annuals to rainfall augmentation. *Journal of Arid Environments* 12: 127-39.

Kelt, D. A., and T. J. Valone. 1995. Effects of grazing on the abundance and diversity of annual plants in Chihuahuan desert scrub habitat. *Oecologia* 103: 191-95.

Lightfoot, K. S. 1991. "Association of annual plants and shrubs in the Northern Chihuahuan desert." M. S. Thesis, New Mexico State University.

Ludwig, J. A., G. L. Cunningham, and P. D. Whitson. 1988. Distribution of annual plants in North American deserts. *Journal of Arid Environments* 15: 221-27.

McKinney, Helen H. 1975. "Reproductive effort in some Chihuahuan Desert annuals." M.S. Thesis, New Mexico State University.

Abstract: Theoretically, desert annuals should expend more energy in reproduction during periods of environmental stress, such as water stress. In this work, the reproductive effort, in relation to moisture, of various Chihuahuan desert annuals was studied. Comparisons of reproductive effort under amended and natural soil moisture conditions were made. Under the amended water conditions, *Euphorbia micromera* had a lower reproductive effort. However, *Bouteloua barbata* and *B. aristidiodes* increased reproductive effort under watered conditions.

Plasticity of reproductive effort was studied by comparison of reproductive effort in closely related species over a 3-year period. Species of the genera *Euphorbia*, *Bouteloua*, and *Eriogonum* responded to seasons with low rainfall by generally increasing reproductive effort. These results follow the expected theory that reproductive effort is higher during periods of moisture stress.

Reproductive effort of summer and winter annuals in relation to moisture was also studied. A significant regression of reproductive effort onto a precipitation ratio was found in the summer annuals, but no significant relationship was found in the winter annuals.

Moorhead, D. L., F. M. Fisher, and W. G. Whitford. 1988. Cover of spring annuals on nitrogen-rich kangaroo rat mounds in a Chihuahuan desert grassland. *American Midland Naturalist* 120: 443-47.

Muller, C. H. 1953. The association of desert annuals with shrubs. *American Journal of Botany* 40: 53-60.

Nelson, J. F., and R. M. Chew. 1977. Factors affecting seed reserves in the soil of a Mojave desert ecosystem, Rock Valley, Nye County, Nevada. *American Midland Naturalist* 97: 300-320.

Abstract: During 1972, a 2nd year of low herb production, there was a significant variation of seed reserves in the upper 2 cm of soil, with a doubling from February to June and a density-independent halving by October. In October 1972 there were 8×10^6 seeds/ha (5.3 kg/ha). After very high herb production in the spring, seed densities in October 1973 were 10-16 times greater under shrubs and 23-27 times greater in exposed areas (max 187.5×10^6 seeds/ha, 84.3 kg/ha). The increase was principally by the winter annual

grass, *Festuca octoflora*. In 1972, when there was a small difference in rodent density between two plots (0.8:1.0), there was no effect of rodents on seed density. In 1973, when there was a 1:17.8 ratio of rodent densities, there was a significant effect on seeds under shrubs. Then from October 1973 to October 1974, seed reserves in exposed areas between shrubs decreased by 20% in the plot with few rodents, and by 40% in the plot with many rodents. Eating of seeds by rodents accounted for 30 to 80% of the seed reserve decreases observed. Germination losses were no more than 25%. There is slight evidence that pocket mice selectively decrease abundance of the heavier species of seeds. Seed density was at least five times greater under shrubs than in exposed areas; density was significantly correlated with the size of shrub canopy. There was also a significant effect of the species of shrub on the density of seeds. During years of low production, under-shrub areas are a refuge for herb seed production, and in such years shrub seeds form a larger portion of the seed crop and new reserves. The difference in response of shrubs and herbs to weather increases the stability of seed reserves. In May 1973 the number of herbs per 100 seeds in the previous October was 16.8 under shrubs and 43.6 in exposed areas; this implies a minimum germination of 24% of seeds over the whole habitat. It takes an exceptional coincidence of events, even in deserts, to cause a severe depletion of seed reserves.

Pake, Catherine E., and D. Lawrence Venable. 1995. Is coexistence of Sonoran desert annuals mediated by temporal variability in reproductive success? *Ecology* 76, no. 1: 246-61.

Abstract: Models of annual plants with a persistent seed bank have shown that temporal variation can promote coexistence if the reproductive success of species is favored in different environments determined by temporally variable conditions. This study investigates whether this mechanism may explain the coexistence of three Sonoran Desert species (*Pectocarya recurvata*, *Plantago patagonica*, *Schismus barbatus*). In a 2-yr experiment, factors that vary across years (water and seedling density) were manipulated. In addition, the dominant spatial feature, presence or absence of *Larrea* cover, was also included as a factor. Our aim was to document fitness hierarchies in different types of years. Seedlings were mapped monthly for survival and reproductive success. To compare species, we used 10 yr of data to calculate the average value that seeds of different species have for population growth. Shifts in fitness hierarchies were found for two species pairs (*Pectocarya*-*Schismus* and *Pectocarya*-*Plantago*), depending on density and either the year or the water level. Surprisingly, all species had higher survival at higher densities in one or another treatment. Habitats were not important to the fitness hierarchies; all species had higher mean survival and fitness in the open than under shrubs.

———. 1996. Seed banks in desert annuals: implications for persistence and coexistence in variable environments. *Ecology* 77, no. 5: 1427-35.

Abstract: It is widely believed that desert annual plants maintain between-year seed banks, yet few field studies actually have measured the proportion of the viable seed bank that remains dormant through a season. Dormancy and germination fractions were quantified for a guild of winter annuals on a creosote flat in the Sonoran Desert for three years. Predictions from two types of theoretical models applicable to temporally variable environments were examined: (1) the evolution of life history traits promoting persistence in the face of temporal variation and (2) the role of temporal variation in mediating species

coexistence. The density of ungerminated seeds was estimated by collecting soil samples after germination, but prior to new seed set. Seedlings were followed in nearby plots to estimate the density of germinated seedlings and their reproductive success. Long-term data collected from permanent plots over a 10-yr period were used to calculate temporal variation in reproductive success for each species. Species with higher temporal variation in reproductive success had lower germination fractions and smaller seeds, consistent with the theory that seed dormancy and large seed size are partially substitutable bet-hedging strategies. The data also suggested that this system possesses traits that are necessary for temporal variation to promote coexistence. First, between-year seed banks, necessary to buffer populations in unfavorable years, were documented for 17 species. Second, there was a strong tendency for year-to-year variation in germination fractions to vary among species. Finally, plants germinated more in years of higher reproductive success. We discuss how a correlation between germination and reproductive success enhances the role of temporal variance in success hierarchies in promoting species coexistence.

Smith, S. D., R. K. Monson, and J. E. Anderson. 1997. *Physiological ecology of North American desert plants.*

Adaptations of Desert Organisms, ed. J. L. Cloudsley-Thompson. Berlin: Springer.

Contents: 1- North American Deserts: Environments and Vegetation; 2- Plant Processes and Responses to Stress; 3- Evergreen Shrubs; 4- Drought-Deciduous Shrubs; 5- CAM Succulents; 6- Perennial Grasses; 7- Phreatophytes; 8- Desert Annuals; 9- Poikilohydric Plants; 10- Exotic Plants

Tielbörger, K., and R. Kadmon. 2000. Indirect effects in a desert plant community: is competition among annuals more intense under shrub canopies? *Plant Ecology* 150: 53-63.

———. 2000. Temporal environmental variation tips the balance between facilitation and interference in desert plants. *Ecology* 81, no. 6: 1544-53.

Abstract: Recently, numerous studies have pointed to the importance of positive interactions in natural communities. There is now a broad consensus that the balance between negative and positive interactions should shift along environmental gradients, with competition prevailing under environmentally benign conditions and positive interactions dominating under harsh conditions. A commonly cited example of the importance of facilitation in harsh environments is the preference of desert annual plants for the areas under the canopy of shrubs. The recognition of apparently positive effects of desert shrubs on annuals, however, has been mostly based on density measurements, while fitness parameters of the understory plants have been ignored. Also, the temporal consistency of such effects has not been previously tested. Based on conceptual ideas about the balance between interference and facilitation, we predicted that positive effects of the shrubs on the understory should dominate in dry years, while in favorable years, negative effects would be stronger. We tested our hypothesis by measuring the direction and magnitude of the shrub effect on demographic responses of four desert annual plant species during four consecutive seasons of differing rainfall. The results contradicted our initial hypothesis. Depending on the species, the effect of the shrubs shifted from either negative to neutral or from neutral to positive with increasing annual rainfall. However, this trend was stronger for the effect of shrubs on plant reproductive success

than on their densities. Our data highlight the importance of measuring fitness parameters in studies of plant–plant interactions. We suggest that the negative effects of shrubs on plant fitness were due to rainfall interception, while positive effects were related to increased nutrient availability beneath shrubs. However, the mechanisms by which the shrubs and annuals interact can only be resolved using an experimental approach. Our results contradict previous hypotheses about the relative importance of positive and negative interactions along environmental gradients. A simple conceptual model summarizing the proposed role of rainfall in determining the direction of shrub effects on their understory annuals is presented.

Valone, T. J., and D. A. Kelt. 1999. Fire and grazing in a shrub-invaded arid grassland community: independent or interactive ecological effects? *Journal of Arid Environments* 42: 15-28.

Abstract: This study examined the response of summer and winter annuals and perennials in a shrub-invaded arid plant community to combinations of fire and grazing by cattle to determine their effects on individual abundances, species richness and diversity. Thirteen species differed significantly in abundance across the burn treatment while nine differed significantly across the grazing treatment. Summer and winter annual plants were significantly more abundant, and summer annual plant species richness and diversity were significantly higher on burn plots. Most species were affected either by burning or grazing indicating that these disturbances affect this plant community relatively independently.

Went, F. W. 1949. Ecology of desert plants. II. The effect of rain and temperature on germination and growth. *Ecology* 30, no. 1: 1-13.

Abstract: Topsoil from 4 different desert areas was collected, and spread thinly over washed sand in flats. When subjected to artificial rain and to a variety of temperatures, many seeds germinated. The heavy initial artificial rain caused 3 to 4 times as many seeds to germinate as germinated without the benefit of that rain. There were also marked differences in the rate of germination according to the temperature conditions and the source of soil. When subjected to 27° day and 26° night temperatures, a typical summer vegetation of annuals developed, comprising *Bouteloua barbata*, *B. aristidoides*, *Pectis papposa*, *Amaranthus fimbriatus*, *Mollugo Cerviana* and *Euphorbia micromera*. None of the typical winter annuals grew. The latter were found in the flats kept during day at 18° and during night at 13 or 8°C. There none of the summer annuals grew, but winter annuals like *Gilia aurea*, *Plantago spinulosa*, *Eriophyllum Wallacei*, *Nemacladus longiflorus* and *Bromus rubens* developed well. When seeds were sown so thickly that 5,000 germinated per m², 56 per cent survived and grew to flowering and fruiting plants.

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