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Responses of Plant Communities to Grazing in the Southwestern United States

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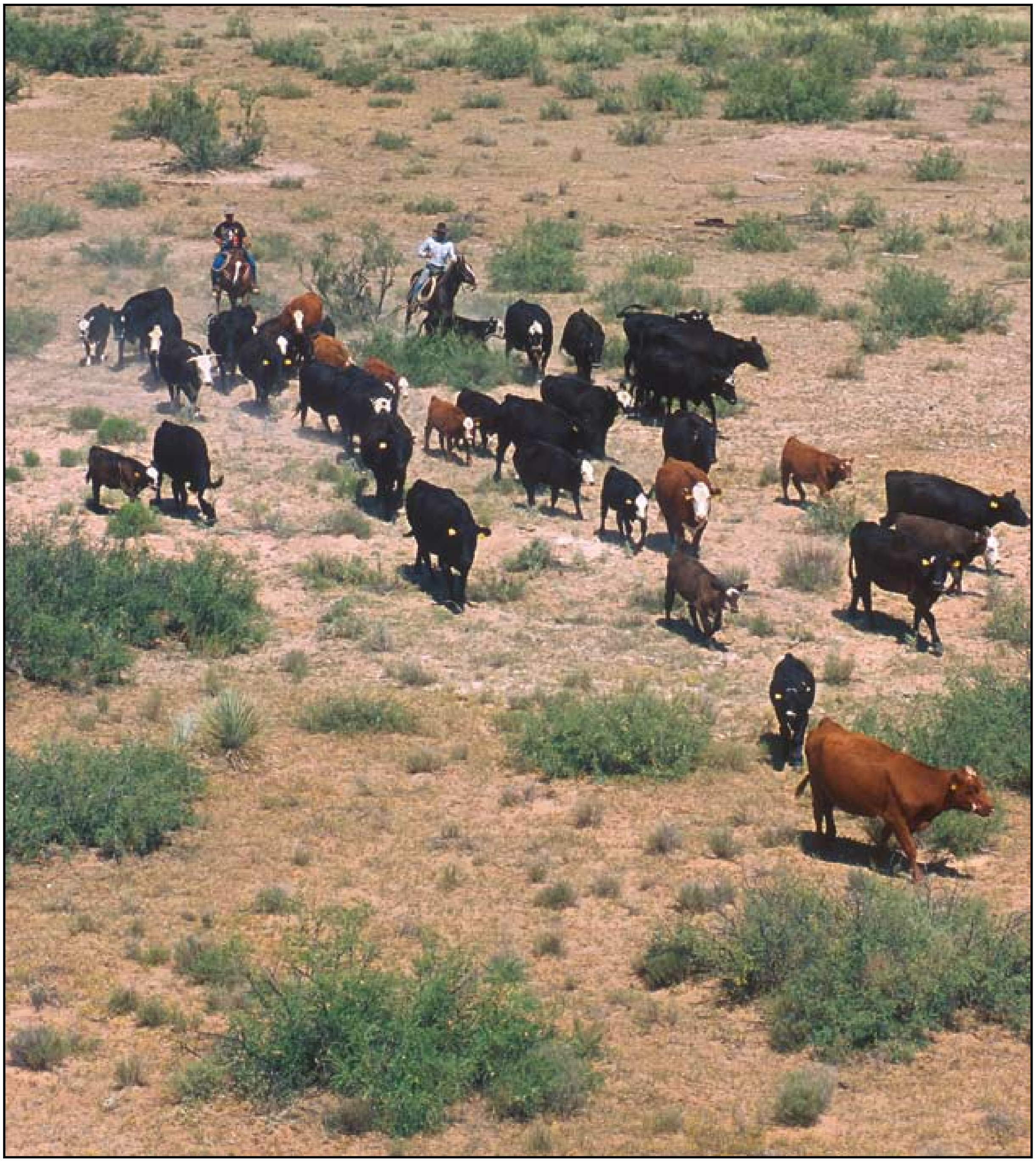

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Abstract

Grazing by wild and domestic mammals can have small to large effects on plant communities, depending on characteristics of the particular community and of the type and intensity of grazing. The broad objective of this report was to extensively review literature on the effects of grazing on 25 plant communities of the southwestern U.S. in terms of plant species composition, aboveground primary productivity, and root and soil attributes. Livestock grazing management and grazing systems are assessed, as are effects of small and large native mammals and feral species, when data are available. Emphasis is placed on the evolutionary history of grazing and productivity of the particular communities as determinants of response. After reviewing available studies for each community type, we compare changes in species composition with grazing among community types. Comparisons are also made between southwestern communities with a relatively short history of grazing and communities of the adjacent Great Plains with a long evolutionary history of grazing. Evidence for grazing as a factor in shifts from grasslands to shrublands is considered. An appendix outlines a new community classification system, which is followed in describing grazing impacts in prior sections.

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Cover photo: *On the 300-square-mile Jornada Experimental Range near Las Cruces, New Mexico, technicians Rob Dunlap (left) and John Smith round up cattle. Photo by Scott Bauer.*

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Executive Summary

Two primary factors determine a plant community's relative response to livestock grazing: the evolutionary history of large-herbivore grazing and the plant community's aboveground primary productivity. Bison were generally not part of the evolutionary history in the southwest, except for the edge of their range (less intense grazing) in far eastern New Mexico where a smaller bodied (more selective) grazer exerted possibly different pressure than that occurring in the central Great Plains. Because aridity (low productivity) and grazing are convergent selection pressures, communities of the southwestern United States may be intermediate in their response to livestock grazing. However, grazing by domestic livestock is controversial in the southwest, and grazing has been considered a reason for shrub encroachment in many communities.

This report assesses the effects of grazing on 25 plant communities of the southwestern United States, in terms of plant species composition, aboveground primary productivity, and root and soil attributes. All possible studies were considered in an attempt to 1) determine the state of knowledge for each community and suggest where research is lacking, 2) assess the relative responses among communities, 3) present an unbiased, literature-based overview of grazing and the shrub encroachment issue, and 4) broadly view grazing responses in the southwest relative to responses observed in adjacent semiarid to subhumid Great Plains communities that have a long evolutionary history of grazing by bison. Responses of individual communities are summarized at the end of each section. Community response to grazing increased, following theoretical predictions, as such: unproductive/long history < unproductive/short history < productive/short history < productive/long history. However, variables such as precipitation, grazing intensity, and years of protection from grazing could much better predict community response on the Great Plains than the southwestern United States. This degree of unpredictability for the southwest, together with a large difference between never-grazed geologic refuges and human-made exclosure comparisons with grazed treatments in the southwest, raises questions as to whether some livestock effects may have been historic, or whether southwestern communities require temporally rare and unpredictable environmental events for change to occur. Riparian communities were particularly responsive to grazing. The response of a plant species common to both Great Plains and some southwestern communities was not the same in the two locations. In general, southwestern communities were more sensitive to grazing than the adjacent shortgrass steppe, but were similar in response to other semiarid/arid and subhumid communities with a short evolutionary history of grazing. Further, the temporal variability in plant community species composition due to weather appears to be much greater in southwestern than in Great Plains communities.

The majority of evidence from experimental literature indicates that shrub encroachment occurs into ungrazed sites as well as grazed sites. There are four possibilities that could still invoke livestock grazing as a factor in this conversion of communities: 1) previous very heavy grazing during the 1800s resulted in an alternate stable state, 2) grazing interacts with fire, 3) there are highly erodible areas where long-term studies have not been in place, where current grazing could initiate alternate stable states, and 4) grazing interacts with some other factor such as climate or rodents. The evidence for these are reviewed and found to be either weak or experimentally untestable under current conditions but having factors that weaken a supporting argument. There is an increasing amount of evidence implicating changes in the seasonal proportions of precipitation as a primary cause of community change in the southwest. However, no one factor alone appears to adequately explain the complex spatial pattern of community change through parts of this region.

Intense non-selective grazing is an exogenous disturbance in most southwestern communities. From a conservation standpoint, there are places where grazing by livestock should be encouraged in the absence of the native grazer, and other places where livestock grazing should be discouraged or at least cautiously managed because similar grazers were not present historically. From a production standpoint, light to moderate grazing can be sustainable in the southwest in many situations. For some communities there are little data to base conclusions, and for other communities there are contradictory findings. However, the fate of private lands will often closely be coupled to use of public lands. Alternatives to ranching such as development and subdivision for ranchettes or agriculture may potentially be a greater threat to the integrity of southwestern ecosystems than ranching of native communities.

Contents

Introduction

The objective of this review is to examine the responses to grazing in plant communities of the southwestern United States. More specifically, the review focuses on 25 plant community types in Arizona and New Mexico and the manner in which grazing affects species composition, primary productivity, soil, and other belowground attributes. Focusing on each particular plant community, rather than a region, allows for a better assessment of the specific states of knowledge and research needs. This review also discusses how the evolutionary history of plant communities interacted with native ungulate grazing to shape responses to grazing by livestock. Grasslands of the Great Plains have a long evolutionary history of grazing by bison. The impact of livestock grazing on the Great Plains differs from the impact of livestock grazing on other lands where native ungulates did not graze as much in the past, such as southwestern lands (Bock and Bock 1993; Milchunas and others 1998; Bock and Bock 2000), the Great Basin, and the far west (Mack and Thompson 1982; Milchunas and others 1988; Lauenroth and others 1994) that did not have similar levels of grazing by large generalist herbivores. Evolutionary history of grazing and environmental moisture or primary productivity interact in determining species adaptations for tolerance or avoidance of herbivory (Milchunas and others 1988) and in community responses to grazing (Milchunas and Lauenroth 1993). While quantitative global-scale analyses have tested the hypotheses concerning the history-productivity interaction (Milchunas and Lauenroth 1993), no specific attempt has been made to compare southwestern with adjacent Great Plains plant communities with respect to relative responses to grazing.

The literature concerning southwestern plant communities often indicate that very large changes in compositions and distributions have taken place within the lifetimes of individuals and coincidental with the period of large-scale introduction of livestock. Controversy over the role of livestock grazing in those changes is high. Some reviews and paper discussion sections in even the scientific literature appear to pick and choose studies or evidence supporting a particular viewpoint. Therefore, an additional objective of this review was to do an extensive coverage of the studies for each community type whereby all available information is presented. The long literature cited section for this paper attests to the volume of studies associated with this endeavor, but also to the possibility that important pieces could have been missed.

Several other procedures/conventions were taken in compiling the effects section to help the reader as well as this author in interpretation. First, observation versus experimentation is differentiated. Observation-based information is a large proportion of the knowledge available for some community types, and less for others. In the case of a plant community type for which a large number of experimental studies were available, an even lesser amount of observational evidence may have been presented. Sections on community types are generally organized by observational works first and experimental second, and presented in a way whereby it is apparent as to which is which. This is not to demean observational information, but I know that I have often been surprised when my experimentation has not supported my perceptions based on observations of a system that I worked in for years.

A second convention was to sometimes comment on particularly good experimental designs and point out interpretive peculiarities of others. In general, however, grazing studies require large pastures and are often inadequately or improperly replicated, leading to an inability for proper characterization and inference (Hurlbert 1984; Brown and Waller 1986). Pseudoreplication and/or complete lack of statistical testing is common especially among early research, yet this research is particularly important for our understanding grazing effects when conducted through long-term weather cycles and when it provides a historical record of previous condition of plant communities. Animals do not graze uniformly across the landscape topography even within areas of a square kilometer in the same general plant community type, and the effects of grazing can differ substantially over this heterogeneity (Milchunas and others 1989) as well as over large regional differences within a plant community type (Sims and others 1978; Milchunas and Lauenroth 1993). Therefore, reaching consensus in results from multiple studies, or differentiating factors that may lead to divergent results, are particularly important potential outcomes of extensive reviews. Alternatively, a lack of studies for particular communities points to the need for additional study.

Third, an attempt was made to mention the type of sampling procedure used by the author. Canopy cover, basal cover, density, and biomass each have advantages and disadvantages depending on the particular objectives of the research, but some can confound current-year removal by the herbivore with longer-term plant population dynamic changes associated with grazing when the objective here is the latter. When contrasted with an ungrazed treatment for example, canopy cover and biomass not sampled from within temporary cages on grazed areas measures both current-year removal by the animal plus any of the longer-term effects of the grazing on mortality and growth capacity, whereas basal cover does not include effects of current removal. Since grazing is by definition removing the canopy, studies where the objective is long-term effects on plant populations would not have wanted to include the confounding effect of utilization inherent in canopy cover, but studies where the objective was the effects on other native consumers would have wanted to include the short-term effects on structure and species availabilities included in current-year removal by the livestock. Density has a size dependent bias, but is also an unbiased estimator of long-term population dynamics. In terms of aboveground net primary production, use of end-of-season peak standing crop from annually-moved temporary cages was considered a valid estimate (see Milchunas and Lauenroth 1992; McNaughton and others 1996 for advantages and disadvantages), but several papers were omitted from production portions of this review when uncaged grazed biomass estimates were called production. Moving cages multiple times throughout a growing season, and clipping caged and uncaged biomass, is a method that captures the effects of current-year grazing on compensatory regrowth but can also result in biases that cause overestimations, and few studies have used this method (McNaughton and others 1996).

The effects on plant communities of herbivory by domestic, feral or exotic, and native animals are considered in this paper. However, the majority of studies available concern domestic livestock. While there may be many reasons for the prevalence of livestock studies, it should not lessen our consideration of the potential importance of the other herbivores. In an introduction to a proceedings on research on exotics in National Parks, Dennis (1980) notes that 14 of 24 papers concerned ungulates. Feral or exotic species often represent a novel perturbation to a system, which can have large impacts. The works of Brown and colleagues on rodents in the southwest are prominent examples of how native small mammals can act as keystone species in their effects on a system (Brown and others 1979; Brown and Heske 1990). The classic textbook example of predator control, herbivore population eruption, damage to plant communities, and then herbivore population crash comes from the Kaibab deer herd in the southwest (Rasmussen 1941; Leopold 1943; Mitchell and Freeman 1993; Young 2002). Deer populations in many areas of North America are at higher densities than they have been in the past several hundred years, because of their opportunistic nature and use of early seral stages created by humans (Rooney 2001). However, there appears to be more studies on the effects of livestock grazing on wildlife populations than on the effects of wildlife on vegetation. Information on these other groups of herbivores/granivores are included when available.

The organization of this paper is to first examine the history of grazing by native and domestic herbivores in the southwest at a broad geographic scale. Additional material specific to particular communities, when available, is included in the section on grazing effects on that community. The summary of available studies on the effects of grazing on each of the communities follows a community classification system recently developed by the USFS (Moir 2000, Appendix 1 provides outline and synonyms from other classification systems). Some departure from the numerical order of communities in the Forest Service classification system is made for the purpose of conceptual flow. In one case, two community types are combined because of difficulty in placement of the available studies into separate categories, the small amount of information available, and similarity between the two communities. Each community type begins with a general description or definition, followed by a discussion of grazing effects on species composition, primary production, and, where available, root responses, soils (including erosion), fire-grazing interactions, and grazing management. A comparison among community types, and between southwestern and Great Plains communities, is made with respect to sensitivity to grazing. Conclusions are based on the within and between community responses. Appendix 2 provides a list of scientific names of plant species referenced in the text.

History of Grazing by Native and Domestic Large Herbivores

The Importance of Evolutionary History and Environmental Conditions in Grazing Responses

A theoretical, generalized model has been proposed to explain the very different sensitivities of plant communities to grazing by large herbivores (Milchunas and others 1988) and has subsequently been validated by quantitative, meta-analyses of grazing studies from around the world (Milchunas and Lauenroth 1993) and various other experimental and synthesis efforts (Painter and others 1993; Proulx and Mazumder 1998; Huisman and Olff 1998; Kotanen and Bergelson 2000; Loreti and others 2001; Osem and others 2002). Basically, the theoretical model views the primary determinants of plant community response to grazing as an interaction between evolutionary history of grazing and site productivity. Various avoidance and tolerance mechanisms develop in plant populations that are exposed to high levels of herbivory (prostrate low-growing morphologies, investment in crown and root storage unavailable to grazers, and so forth). However, adaptations for successfully competing in water limited semiarid systems are convergent (act in the same manner) to those inferring tolerance and/or avoidance to grazing, while adaptations for successfully competing in productive environments are divergent (act in the opposite manner) to those inferring tolerance and/or avoidance to grazing. Relatively greater investment in crown and root structures are positively associated with the ability to compete for limiting soil-water resources in semiarid areas, and is also an avoidance of grazers because a greater proportion of the plant is unavailable to large ungulates and supplies necessary resources for regrowth after a defoliation event. In contrast, light in a space-restricted canopy can become relatively more limiting in productive environments where belowground resources are relatively not as limiting. Adaptations for competition in the canopy (tall growth forms, relatively more proportional aboveground investments) make a plant more susceptible to greater injury and lower potential regrowth reserves following defoliation. Further, large herbivores consume the plant canopy, thereby having a direct influence on mechanisms of plant-plant competition in productive communities, while only indirectly influencing belowground competition in semiarid environments. The role of small herbivores and granivores can also be large in some systems (Brown and Heske 1990), but less experimental and theoretical work has been done on their potential effects on plant communities.

The interaction between evolutionary history of grazing and precipitation/primary production result in differences in the response to grazing that can be described by four extreme cases along the two continuous axes (Fig. 1). At one extreme, rapid switching in species adapted to competing in the canopy and those adapted to grazing tolerance and avoidance in productive communities with a long evolutionary history of intense grazing result in large changes in species composition and diversity when ungrazed-grazed comparisons are made. At the opposite extreme, communities of low production and short history of grazing are not as responsive to grazing as the former in terms of changes in species composition and diversity, but can be more susceptible to invasions by exotics than systems with a long history of grazing. Adaptations to semiaridity temper the drastic changes seen in productive communities with a short history of grazing, but are greater than responses in semiarid communities with long history of grazing because grazing pressure was not similar to aridity pressures when acting on the evolution of adaptations. Plant basal cover is more likely to increase in semiarid communities with a long grazing history and

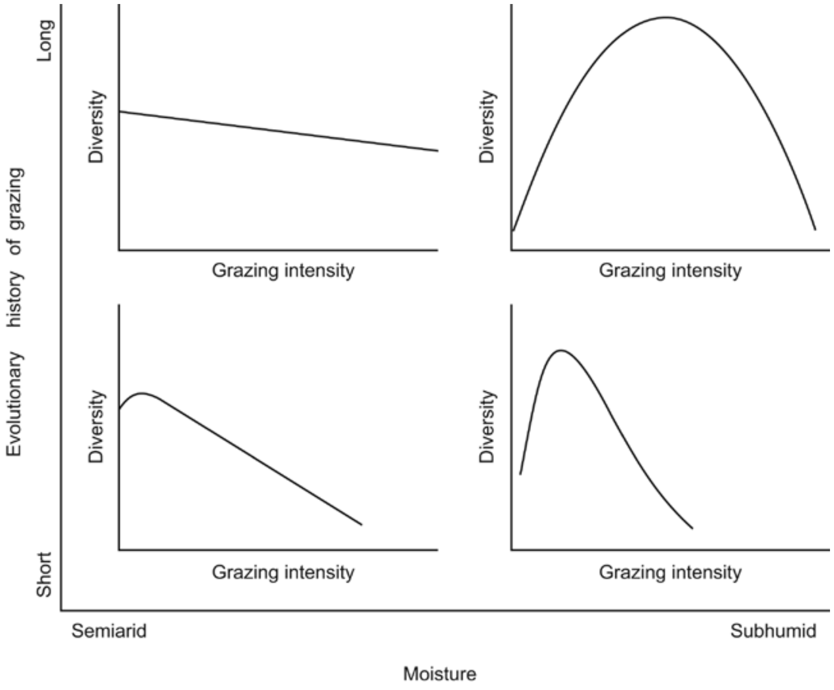

Figure 1—Theoretical model of plant community species diversity response to grazing intensity over gradients of precipitation and evolutionary history of grazing. The semiarid to subhumid precipitation gradient (approximately >250 to <1000 mm/yr average) is considered interchangeable with low to high aboveground primary production. The four graphs represent the four extreme cases over the environmental gradients, and intermediate gradations occur from one curve to another. Grazing is for large generalist herbivores such as cattle, sheep, bison, and so forth. The effects of, or interactions with, small specialists herbivores are not included in the model. Adapted from Milchunas and others (1988).

decrease in semiarid communities with a short grazing history because of differences in grazing tolerance and avoidance mechanisms (Milchunas et al. 1988, 1989). Invasion of exotic or native opportunistic species is more likely where unoccupied space increases rather than decreases (Milchunas and others 1992).

The importance of evolutionary history of grazing and community productivity in determining responses to grazing in plant community species composition and net primary production was quantitatively assessed over 236 ungrazed-grazed comparisons from around the world (Milchunas and Lauenroth 1993). At this global scale, sensitivity to grazing was more explained by ecosystem and environmental variables (evolutionary history of grazing, productivity, and so forth) than by current grazing-related variables (intensity, years of protection, and so forth). Current grazing practices undoubtedly become important within communities or regions. Because of the importance of evolutionary history of grazing and plant community productivity, I first review the evolutionary history of grazing in southwestern communities, and in the Plant Community response section I include information on primary productivity when available.

The Milchunas and others (1988) theoretical model is entirely based on plant-plant interactions as historically and currently influenced by large generalist herbivores over a semiarid to subhumid gradient. This may be a partial weakness of the model when arid or highly erodible systems are considered. Soil processes mediated by large herbivores have also been suggested in a model describing responses to grazing in arid-to-semiarid regions in the southwestern United States (Schlesinger and others 1990; Whitford 2002) and elsewhere (van de Koppel and others 1997). Effects of intensive grazing on albedo feeding back on local climate change has also been suggested as a model for community desertification and drought cycles in the Sahel (Charney 1975). The El Nino Southern Oscillation has also been implicated as interacting with herbivores in affecting the dynamics of plant communities (Holmgren and others 2001). There is evidence supporting all of these models, and it is possible that all or some operate simultaneously at any particular location. This possibility in reference to the southwest will be further pursued in the conclusion section of this paper, after reviewing literature regarding plant community responses.

Evolutionary History of Grazing in Southwestern U.S. Plant Communities__________

Bison were the primary large, generalist herbivore that was important in structuring plant communities of the Great Plains. Although other herbivores such as deer and elk also occurred throughout much of the region, in the plains they generally did not reach the large herd sizes associated with bison. Further, the body size and therefore diet of bison and cattle are generally similar, although bison are a little more of a generalist, non-selective “lawn mower” type grazer than cattle in

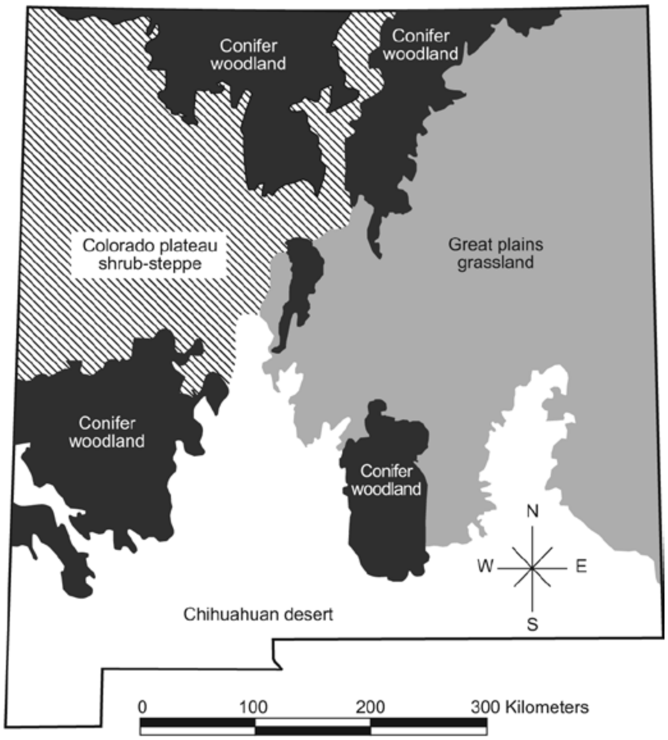

Figure 2—Distribution of four major biomes in the state of New Mexico. Adapted from Gosz and Gosz (1996).

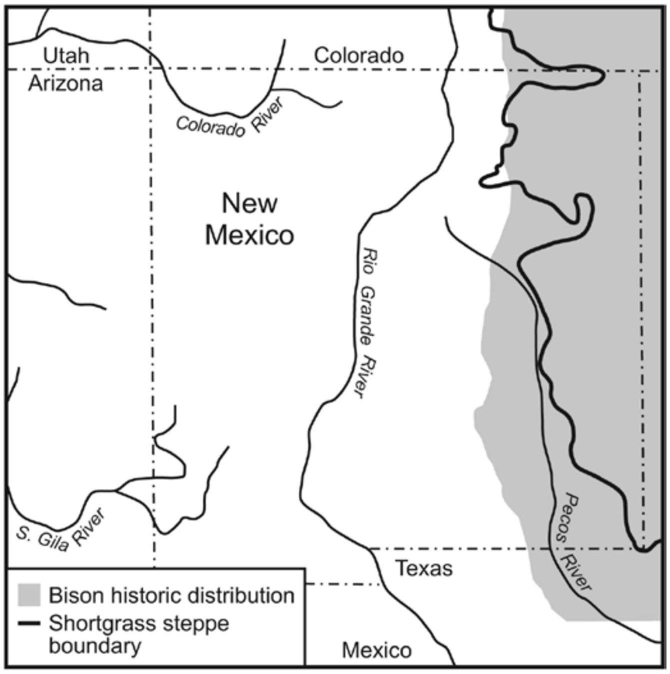

Figure 3—Historic estimated distribution of bison in Arizona and New Mexico based on several sources and locations where archeological remains have been found (adapted from Truett 1996) with the boundary of the shortgrass steppe superimposed (as mapped in Lauenroth and Milchunas 1991).

shortgrass steppe communities (Lauenroth and Milchunas 1991). There are numerous accounts illustrating the intense grazing pressure that was applied by a large herd of bison. For example, Hornaday (1889, quoted in Larson [1940]) wrote that bison "at times so completely consumed the herbage of the plains that detachments of the United States Army found it difficult to find sufficient grass for their mules and horses." Col. Dodge was reported to have estimated one herd at over four million individuals (Roe 1951). Seton (1953) estimated numbers at 40 million in the "open plains" and 30 million in the "prairies". Lott (2002) estimated an average population size of 24 to 27 million bison in North America, based on carrying capacity estimates and population time-lags in responding to weather cycle effects on resource availability. Because of the intensity of grazing by bison for 10,000 years and general similarities between the animals, herbivore adapted grasses in the *Bouteloua* (grama grass) Provence east of the Rocky Mountains in North America were not adversely affected by the introduction of domestic livestock (Mack and Thompson 1982; Milchunas and others 1988). However, the steppe of the *Agropyron* (wheatgrass) Provence west of the Rockies, which lacked large herds of mammals throughout the Holocene and hence dominant caespitose plants not well adapted to herbivory, showed declines in herbaceous vegetation and increases in opportunistic species with the introduction of livestock. In these grasslands, the dominant C_3 grasses and the prominent cryptogram layer were soon altered by domestic livestock and replaced largely by alien winter annuals. Further, in the Great Basin, a greater pressure on the shrub component in sagebrush shrubsteppe occurred during the Pleistocene by browsers such as camels and ground sloths (Martin 1970, see Great Basin sagebrush shrubsteppe section).

With respect to range of bison in the southwestern United States, elevation and latitudinal/longitudinal factors with the adjacent Great Plains grasslands were involved in distributional patterns. Large generalist herd animals such as bison generally do not utilize areas of steep topography (see evolutionary history part of Alpine Tundra section below). Since bison proliferated in the Great Plains, but existed for a relatively short period, or in isolated locations west of the Rockies, the potential for an influence of bison on southwestern communities could only come from the east and northeast, similar to the locations of the major biomes (Fig. 2). However, Gosz and Gosz (1996) delineate the boundary for Great Plains grasslands farther west than Lauenroth and Milchunas (1991) delineate the boundary for the shortgrass steppe (Fig. 2 vs. Fig. 3), because of the influence of blue grama in plant communities further west than what may be considered shortgrass steppe, but also because the Great Plains geomorphic province extends farther west than the shortgrass steppe biotic community (Sims and others 1978). Although grasslands in southeastern Arizona have been designated as "Plains and Great Basin Grasslands" and have some species in common with the Great Plains, similarities of the flora are greater to the southeast (Mexico and southwestern Texas) than to the northeast (central U.S.) (McLaughlin and others 2001). Madrean and Apachian elements are the largest part of the native flora.

Interestingly, the distribution of bison into the southwest has been mapped intermediately between boundary of the shortgrass steppe, which is more to the east (Fig. 3), and the boundary of the Great Plains biome, which is more to the west (Fig. 2). Clearly, biomes, communities, or animal distributions usually do not have sharp well-defined boundaries, but they gradually merge in broad ecotone transitional zones. In reviewing the evidence for distributions of both bison and elk, Truett (1996) used the Bailey (1931) range map and early explorer accounts that indicated only occasional occurrence west of the Pecos River. Bison remains have been found at many sites in other areas of New Mexico and Arizona (Parmenter and Van Devender 1995; Truett 1996), but numbers were generally thought to be very low. Effinger and Lucas (1990) also map most bison remains in eastern New Mexico. Bailey concluded that bison never occupied the Rio Grande Valley in large numbers, because of the barrier provided by arid valleys and due to hunting by the Navajo and Pueblo Indians that inhabited the valley. There are no explorer accounts of bison in the Rio Grande Valley, but there were numerous reports of bison along the Pecos River, named Rio de las Vacas for the abundance of bison. Bailey quotes Coronado from the mid 1500s as saying "the plains are as full of crooked-back oxen as the Mountain Serene in Spain is of sheep," and Espejo in reference to the Pecos Valley in 1584 with "all the way passing through great herds of buffaloes." Truett also maps the historic distribution of elk in New Mexico and Arizona (based on a number of early references) as very limited and in only some mountain ranges, about only half of today's range. Truett investigated a number of potential reasons for the scarcity of these large herbivores in the southwest and concluded that the most important causes were the restricted distribution of perennial water together with hunting by late-prehistoric peoples. Archeological site excavations suggest a relative abundance of the smaller, more dietary specialist deer and pronghorn antelope in the region. These accounts cover the more recent, 11,000-year history during the Holocene. Bison species originally immigrated to North America about 150,000 years ago in the late Pleistocene and occupied not only the Great Plains, but much of the southwest as well (Van Devender 1995). About two-thirds of the large mammals of North America went extinct 11,000 years ago, and desert grasslands after that time have had the poorest fauna of large herbivores ever in the last 20 million years of its history. Lott (2002) also mapped bison distribution in 1500 as extending only into the eastern strip of New Mexico, but he suggested dense numbers only in the northeastern corner of New Mexico with southeastern New Mexico being only "sparsely occupied during periods of typical climate." Carrera and Ballard (2003) reviewed the evidence of elk distributions, and conclude that Arizona, New Mexico, and northern Texas were the southernmost edge of the distribution in the late Holocene and that elk never occurred naturally in Mexico.

It can be concluded that only a small eastern strip of New Mexico was subjected to the long-evolutionary history of grazing that was a strong force in shaping recent species adaptations and plant communities in the adjacent Great Plains region. More specialist herbivores were present, and specialist herbivores alone rarely consume a large percentage of plant production in communities, except under occasional population outbreaks. Both the type and intensity of herbivory differed between the adjacent shortgrass steppe and much of the southwestern United States. Further, the Indians recognized two types of bison, a smaller southern type and a northern larger bodied animal (Bailey 1931). Bailey places the larger bison in the Arkansas River area and northward, and the smaller animal as ranging through Texas and eastern New Mexico. Allen (1874 cited in Bailey 1931) also reported that the Indians and Mexicans recognized a 'mountain buffalo' and a 'plains buffalo', but Allen did not consider two separate species due to conflicting accounts of characteristics of the mountain buffalo. Bailey's talks with Indians indicate that a cow of the northern type was as large as a bull of the southern type. A body size that different may also suggest a more selective grazer in the south than in the north, possibly representing a somewhat different pressure by bison grazing of southern compared to northern shortgrass steppe communities. Therefore, not only was it a small eastern strip of New Mexico that was subjected to bison grazing, but the type of grazing pressure received at this limited border of occupation could well have been by a relatively more selective grazer than current-day cattle. Responses of even these communities to the novel grazing pressure of domestic livestock may, therefore, be greater than in the Great Plains where past and current grazing pressure may have been more similar. Further, plant populations near the edge of their range may also be more susceptible to change.

History of Grazing by Domestic, Feral, and Exotic Animals in the Southwest United States

There have been many detailed reviews of the history of livestock grazing in the southwest (Wagoner 1952; Schickedanz 1980; Bahre 1991; Elson 1992; Cartledge and Propper 1993; Scurlock 1995; Brugge and Gerow 2000; Eastman and others 2000; Fowler 2000), and it is not the objective of this paper to repeat that here. It is, however, important in the context of this paper to examine the degree and extent of overgrazing in the late 1800s to early 1900s, and to place this in a temporal context to evaluate in the discussion of grazing impacts and interactions with other stressors that are addressed later in this paper. This is because of the coincidence in the period of intense, unregulated grazing with the start of profound changes in plant community species compositions and distributions. We therefore present only a brief outline of the history of grazing by domestic livestock to illustrate the time frame and extent of the grazing. "Overgrazing" is a qualitative term that is difficult to define scientifically, because it requires knowledge of a particular threshold. The term is used here only in the context of the historic period of unregulated, intense grazing of large, unfenced areas to emphasize the situation that is generally acknowledged by ranchers, range managers, and scientists as a period of overgrazing.

Humans occupied and modified southwestern ecosystems long before domestic livestock were introduced. Evidence of humans dates back earlier than 10,000 B.C., although permanent habitation did not occur until 300 B.C. (Elson 1992). The Anasazi were the dominant Indian communities around 1100 to 1300 and possibly had large impacts on plant communities through the gathering of fuel wood and food and cultivation activities (Cartledge and Propper 1993). There are several lines of evidence that indicate significant deforestation due to the activities of these people.

The first cattle were brought into Mexico in 1521 by the Spanish (Wagoner 1952). They were of the Andalusian breed originally from western Spain. Coming from a similar environment, they were well-adapted to the semiarid southwest. Cattle were first brought into what would become southwestern United States by Coronado in 1540, and many were abandoned. Thousands of their descendants were discovered later by frontiersmen. There were 75,000 head by 1586. Wild asses or burros were similarly introduced (Douglas and Leslie 1996). The numbers of cattle, sheep, and goats owned by Spanish and Indians, and that were wild, increased through the 1700s (Wagoner 1952). By 1757 there were 7,000 horses, 16,000 cattle, and 112,000 sheep in New Mexico, primarily in the Rio Grande Valley (Elson 1992). Some signs of overgrazing began to appear locally by 1846: in the plains south and east of Santa Fe, the Rio Grande Valley, and the Rio Puerco watershed. Bahre's (1991) review of the historical status of Arizona borderlands concludes that overgrazing was insignificant through the mid-1800s and much of the descriptions of southeastern Arizona were of pristine conditions. While the history of domestic livestock grazing is longest in the southwest than anywhere else in the western United States, areas heavily impacted by grazing prior to Anglo entry in the mid-1800s were usually near settlements along major drainages or on some Indian occupied areas (Bahre 1991).

The end of the Civil War, the establishment of railways, and removal of Indian threats to settlement all combined to produce a boom in the cattle industry in the 1880s. Based on accounts of locals in southeastern Arizona at the time, Bahre (1991) writes that "every running stream and permanent spring had been claimed and adjacent ranges stocked" and "the entire region must have looked like one big cattle ranch." A major drought in 1891 to 1893 killed large proportions of the livestock and many areas experienced major topsoil erosion after loss of vegetative cover. Overstocking continued after the drought, but animal numbers had peaked in 1891. Wagoner (1952 appendix I) lists numbers of cattle for Pima county, Arizona, as 11,741 in 1880, 121,377 in 1891, and 49,599 in 1893. Cable (1975 citing Croxen 1926) describes the stocking of Tonto National Forest as peaking in about 1900 at 15 to 20 times the number present in 1926. The decline in mining and introduction of railroads led also to abandonment of burros (Douglas and Leslie 1996).

The 1880s through early 1900s represented a period of grazing at extreme intensities greatly over carrying capacity of the plant communities. Bahre (1991) considered Forest Service land to have been overgrazed through 1906, and Bureau of Land Management land continued to be heavily overgrazed until enactment of the Taylor Grazing Act in 1934. Homesteading in the 1910 to '20s resulted in decreasing amounts of open, unfenced range, and Forest Service lands were generally fenced by 1930.

Changes in fire regimes also occurred along with settlement and fencing and management of public lands. Fire suppression accentuated lower frequencies of fires due to lowering of fuel loads by livestock removal of the forage. Frequent fires started by Indians were also no longer a part of the environment. Grazing, but also grazing as interacting with fire, became a primary suspect in the very large changes in plant community species composition and in the distributions of plant communities that were also occurring in the late 1880s and continue to present. Bahre (1991) provides an overview review of fire incidence in the southwest, and more recent reports and analyses relevant to grazing are examined below for each particular community type. Several free-ranging exotic animals are also found in New Mexico, and include Barbary sheep, gemsbok, Persian wild goats, and Siberian ibex (Douglas and Leslie 1996).

Grazing Effects on Plant Communities

There are several classification systems that cover southwest U.S. plant communities. In this report, we follow a recent one developed by W. H. Moir (2000) for the Forest Service in New Mexico and Arizona. Synonyms for each community that are associated with other classification systems are listed in Appendix 1. A list of scientific names for the common names of plants used in the text appears in Appendix 2.

Alpine Tundra

Alpine plant communities are subject to many environmental stresses such as high wind and UV-radiation, cold temperatures, and short growing seasons. Plants in this environment, therefore, grow very slowly and have low annual primary productivity. These characteristics make alpine systems particularly susceptible to aboveground disturbances such as grazing. Alternatively, alpine plant communities are generally considered to have high root to shoot ratios (Paulsen 1975; Billings 1979; Thilenius 1979), which is a characteristic of systems that imparts avoidance and tolerance to grazing (Milchunas and others 1988; Milchunas and Noy-Meir 2002). Reserves in crowns and roots are inaccessible to large aboveground herbivores and serve as a source of carbohydrates for regrowth following defoliation. Thilenius (1975) and Paulsen (1975) report that 80 to 95 percent of alpine plant biomass in the Rockies is belowground and proportions are greater for forbs than for grasses, and Billings (1979) gives a range in root:shoot ratios from 1 to 6. In comparison, however, root:shoot ratios for North American grasslands range from 2 to 24, from 2 to 4 for a desert grassland site in New Mexico (Sims and others 1978), and 10 to 15 for the highly grazing tolerant shortgrass steppe in Colorado (Sims and others 1978; Milchunas and Lauenroth 2001). Tundra plants growing under low temperatures have high carbohydrate contents, which may account for the high degree of tolerance to defoliation of some graminoids (Tieszen and Archer 1979). Thilenius (1975) speculated that competition among alpine plants is less intense than for plants in lower elevations, and that they respond more to environmental conditions than to biotic influences. If true, then the effects of grazing would need to manifest through direct mortality or modification of the environment rather than by altering competitive outcomes. However, Griggs' (1956) observations suggest competition is important in harsh alpine communities, and Fowler (1986) reviewed evidence that supports the importance of competition in harsh arid environments.

The evolutionary history of grazing in alpine communities is not well understood but may have had only a minor role in structuring these systems (Tieszen and Archer 1979). Basic similarities of alpine communities in areas where large herbivores were and were not present indicates convergence (similarly structured communities) regardless of herbivore presence (Tieszen and Archer 1979), and the number and density of herbivores in alpine systems is generally much lower than lower-elevation grasslands in the same region (Hoffman 1974). Other reports in the literature appear contradictory. Tieszen and Archer (1979) cite studies in New Zealand and Ethiopia (Mark 1965; Klotzli 1977) as showing tall tussock communities changing to short-tussock communities when defoliated or grazed, suggesting that these systems that evolved in the absence of large herbivores display unusually dramatic responses. However, the responses may be due to the unusual tall structure of these particular communities. Bock and others (1995) specifically attempted to test the hypothesis that responses to defoliation would be different between alpine communities in the Republic of Georgia with a 2000 yr history of livestock use and a Rocky Mountain National Park, Colorado, alpine community lacking a history of settlement and livestock grazing. These authors found defoliation decreased productivity in both systems, and they found an even greater depression in the Georgian plants. The clipping studies did not support directional selection by a long history of grazing in this system, but plant family patterns and morphology may have resulted. Grazing can rapidly change species composition and morphology of communities, but 2000 years may be insufficient for individual or population level changes. However, if prior, longer-term selection had been acting, a genetic pool containing characteristics relating to tolerance or avoidance would have been present and influenced community dynamics when domestic animals were introduced. Bock and others (1995) did observe differences in community species composition and plant height structure that indicate selection at this level.

There are not large amounts of alpine vegetation in Arizona and New Mexico. Two plant associations with 140 plant species have been described for New Mexico, and three associations with 80 species in Arizona (Chambers and Holthausen 2000). For alpine areas elsewhere and in general, Thilenius (1975) considered that no more than 200 to 300 species usually occupied the alpine zone of a particular mountain range. Although the alpine areas in Arizona and New Mexico were used for sheep grazing in early settlement years, they are no longer intensively grazed. Sheep numbers in the United States were highest from the 1880s through the 1940s and have declined since (Joyce 1989). Cattle are poorly adapted to this environment (heart damage - brisket disease) but can be acclimated (Thilenius 1979).

No studies of the effects of grazing on southwestern alpine plant communities could be located. Thilenius (1975, 1979) and Tieszen and Archer (1979) reviewed research concerning grazing of alpine communities in other locations. Since grazing study sites are potentially very different from those in the southwest, specific changes in structure or function of alpine communities cannot be considered here. Some very general conclusions reached by these authors, that may or may not be applicable to southwestern alpine communities, include: 1) Some graminoids show good regrowth after even chronic grazing pressure, whereas deciduous and evergreen shrubs can be damaged more severely. 2) The regrowth of graminoids results in reduced root growth which can take more than two years to replace. 3) There is the potential for changes in species composition, but the small amount of work in this area makes grazing management of these systems largely empirically derived. 4) A reasonable average production for grazable alpine vegetation is ~90 to 100 g/m^2 and wetter or drier sites should be considered unsuitable range because wet sites are susceptible to trampling damage and drier sites are susceptible to erosion. Costin (1967) also concluded that the low productivity is a management problem, and makes alpine areas unsuitable for efficient grazing use. Chapin (1980) commented on the potential for defoliation to deplete nutrients in plants growing in nutrient-poor soils such as those found in arctic and alpine habitats.

Particular problems of grazing management in these systems include proper animal distribution due to shelter from wind, topography, and snow-melt distributions, and trampling impacts in saturated soils below snowdrifts (Thilenius 1975, 1979). Light to moderate use is generally considered to be 20 to 30 percent of aboveground biomass, but actual grazing is often lighter at 7 to 10 percent. The 20 to 30 percent utilization recommendation is the lightest of all plant-community types in New Mexico (Holechek and Pieper 1992). Past and most current grazing uses a sheep herder, although herderless grazing may also occur. Paulsen (1975) and Thilenius (1975, 1979) outlined USDA-Forest Service herding practices that would seldom show excessive use, improve range condition, and show reduced erosion. These included slow moving, loosely bunched distributions, watered once a day, one-time per season defoliations, and one-night beddings where salt is provided in movable containers. Grazing should be deferred until after the period of most active plant growth, and rest-rotation systems may also improve range condition. Slopes of greater than 40 percent are considered ungrazable due to the high potential for erosion problems to develop. Thilenius (1975, 1979) also stressed that condition standards for Rocky Mountain alpine communities are poorly understood, and current guidelines are of doubtful value. Recovery of misused alpine systems requires long time periods. While extensive proportions of alpine areas have been disturbed by grazing at some point in time, Johnson and Brown (1979) considered other types of disturbances to be currently more intensive.

Boreal Forest

Boreal forest occupies approximately 500,000 ha in the southwest, with 80 percent in New Mexico (Chambers and Holthausen 2000). Precipitation ranges from 580 to 880 mm/yr and is the second highest for all Arizona - New Mexico community types. At five sites in Arizona, understory productivity of grasses and forbs averaged a little over 8 g/m^2 in conifer forest and 51 g/m^2 in associated aspen stands (Reynolds 1969). This is extremely low herbaceous production. Reynolds (1962) considered this community type to be of little importance for range production, but of high value for water yields and recreation. Logging or thinning of overstory increases forage production (Ffolliott 1979), but the inverse relationship between overstory-understory production is not as evident in the spruce-fir type as in other coniferous forests in the region (Ffolliott and Gottfried 1999). Understory in closed-canopy spruce-fir is mainly lichens, fungi, sedges, mosses, and liverworts, with grasses, forbs, and half-shrubs becoming more abundant with opening of the canopy by disturbances. In addition to low forage production, the growing season is short—often less than 75 days.

There is little actual grazing in the spruce-fir community as animals primarily utilize meadows within this type, and grazing capacity of the area is based on the meadow communities within. Deer and cattle use of associated aspen stands can also be greater than use of the conifer forest (Reynolds 1969). As with alpine communities, the boreal forest type is considered more suitable for sheep than cattle grazing (Reynolds 1962). Sheep can, however, be more damaging to vegetation than cattle when heavy grazing occurs because they are capable of grazing plants closer to the ground. It is unlikely that boreal forest types are or were heavily grazed by native large herbivores, although use for cover may be high. Plant-herbivore relationships are probably poorly developed, except for associated aspen stands where utilization can be heavy.

Chambers and Holthausen (2000) commented that there is very little literature quantifying the effects of grazing in montane communities in the southwest, and they list some important research needs. I was unable to locate any quantitative data comparing ungrazed and grazed plant communities for boreal forest types.

Grazing has been considered by some to be an indirect factor in changes in many southwestern community types through its effect on reducing fuel loads and altering natural fire regimes (see other community type sections below). This may not be an effect of grazing in the boreal forest type, since the natural fire return interval is very infrequent anyway. White and Vankat (1993) estimated the natural fire return interval for boreal forest was 70 to 250 years, which is relatively infrequent compared to lower elevation communities.

High value for recreational use would conflict with use as grazing land. Further, the spruce-fir type is estimated to require twice the area than pine-fir forest to support an AUM, and six-times the area for mountain grassland (Reynolds 1962). Aspen stands within this type provide much more forage, but heavy grazing of young aspen shoots by wild or domestic large herbivores can eliminate reproduction and result in old, relatively even-aged stands. Chambers and Holthausen (2000) suggested livestock grazing should be avoided in communities where animal dietary preference for regenerating trees is high.

Mixed Conifer Forest

The two community types differentiated according to Appendix 1 are combined for the purpose of assessing grazing impacts because no data specific to Madrean montane forests were located. Data located is applicable to the upper montane forest, white fir/douglas-fir, pine/douglas-fir, and Petran conifer forest type.

Annual precipitation ranges from 450 to 800 mm in this and the Madrean mixed conifer type (Ffolliott and Gottfried 1999). Grasses and forbs are more abundant than in adjoining higher elevation boreal forest, although dense canopies and high litter buildup can limit understory production. Management practices closely parallel those in adjoining, lower elevation ponderosa pine communities. These communities have high value for recreation and wildlife habitat, and are valuable for summer forage for mule deer and elk. Exotic or noxious plants are not important components of this community, although Kentucky bluegrass is an introduced species that is considered a good livestock forage (Chambers and Holthausen 2000) but is primarily associated with grassland openings in the forest. Gambel oak may replace ponderosa pine and Douglas fir stands after removal by fire or logging in southern Colorado (Engle and others 1983).

Humphrey (1960) described "fir" forests as "…so dense as to let little sunlight reach the ground and, as a result, except for a few shrubs and weeds and an occasional grass, there is little available to serve as feed for either game or livestock." Timber harvesting of overstory can increase grass and forb production from 11 to 17 g/m^2/yr and increase deer use of the habitat (Patton 1976). Thill and others (1983) reported understory production values from 4 to 16 g/m^2 in unlogged mixed conifer forests, depending on tree basal area. Comparable values for thinned sites increased up to 74 g/m^2/yr for lowest basal area sites. Small clear cuts can increase forage for both domestic and native large herbivores from 8 to 28 g/m^2/yr (Ffolliott and Gottfried 1989). Utilization by livestock and wildlife can increase but varies considerably between cleared patches. The very low forage production for this community would suggest that it would be easy to overutilize the forage base with only slight overstocking. Clearcutting of aspen stands in Colorado, however, resulted in few major changes in understory characteristics (Crouch 1983).

Production of grasses, forbs, and shrubs was similar to uncut stands, except for some depression the first year after cutting. The largest effect of cutting was to increase aspen sprouting. Utilization by cattle was greater on older than recently logged or uncut sites. Reynolds (1962) recommended stocking rates of 10+ acres/AUM for pine-fir forests and 2 to 4 acres/AUM for associated grasslands.

Natural fire return intervals are considered to have been less frequent than those in the ponderosa pine community, but fire has played a role in structuring mixed conifer forests (Chambers and Holthausen 2000). Fire return intervals have been reported to be from 2 to 27 years to 6 to 27 years, depending on forest type. However, Grissino-Mayer and others (1994) suggest a low intensity surface fire return interval of 4 to 6 years in the Pinaleno Mountains, based on fire scar data. This is similar to that for ponderosa pine communities. Fire regimes changed after European settlement. These authors suggest that spreading fires initiated naturally and by Native Americans were common until the period when livestock grazing intensified and fire suppression was initiated, and that grasses were an important component of fine fuel loads. Kaib and others (1999) and Swetnam and others (2001) studied fire scar data traversing a gradient in community type from desert grassland, Madrean pine (canyon pine-oak), to mixed conifer (Madrean) and estimated fire return intervals of 4 to 8, 3 to 7, and 4 to 9 years, respectively, based on scars on at least 10 to 25 percent of the trees sampled.

There is only one quantitative grazing intensity comparison for this community type in Arizona and New Mexico. One of the 34 grazing exclosure plots assessed by Potter and Krenetsky (1967) and Krenetsky (1971) in the upper range of the ponderosa pine type was dominated by Douglas-fir. Grazing intensity at this site was probably moderate from ~1940 through 1951, when the grazing allotment was closed to grazing and use was only by recreationists. Grazing was for two months of the year by sheep, and the plot was in good condition and underutilized when the exclosure was established. Re-sampling of the plot was done in 1964, thus the area outside the exclosure was also ungrazed by livestock the previous 13 years. Unlike some other sites in this study, protection from grazing favored tree growth. Krenetsky (1971) concluded that this hindered grass recovery, but grass cover increased from 1940 to 1964 to a greater extent in the exclosure (0.9 to 6.7 percent) than outside (0.2 to 3.5 percent). Largest increase in grass was for creeping muhly. Forb cover decreased with protection from grazing, although it was always below 1 percent cover. The large increase in browse was primarily due to Douglas fir, which showed a 22 percentage-unit greater increase in the ungrazed compared to the grazed plot. Total vegetative cover was 4.4 and 36.6 percent in the ungrazed area in 1940 and 1964, respectively, compared to 0.8 and 8.85 percent in the adjacent grazed area. The diversity (richness) of plant species sampled decreased from 17 to 9 in the exclosure from 1940 to 1964, respectively, but increased from 9 to 12 in the grazed area. The loss of species with protection from grazing was due to the increase in tree cover and a loss of forbs and grasses that were minor components of the 1940 cover. Exclosure from grazing resulted in greater soil infiltration rates and concentrations of Ca and Mg, with other characteristics similar to the grazed area. Litter biomass was also similar between grazing treatments. The very low cover of grasses and forbs compares well with a geologic refuge (butte) in southern Utah that has never been grazed by domestic livestock and has a cover of less than 3 percent for the grass plus forb component (Mandany and West 1984).

Browsing of fir, spruce, and pine species by deer is considered in the next section (Ponderosa Pine).

No solid conclusions should be attempted concerning the effects of grazing on mixed conifer forests of the southwest based on only a single-site ungrazed/grazed comparison.

Ponderosa Pine and Madrean Pine Forests

The Madrean pine forests (often dominated by ponderosa pine) and ponderosa pine types are included in one section because of a general lack of information for the Madraen type. The latter type is differentiated in the text when possible.

Grazing of domestic livestock in the ponderosa type became intense during the 1880 to ‘90s (Currie 1975). Grazing was primarily by cattle until World War I, when sheep grazing became more important. Livestock numbers declined after the mid-1930s and are now less than one-third of peak numbers.

Reynolds (1962) considered the ponderosa pine type to be the most important community in the southwest with respect to timber production, water yields, trout habitat, and recreational use, second most important in big game habitat, and third in range production. Ponderosa pine communities of the southwest are sometimes separated into those occurring in the southern Rocky Mountains of Arizona, and those in the central Rocky Mountains from northern New Mexico, through Colorado and into the mountains of southern Wyoming. A large amount of the controlled experimental grazing work in the ponderosa pine type has been done at the USFS Manitou Experimental Forest in central Colorado. These communities are similar enough to those in New Mexico that we here include results and conclusions from the Colorado studies.

Precipitation in the Arizona communities ranges from 356 to 457 mm/yr, and falls in two pronounced periods of winter and summer (Paulsen 1975). Precipitation in the central Rocky communities falls primarily during the April through September growing season, with means from 381 mm in New Mexico, 391 mm/yr at Manitou in central Colorado, to 635 mm/yr in Wyoming (Smith 1967; Paulsen 1975).

Mountain meadow grasslands are interspersed throughout ponderosa pine stands of varying density. These grassland types are considered below in the montane meadow community type. As with other montane forest types, cattle often prefer grazing the grassland meadows over the forested sites (Smith 1967; Paulsen 1975), making stocking rate determinations more difficult.

Species Composition

Farish (1889, cited in Cooper 1960) reported at the height of historic very heavy grazing in Arizona that much of the better forage plants had been lost within 12 years (see History of Grazing by Domestic Animals section). Very high stocking rates coupled with a drought caused heavy losses of livestock. Governor Hughes (1893, cited in Cooper 1960) stated in his annual report: "In nearly all districts, owing to overstocking, many weeds have taken the place of the best grasses. In other places where ten years ago the end of the wet season would find a rich growth of grass, now is of inferior quality, or less quantity, or does not exist at all."

In terms of species composition today, the understory of Arizona ponderosa communities on the Colorado Plateau are dominated by Arizona fescue and mountain and screwleaf muhlenbergias (Paulsen 1975). Central Rocky Mountain communities in the south are Arizona fescue and mountain muhly dominated, and Idaho fescue can replace Arizona fescue in the north or upper elevation limits, while Thurber and Idaho fescue may replace Arizona fescue in western Colorado and northern New Mexico. Forbs and shrubs are generally small components, and variable in space and time.

Arnold (1955) and Clary (1975) outlined successional stages of degradation due to grazing for Arizona ponderosa pine in forest openings:

- Bunchgrass stage (Arizona fescue and mountain or screwleaf muhly)
- Sod-forming grass stage (black dropseed, Kentucky bluegrass, blue grama)
- Prostrate perennial forbs stage (pussytoes and sandwort)
- Short-lived half-shrub stage (broom snakeweed and hymenoxys)
- Annual stage (annual dropseed)
- Denuded soil stage

Species in each progressively lower stage are shorter-lived. Arnold emphasized the use of life-forms in assessing condition of ponderosa range due to grazing. The replacement of tall and/or midgrasses by shortgrasses with grazing is a common response to grazing across plant communities worldwide (Milchunas and Lauenroth 1993; Diaz and others 2006). However, the presence of "sod-grass" forming species is often related to systems with a long evolutionary history of grazing (Milchunas and others 1988). While that is not the case for these systems, a sod-forming stage contributes a degree of protection from grazing to the system whereby erosion potentials are lowered even though species composition changes are occurring. Recovery from the denuded stage to a bunchgrass stage may require 100 years even under reduced grazing pressure, based on observations of a half-shrub stage after 30 years (Clary 1975). Successional stages of recovery may not follow degradation stages after complete protection from grazing, because bunchgrasses may establish immediately along with annuals and other life-forms, including pine. The savanna structure of ponderosa pine climax is confirmed by accounts of early explorers (Cooper 1960) as well as examination of relict stands on geologic refuges (mesas, and so forth) (Mandany and West 1984). Natural fire is a reason stands are not closed canopy (see section below). Forests are much more dense today than in the past, and succession in the absence of fire can proceed to a closed canopy structure (Cooper 1960).

The successional scheme described above by Arnold (1950) was based on five exclosures and adjacent grazed areas that were established in 1912 and resampled 36 years later. Within the grazing treatments there were areas ranging from open to relatively closed stands. Plant species were grouped into bunchgrasses, grasses that avoid or tolerate grazing (sod grasses), and "weeds" (colonizing ruderals). Under protection from grazing 1) bunchgrasses increased (mountain muhly, Arizona fescue, mutton grass, pine dropseed, and less abundant spike muhly, deergrass, little bluestem, junegrass, and needle grasses), 2) sodgrasses decreased from their dominance in grazed treatments (blue grama, squirreltail, black dropseed, Fendler threeawn, and Arizona threeawn 3) "weeds" (colonizing ruderals) were a small proportion of the total and consisted of mainly perennials (yarrow, pussytoes, sandworts, thistles, daisies, asters, and penstemons), compared to mainly annual opportunistic ruderals in the grazed treatments. Blue grama and black dropseed dominated grazed communities. Even these short prostrate species declined in open-canopied sites where grazing pressure was relatively much more intense. Thus, greatest herbaceous cover was found in ungrazed open-canopied sites, whereas the least was found in grazed open canopied sites. Bunchgrasses in grazed treatments were often confined to refugia under denser pine cover. The survival of the awned species under grazing was attributed to the defensive structure of awns and that some were cool-season species that grew largely before the grazing season began. Arnold concluded that canopy closure under ungrazed conditions reduced productivity but had little effect on species composition. Grazing reduced productivity and had effects on species composition. Further, declines in production caused by canopy closure "will in time encourage improper grazing use and thus bring about discernable changes in plant composition." Managers need to continually adjust stocking rates when overstory canopy conditions are in transition.

Cooper (1960) described a site where "livestock have been virtually excluded"…"ground cover approximates to some degree that of pre-white man days…" as "…as dense as is to be found anywhere in the southwestern pine zone," and composed of 90 percent screwleaf muhly with few other grasses and forbs. However, Hanks and others (1983) classification of ponderosa pine types includes a description of a ponderosa/screwleaf muhly type which is the wettest most productive habitat, with screwleaf muhly as the dominant.

Potter and Krenetsky (1967) and Krenetsky's (1971) reassessment of plots inside and outside grazing exclosures after 25 years of treatment included six locations in ponderosa pine. They report a definite increase in understory cover with protection, primarily due to grasses, but depending on elevation (see below). The increase in grasses was the greatest for any of the seven community types studied. Grass species increasing with protection from grazing were blue grama, Arizona fescue, prairie junegrass, and creeping muhly. It is interesting to note that blue grama displayed the greatest increase, because 25 years is a considerable period and blue grama is a component of Arnold's (1955) and Clary's (1975) second seral stage. Blue grama is generally considered an increaser with grazing throughout all Great Plains grasslands (Lauenroth and others 1994), and it decreases with protection from grazing in the shortgrass steppe with a long evolutionary history of grazing (Milchunas and others 1989). Potter and Krenetsky (1967) and Krenetsky (1971) observed no effect of protection on forbs, which were minor overall components. Browse increased more under protection than under grazing, and this was the only community studied where ponderosa pine increased under protection rather than when grazed.

An important relationship between response to protection and elevation of the site was discussed by Krenetsky (1971). Recovery of grasses with protection was only found for the two low elevation sites. At the next highest elevation site, there were no significant effects of protection on grass or shrub cover, although vegetation was sparse at this site. At the next higher elevation site, there was greater browse cover and protection favored tree overstory cover. At the highest elevation site, grazing significantly favored the overstory, with no significant effect on grass cover. Similar relationships were observed for sites in the pinyon-juniper type (see section below).

In northwestern New Mexico, Gardner and Hubbell (1943) studied two paired grazed and ungrazed plots after eight years of protection that were selected for study because they were severely overgrazed and invaded by the "weed" pingue, an indigenous bare-ground colonizing species. Heavy grazing continued on one of the grazed treatment sites and was reduced to light grazing on the other site. The sites were in openings in open savanna stands, so it is difficult in this case to classify as a ponderosa type or a mountain meadow type. Pingue decreased slightly over the eight year period on the heavily grazed treatment, compared to "marked" decreases on the ungrazed and lightly grazed plots. Three species of forbs greatly increased on the ungrazed and lightly grazed plots. Of the grass species sampled, sand dropseed decreased and bottlebrush squirreltail increased. New pine trees in the heavily grazed plot were shorter than those in the other three, although this was based on a limited amount of data. This is contradictory to other reports indicating increases in pine cover with fire suppression and grazing (see section below).

Quantitative controlled studies of grazing at the Manitou Experimental Forest in Colorado provide the most detailed accounts of grazing effects on plant species composition in the ponderosa type. Cattle favored open grassland areas within the large pastures (Smith 1967). Utilization of open and timbered stands increased with increasing intensity of grazing. Use of the open ponderosa type was very low under light stocking levels. Use of dense timber areas was never greater than 13 to 14 percent even under heavy stocking rates, and uniform utilization between grassland and open ponderosa was not achieved even with heavy stocking. Percent utilization was more closely related to the number of individual plants grazed than to the amount removed from an individual plant. Arizona fescue and mountain muhly were the most important forage species. Little bluestem and sedge were also palatable, but blue grama and fringed sagebrush were relatively unpalatable although the former provided a significant amount of forage biomass later in the season.

Responses of the plant communities at Manitou were studied over 14 years, although the period also included a seven year drought in the 1950s. For the ponderosa type, total plant canopy cover remained similar between 1940 and 1957 on lightly (10 to 20 percent utilization) and moderately (20 to 40 percent utilization) grazed treatments but declined considerably on heavily (>50 percent utilization) grazed treatment (Smith 1967). These responses were due to grasses and sedges, rather than to forbs and other plant groups. Mountain muhly was resistant to grazing at light and moderate levels, although cover decreased by half on heavily grazed treatment. Arizona fescue decreased slightly under light and moderate grazing in grassland and remained similar in ponderosa, but it was reduced even more than muhly with heavy grazing. Blue grama increased in grassland but was not found commonly in the timbered stands. Cover of the short statured blue grama generally increases with grazing throughout its range (see references in Smith 1967 and Lauenroth and others 1994). Bottlebrush squirreltail increased with light grazing and declined with increasing intensity of grazing after that. Lupines, bearberry, Arkansas rose, and mountain mahogany all declined with grazing. Increasers with grazing, especially heavy, included a variety of colonizing ruderals species that were either annuals, low-growing, or stoloniferous and included tumblegrass, pussytoes, groundsels, and goosefoots. Sun sedge and fringed sagebrush showed no responses to the grazing intensities. A large number of species increased on protected sites, but only blue grama, pussytoes, and fendler sandwort decreased. The number of Arizona fescue, mountain muhly, or blue grama plants bearing flower stalks were generally similar for light and moderately grazed treatments, but all declined with heavy grazing. A study conducted to assess time for recovery of flower stalk production of heavily grazed plants after complete protection indicated three years was required for Arizona fescue and mountain muhly.

Grazing may also affect ponderosa pine regeneration through its effect on fuel loads and fire (see section below), by reducing competition between grasses and pine seedlings, or directly through trampling and consumption. Koehler and others (1989) found that mechanical removal of other plants around seedlings significantly increased their growth in both height and diameter, whereas chemical removal increased only height. A further study involving grazing cattle in enclosures resulted in enhanced growth of seedlings while causing only one percent mortality. A third study used large areas of ungrazed, moderately grazed in alternate years, and moderately grazed in consecutive years. Growth of pine increased with increasing grazing frequency, but density of seedlings was not affected by the grazing treatments. Currie and others (1978) found that seedling damage was high on heavily grazed treatments, but not on moderately or lightly grazed treatments. Rodents and rabbits caused more damage than cattle on the lightly and moderately grazed treatments. However, average height growth was greater in the lightly than either moderately or heavily grazed treatment in this study. Similar results for pine seedling mortality from other parts of the country are discussed by Koehler and others (1989). Although not in the southwestern United States, Neils and others (1956) reported that 90 percent of ponderosa pine seeds were consumed by small mammals before they had time to germinate, and that 60 percent seedling mortality due to deer occurred in one year, and 99 percent mortality over three years.

In Colorado, Currie and others (1977) noted consumption of ponderosa pine seedlings when deer "happened upon them," and that they bit off the terminal bud and upper needles. Newly fallen dead needles and live needles on lower branches of mature trees are also readily consumed. Fungi and dwarf mistletoe were large parts of the diet in heavily forested areas. Although grasses are a large part of the diet in more open habitat, there is little dietary overlap between deer and cattle, so grazing effects on the plant community would be expected to be different. Ponderosa pine is a considerable component of the diets of mule deer in many areas (Kufeld and others 1973), and most commonly in winter (Crouch 1981). Deer can damage ponderosa pine as well as several fir and spruce species, but it is generally not considered as economically important in the southwest as it is in the northwest or northern Rockies (Crouch 1981). Local damage can be intense in some instances but is generally not widespread (Heidmann 1972). On the other hand, the classic example of herbivore overpopulating a range after predator control and drastically affecting plant communities comes from the Kaibab Plateau herd in the 1910s through 1930s (Rasmussen 1941; Leopold 1943; Young 2002). While this example of deer altering plant communities includes ponderosa pine habitat, the Kaibab deer eruption is discussed in the Pinyon-Juniper section below. Browsing of understory gambel oak may be considerable, because it is a large component in the diet of mule deer in northern Arizona (Neff 1974 cited in Carpenter and Wallmo 1981), but heavy browsing stimulates sprouting that is considered desirable for wildlife (Sheperd 1971 cited in Carpenter and Wallmo 1981). Elk were observed to browse an average of 57 percent of the current-year branches of buckbrush. This shrub is an important component of midstory structure in ponderosa communities in the southwest and therefore important for diversity of other wildlife. These authors indicate that Rocky Mountain elk introduced into the area to replace the extirpated Merriam's elk have increased in numbers to about 30,000 in Arizona and about 45,000 in New Mexico, and that these numbers are greater and the elk's distribution greater than in the past.

There are not a large number of studies to base conclusions on the effects of grazing on species composition in ponderosa pine communities. Some results differ among studies, which may be due to elevation as suggested by one study, or simply to site or treatment differences. The studies suggest lower abundance of colonizing ruderal, annual, and low growing species in exclosures compared to grazed sites. A long-term well documented study showed little change through time in communities lightly or moderately grazed, but declines in understory cover with heavy grazing. There is contradictory evidence concerning the effect of grazing on ponderosa pine.

Aspen Communities

Aspen communities within the ponderosa type are important habitat for wildlife, and utilization can be high (Patton and Jones 1977; DeByle and Winokur 1985). This community can also be found interspersed within boreal forest and mixed conifer forest types. Understory productivity of grasses and forbs can be six times that in adjacent conifer forest (Reynolds 1969), making it particularly attractive to wild and domestic grazers. When grassland surrounds aspen stands, livestock prefer the grasslands, but use of the stands for shade can be heavy (DeByle 1985a).

Browsing of new aspen shoots by elk can be heavy under some circumstances and in some locations. Bailey and Whitham (2002) found that there was a positive relationship between severity of a burn and aspen sprouting in the absence of elk (in exclosures). However, elk selectively browsed aspen sprouts in the more severely burned sites, averaging 85 percent of shoots compared to only 36 percent in intermediately burned sites. The heavy browsing by elk more than negated the positive effect of intense burning on regeneration, and intermediately burned sites showed much greater regeneration. The differences in standing biomasses in the severely burned browsed and unbrowsed sites were dramatic, with 8967 g/m^2 in the unbrowsed and 135 g/m^2 in the browsed stands. Each combination of burning intensity and browsing intensity resulted in distinctly different arthropod communities associated with the different plant communities. Lack of regeneration of aspen in Rocky Mountain National Park in Colorado due to elk grazing has been of concern for many years, but survey studies indicate the problem to be of local and not regional or landscape concern. Kaye and others (2003) found a very patchy distribution of stand structure, no difference in regeneration between concentrated-elk-use winter range stands and dispersed-elk-use summer range stands, and no evidence of aspen decline. Suzuki and others (1999) found that regeneration was common within stands except in local areas of high elk utilization. It can take 6 to 8 years for sprouts to go to a height out of reach of elk (Patton and Avant 1970). Elk also chew the bark of mature trees during winter, and this can have an impact on stands by providing an entry way for pathogens, while complete girdling is not common (Debyle 1985a; DeByle and Winokur 1985). The effects of elk grazing on other plant communities has been reviewed by Wisdom and Thomas (1996). Deer, lagomorphs, and rodents may also remove bark, twigs, and sprouts for food, and these herbivores and birds utilize buds (DeByle 1985a,b; DeByle and Winokur 1985). Both aspen sprouts and aspen bark are high quality forages in term of nitrogen and digestibility (Mueggler 1985; DeByle 1985b).

Gophers were estimated to consume from 6 to 39 percent of the annual belowground primary production in aspen stands in Utah, and from 10 to 31 percent in meadow, and 5 to 6 percent in fir communities (Andersen and MacMahon 1981). However, means of estimating belowground net primary production at that time were limited and open to many serious errors and biases (Milchunas and Lauenroth 1992). A study by Cantor and Whitham (1989) suggests that belowground consumption of aspen by gophers in meadow communities in northern Arizona may be substantial, to the point that gophers limit the distribution of aspen communities to rock outcrop refugia where gophers cannot forage effectively. Mortality of aspen was 90 percent at meadow edges where gopher densities were high, compared to mortality of less than 20 percent where gophers were in low abundance. Aspen survival increased 3.5 times over control when gophers were removed, and tree growth rates increased 3 times.

Sheep compared to cattle grazing can be particularly hard on aspen sprouts, weakening a stand's capacity to produce suckers after several years of heavy browsing (Patton and Jones 1977, DeByle 1985a). Grazing by both animals, if heavy, can have very large impacts on the community, as sheep remove forbs and browse and cattle remove grasses (DeByle 1985a). Heavy prolonged grazing generally results in a loss of plant species diversity and greater composition of less palatable species (Mueggler 1985). DeByle reviews grazing in the aspen type throughout its range and discusses competition between the various types of herbivores that may utilize the habitat.

Primary Production

Clary (1975) reviewed literature for understory aboveground primary production in Arizona ponderosa pine and gave typical ranges of 22 to 36 $g/m^2/yr$. Exponential and linear negative relationships with overstory basal area have been reported. Productive sites with dense overstory may produce 6 to 8 $g/m^2/yr$ and ungrazed open productive sites may reach 156 $g/m^2/yr$, while sites with infertile, shallow soils may be half as productive. In Colorado, understory aboveground production in ungrazed open timber compared to surrounding grassland was 37 and 181 $g/m^2/yr$, respectively (Smith 1967). Grasses and forbs are a large component of the herbaceous standing crop, and most are perennials. Grasses, forbs, and shrubs comprised 63, 29, and 8 percent, respectively, of the production on cutover stands with a moderate canopy (Brown and others 1974), while for dense canopy stands values were 86, 17, and trace percent, respectively (Pearson 1964). The largest variability in production due to year-to-year fluctuations in weather were found where overstory canopy coverage was least (Paulsen 1975).

Several investigators have examined the effects of grazing on understory aboveground primary production, and some of these entailed controlled experiments and quantitative measurements. An early account of grazing effects was that of Arnold (1955), where values of production were given for range sites in excellent, good, fair, and poor condition classes in Arizona. Although experimental plots were described for species cover measurements (Arnold 1950), it is not clear how they were sampled for production, but graphs made from the Arnold values for two different community types appear similar and curves appear rather artificially smooth (Fig. 4A). This may lead one to possibly doubt that these sites were actually measured, and that values represent qualitative estimates by the author. Sites in excellent condition were based on observation of relict areas and represent the ungrazed condition. If heavily grazed sites were represented as poor condition, then they produced only 36 percent of that on the ungrazed excellent condition site.

Data from controlled studies in Colorado do not show a continual decline in production with increasing grazing pressure (Fig. 4B; Smith 1967). There were no differences among treatments two years after initiation. This was possibly because timbered sites were in relatively good condition prior to initiating the treatments, as cattle grazed associated grasslands more heavily. Associated grassland sites even increased production in response to a reduction in grazing pressure imposed two years before starting the grazing treatments. Understory production of ponderosa sites were not different among ungrazed, light (10 to 20 percent utilization), and moderate (30 to 40 percent utilization) grazing after 7 years of treatment, but heavily (>50 percent utilization) grazed sites produced 58 percent of ungrazed sites. After 17 years of treatment, moderately grazed sites had greater production than ungrazed or lightly grazed sites, and heavily grazed sites produced 46 percent of ungrazed sites. Heavy grazing affected early leaf growth, as indicated by leaf height measurements. Flower stalk production is discussed in the above section.

There is very little evidence to base conclusions concerning grazing effects on ponderosa pine community understory production. Both an apparent observational report of condition classes that may confound site with grazing effect and a well sampled controlled experiment suggest decreases in production with heavy grazing.

Root Responses

Root biomass in response to grazing exclosure, moderate, and heavy use was studied at the Manitou site in Colorado after 18 years of treatment (Schuster 1963; Smith 1967). Root biomass decreased with increasing intensity of grazing, and grazing resulted in a vertical distribution of roots (mostly grasses) more concentrated near the surface. Average maximum root depth was significantly reduced by heavy grazing, but there was no difference between moderately grazed and ungrazed treatments. There was a trend for lateral spread of roots to decrease with increasing grazing intensity, but this was not statistically significant. Individual roots

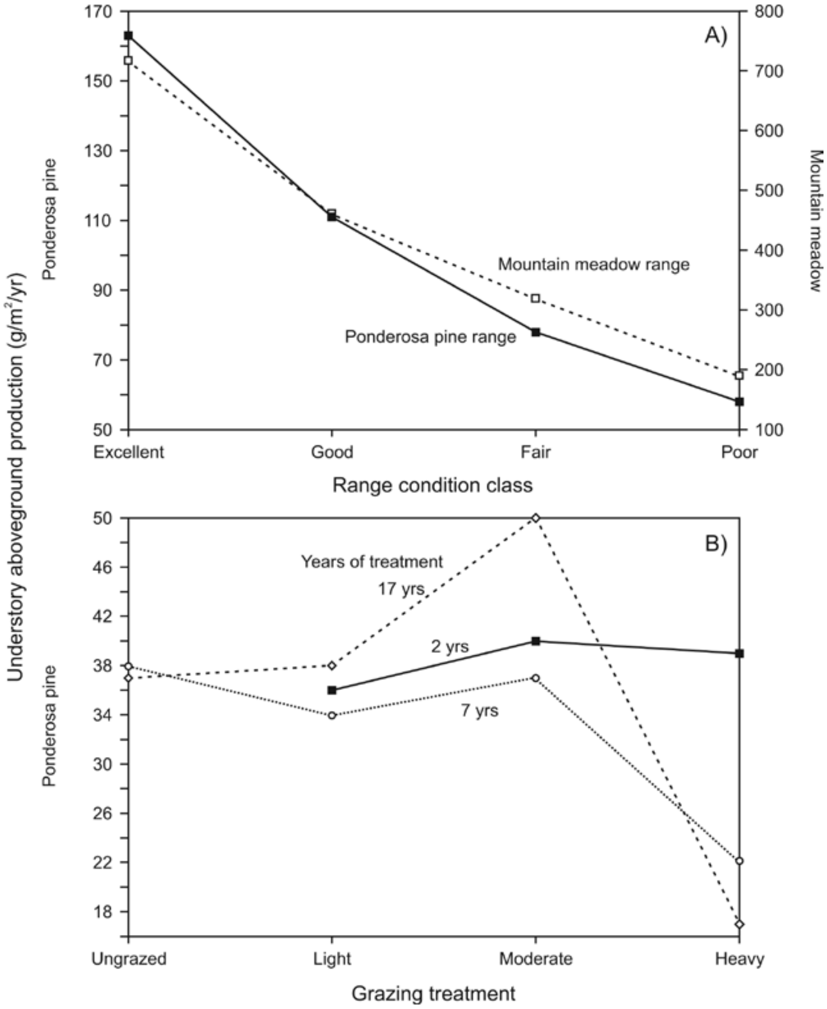

Figure 4—Understory aboveground primary production ($g/m^2/yr$) for A) ponderosa pine and mountain meadow communities in excellent, good, fair, or poor range condition classes (Data from Arnold 1950, 1955), and B) ponderosa pine communities ungrazed, lightly (10 to 20 percent utilization), and moderately (30 to 40 percent utilization), and heavily (>50 percent utilization) grazed for 2, 7, and 17 years (Data from Smith 1967).

of three important grass species were smaller in diameter and branched less under heavy grazing than those under lesser grazing intensities. Smaller effects on these variables were observed in moderately grazed treatments, and this may have been due to a lack of response by blue grama roots. Root biomass of blue grama is also very tolerant of grazing in shortgrass steppe (Milchunas and Lauenroth 1989).

Soils

Infiltration and erosion in response to light, moderate, and heavy grazing use were studied at the Manitou site in Colorado after 12 years of treatment, and in exclosures and adjacent grazed sites after 7 and 14 years of treatment (Dortignac and Love 1961; Smith 1967). No differences in infiltration were detected among light, moderate, and heavy use treatments, but data were highly variable. Infiltration inside exclosures in open ponderosa were greater than in grazed sites after 7 years but did not increase further after 14 years of protection. Erosion rates in grazing exclosures tended to be less than in lightly and moderately grazed treatments but were substantially greater in heavily grazed treatment. However, the rates of erosion in the heavily grazed treatment were not considered excessive by the authors. Dunford (1954) reported increased runoff from these treatments with increasing grazing intensity, with no effect of moderate grazing on soil loss. Arnold (1950) mentioned that soils were less compacted, and organic matter greater, inside exclosures after 36 years of protection of northern Arizona ponderosa pine communities, but no data were provided.

Fire-Grazing Interactions

Mean fire return intervals for southern ponderosa pine (Madrean, canyon pine-oak) forests were estimated to be 3 to 7 years, based on fire-scar data (Kaib and others 1999; Swetnam and others 2001). Grazing by domestic livestock and subsequent fire suppression with increased settlement by European humans resulted in very evident reductions in fire frequencies throughout the southwest starting about 1880 to 1890 and continue to decline to present (Swetnam and Betancourt 1998). Cooper (1960) believed that fire suppression was the most important of the two but that grazing may have had an indirect effect on fire frequency through lowering of fuel loads. Prior to settlement, Indians had set fires for 10,000 years and lightning fires occurred naturally even prior to that. Removal of competition for pine seedlings and greater cover of bare mineral soil resulted in dense thickets of pine regeneration. A more open nature of the stands was reported by early explorers (Cooper 1960) and is also found on relict areas large enough to be exposed to lightning fires (Mandany and West 1984). Cooper found that fire thinned stands of young trees; only 18 percent of trees less than 1 inch dbh survived. Stands not exposed to fire had diameter distributions skewed toward smaller trees.

Fire suppression efforts and grazing effects on fuel loads were believed by most in the past to be the sole reason for the even-aged dense stands of ponderosa pine that established in the early 1900s. Cooper (1960) concluded that "long term climate changes do not appear to be a factor contributing to these changes." However, Savage and Swetnam (1990) found that fire-scar records from stands in the Chuska Mountains showed a reduction in fire frequency four decades earlier than other parts of the southwest, but that dense even-aged stands established at the same time everywhere. The coincidence of the earlier decline in fire on this Navajo Reservation with its earlier history of heavy grazing by livestock supported the hypothesis that livestock grazing has had large effects on fire frequencies in the ponderosa type. Further, the decline in fire for the southwest in general preceded organized fire suppression. However, the regeneration pulses in forests both within and outside the reservation could be attributed to periods of both good seed supply and temperature and precipitation patterns highly favorable to seedling establishment. These authors concluded that the structure of present-day ponderosa stands was a complex interaction of anthropogenic disturbance and climatic conditions, and that fire and grazing regimes alone were not sufficient to cause the regeneration pulses. Swetnam and Betancourt (1998) present further evidence indicating a very important role of long-term weather cycles in driving recruitment/mortality cycles. Drought was shown to have large impacts on tree populations, and when preceded by cycles of high production, also resulted in high fuel loads/dry conditions with widespread fires across the region. Grazing may play a role in these weather/fire cycles, but the primary driver is weather. Based on preliminary studies, Curtin (2002a) also stresses that "climate is the overriding factor determining the outcome of management actions." Because "climatic trends may not be reflected in the age structure of a single forest or woodland" (Swetnam and Betancourt 1998), early researchers studying single stands would be likely to miss or underestimate the importance of these longer-term cycles. It is interesting to note, however, that Ellison (1960) surmised the importance of drought in woody-plant mortality, but also suggested an interaction with grazing based on Young's (1956) drought observations of greater mortality on lightly than heavily grazed ranges due to greater herbaceous cover effects on soil water. Young also noted that pricklypear cactus and mesquite were not as affected by drought.

Grazing Management

Approximately 80 percent of the ponderosa range in Arizona is grazed only in summer due to cold temperatures and snow accumulations (Clary 1975). At the time of the Clary report, continuous grazing occurred on 9 percent of the USFS allotments, rotation 15 percent, deferred 19 percent, rest-rotation 42 percent, and deferred-rotation 11 percent. Studies of advantages or disadvantages to different grazing systems have not been investigated for this range type. Currie (1976) reported no significant difference in production of montane meadows within ponderosa pine type to several grazing systems (see Montane Meadows section below).

Average grazing capacities were estimated at 7, 10, 18, and 41 acres/AUM for good, fair, poor, and very poor range-class conditions, which is approximately 30 to 40 percent utilization (Clary 1975). Currie (1975) based recommendations on slope and condition class with lower stocking on steeper slopes. Average acres/AUM were estimated at 2 to 6, 3 to 12, 4 to no grazing, and 8 to no grazing for excellent, good, fair, and poor range-class conditions. Currie suggested that stubble heights of Arizona fescue should be 5 to 6 inches, and mountain muhly 1.5 to 2 inches, at the end of the grazing season to obtain the 30 to 40 percent utilization. Steepness and length of slope (except in extreme cases) and distance to water were factors important in utilization of ponderosa ranges based on an early study (Glendening 1944), but not in a similar study conducted by Clary and others (1978). This was attributed to fencing to smaller pastures and increased development of water-site densities. Holecheck and Pieper (1992) also recommended 30 to 40 percent utilization, but of key species. This amount of utilization would agree with the studies at Manitou in Colorado (see above) that found few negative effects of moderate grazing at 30 to 40 percent. However, utilization in the ponderosa type was much less than that for grassland meadows within the ponderosa pastures. Utilization of grasslands in moderately stocked pastures ranged from 24 to 53 percent, whereas utilization of open ponderosa stands in the same pasture/years ranged from 11 to 40 percent, and dense stands from 0 to 4 percent. Management of ponderosa communities cannot be done independently of the associated mountain grasslands that are interspersed in varying amounts. Possibly a better approach would be to manage to keep associated meadow grasslands in a productive state, utilizing the forested sites even less, since light to moderate grazing may be sustainable in this system based on the Manitou studies. Sustainable in this case refers to primary production and secondary livestock production, not necessarily wildlife populations or desirable plant species composition.

Pinyon-Juniper

The pinyon-juniper type is one of the largest communities in the southwest in terms of area occupied (Gottfried and Pieper 2000). There is large variability in climate, topography, soils, and therefore plant species composition and stand structure (Springfield 1976). Precipitation generally ranges from 280 to 560 mm/yr, and amounts and seasonal distributions vary with elevation and geographic location. Precipitation is relatively more Mediterranean (45 percent April to September) in northwestern Arizona and understories have affinities to Great Basin plant communities, whereas in eastern New Mexico precipitation is continental (75 percent growing season) and plant communities have affinities to shortgrass steppe Great Plains grasslands (Lavin 1953, 1964 cited in Springfield 1976). Mediterranean climates favor annual species and deep-rooted (shrub) communities over continental climates if annual average precipitation and temperatures are held constant, so responses to and thresholds to grazing may be different. Further, the long, intense evolutionary history of grazing by native bison in the Great Plains compared to the low intensity of historical grazing in Great Basin plant communities can also shape responses to current-day grazing by domestic herbivores (Mack and Thompson 1982; Milchunas and others 1988), and this may or may not translate through affinities in communities that were not actually historically grazed.

The history of livestock grazing in the pinyon-juniper type follows the general history for lower elevation sites (see history section above), except that Gottfried and Pieper (2000) mention that most of the major Spanish settlements and Indian Pueblos were located within or close to pinyon-juniper communities. Gottfried and Pieper (2000) present an excellent summary and conceptual model of historical pinyon-juniper changes on the Pajarito Plateau, New Mexico (Fig. 5). Four main periods and five general states of pinyon-juniper communities are outlined. A dense understory vegetation and an open woodland structure were maintained by periodic fires prior to the Anasazi impacts from A.D. 1200 to 1550. During this period, there was possibly an increase in fire frequency due to the use of fire by the Indians and a decrease in grazing by wildlife due to hunting. This resulted in a decreased cover of pinyon-juniper due to fire and cutting and an increase in understory as a result of the lower overstory and reduced grazing, and little overall effect on erosion due to localized farming and settlement. The Spanish colonization period from the late 1500s through the early 1800s saw some cutting of pinyon-juniper and limited introduction of domestic livestock, resulting in only localized changes in vegetation and soil erosion. Anglo settlement after 1880 brought similar conditions described for other communities above: large increases in domestic livestock and reduced fuel loads, fire suppression, and several periods of drought, and several changes in wildlife populations some of which may be particular to this location. These conditions combined to increase pinyon-juniper cover, bare soil and erosion, and the difficulty for herbaceous plant re-establishment, resulting in unstable “pinyon-juniper rocklands.”

Species Composition

The response of pinyon-juniper communities to grazing may depend in part on the successional stage being grazed. Gottfried and Pieper (2000) show three successional scenarios for the pinyon-juniper type based on different authors and different parts of the country. Fire is the succession initiating force in all three models. Annual, perennial grass - forb - shrub, and woodland stages are common to all. There are few large-scale problems with exotic species invasions into pinyon-juniper communities, although Russian thistle is widespread with many less abundant taxa. The effects of grazing on fire regimes is discussed in the Fire - Grazing Interactions section below.

Preference for particular species by livestock is one of several factors that can influence the directional change the species may take with grazing. In northern Arizona,

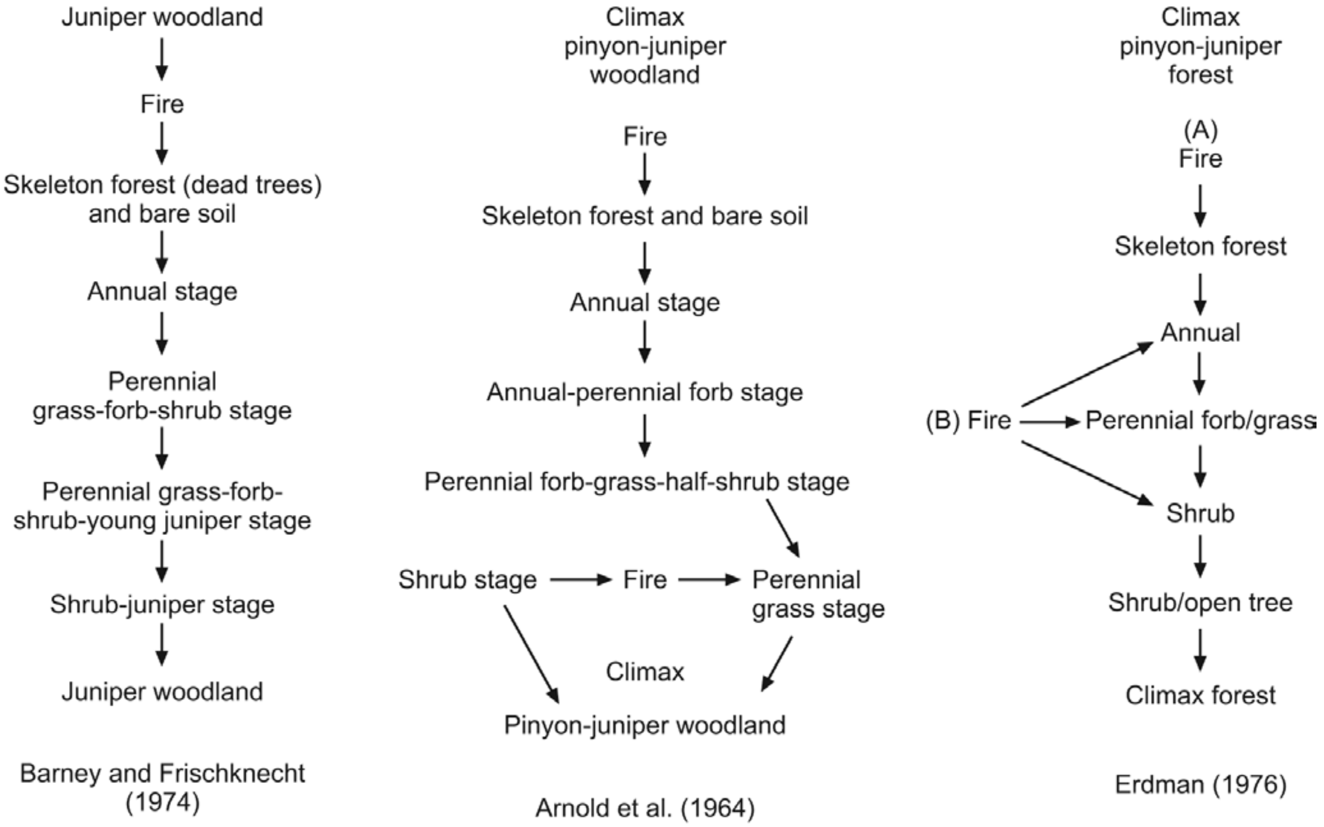

Figure 5—Three successional models for pinyon-juniper communities in different locations. From Gottfried and Pieper (2000).

Clary and Pearson (1969) observed the following preferences (percent utilization): prairie junegrass 43 percent, bottlebrush squirreltail 40 percent, mutton bluegrass 33 percent, sideoats grama 30 percent, black dropseed 15 percent, blue grama 5 percent, and spike muhly 4 percent. Blue grama is generally the most abundant grass in the pinyon-juniper type (Gottfried and Pieper 2000), which may account for its low preference.

Qualitatively, Paulsen (1975) suggested that spring grazing has been especially detrimental to cool-season grasses such as muttongrass, bottlebrush squirrel-tail, and western wheatgrass. Humphrey (1960) described condition classes for Arizona pinyon-juniper type. Excellent condition was considered to have almost entirely palatable perennial grasses such as hairy and sideoats grama, plains lovegrass, woolly bunchgrass, pinyon ricegrass, Texas beardgrass, little bluestem, and curly mesquite. This condition was thought to be sustainable if proper utilization levels were maintained, but condition could decline during drought. Grazing intensities should be especially watched and adjusted under drought conditions. Good condition range has enough cover, and of the palatable species, to resist erosion losses. Junipers are widely spaced. Fair condition is marked by low cover and density of vegetation, although it is still composed of perennial grasses. Production is half of potential, and grazing should be deferred during the summer at least every third year. Poor condition range produces almost no forage, and plants that are there produce little seed or vegetative reproduction. Removal of grazers for a couple of growing seasons and re-seeding of native forage plants was recommended.

There are several studies of pinyon-juniper communities on isolated, "relict" geologic refuge sites. Large geologic refuges such as buttes and mesas have advantages and disadvantages when used to compare to mainland conditions (Milchunas and Noy-Meir 2002). An advantage is that the refuge communities have never been grazed by very large herbivores such as domestic animals, whereby potential shifts to alternate states due to historical very heavy grazing before scientific study can be eliminated as a potential confounding factor in present-day condition. On the other hand, these isolated islands can differ in abiotic conditions, fire frequency may be lower than the historical average because spread of natural fires to the isolated area may have also been inhibited, and in some cases the small mammal and even insect assemblages may be limited by dispersal capabilities. In other cases, a large size can allow good chances for lightning strikes and fire spread, and ease of accessibility to all but large herbivores can make these communities important for comparative purposes.

Baxter (1977) compared a 10 acre mesa in north-central Arizona to surrounding grazed sites that were either continuously grazed or under a rest-rotation system with an apparently lower grazing intensity. The mesa was accessible to rabbits, but fire was probably not common on this small, isolated area. Baxter states that he used to think blue grama was an important forage species of woodland sites where it often heavily dominates, and that many in the area think "blue grama has been the salvation of the rancher" in the southwest because other species had been eliminated by grazing long ago. Observations and measurements taken on the mesa show a plant community where the cool-season grasses mutton bluegrass and bottlebrush squirreltail make up 60 percent of the plant community, and blue grama only 7 percent. In contrast, the two cool-season grasses were not encountered on the continuously grazed site, and blue grama comprised 77 percent of species composition. Cool-season grasses and blue grama were equally abundant in the rest-rotation site (35 percent each). Forbs did not vary much with grazing treatments. Bare ground was 65 percent on the continuously grazed, 25 percent on the rest rotation site, and 8 percent on the mesa. A lack of juniper on the mesa was attributed to the competition from grasses, since fire was probably not a factor. Production was estimated to be about 100 g/m^2 compared to 10 g/m^2 in the grazed area. Biomass sampling appears very weak, but Baxter believed that there were very large differences between the three sites. The continuous versus the rest-rotation system comparison was confounded by also having differences in grazing intensity, and it was considered a "managed" versus non-managed comparison. The responses reported occurred over a 20-year period.

Schmutz and others (1976) studied another relict, geologic refuge area in northeastern Arizona. The 12 ha (30 acre) butte is protected from grazers by 150 to 350 m high sheer cliffs, so small mammal populations and fire may also be affected by the butte structure. Comparable grazed areas were not sampled, so only qualitative visual observations suggested "a marked contrast in luxuriance of growth of grasses on ungrazed" compared to "the typically overgrazed areas on the mainland." Plant communities were dominated by perennials, with almost no annuals. However, the perennials were species of low to moderate palatability similar to those on the mainland, which may be attributed to the shallow soils of the butte. Thatcher and Hart (1974) reached similar conclusions after studying another 40 acre mesa in northern Arizona. Some parts of the mesa had pure stands of grass and pinyon, juniper, shrubs, and very little grass in others. Differences could be attributed to soil types and fire frequency. Pinyon-juniper was dominant in the absence of fire regardless of soil type, but grass was abundant after fires only on the sandy surface-textured soils. Mandany and West (1984) observed very low herbaceous cover in a pinyon-juniper community on an ungrazed mesa in southern Utah. Johnson (1983) studied five ungrazed buttes and a grazed area in southern Utah and reported floristic similarity between grazed and ungrazed sites but that the grazed area had only one species of grass while each butte site had at least six. However, some of these buttes did not have similar small mammal and insect populations as found on the grazed mainland site. (See also the relict, geologic refuge studies in the Great Basin Juniper-Sagebrush savanna section below because of similarities with this community type.)

The overall conclusion from the studies of relict, geologic refuges never grazed by domestic livestock compared to grazed areas is that there are sometimes very large differences in species composition and species richness and other times there are not, and this may be attributed to soil type and fire history. In some locations, infertile shallow soils rather than past or current grazing abuse may be responsible for low coverage of herbaceous understory plants. More highly productive sites are more likely to show effects of grazing, which is consistent with qualitative and quantitative models at a global scale (Milchunas and others 1988; Milchunas and Lauenroth 1993).

There are only a few controlled studies on the effects of grazing on species composition of the pinyon-juniper type. This seems unusual given the extensive distribution and use of this type for grazing. Springfield (1959 cited in Springfield 1976) indicated that responses to grazing protection for 10 to 14 years depended on tree canopy cover. The effects of grazing were "negligible" when the canopy was greater than 30 percent, whereas perennial grasses increased "substantially" with protection when tree cover was less than 20 percent. This would suggest poor possibility for improving conditions in dense woodland by protecting them from grazing (Potter and Krenetsky 1967). Springfield did not suggest why this may have occurred, provide grazing intensity or distributions at the grazed sites, or indicate the prior condition of the exclosure(s). However, the common response to grazing worldwide (Milchunas and Lauenroth 1993) was observed, whereby short prostrate species increase with grazing and midgrasses such as sideoats grama increase with protection. Springfield also noted that annuals increased with grazing and the palatable fourwing saltbush decreased. While shrubs are more likely to increase worldwide with grazing (Milchunas and Lauenroth 1993), the highly nutritious and palatable C_3 shrub fourwing saltbush generally declines with grazing throughout its range.

Potter and Krenetsky (1967) and Krenetsky (1971) re-evaluated six exclosures at five different sites in the pinyon-juniper type 25 years after their establishment. These were the same sites examined by Springfield (1959 cited in Springfield 1976) after 10 to 14 years of protection (paragraph above). Potter and Krenetsky (1967) and Krenetsky (1971) analyzed and presented the same data differently. Potter and Krenetsky's (1967) analysis did not relate changes to differences in canopy cover as did the earlier Springfield assessment or the Krenetsky (1971) analysis. Language in the Potter and Krenetsky (1971) paper is confusing and not well defined, but apparently states that grass cover was "consistently" higher in ungrazed than grazed sites, with prairie junegrass becoming more abundant. Forbs may be slightly greater on grazed sites, and shrub cover as well as pine and juniper cover increased over time to a greater extent in grazed sites. Krenetsky (1971), in the more detailed dissertation, specifically differentiates between overstory cover and response to grazing, and he relates tree cover to elevation. Development of overstory cover was positively related to increasing elevation, as was also observed for the ponderosa pine type. Differentiating in this respect resulted in similar conclusions as those of Springfield; grass recovery was favored by protection when canopy cover was lower. This, however, was based on two low elevation sites where grass was significantly greater with protection, compared to three higher elevation sites with greater overstory cover where differences between grazing were not significant. Krenetsky (1971) placed some confidence in these findings because they appeared consistent in other vegetation types as well as in pinyon-juniper, but the response was strongest in pinyon-juniper vegetation. Krenetsky's overriding conclusion was that recovery of ranges by even complete protection must in some cases "be seriously questioned."

At a southeastern New Mexico pinyon-juniper site (precipitation 389 mm/yr), Pieper (1968) studied grazed (intensities not provided) and adjacent ungrazed sites for 12 years on loamy uplands and lowlands and a stony hills site. The loamy sites were open grasslands and the stony hills site had an overstory. Plant cover was not affected by grazing treatment on either loamy site, but it was greater on grazed sides of the fence on the stony hills site (possibly due to blue grama increase). In terms of compositional percentages, no statistically significant differences were observed on the stony hills site, and means were generally close. Some compositional changes were observed on the two loamy sites. On bottomlands that were probably relatively heavily grazed, blue grama and western wheatgrass composition declined with grazing while mat muhly increased. On loamy upland sites, mat muhly also significantly increased with grazing, while Carruther's sagewort significantly decreased and blue grama tended to decrease. At the same research station, Gamougoun and others (1984) estimated vegetative cover in exclosures to be 43 percent compared to 50 percent in moderately stocked treatment, 40 percent in heavily stocked, 35 percent in rested rotation pastures, and 36 percent in grazed rotation pastures. It is interesting to note that blue grama, a species that increases throughout Great Plains grasslands (Lauenroth and others 1994), sometimes decreases even in this area possibly influenced by bison grazing (see Fig. 3).

Long-term (40 yrs) protection from grazing was studied in northeastern Arizona and compared to areas moderately to heavily grazed with sheep and cattle (Brotherson and others 1983). This is a relatively dry site receiving only 290 mm/yr precipitation. Vascular plant and litter cover showed no differences among treatments, although bare soil cover was greater in grazed areas due to loss of cryptogamic crusts (see below). Trees, shrubs, and forbs had similar covers between treatments, but grasses were 2 ½ times greater on ungrazed compared to grazed areas. Some species increased in response to long-term protection (prickly gilia, brittle pricklypear, Indian ricegrass, longtongue muttongrass) and some decreased (slenderbush eriogonum, slender gilia, sandhill muhly).

There have been a couple studies of cryptogamic crusts of ungrazed and comparable grazed sites in the pinyon-juniper type. Beymer and Klopatek (1992) studied five sites in northern Arizona that ranged from a never-grazed relict, to sites not grazed since the 1930s, to sites currently grazed. Unlike findings from other communities, these authors reported that species presence was not related to the amount of grazing. Grazing reduced cover of cryptogamic crusts from 23 to 5 percent but did not result in loss of species. Brotherson and others (1983) studied cryptogamic crusts in northeastern Arizona in heavily grazed and adjacent ungrazed sites fenced for 40 years. Vascular plants were less affected by grazing than cryptogamic crusts. Mosses and lichens declined more than 80 percent with grazing, while algal and grass cover were reduced less than 60 percent.

Twenty-two species were sampled on the ungrazed treatment compared to only 8 on the grazed. These authors suggested periods of rest from grazing may enhance reestablishment. Ladyman and Muldavin (1996) reviewed the effects of grazing on cryptogamic crusts in a number of arid western communities and concluded that recovery times can be substantial. Grazing during periods of the year when crusts are more likely to be wet minimizes the impacts, and they are also less susceptible to damage in winter as well. However, climatic conditions in some parts of the pinyon-juniper range in the southwest are never conducive to mitigating grazing impacts on this sensitive part of the community.

Grazing by feral animals is an important factor in many parts and in many plant communities of the southwest. Feral burros were first observed in Bandelier National Monument in north central New Mexico in the late 1930s. A canyon that is a barrier to burro migration provided a comparison between burro-impacted and relatively ungrazed sections of the monument (Koehler1974). Large differences in condition of pinyon-juniper vegetation was observed on opposite sides of the canyon. Under very heavy grazing pressure, grasses occurred only under protection of Opuntia or dense brush cover. Common wolfstail, sideoats grama, and New Mexico feathergrass were among the species most sensitive to grazing, while blue grama, threeawn species, and ring muhly were the least sensitive. Heavily grazed sites showed a high degree of pedestalling of plant crowns and little reproductive output. Some use of ponderosa pine communities was also observed, but there was limited use of higher elevations, heavily forested areas, or steep slopes. Utilization of forages in heavily grazed sites was estimated to be up to 80 percent. Deer and trespass cows also contributed to the observed conditions. The effects of burro grazing on vegetation translated into impacts on bird populations as well, and these effects were most pronounced on foliage nesting birds, which showed a proportionately greater decline on burro-grazed compared to ungrazed areas of the park than other nesting guilds (Wauer and Dennis 1980).

The Kaibab Plateau in north-central Arizona is a mix of pinyon-juniper at lower elevations, leading to ponderosa pine, and then spruce-fir mixed conifer forest with aspen as elevation increases (Rasmussen 1941). For a large part of the 1900s the Kaibab deer eruption was cited as the classic example of predator control, herbivore population eruption, destruction of forage base, followed by population crash and decline to lower than historic levels (Rasmussen 1941; Leopold 1943; Kimball and Watkins 1951; Mitchell and Freeman 1993; Young 2002). Large numbers of mountain lions, wolves, coyotes, and bobcats had been killed in predator control efforts that were popular wildlife management techniques of that time (Rasmussen 1941; Mitchell and Freeman 1993; Young 2002). In 1970, Caughley argued that habitat and resource supply, not predation, is generally most likely to result in eruptions, which lead to much debate over the classic story involving predator control. Mitchell and Freeman (1993) conducted a review of the evidence for the Kaibab situation and concluded that the eruption was due to predator control (primarily mountain lion), removal of large numbers of livestock prior to the eruption and the release of the forage base, and a prohibition of hunting in an area that had traditionally been heavy hunted by Native Americans. They concluded that the decline of the deer herd was also due to multiple factors that included the extreme overutilization of the forage by the large numbers of deer, the effects of the new fire control efforts of the time on decreasing understory production, and a drought that coincided with the peak of the eruption. These are basically the original factors presented by Rasmussen (1941). Although removal of predators was one primary reason for the irruption, the historical simplification of the situation for textbook purposes and for a philosophical need at the time to emphasize the importance of predators as a component of the ecosystem rather than an evil led to the Kaibab herd becoming the classic story that it has become. Regardless of specific reasons, the Kaibab deer herd represents an unusual situation where a number of rapidly changing factors coincided to produce very large effects of a wild herbivore population on vegetation communities. It was estimated that 60,000 deer starved to death within an area of 2,980 km^2. Reports from the time indicate that juniper, pine, fir, spruce, and a variety of shrubs were severely utilized and damaged (Kimball and Watkins 1951). Leopold (1943) reported that the effect on winter food plants was very severe. Boone (1938) suggested the damage was so severe that there was a loss in carrying capacity of as high as 90 percent. Vegetation that was first observed to be in a downward trend in 1919 was not considered to have generally recovered until 1941 (Kimball and Watkins 1951).

Krausman and others (1992) conducted a followup to an earlier Leopold and others (1947) survey of "over-populated deer herds" in the United States. The Leopold survey identified nearly 100 herds, six of which were in Arizona and eight were in New Mexico. Of these herds, all were considered to be at or below carrying capacity in the 1980s, except for occasional or limited overbrowsing at the Kaibab north and Kaibab south ranges. However, the original Leopold term of over-populated as well as current terms concerning carrying capacity are now considered value laden and/or difficult to scientifically define.

There are several studies of grazing effects on species composition in the pinyon-juniper type. However, it is a widespread community type that varies greatly in species composition. Soil type, tree cover, and proximity to areas historically grazed by bison may affect level of response to grazing. Cryptograms generally show large declines with grazing. There is some evidence that increasing overstory cover can override grazing effects, but that in more open sites there is loss of species palatable to livestock and increases in annuals. Sites in proximity to areas historically grazed by bison may display less loss of overall cover due to increases in species with low growing prostrate growth form. However, even at these sites the soil type has influences on response to grazing. Blue grama may or may not increase with grazing, depending on site, even though it is a consistent increaser in Great Plains grasslands.

Primary Production

As with many other woodland types in the southwest, tree canopy cover can vary from dense to open savanna; precipitation in open stands is generally at the low annual average end and is at the high end in dense woodlands (Springfield 1976). Productivity can vary up to 50 percent with local soil types in northern Arizona (Jameson and Dodd 1969). Thatcher and Hart (1974) estimated production on a never-grazed relict in northern Arizona and found a range across soil types of 45 to 147 g/m^2/yr. Pieper (1995) found temporal variation in productivity ranging from 19 to 73 and 30 to 100 g/m^2/yr for locations over 12 years of measurement. Clary (1987) reviewed seven studies across a geographic range through Arizona and New Mexico and reported from 7 to 93 g/m^2/yr. Kruse and Perry (1995) studied mature old-growth stands and reported understory production of only 3 to 14 g/m^2/yr. There are extreme effects of overstory canopy cover on productivity; Jameson and Dodd (1969) report 58 g/m^2/yr when canopy cover was 2 percent to 10 g/m^2/yr when cover was 30 percent. Clary (1987) and Pieper (1995) reviewed the large number of studies on overstory-understory relationships. Increases in production after pinyon-juniper control ranged from 33 to 2900 percent based on six studies across eight locations (Pieper 1995). Springfield (1976) states that there are some stands, usually dominated by pinyon pine, so dense as to have practically no understory and have little or no value for grazing.

Because of the generally low forage productivity, increases in juniper cover and invasion into grassland and drier areas of ponderosa pine led to large numbers of conversion projects after World War II, which were and still are controversial (Gottfried and Pieper 2000). Springfield (1976) states that there is more information about control of pinyon and juniper than any other aspect of management of this community. Clary and others (1974) concluded that increased yields were not sustained long enough to make conversion economically justifiable. Recently, Ffolliott and Gottfried (2002) questioned earlier perceptions of "massive invasion" by trees. A site followed from 1938 to 1991 showed an increase of only 1.2 trees/acre, but large increases in tree crown diameter and height could possibly be misperceived as invasion. An additional alternative view is that invasion may not necessarily be into new areas, but just be a re-occupation of previously occupied areas (Gottfried and Pieper 2000). Conversion to improve livestock forage production or wildlife habitat is a human decision and action, not a direct or indirect effect of the grazing animal, so it will not be discussed in detail here. However, Lanner (1993) argues that conversion, which he terms "deforestation," 1) economically only breaks even in terms of forage production for even successful projects, 2) does not increase water yields as hypothesized, 3) does not reduce erosion, and 4) fragments habitat for wildlife rather than improves wildlife habitat because any manipulation of habitat is beneficial for some species and detrimental for others.

The effects of grazing on primary production of the pinyon-juniper type have been assessed both qualitatively and quantitatively, although data are very limited for both. Clary (1987) reviewed production values for grazed sites and separate independent sites that were not grazed (sites were not experimentally paired, but were from different studies), and estimated that ungrazed sites often produced more than 135 g/m^2/yr compared to generally less than 100 g/m^2/yr for grazed sites. Apparently based on ocular estimates, Baxter (1977) estimated production on a relict mesa to be approximately 100 g/m^2/yr compared to 10 g/m^2/yr on nearby grazing allotments.

There are only two quantitative studies of production in the pinyon-juniper type, and only one provides any statistical tests. Springfield (1959, cited in Potter and Krenetsky 1967 from the sites described above in Species Composition section) gave estimates for dense woodlands of from 20 to 26 g/m^2/yr in protected compared to from 13 to 25 g/m^2/yr in grazed plots. These values are very similar, as were differences between grazing treatments in species composition. However, in open pinyon-juniper sites production on protected sites was twice as much as on grazed sites. Pieper (1968) provides production estimates for 12-year-protected and grazed stony hill topographic sites of 63 and 53 $g/m^2/yr$, respectively, for loamy bottomland of 68 and 33 $g/m^2/yr$ and for loamy upland of 73 and 62 $g/m^2/yr$, for the respective treatments. All three protected vs. grazed comparisons were statistically significant. The large difference with grazing in production on bottomlands represents the relatively high grazing pressure in this topographic position within a particular pasture stocking rate. Other locations show small decreases in production with grazing. This site is in southeastern New Mexico, in an area possibly influenced by bison grazing.

Reproductive effort of plants is often used as an indication of condition or stress. In a review of this concept, Obeso (1993) found defoliation caused mainly reductions in the reproductive output of herbaceous perennials. Pieper (1968) measured the number of seed stalks per unit ground area in protected and grazed pinyon-juniper and observed significant reductions on loamy bottomland and upland sites, but not on stony hill sites. Stony hill sites were more heavily dominated by blue grama, and there were no differences in species composition between grazing treatments. Average heights of seed stalks were significantly lower in grazed compared to protected treatments at all three topographic sites.

No data were located concerning root responses to grazing in the pinyon-juniper type.

There are few studies to base conclusions on effects of grazing on primary production of the pinyon-juniper type. Available evidence suggests large declines in production in open-canopy juniper communities distant from the geographic range of bison, small declines in dense woodland, and relatively small declines in communities within the historic distribution of bison.

Soils

Grazing can affect both soil nutrient and water-holding capacity through influences on erosion of topsoil with reductions in plant cover and by decreasing infiltration rates through soil compaction. Soil organic matter can be lost through erosion as well, and/or inputs of carbon to soils can be reduced if primary production decreases or decomposition increases due to increased soil temperatures. While pinyon-juniper systems are generally nitrogen deficient, and sometimes phosphorus and potassium deficient, water stress more often limits plant growth (Gottfried and Pieper 2000). Very little data are available on grazing effects on soil nutrient or carbon levels in the pinyon-juniper type. Beymer and Klopatek (1992) did not find trends in soil organic carbon, texture, or pH over a five-site gradient from ungrazed to increasing grazing pressure. Grazed rather than ungrazed sites tended to have insignificantly higher soil nitrogen concentrations. Krenetsky (1971) found no consistent directional differences between grazed and ungrazed plots at five sites for soil texture, N, P, K, Ca, or Mg concentrations. Wilcox and Wood (1988) found only slight differences between two ungrazed and two lightly grazed sites in southeastern New Mexico; ungrazed sites had lower organic carbon and sand content. No differences were apparent between grazing levels and soil bulk density or soil depth. Organic carbon was also lower in exclosures compared to moderate or heavy continuous grazing or rested or grazed short duration treatments in central New Mexico at one site, but not at another (Weltz and Wood 1986).

Erosion in the pinyon-juniper type is highly variable both within and between geographic location (Gottfried and Pieper 2000). Within site, movement of water and soil is least under trees where litter buildups produce micro-topographic hummocking, and greatest between trees where there can be less cover and greater compaction by livestock and wildlife. Between sites, observations from studies are often inconsistent (see review in Gottfried and Pieper 2000). Davenport and others (1998) proposed a threshold model that operates very differently under different site conditions to explain the reason why some pinyon-juniper systems are undergoing accelerated, heavy erosion, others are undergoing little or no erosion, and few intermediate cases exist. On sites with high soil erosion potential (due to climate, soil type, geomorphology), erosion rates are very sensitive to even small changes in cover. Conversely, increasing site erosion potential has little effect on erosion under high cover, but under low cover erosion rate is very sensitive to increasing site erosion potential. The tree component can be important in contributing to the threshold through its influence on understory cover. Grazing can lead to threshold conditions directly by affecting understory cover, and indirectly by reducing competition for tree establishment or by reducing fuel-loads and tree mortality by fire, thereby further decreasing understory cover. Jameson (1987) also proposed a cusp-catastrophe model of alternative steady states for pinyon-juniper communities, where fire, grazing, and climate interact in producing the alternate states.

At locations where erosion rates have been high, reestablishment of understory cover is difficult (Gottfried and others 1995). Wildlife may be limiting seed availability through consumption, and eroded soils are more xeric, nutrient poor, and warmer, thereby limiting seedling establishment. Gottfried and others (1995) indicate that simply eliminating livestock that contributed to the high erosion situation will not halt or reverse the problem because the system is currently driven by physical abiotic processes rather than by biological processes. This was evident from areas where livestock were removed in 1932 and 1943 and erosion continued to be high.

However, there are only a few actual studies of infiltration/erosion in pinyon-juniper communities. At a 384 mm/yr precipitation site in south-central New Mexico on fine-loamy soils, Gamougoun and others (1984) found greater infiltration rates in exclosures (ungrazed 30 years) than in continuous moderately or heavily grazed treatments, and the latter had greater infiltration than rested and grazed pastures in a rotation system. There were no differences between moderate and heavy grazing treatments. Sediment production was highly variable within and between years. Sediment production tended to be less in ungrazed exclosures than all grazing treatments in all three years, but it was significantly less in the ungrazed exclosure in all years only when compared to the grazed rotation pasture. Significantly less sediment production was observed in the exclosure compared to the continuous heavily grazed pasture in only one of the three years and was never statistically different between the exclosure and the moderately grazed pasture. At the same site during a fourth year of study, Weltz and Wood (1986) observed greater infiltration rates in the exclosure than any of the grazed treatments, and greater rates in moderately grazed than heavily grazed treatments. At a second fine-loamy site where the exclosure had been ungrazed since the turn of the century, infiltration rates were not different among ungrazed, moderately grazed, and a rested short duration pasture. The grazed short duration pasture showed much lower infiltration rates than any of the other three sites. At a site in southeastern New Mexico with 500 mm/yr precipitation and shallow gravelly loams to clay loams, Wilcox and Wood (1988) found 12 to 17 percent lower infiltration on ungrazed compared to lightly grazed slopes averaging a 50 percent steepness when soil was initially dry or wet, respectively. The difference was significant, however, only for the dry soil condition. Sediment concentrations were similar between grazing treatments for initially wet soil conditions, and only slightly higher with grazing for dry soil conditions. Sediment production values between treatments were similar to results for infiltration.

Fire-Grazing Interactions

Interactions between grazing and fire frequency and the effects on community structure in pinyon-juniper communities is similar to that reported in the ponderosa pine section above and will not be repeated here. Fig. 5 gives an overview of the history and role of fire in the pinyon-juniper community. Estimates of natural fire-return intervals for pinyon-juniper are rare and studies were in the upper border where it occurs with ponderosa (Gottfried and others 1995). Fire scars on pinyon are rare (trees are often killed), and junipers cannot be accurately dated due to numerous false and missing rings. Gottfried and others (1995) reviewed the available studies and give estimates of 11 scars over 200 years, a 20 to 30 year return interval, and a 15 to 20 year return interval.

Jameson (1987) considered not only grazing-fire interactions in driving alternative steady states in the pinyon-juniper type, but also the interaction between grazing and weather. Years of precipitation sufficient for tree establishment would be less common in ungrazed sites where grasses compete for soil water but more common when grazing removed the vegetation.

Grazing Management

As mentioned earlier, there is probably more research concerning control, conversion, and thinning of pinyon-juniper than any other aspect of management, use, or ecology of the system. While large-scale conversions are presently controversial from both ecological and economical standpoints, some modification is still considered a management option (Gottfried and others 1995; Gottfried and Pieper 2000). These authors suggest that clearing small, dispersed areas can create a mosaic of habitats that would increase diversity and abundance of large and small mammalian wildlife and birds, as well as increase forage production for livestock. Open areas should be designed so that the longest distance an animal could be seen across would be 182 m and continuous corridors of adequate width be maintained. In some cases, thinning and seeding with native understory species has increased ground cover and reduced soil erosion losses (Chong 1994, cited in Loftin and others 1995). Grazing should be deferred two growing seasons after either thinning, conversion, or seeding to allow plants to establish (Gottfried and others 1995).

Very little work has been done concerning different grazing systems on pinyon-juniper communities. However, given the potential in some of the communities for thresholds in erosion mediated by plant cover, the positive feedback mechanism for continued erosion once the threshold is passed regardless of a grazing factor, and the observations that some grazing systems that concentrate animals even for short periods can increase erosional losses (see soils section above), it would seem prudent to base all grazing management on maintaining critical cover at all times, regardless of the duration or frequency of rest periods following the grazing. Point-in-time grazing intensity maximums should be tightly regulated even if long periods of rest or deferment are scheduled in the future.

Several grazing intensity guidelines have been proposed for pinyon-juniper communities. Reynolds (1962) recommended 3 to 10 acres/AUM, depending on site condition and potential. Holechek and Pieper (1992) recommended 30 to 40 percent use of key species as a moderate intensity, with the high end being for sites in good condition or grazed during the dormant season. Holechek and Galt (2000) combine the shortgrass and the pinyon-juniper type together and use some guidelines developed by Bement (1969) for shortgrass steppe in the eastern Colorado Great Plains. Moderate in this case is 41 to 50 percent utilization, which is similar to moderate for shortgrass steppe (Klipple and Costello 1960; Bement 1969). A stubble height of 1.5 to 2 inches is an indicator of this level of use. However, there can be a major difference in the response of the dominant species in these two systems. Blue grama increases with even heavy grazing in the shortgrass steppe and in other grasslands of the Great Plains (Milchunas and others 1989; Lauenroth and others 1994), resulting in greater cover of vegetation and exploitation of soil volumes (Milchunas and Lauenroth 1989). The cover of blue grama and of total vegetation in some pinyon-juniper communities can decrease with grazing (see sections above). While Holechek and Galt (2000) state that observations of blue grama residues in New Mexico blue grama rangelands match those developed for shortgrass steppe by Bement (1969), differences in behavior of the dominant species in some pinyon-juniper communities should raise caution in applying blue grama stubble height as a guide and using similar estimates of what "moderate grazing" entails. Holechek and Galt (2000) provide guidelines for conservative and light to non-use grazing intensity categories representing 31 to 40 percent and 0 to 30 percent utilization. Their "conservative" level would be similar to a lower range moderate in shortgrass steppe and may better apply as moderate in those particular communities where vegetative cover declines with grazing. Paulsen (1975) states that most range managers consider use of more than 40 percent of forage grasses to be detrimental, and he recommends leaving one-third of the culms ungrazed at the end of the season. This is similar to Holechek and Galt's (2000) conservative level of grazing, where one-third to one-half of primary forage species show use on key areas.

Humphrey (1955), Paulsen (1975), and Springfield (1976) also recommended resting areas that are in poor condition every summer, fair condition range every other summer, and good condition range every third summer. Springfield (1976) indicates that some system of seasonal use in conjunction with deferment is preferable to year-long grazing. The grazing system should allow for rest for both cool- and warm-season grasses, and guidelines for timing to accomplish this are provided in Springfield (1976). This author reviewed the potentials for using controlled burning as a management tool.

Humphrey (1955) provides indicator species for good condition range as black, blue, and sideoats gramas, Indian ricegrass, junegrass, western wheatgrass, and galleta, and those for poor condition as ring muhly, blue grama, sand dropseed, snakeweed, pingue, and rabbitbrush.

Madrean Woodland

Precipitation in these communities exceeds 400 mm/yr, of which half to two-thirds falls during the growing season (Brown 1982; Ffolliott and Guertin 1987; Gottfried and others 1994). Ffolliott (1999a) gives general ranges of 300 to 560 mm/yr, and up to 800 mm/yr in some locations. There are 12 habitat types in the southwest, and they generally occur on thin soils, rocky slopes, and along drainages (three major types are described in the Plant Community Descriptions Appendix 1). This characteristic could make them susceptible to erosion when grazed. Because the dominant trees are hardwood oaks, important uses of these communities includes fuelwood and fenceposts. However, silva-pastoral management is considered of particular importance in these woodlands. The history of land-use in these communities is similar to that of the pinyon-juniper type, but some areas were settled somewhat later due to their more mountainous terrain (Ffolliott 1999a). McClaran and others (1992) reviewed the history of settlement in this plant community and came to a similar conclusion concerning terrain, but they also concluded that Indian attacks prevented ranch establishment until chief Geronimo surrendered in 1886. Nearly three-quarters of these communities are part of the Coronado National Forest and were closed to settlement between 1902 and 1910. Most grazing occurred in lower desert grasslands until the mid to late 1930s, when state and federal programs developed stock-watering facilities and fencing.

Extremely little is known of the effects of grazing by domestic livestock in Madrean woodland. There are few controlled quantitative experiments and even very little qualitative descriptive information. Little is even known in terms of silviculture practices (Gottfried and others 1994). Large-scale range improvement practices have generally not been undertaken in these communities (Ffolliott and Guertin 1987). However, grazing is an important land-use (McClaran and others 1992; Ffolliott 1999b), and Humphrey (1960) considered these communities as providing "some of the best grazing in the state." Brown (1982) considered it the "principal biotic community for the white-tailed deer." An estimate of herbaceous production may be obtained from Caprio and Zwolinski's (1994) data of litter plus plant biomass, because they sampled 10 months after burning (litter removed and plants grew for 10 months). These data indicate levels of herbaceous production of 108, 150, and 136 g/m^2/yr on south, east, and north slopes, respectively. Standing biomass of herbaceous understory can be very large; Haworth and McPherson (1994) gives estimates of from 800 g/m^2 within tree canopies, more than 1200 g/m^2 2 m from canopy edge, to over 1500 g/m^2 in interstices between trees. Natural Resource Conservation Service gives estimates of production from 22 to 34 g/m^2/yr in mountainous sites to 112 to 280 g/m^2/yr in deep sandy loam soils of only 1 to 15 percent slopes and 20 percent canopy cover (Soil Conservation Service 1988 cited in McClaran and others 1992). Humphrey (1960) comments that this is a relatively productive range with adequate precipitation to support a variety of grass and shrub forage plants. Carrying capacity of range in excellent condition is about 10 to 15 animal units per section year-long.

While thinning overstory increases understory production in many systems, the effects of thinning oaks for wild or domestic herbivore forage may be small in this system (Haworth and McPherson 1994). McPherson (1993) reported increased forage production of 10 to 20 g/m^2/yr with canopy removal. Increases are short-lived due to rapid resprouting of oaks (McClaran and others 1992). Regeneration by sprouting after cutting can be highly variable, and reproduction by seed is episodic, whereby sustainability of coppicing is not known (Gottfried and others 1994). Extremely dense stands can hinder animal movement, and thinning of stands has been attempted to improve wildlife and cattle habitat (Clary and Tiedemann 1992). Animal weight gains increased 60 percent after clearing of oaks in southern Colorado (Marquiss 1972). Changes in species composition with cutting of Emory oak overstory were also small (Haworth and McPherson 1994). Ffolliott (2002) recommended that openings to improve livestock forage should be less than 15 to 200 m wide, but that these could improve insect abundance for wild turkey populations. Cutting of oaks in these communities is not always necessary to open stands, because tree densities naturally vary from few, scattered trees to over 150/ha, and grasses and forbs occur in savannah-like mosaics (Ffolliott 1985, cited in Ffolliott and Guertin 1987; Ffolliott 1999b). Herbaceous species canopy cover at a savannah-like site averaged about 60 percent, and grasses contributed a substantial proportion (Caprio and Zwolinski 1994).

Ffolliott (1999b) suggested that grazing may favor oak seedling establishment if competition with herbaceous species is reduced, but Phillips (1912, cited in Ffolliott 1999b) and Bahre (1977) suggested that poor regeneration from seed was due to livestock grazing. McClaran and others (1992) states there is no obvious difference between oak recruitment in ungrazed exclosures compared to adjacent grazed areas, and indicates this is different from the situation in less productive California oak communities. Humphrey (1960) also mentions that there was more grass and fewer trees in the past than there is today, but this could be due directly to fire thinning of young trees (McPherson 1992). Bahre (1977) and McPherson (1992) think tree density has decreased over the last century. In general however, fire favors oaks, but use for fuelwood, fenceposts and other types of construction can have impacts on their abundance (McPherson 1992). McPherson (1993) showed that seedling mortality was directly linked to belowground competition from other plants. Defoliation of plants growing in the field was a major cause of mortality, but defoliation in growth chambers was not. The majority of mortality due to defoliation was from invertebrates. Humphrey (1960) suggests that junipers have increased on some sites, but not as much as in other communities with junipers present. There does not appear to be a consensus in opinion concerning tree densities condition in these communities, let alone the direct and/or indirect effect of grazing. Cattle are generally not large consumers of the mature oaks themselves, although some consumption of Emory and silverleaf may occur in winter (McClaran and others 1992).

In some cases the increase in pinyon and junipers has been reported to be substantial. Tolisano (1995) indicate an increase from 20 to 40 percent, with decreases in Madrean woodland communities over a nearly 30 year period in Apache National Forest. Some quantitative data on range condition were collected between 1962 and 1968 and again in 1993 to 94. Intermediately, cattle were removed from one grazing allotment in 1983. A comparison of the 10 year ungrazed and adjacent grazed allotments indicated some recovery of tall bunch grasses and cool-season grasses and increased grass and forb diversity for one-third of the study plots (Tolisano 1995). One-third of the plots showed no trend in recovery, and one-third showed some declines in cover. The author indicated that some deterioration of the range may have occurred between the time of the initial sampling and the removal of cattle but concluded that a century of rest from grazing had not resulted in large improvement, suggesting a very slow recovery that may take centuries.

Humphrey (1960) described range condition classes as follows: Excellent - perennial grasses make up 90 percent of plant cover; plants are "vigorous" and there is no erosion. Good - understory is primarily good-forage grasses and low-shrubs, but there are more oaks and bare ground present, which could be improved by thinning of oaks with no reduction in stocking rate. Fair - density of perennial grasses is low and plants are small, producing few seeds, and there are patches of bare ground. Poor - forage production is 25 percent of range in excellent condition, perennial grasses are replaced by annual grasses and weeds (colonizing ruderals) and unpalatable shrubs, and erosion is evident and can be severe. Ranges in poor condition should be left ungrazed for 3 to 5 years, or grazing should at least be discontinued during July through September with grazing intensities reaching no more than 50 percent by this time. Carrying capacity of cows for range in poor condition is reduced by a quarter. Holechek and Pieper (1992) recommend 30 to 40 percent utilization of key forage species as a moderate grazing intensity. Brown (1982) also commented on bare ground as an indicator of very heavy grazing of these communities, although Ffolliott and Guertin (1987) suggest similar or lower erosion potentials in these systems as for pinyon-juniper communities, based on observation. The characteristic steep slopes and thin soils on which these communities are commonly found would suggest high erosion potentials should soil become unprotected due to loss of vegetative cover.

Actual grazing intensities reported in 1991 on the 150 allotments in Coronado National Forest averaged 35 to 55 percent utilization of herbaceous understory vegetation (McClaran and others 1992). This was 3.8 acres/cow/month, or 2.5 acres/cow/month if unsuitable steep slopes were removed from the grazable area. Yearlong or seasonal grazing was the most common grazing practice at this time, although two or three-pasture rest-rotation systems were becoming more common. There are no data to base conclusions on as to whether the grazing systems improve range condition or not. Ffolliott (2002) suggested a maximum forage utilization of 35 percent in areas managed for Merriam's turkeys and that grazing be deferred until September 1 in high density brood habitat.

Grazing can reduce fuel loads in terms of herbaceous canopy and litter biomass and can affect site productivity, thereby influencing fire regimes. There is evidence that oak woodlands were historically a part of a fire chain, whereby fires started in lower elevation grasslands spread through oak woodlands and into higher elevation mixed-conifer forests (Bahre 1991). In this case, heavy grazing of fuel loads and fire suppression in lower elevation grassland affected fire regimes of neighbor communities. However, McPherson (1992) and Bennett and Kunzmann (1992) comment that the absence of reliable data make it difficult to estimate fire frequencies. However, Swetnam and others (1992) conducted fire-scar studies in southeastern Arizona oak-pine woodland and estimated a mean fire return interval of 3.9 years for any one tree, and 13.2 years for fires scarring 25 percent of the trees. They concluded that surface fires occurred every 1 to 38 years up until 1890 when livestock grazing became an important landuse. Caprio and Zwolinski's (1994) study of fire effects in Madrean woodland show large effects on species composition. Woody species were reduced and grasses and forbs increased after an initial depression. Oak species resprouted well after fire but had about a 15 percent mortality. The rapid accumulation of fuels in these communities suggest a potential short interval between fires of 1 to 2 years prior to fire suppression and grazing by livestock.

There are no controlled grazing studies to base any conclusions concerning effects of livestock in these communities. However, the qualitatively described switch from perennial grass dominated vegetation to annuals with heavy grazing pressure, and the potential for large areas of bare ground to develop and erode, would suggest this is not a system well adapted to heavy grazing. Productive communities with a long evolutionary history of grazing can display a rapid switching from perennial tall grasses to perennial short "sod grasses" with changes in grazing pressure over short periods of time, and semiarid communities with a long history of grazing can display increases in basal cover of prostrate, grazing tolerant, perennial short grasses (Milchunas and others 1988). While blue grama is a dominant in the latter, nearby shortgrass steppe communities and can be a component of Madrean woodland communities as well, it is interesting to note that genotypes of blue grama here may not respond to grazing as they do in shortgrass steppe (Milchunas and others 1989; Milchunas and Lauenroth 1989) or blue grama may not be present in sufficient quantities to detect a response at the community level.

Great Basin Juniper-Sagebrush

Some of the general literature overlaps when differentiating between pinyon-juniper woodlands and Great Basin juniper-sagebrush community types, and between Great Basin juniper-sagebrush and Great Basin sagebrush shrubsteppe, or between Great Basin sagebrush shrubsteppe and Intermountain sagebrush steppe. In the case of the former, sagebrush is an important component of one but not the other, but pinyon-juniper is sometimes applied regardless of understory components. Schmutz and others (1967) considered their study site "borderline between the sagebrush northern desert shrub and the pinyon-juniper," although the site is dominated by sagebrush. In the case of the middle, relative amounts of the overstory can determine the classification, and juniper and pinyon can invade Great Basin sagebrush shrubsteppe (Ellison 1960; Rowlands and Brian 2001). Community analysis of a Great Basin juniper-sagebrush and a Great Basin sagebrush shrubsteppe suggested that the classification is based primarily on just the absence/presence of pinyon and juniper. In the case of Great Basin sagebrush shrubsteppe and Intermountain sagebrush steppe, West (1983a) states that, because of structural similarities, the two types have often been combined in reviews, but the more arid Great Basin sagebrush shrubsteppe reacts to disturbance more like a desert and the Intermountain sagebrush steppe more like a semi-arid grassland. However, because of these gradients and some similarities between pinyon-juniper, Great Basin juniper-sagebrush, and Great Basin sagebrush shrubsteppe, and because of lack of abundant data for all, cross referencing between the three types covered in this review and outside reviews of Intermountain sagebrush steppe may be helpful to the reader. Specific to this review, abiotic conditions, primary productivity, and grazing management for this community are covered in the general references contained in the pinyon-juniper section above or the Great Basin sagebrush shrubsteppe section below.

There are only four studies of grazing effects in this community type at three locations. Jameson and others (1962) studied a large 1,430 acre mesa in northwestern Arizona in 1958, and Rowlands and Brian (2001) returned to the same mesa in 1996. The mesa is grazed by deer but is inaccessible to livestock. Jameson and others noted that fires had occurred long ago, that trees would dominate nearly 90 percent of the area were it not for fires, and that burned areas were not rapidly reinvaded by trees. Pinyon density was increasing some, as evidenced by the presence of seedlings and young trees. However, junipers were mature and even-aged. This indicates a direct effect of fire on the tree component and suggests that the lack of grazing may slow invasion by juniper but not necessarily pinyon. Deer grazing was "appreciable" but generally did not cause severe damage to the vegetation. Muttongrass was the dominant grass of the mesa but was not reported in studies on the mainland. In contrast, blue grama was the dominant on the mainland but was in very low abundance on the mesa except on hard shallow soils. Rowland and Brian's intensive sampling revealed that the cover of most species had remained stable over the 38 year interval since the Jameson and others study. However, a few changes were noted. Muttongrass had increased, while Torrey jointfir, prickly pear cactus, and snakeweed had decreased. Sagebrush, juniper, and pinyon pine showed no change.

Daddy and others (1988) compared an area protected from grazing for 21 years with moderately and heavily grazed areas in northwestern New Mexico. The measurements were quantitative, but statistical power was poor, whereby differences reported as not significant may be due to high variance. Excluding large herbivores did not retard woody plant growth. Big sagebrush did not differ between treatments but appeared more "luxuriant" in the exclosure. West (1983a) also commented that sagebrush dominates Great Basin sagebrush shrubsteppe communities even when they are pristine or near-pristine sites. Daddy and others do not give data for juniper. Total herbaceous cover and biomass were greatest in the moderately grazed treatment, primarily due to large amounts of galleta. Because the sites were not grazed during the year of study, end of season biomass values can be used as estimates of primary production. Protection for 21 years did not result in increases in production, as values were 19, 50, and 25 g/m^2/yr for the exclosure, moderately, and heavily grazed treatments, respectively. Precipitation at this site is only 200 mm/yr. Blue grama tended to increase with increasing grazing intensity, but differences were not significant. The heavily grazed treatment had a large proportion of opportunistic ruderals (three-awns) and exotics (cheatgrass, *Bromus tectorum*). Species diversity was greatest in the moderately grazed treatment and similarly lower in the heavily grazed and ungrazed treatments.

There were no differences among grazing treatments in root biomass. However, root distribution was deeper in the exclosure, where only 40 percent of the biomass was in the 0 to 40 cm depth compared to 80 percent in the grazed treatments. Soil water content was lowest in the heavily grazed treatment and highest in the moderately grazed. The heavily grazed treatment was driest near the surface.

Pinyon-juniper communities in Grand Canyon National Park were heavily impacted by feral burro grazing. Bennett and others (1980) noted reductions in palatable perennial grasses, seed production, total plant cover and density, and plant diversity in both richness and evenness components.

These very limited number of studies suggest large effects of protection from grazing on species composition but little effect on recovery of production. West (1983a) also commented that damage to the somewhat similar Great Basin sagebrush shrubsteppe is much less reversible, and manipulations less successful, than for the more mesic Intermountain sagebrush steppe.

Interior Chaparral

Chaparral of the southwest is located almost exclusively in a discontinuous strip across central Arizona and occupies only 13,000 km^2 (Cable 1975). Mean annual precipitation averages about 480 mm/yr in the center, with a range from 480 to 635 mm/yr. Approximately half the precipitation falls from May through October. Chaparral is found on coarse soils, particularly on steep slopes, where precipitation is equally divided between summer and winter (McGinnies and others 1971, cited in Cable 1975). Heavier soils are occupied by grassland, and grazing can favor invasion of chaparral into grassland. Oak woodland occurs under similar environmental conditions but where there is more precipitation. Shrub live oak is from 45 to 80 percent of the total shrub cover, which varies from 25 to 80 percent with increasing elevation and precipitation Cable 1975). Herbaceous understory species are sparse where the overstory cover is high. As with the pinyon-juniper type, there have been some attempts to thin overstories in order to increase forage production (Reynolds 1962, Cable 1975). Root-plowing is most effective and fire or herbicides are not effective means of shrub control. In the past, exotic species such as Lehmann lovegrass or crested wheatgrass have sometimes been seeded after shrub control efforts. Productivity of the herbaceous understory can increase from near zero when shrub cover is 30 percent or more to about 200 g/m^2/yr where shrub cover is 5 percent or less (Pond 1961, cited in Reynolds 1962). Reynolds (1962) list the more important uses of chaparral as wildlife habitat and rates this community very low for range production.

The history of grazing by domestic livestock is a little different for the chaparral than for other community types because of the rough topography (Cable 1975). The first cattle were brought in 1874, and most of the chaparral was stocked within 10 years. Early reports were that the shrub stands were quite open with productive grass cover between (Croxen 1926 cited in Cable 1975). Livestock numbers peaked in 1900 at about 15 to 20 times the number present in 1926 when numbers were reduced to the approximate carrying capacity. By 1926 chaparral was dense shrub stands with only a small proportion of the previous grass production. McGinnes and others (1941, cited in Cable 1975) also commented on the change from open shrub with good grass cover to dense shrub with little herbaceous cover over 30 years due to fire and excessive grazing. As a result, there has been invasion of this community type into adjacent types and loss of perennial grasses such as blue, black, hairy and sideoats gramas, dropseeds, threeawns, curly mesquite, bluestems, and wolftail. Grazing of chaparral today is primarily by cattle, but goats were an important component as late as 1942 (Cable 1975). Rigden and Parker in 1943 commented that as many as 250 goats and 10 cows per section (259 ha) grazed many chaparral areas year-long, and that this intensity of grazing resulted in mortality of perennial grasses and was not sustainable. Goats are browsers while cattle are generalist grazers. Dual grazing by goats with cattle would tend to balance grazing pressure, with goats utilizing more of the shrubby component. The two-animal system was economically beneficial (Cable 1975).

Grazing of goats in chaparral can, however, have some undesirable consequences as well. Severson and Debano (1991) studied four stocking levels of goats in a short duration grazing system for four and a half years. Total shrub cover was lowered by goat grazing at heavy (38 percent cover), moderate (39 percent), and light (35 percent) stocking densities compared to unstocked controls (51 percent cover). A shrub-crushing treatment further increased the effectiveness of the goats. However, shrub species not preferred by the goats were not affected, and neither were perennial understory species. Annual grasses increased due to soil disturbance by either the hoof action of the goats or the mechanical crusher. Lower amounts of litter were found between shrubs, and this translated to lower soil organic matter levels. Concentrations of N and P were also lowered under some shrub species and soil bulk densities increased. Shrubs preferred by goats were also those preferred by deer, and heavy browsing of nitrogen-fixing shrubs could eliminate these, lower forage diversity, and possibly lead to increased nutritional stress for wildlife. The lower litter accumulation and reduced tissue quality was thought to have potential long-term effects on stability of the system by affecting decomposition processes. This and two other goat browsing studies in Arizona suggest limited success in using goats to control shrubs in chaparral. Goat browsing of gambel oak was found to not be a useful control measure in ponderosa stands in southern Colorado unless combined with other mechanical treatments, suggesting that this may apply to other communities as well. Shrubs are a very important component of deer diets in chaparral, but little information exists on their impact on the plant community (Urness 1981; Wallmo and others 1981).

Rigden and Parker (1943) emphasized the need to balance carefully the numbers of goats and cattle in relation to the proportions of shrub and herbaceous forage. They also conducted one of the few exclosure experiments in chaparral, for five years on two ranches grazing both cattle and goats and for two years on an additional goat only ranch. Perennial grasses increased with time of protection from grazing. Half-shrubs also increased with protection, but the ruderal half-shrub snakeweed decreased slightly even though it increased over time in the grazed treatments. Browse increased slightly under protection from grazing only at one site. While very heavy grazing can kill shrub species, the usual impact under less intense grazing is to gradually shift species composition from a mix of palatable/unpalatable species towards a dominance of unpalatable species. Less palatable species include scrub live oak and manzanita, and palatable shrubs include cliffrose and desert ceanothus. Rigden and Parker (1943) also mention that heavy grazing and brush fires reduce the litter layer and soil organic matter, thereby resulting in dryer conditions that will not support a good grass cover. Grasses dependent on heavy summer rains that come as large events. These events produce more runoff if a good litter cover is not present. In contrast, deep rooted shrubs are favored by winter precipitation that comes as small events but that accumulates through time deep into the soil profile.

Rich and Reynolds (1963) compared watersheds moderately grazed (40 percent utilization) and heavily grazed (80 percent utilization) to sites ungrazed for 9 to 12 years. Perennial grasses and half-shrubs declined in composition with heavy grazing, cacti increased, and shrubs did not appear to respond greatly. The moderately grazed watershed was generally similar to ungrazed sites, with perennial grass and half-shrub composition slightly higher than the ungrazed sites. Data were presented in terms of composition as a percent of total, so actual quantities are not known from the data presented.

A range condition classification for chaparral was developed by Rigden and Parker (1943) as follows:

- “Good. Perennial vegetation cover 1/3 to ½ of ground surface; blue, hairy, sideoats, and black gramas compose 20 percent of all vegetation; shrubby buckwheat and menodora plentiful; shrubs compose about 70 percent of all vegetation; most palatable species such as Ceanothus, Garrya, and mountain-mahogany in healthy growth; use on scrub oak light.
- Fair or Unsatisfactory. Perennial vegetation usually covers 1/5 to 1/3 of ground surface. Grama grasses compose less than 10 percent of vegetation but increase of 3-awn grasses may raise total to 20 percent; half-shrubs such as snakeweed increasing; may comprise 20 percent of vegetation. Palatable shrubs disappearing from range.
- Poor or deteriorated. Vegetation usually covers less than 1/5 of ground surface. Perennial grasses including 3-awns absent or confined to protection of shrubs and rocks. Soil unstable, erosion active, no litter. Increase in snakeweed and pricklypear. Hillsides covered with prominent pattern of criss-cross livestock trails and trampling excessive. Shrubs dying out with many dead and half-dead plants.
- Spring annuals such as filaree will occur in all condition classes but not dependable every year for forage.”

Humphrey (1960) also described range condition classes for chaparral in the somewhat more productive southern ranges. In addition to the generalizations given by Rigden and Parker (1943) above, Humphrey suggests burning as a means of killing manzanita while leaving large oaks for shade. This author also suggests stocking steep slopes at lighter rates and very steep slopes left ungrazed. Ranges in poor condition should be left ungrazed for a two to three year period, or at least deferred during July, August, and September leaving at least 50 percent of the grass production as residual.

A rotation-deferred grazing system was described by Freeman (1961) whereby one or more pastures are rested during the growing season and use of other pastures is rotated. Although there were no data, the grazing system was reported to have improved range condition and grass production. Salting a good distance away from watering locations was an additional important aspect in recovery of especially degraded areas near water. Yearlong grazing is often practiced in the chaparral because shrubs provide some winter forage and grasses summer forage, and because weather is mild throughout the year (Cable 1975). Suggested grazing intensities range from 40 percent utilization of perennial grasses to 30 to 35 percent of current-year twig growth of shrubs.

Mule deer are the common deer species of chaparral, but Coues white-tailed deer can be locally abundant (McCulloch 1972, cited in Wallmo and others 1981). Wallmo and others (1981) reviewed literature on densities of deer in chaparral and reported 4 to 5 deer/km^2 usual, with local densities that reached 20 to 30 deer/km^2. All shrubs except possibly pringle manzanita were found in diets, but effects on the plant community are generally not known.

Runoff and erosion on ungrazed (9 to 12 yrs) and moderately and heavily grazed watersheds were estimated by Rich and Reynolds (1963). No significant effects of grazing were found for water yield, and differences among treatment means were small. Sediment trapped was so variable that differences among grazing treatments were not significant. Slopes in the study watersheds were moderate. The authors concluded that reductions in densities of perennial grasses must be severe in order to change runoff from subsurface to surface phenomena. However, Humphrey (1960), Freeman (1961), and Rigden and Parker (1943) mention grazing-induced erosion in relation to range condition. Rigden and Parker (1943) even use the terms "erosional pavement is pronounced" and "grasses are distinctly pedestaled" in relation to poor or deteriorated range condition class. Water yields generally increase following conversion from shrub to grass (Cable 1975). Increases are attributed to reduced transpiration from deep rooted shrubs compared to shallow rooted grasses. Erosion following fire that removes the shrub and litter cover can be extensive, but sediment movement declines sharply as cover recovers and returns to the normal small amounts about four years after the fire (Pase and Ingebo 1965, cited in Cable 1975).

The role of fire and grazing by fire interactions in chaparral may not be as important as in many other southwestern communities. Shrub cover in chaparral recovers rapidly after fire with only minor changes due to prolific seedling establishment of fire-scarified seed or by sprouting (Paulsen 1975; Cable 1975). Cable suggests that fire is an advantage to the shrub component after a short period when grasses and forbs are favored. Knipe (1983) noted that the only shrubs killed by fire were manzanita and desert ceanothus, but that fire stimulated germination of their seeds. Because other means of shrub conversion, such as root plowing, are not feasible over much of the rugged terrain and rocky soils this community occurs on, Knipe (1983) assessed the possibility of using goat browsing following burning and seeding of range to trample seeds into the soil and utilize new shrub sprouts until the grasses became established. The system of fire and timed grazing was more successful than fire alone. Trampling of the seed into the soil and the use of a wider range of vegetation than that used by livestock and wildlife were considered positive aspects of the treatment, although heaviest use was of species preferred by cattle, deer, and elk. Desert bighorn sheep may act similarly, but numbers may not be great enough to have much of an impact. Krausman and others (1989) found that diets of desert bighorn sheep contained a large browse component, and that diet overlap was insignificant among the bighorn sheep, desert mule deer, and feral burros.

Rigden and Parker (1943) made a very important point concerning the balance between the way a shift in the half summer and half winter precipitation pattern could favor grasses versus shrubs respectively. Mediterranean climates favor deep rooted shrubs due to over-winter storage of soil water that can accumulate deep in the soil profile in the absence of large surface-evaporative and surface transpirational demands. Annuals are also favored in this type of climate because they can rapidly utilize stored water in spring before the perennials are active. Severson and DeBano's (1991) observation of increased annuals with grazing may not have been due to hoof action as suggested, but could possibly be due to shifts in temporal dynamics of soil water availability. Grazing in these systems can shift the balance, or they can create an alternate stable point if a successful shrub or exotic annual invades. This is evident in the case of cheatgrass and the conversion of California perennial grasslands to an annual dominated system. Both Rigden and Parker (1943) and Severson and DeBano (1991) consider litter and soil organic matter to control the balance in chaparral through their effects on soil water dynamics. Litter cover can rapidly be recovered with protection from or reductions in grazing pressure, but soil organic matter has fast, intermediate, and recalcitrant pools (Burke and others 1997). Recalcitrant pools can have turnover times in the hundreds of years, and loss of this pool through erosional processes could lead to an alternate stable point in ecological time.

There are insufficient studies in the chaparral to suggest whether a shiftable balance exists or whether an alternate state has been reached. Rigden and Parker's (1943) results show perennial grass recovery is possible, whereas Severson and DeBano (1991) results suggest that perennial grass may not respond. The latter is unclear since the consumption of some grass by goats may have countered the effects of shrub overstory reduction.

Subalpine Grassland

Subalpine grassland is associated with and interspersed through boreal forest with 500 to 1000 mm/yr precipitation, of which 150 to 250 mm/yr falls in the summer (Paulsen 1975; Turner and Paulsen 1976). Most of this community type occurs in Colorado, small amounts in New Mexico, and only a few isolated locations in Arizona. Herbaceous primary production ranges from 115 to 225 g/m^2/yr and can reach as high as 335 g/m^2/yr. There is very high variability in production from year to year within a site, and the grass component can vary from 35 to 62 percent of total vegetation. Along with the patchy distribution of the grassland within the forest type (see section above), this potentially makes it difficult to adjust stocking rates to available forage without grazing the community more heavily than desired.

Paulsen (1975) and Turner and Paulsen (1976) describe range condition changes associated with livestock grazing. Thurber fescue is an important component of the community, is sensitive to grazing, and may be replaced by other small bunchgrasses. Forbs and secondary grasses increase as Thurber fescue and Parry oatgrass decline. Unpalatable forbs and shrubs are more likely to replace palatable grasses with cattle grazing, whereas sheep grazing is more likely to result in a shift from palatable forbs to grasses. Total cover may remain similar in this early stage of range deterioration, and primary production and litter may decrease only slightly. In poor condition range, bare soil and erosion become more evident, and species composition becomes forb and shrub dominated. Costello (1944) observed Thurber fescue becoming the dominant species within aspen stands after prolonged heavy grazing eliminated preferred forbs and grasses. Moir (1967) suggested Kentucky bluegrass replaced Thurber fescue after heavy grazing. After protection from grazing, Paulsen (1970) observed increases through time in slender wheatgrass and butterweed groundsel and decreases in Letterman needlegrass and Fremont geranium. Based on this study, however, Turner and Paulsen (1976) suggested that protection from grazing for eight years had little effect on grass-forb composition.

Several studies of grazing effects in subalpine grassland have been conducted. A study in western Colorado conducted by Klemmedson (1956) must be interpreted with extreme caution. Study sites were chosen by following a "Range Condition and Site Guide" based on a listing of species thought to be increasers, decreasers, and invaders with grazing, and then various aspects of the vegetation and soil were measured. No indication is given of actual previous grazing intensities on the different sites. Studies such as this may be of limited use to confirm accuracy of condition guides based on species composition if soil type remained constant among sites, but this information is not provided either. Total vegetative cover declined from 48 percent for 'good' condition range to 42 percent for fair and 24 percent for poor, possibly confirming the use of Thurber fescue, *Carex* species, nodding brome, and sheep fescue as "desirable" species and a number of forbs and half-shrubs as "undesirable." Soil organic matter, degree of plant pedestaling, some erosion indices, and infiltration were also measured, all of which followed the predetermined condition classification.

In a similar situation again in western Colorado, Turner and Dortignac (1954) chose "six common plant-cover types which are readily recognizable by those directly concerned with the management of mountain grasslands." No indication is given of previous grazing histories of the sites or of soil types. The potential for different responses to grazing on different soil types is recognized. The authors' observations indicate that Thurber fescue is commonly replaced by Idaho fescue and needlegrasses with heavy grazing on coarse-textured soils, and by Kentucky bluegrass on fine-textured soils. The six community types studied were dense Thurber fescue, open Thurber fescue, bluegrass, needlegrass, lush-weed, and poor-weed. Over this gradient of community types, grass biomass declined from 228 to 21 g/m^2, while opportunistic ruderals increased from 48 to 125 g/m^2. Litter declined over the community gradient from 1148 to 57 g/m^2, while bare ground cover increased from 6 to 58 percent. Infiltration was slowest in the needlegrass and the poor-weed community and highest in the dense Thurber fescue. Erosion losses ranged from 9 g/m^2 in dense fescue to 490 g/m^2 from the poor-weed community.

One of the Potter and Krenetsky (1967) and Krenetsky (1971) exclosures in this type showed increases in Thurber fescue and Columbia needle-grass after 25 years. *Carex* species, Arizona fescue, and Kentucky bluegrass declined with protection. Forbs declined with protection, while increasing through time on the grazed site. Browse increased from 1939 to 1963 on both grazing treatments. Part of an aspen stand contained in the original exclosure increased inside but not outside the fence where sheep grazed, and the aspen stand in turn was displaced by a mixed conifer association. Overall, however, grass cover and total herbaceous cover increased through time more in the grazed area than the ungrazed, and this led Krenetsky to conclude protection does not speed grass recovery. This site was in good condition when the exclosure was built in 1939 and had been grazed by sheep.

A controlled but complex study of interactions between gophers and cattle grazing, and by a change from heavy to light grazing, was conducted on a mesa near Grand Junction, Colorado (Turner 1969). The area had been heavily grazed to the point where dense stands of Thurber fescue that were documented in 1889 had been replaced or obscured by sagebrush and orange sneezeweed. The area had also become heavily infested with pocket gophers. Condition of the site at the start of the study was described as very poor. Initial treatments included construction of replicated grazing exclosures and reduction in grazing intensity by one-half, and gopher control or no gopher control. Averaged over gopher treatments, grazed sites had beginning and 19-year-later grass biomass of 14 and 34 g/m^2 , compared to 15 and 40 g/m^2 beginning and 19-year-later biomass, respectively, for the ungrazed. The switch to light grazing had nearly as much of an effect as complete protection for grass recovery. For forbs, grazed sites had beginning and 19-year-later biomass of 63 and 49 g/m^2 compared to beginning and 19-year-later biomass of 67 and 49 g/m^2 for the ungrazed. The switch from heavy to light grazing in this case had the same effect as complete protection. However, sneezeweed production was reduced only half as much when heavy grazing was reduced to light grazing compared to heavy grazing being reduced to no grazing at all. Shrubs increased slightly on grazed sites and did not change from initial values on protected sites, but differences were not significant. There was an apparent gopher treatment by grazing treatment interaction, whereby grass recovery was greatest when gophers were present on ungrazed sites and grass recovery was least when gophers were controlled on grazed sites. Species composition changes were large. The 19-year protection resulted in initial and final values of 35 and 18 percent for Letterman needlegrass, 8 to 34 percent for slender wheatgrass, and both bromegrass and trisetum increased from 3 to 15 percent each. Forb composition did not change as much as grass species, but western yarrow was a decreaser and agoseris was an increaser. The improved conditions on ungrazed and lightly grazed compared with previous heavily grazed conditions were also evidenced by increased flower stalk height for many of the later seral stage species. The authors concluded that "deteriorated mountain grassland range may improve almost as rapidly under light grazing as under non-use."

A third study, conducted in western Colorado in moderately grazed areas with occasional heavy use, indicated that 8 years of protection had very little effect on plant community species composition. Deep rooted shrubs, and proportions of grasses and forbs, remained generally unchanged (Paulsen 1970). Thurber fescue was increased under protection.

Little literature exists concerning grazing management in this community. Paulsen (1975) suggests less than 40 to 45 percent utilization of palatable grasses. Forbs are more abundant earlier in the growing season and grasses later, whereby seasonal grazing can be used to vary pressure on these components. Palatable perennial grasses should be headed out, and soil sufficiently dry to avoid excessive compaction and trampling before animals are released onto the range in the spring. Although conducted in a Wyoming mountain grassland, a seven-year comparison of continuous grazing versus a rotational grazing system did not show conclusive differences (Pond and Smith 1971, cited in Turner and Paulsen 1976). Little is known of fire effects on this community, although fire tends to maintain grassland openings from tree encroachment (Wright 1971, cited in Turner and Paulsen 1976). However, this grassland is interspersed within the boreal forest type and White and Vankat (1993) estimated the natural fire return interval for boreal forest was 70 to 250 years. This is a relatively very infrequent fire return interval compared to lower elevation communities. Primary production may be increased when fire removes large buildups of litter in productive sites. Litter can regulate soil temperatures and therefore soil water dynamics, tie up nutrients, and provide a positive or negative microsite for seed germination depending on particular species requirements (Facelli and Pickett 1991). However, the effects of fire on primary production may vary with climatic conditions after the fire, whereby production may be increased when sufficient moisture is available or decreased when conditions are dry after the a fire (Turner and Paulsen 1976).

There is very little information to base general conclusions of the effects of grazing on subalpine grasslands. Based on qualitative, observational evidence, there would appear to be very large differences in condition classes ranging from poor to good. Actual experimental evidence for improving condition classes through changes in grazing management must be based on only three studies. These would suggest that a change in management from heavy grazing to either light grazing or no grazing gives similar results when initial condition is an early seral stage, and ranges in later seral stages initially may not change with complete protection.

Montane Meadow

This community type is closely associated with and interspersed among primarily the ponderosa pine and some mixed conifer types. Therefore, much of the information reviewed in the ponderosa pine section above is relevant to this community and will not be repeated here, particularly concerning overstory-understory relationships and primary production, tree encroachment, fire, and grazing management. This section will focus only on plant community response directly to grazing treatments. Small areas of this grassland among ponderosa pine can occur on the same soil types, but larger areas can be on different soil types than the adjacent forest (Klemmedson and Smith 1979, cited in Chambers and Holthausen 2000).

Species Composition

A shift to short, prostrate growth forms has throughout the world been associated with increased grazing, especially in systems with a long evolutionary history of grazing (McNaughton 1984; Milchunas and others 1988; Lauenroth and others 1994). Arnold (1955) observed similar changes in montane meadows of northern Arizona. A difference between the montane meadow and systems with a long history of grazing arises in the increase in weed (colonizing ruderals) or exotic species with grazing in the former (Arnold 1955; Johnson 1956) and the absence of weed increases in systems such as the shortgrass steppe or Serengeti grasslands (Milchunas and others 1988). Arnold considered indicators of deteriorated range condition in montane meadow to be closely associated with increasing composition of decreasingly desirable growth-forms from perennial tall grasses (redtop, timothy), perennial midgrasses (Arizona fescue, mountain muhly), perennial short grasses (black and pine dropseed, blue grama), perennial prostrate forbs (pussytoes, sandworts), short-lived unpalatable half-shrubs (snakeweed), to annuals (annual dropseed).

Quantitative studies in general somewhat support Arnold's classification, but there is not necessarily a linear relationship of increasing grazing intensity and the indicators described above. In a controlled replicated study in central Colorado (Manitou Experimental Forest), Johnson (1956) sampled 3 replicate blocks of meadows ungrazed 10 years, and 9 years of lightly, moderately, and heavily grazed treatments. Grazing was June through October, and the treatments represented utilization of approximately 0, 10 to 20, 30 to 40, and 50 percent or greater for the ungrazed, lightly, moderately, and heavily grazed treatments, respectively. The treatments were sampled for four years, the last of which was a drought year. Johnson (1956) observed similar species composition between ungrazed and lightly grazed treatments, and similar grass and colonizing ruderal compositions among ungrazed, lightly, and moderately grazed treatments (Table 1). Species composition on heavily grazed treatments differed considerably from the other three treatments. Species considered weeds (colonizing ruderals) were approximately 50 percent of the heavily grazed community and 25 to 30 percent of the other three treatments. For grasses, mountain muhly and blue grama dominated composition of the heavily grazed treatment while mountain muhly and Arizona fescue dominated the exclosures. Density was related to grazing intensity for most species. Sedges and rose pussytoes were most abundant in the heavily grazed treatment, and sedges and mountain muhly were most abundant on the ungrazed treatment (Table 2). Total density of all species was greatest in the heavily grazed treatment, but plants were smaller and the greater number may have been due to disintegration of originally large clumps. In many cases, species considered unpalatable were more abundant in moderately and heavily than in lightly or ungrazed treatments. Heavy grazing resulted in more prostrate, short plants with sod-like physiognomy compared to those in the ungrazed treatment. Colonizing ruderal seedlings of three of four species were more abundant on heavily grazed than ungrazed treatment. Smith (1967) reported on the same treatments initiated by Johnson (1956) but after 17 years of treatment. Plants were categorized into those favored by lighter grazing (mountain muhly, Arizona fescue, blue grama, bottlebrush squirreltail lupines, bearberry, and Arkansas rose), those favored by heavy grazing (tumblegrass, pussytoes, groundsels, and goosefoot), and those not affected (sun sedge and fringed sagebrush). However, the only species with greater cover after 17 years of heavy grazing compared to initial values were blue grama and goosefoot. In terms of composition, perennial forbs increased and perennial grasses decreased over the 17 years (Table 1).

At the same research station as the Johnson (1956) study, Currie (1976) assessed treatments of protection,

Table 1—Species composition (percent of total weight) of four grazing treatments in montane meadow communities. Treatments were initiated in 1941. Data for 1949 to 50 adapted from Johnson (1956), and 1940 and 1957 adapted from Smith (1967)

	Grazing treatment species composition (percent)										
	Heavy			Moderate			Light			None	
Species	**1940**	**’49-’50**	**1957**	**1940**	**’49-’50**	**1957**	**1940**	**’49-’50**	**1957**	**’49-’50**	**1957**
Grass											
Blue grama	2.8	16.2	7.7	4.6	7.1	9.8	1.3	2.1	5.8	1.3	
Arizona fescue	8.0	1.8	1.5	8.7	29.5	8.2	4.5	15.6	4.1	14.9	
Mountain muhly	20.8	20.1	14.6	17.2	26.9	15.4	19.1	30.4	19.4	45.0	
Other grasses		24.6			1.9			23		8.1	
Sedge	4.9	5.1	4.5	3.5	5.0	2.7	3.7	3.2	3.2	5.8	
Total grass & sedge	44.0	47.6	34.0	36.0	70.3	51.0	35.0	74.3	51.0	74.9	59.0
Weeds (ruderals)											
Rose pussytoes		22.4			6.5			8.6		3.9	
Nickleaf milkvetch		1.6			1.3			0.7		2.3	
Trailing fleabane		2.3			0.4			1.0		0.5	
Fringed sagebrush	14.1	14.2	16.1	13.3	7.0	12.1	10.2	2.6	11.3	12.3	
Other ruderals		12.2			14.5			12.9		6.1	
Total ruderals		52.4			29.7			25.7		25.1	
Perennial forbs	55.0	63.0		62.0		46.0	53.0		47.0		36.0
Total	99.0	100.0	97.0	98.0	100.0	97.0	98.0	100.0	98.0	100.0	95.0

alternate rest, or seasonal spring or fall grazing on montane meadow that previously had been heavily grazed season-long (June thru October) for 23 years. The experiment had three replicates and also included fertilizer and herbicide treatments in a randomized split-block design. The concentration of livestock in the meadow areas of the surrounding ponderosa pine range had led to dominance by unpalatable species. Grazing intensities remained at the previous heavy rate of 55 percent utilization. The study included a pre-treatment sampling year followed by four years of treatments and measurements. Total plant density was not affected by grazing treatments, and only two species responded to the grazing treatments. Pennsylvania and horse cinquefoil were greater in plots grazed in spring or season-long compared to the other treatments. Currie concluded that no season or system of grazing, including complete protection, was more efficient in promoting recovery of depleted range. Currie did not comment on why his results were different from those of Johnson (1956) at the same research station. Currie’s sites were described as previously depleted, while Smith (1967) described Johnson’s sites as at one time heavily grazed but does not indicate a depleted condition.

Table 2—Plant species density (number of individuals/0.93 m^2) of four grazing treatments in montane meadow communities. Treatments were initiated in 1941 and values are an average for sampling from 1949 and 1950, adapted from Johnson (1956).

	Grazing treatment plant density (number/plot)			
Species	**Heavy**	**Moderate**	**Light**	**None**
Grass				
Blue grama	30.1	24.0	5.9	7.8
Arizona fescue	2.0	8.8	4.0	12.7
Mountain muhly	38.8	37.0	29.0	25.9
Sedge	106.7	58.9	44.0	53.8
Weeds (ruderals)				
Rose pussytoes	60.3	32.1	21.4	10.0
Nickleaf milkvetch	3.2	4.6	2.2	6.1
Trailing fleabane	20.7	11.0	14.6	7.0
Fringed sagebrush	19.5	12.1	5.2	14.8

In Arizona montane meadows, Rambo and Faeth (1999) studied three paired grazed and 8 to 9 year ungrazed sites where consumption by cattle, elk, and deer was about 70 percent of standing crops. No consistent differences between grazing treatments were observed for the relative abundance of grasses, forbs, shrubs, or introduced exotic species. However, the method for estimating abundance was not presented (cover, density, biomass), and sampling too close to fence lines may have biased results. Some individual species and diversity responses were seen. Ungrazed sites had lower percentages of the abundant western yarrow,

Table 3—Primary production (g/m^2/yr) of four grazing treatments in montane meadow communities. Treatments were initiated in 1941. Adapted from Johnson (1956).

	Grazing treatment primary production (g/m^2/yr)							
	Heavy		**Moderate**		**Light**		**None**	
Species	**1949**	**1950**	**1949**	**1950**	**1949**	**1950**	**1949**	**1950**
Grass								
Blue grama	15.7	14.9	8.3	7.3	1.3	2.2	2.4	1.7
Arizona fescue	2.5	1.0	38.4	27.7	2.5	8.3	28.5	18.5
Mountain muhly	22.9	16.0	33.5	26.1	38.0	22.3	109.7	43.9
Other grasses	6.7	2.2	2.9	1.5	24.3	19.5	17.9	8.5
Total grasses	47.8	34.2	83.2	62.5	88.6	52.3	158.5	72.6
Sedge	5.7	4.1	4.8	5.9	5.7	1.3	8.9	8.2
Total grass & sedge	4.9	38.3	88.0	68.5	94.3	53.7	167.4	80.8
Weeds (ruderals)								
Rose pussytoes	19.1	22.9	9.9	4.9	8.5	7.6	10.0	3.6
Nickleaf milkvetch	2.4	0.8	1.6	1.2	0.9	0.6	4.1	2.9
Trailing fleabane	4.0	0.6	0.3	0.6	0.3	1.2	0.2	1.0
Other weeds	14.8	8.7	24.7	9.6	19.5	7.4	18.2	4.4
Total ruderals	40.2	33.0	36.4	16.3	29.3	16.8	32.5	11.9
Fringed sagebrush	14.6	14.9	7.3	8.1	1.5	2.9	22.1	15.9
Total	105.3	86.2	131.7	92.8	125.0	73.4	221.9	108.6

thereby increasing evenness. Species richness was greater on two of the three grazed sites.

Primary Production

Results from studies of primary production responses to grazing of montane meadows vary. For montane meadows in northern Arizona, Arnold (1955) reported primary productivity values declined in a nearly linear fashion with decreasing range condition from excellent to very poor (Fig. 4A). Very poor condition meadows supported only 21 percent the productivity of meadows in excellent condition. As noted in the ponderosa pine section, however, side-by-side plotting of the Arnold production values for montane meadows and openings between ponderosa pine trees gave similar and smooth curves, and it is not described how the sites were chosen or the data were collected. As described in the section above, early studies sometimes chose sites based on preconceived ideas of condition, and then sampled these condition classes. No indication of grazing intensity or history is given for the sites.

In the Johnson (1956) study described above, primary production of the heavily grazed treatment was 47 and 79 percent of the ungrazed treatment for the normal and drought year, respectively (Table 3). Grazing effects on total production were less under drought condition. The effect of drought on lessening differences between the heavier and lighter grazing treatments was also evident in grass and sedge production. The drought reduced primary production 28, 22, 43, and 51 percent from the previous year's level on the heavily, moderately, lightly grazed, and ungrazed treatments, respectively. Johnson suggested additional study to explain causes of this unusual result. Production in the normal year was generally heavy < light, moderate < ungrazed, while differences among means in the drought year could be attributed to variance in the data. Weed (colonizing ruderal) production was always highest on the heavily grazed and lowest on the ungrazed treatment. Decreased seed stalk production with increasing grazing intensity was observed for only two species (mountain muhly and little bluestem), and not for any other species sampled. After 17 years of treatment, Smith (1967) reported nearly five times the production of grass and sedge on protected versus heavily grazed meadows, while moderately and lightly grazed treatments were approximately 25 and 50 percent of protected areas. Smith concluded that light and moderate grazing maintained satisfactory production throughout the study, while heavy grazing resulted in increasingly reduced production.

In the Currie (1976) study of protection, alternate rest, or seasonal spring or fall grazing (see details above) there were no significant effects of treatment by year or main effect of treatment on primary production, and average range among treatments was low at 125 to 135 g/m^2/yr. Although protection or grazing seasons or systems did not promote recovery, fertilizer and herbicide treatments were effective in improving condition of depleted range. Again, Currie did not comment on why his results were different from those of Johnson (1956) at the same research station.

Rooting Characteristics and Soil Properties

Various aspects of root biomass and distributions and soil properties were assessed in the Colorado studies described above. Johnson (1956) found no significant differences among ungrazed, lightly, and moderately grazed treatments in aboveground to belowground ratios of little bluestem, Arizona fescue, or mountain muhly. However, the ratios were about 2.5 for heavily grazed treatment compared to 3.5 for the three treatments under lower grazing intensity. Heavy grazing reduced root biomass in the upper soil profile. After 17 years of treatment, Smith (1967) extracted root monoliths from the treatments to a depth of three feet. Root biomass in moderately grazed treatments was 84 percent of that in ungrazed, and heavily grazed was 68 percent of that in ungrazed treatment. Differences were due to the grass component. The vertical distribution of roots was shallower under heavy grazing intensity, with 81 percent in the top third of the profile in ungrazed treatment compared with 86 percent in the heavily grazed treatment. Lateral spread of grass roots tended to decrease with increasing grazing intensity, but differences were not significant. Lateral spread of fringed sagebrush and pussytoes roots was greatest under moderate grazing intensity. The diameter and strength of primary roots and the number of branch rootlets of mountain muhly and Arizona fescue decreased with increasing grazing intensity. In contrast, ungrazed and moderately grazed blue grama roots did not differ, but declined only with heavy grazing. Roots are the primary form of input of organic matter to grassland soils, whereby differences with grazing would eventually manifest as differences in soil carbon contents.

Infiltration rates on the grazed treatments were highly variable and generally did not change over the period of study. Results were clear only in the ungrazed exclosures, where rates were 116 percent of initial after 6 years of protection and 167 percent after 13 years. Erosion rates were measured only after 11 years of treatment. Erosion rates on lightly and moderately grazed treatments did not differ, but were 66 percent of those on heavily grazed treatment. Losses of root biomass and aboveground plant cover under heavy grazing were great enough to affect soil loss, thereby affecting potential recovery rates of the system even if grazing management changes were undertaken.

Overall, there are too few controlled studies of the effects of grazing on montane grassland to base any strong conclusions. The two strong studies that are available reach different conclusions possibly due to different initial conditions or to the length of the studies. Heavy grazing appears detrimental to the aboveground and belowground plant community and to soil properties.

Temperate Grassland

The temperate grassland group is a very large mix of communities in semiarid to subhumid environments and with short to long evolutionary histories of grazing (see History of Grazing by Native and Domestic Large Herbivores section above). With a long history of grazing by bison of the Great Plains, the shortgrass steppe which occupies the far-western part of New Mexico (Lauenroth and Milchunas 1991; Fig. 3) would be expected to be particularly tolerant of grazing by large herbivores, while other communities in this type that occur in conjunction with Great Basin communities would be expected to be sensitive to grazing (Mack and Thompson 1982; Milchunas and others 1988). Gosz and Gosz (1996) map of the Great Plains grasslands extends farther west than Lauenroth and Milchunas's (1991) map of the shortgrass steppe (Fig. 3), because of the influence of blue grama in plant communities farther west than what may be considered shortgrass steppe, but also because the Great Plains geomorphic province extends farther west than the shortgrass steppe biotic community (Sims and others 1978). Blue grama is the overwhelming dominant of the shortgrass steppe and one of the species that imparts tolerance to aboveground disturbances such as grazing or fire (Milchunas and others 1990). Blue grama may or may not respond similarly to grazing in different locations. The behavior of blue grama in response to grazing in different communities and locations is discussed further in the Conclusions section below. In this section, we start with assessment of the southern shortgrass steppe, followed by other communities dominated by short grass species, and then examine other plant communities, thereby attempting to organize the studies from long to short history of grazing.

Species Composition

The northern shortgrass steppe is among the communities most resistant to grazing in the world (see Fig.

Table 4—Plant biomass, functional group composition, and species composition based on biomass at an ungrazed or grazed southern shortgrass steppe site in western Texas. Adapted from Sims and others (1978) and Grant (1971).

	Ungrazed	Grazed
Biomass component	**Plant biomass (g/m²)**	
Live	70	86
Recent dead	33	33
Old dead	96	79
Total above ground standing crop	200	199
Litter	232	215
Crown	254	299
Roots in upper soil layer	530	668
Total roots	620	725
Groups	**Functional group composition (percent)**	
Warm-season grasses	75	69
Cool-season grasses	5	5
Warm-season forbs	7	2
Cool-season forbs	5	3
Cacti	10	22
Species	**Species composition (percent)**	
Blue grama	40.2	56.7
Buffalograss	1.2	2.4
Hedgehog cactus	0.0	0.0
Plains prickly pear	56.3	40.3
Prairie coneflower	1.9	0.0
Scarlet globemallow	0.0	0.5

13 in Comparison of Southwestern Communities with Great Plains Communities section below). However, some differences exist between the southern and northern shortgrass steppe, including greater precipitation, temperature, and aboveground plant production in the south (Sims and others 1978; Sims and Singh 1978a, b). In west Texas near Amarillo, the IBP Pantex southern shortgrass steppe site is included here because of its proximity to, and similar latitude of, New Mexican shortgrass steppe. Precipitation averages 499 mm/yr. A five-year-old exclosure was compared to heavily grazed communities where utilization of aboveground production was 65 percent. This is very heavy utilization compared with that generally given for other communities reviewed in this report but is similar to the 60 percent utilization for heavy grazing treatments in the northern shortgrass steppe (Milchunas and others 1989). Grazing treatments did not affect the composition of warm- or cool-season grasses, which together comprised 75 percent or more of the vegetation (Table 4; Sims and others 1978). Forbs were less than 10 percent of the community and were greater on ungrazed treatment. Cacti were important but too patchily distributed to accurately assess with the number of quadrats used. In terms of species composition, blue grama increased from 40 percent of the vegetation on ungrazed treatment to 57 percent on the very heavily grazed treatment (Table 4; Grant 1971). Buffalo grass (a very short stoloniferous species) and scarlet globemallow (a very deep rooted, rhizomatous forb) also increased with heavy grazing. Overall, however, there were very small differences between the grazed and ungrazed plant communities, with a calculated a similarity index of 96 percent (Grant 1971). That degree of similarity was equal to or greater than what was observed for the other nine IBP grassland sites in North America, with the northern shortgrass steppe site having a value of 88 percent similarity for heavily grazed compared to ungrazed and 90 percent for moderately grazed compared to ungrazed. Other aspects of community structure also showed little difference between grazing treatments. Live plant biomass was slightly greater in grazed than ungrazed treatment, whereas old-standing dead material was greater on ungrazed. This resulted in no difference between standing plant biomass between heavily grazed and ungrazed treatments. Both root biomass and crown biomass were greater on heavily grazed compared to ungrazed treatment, probably due to the increase in blue

grama with large crown and root biomass compared to aboveground biomass. Similar results have been observed for northern shortgrass steppe (Milchunas and Lauenroth 1989; Milchunas and others 1989), but will not be reviewed here because of their distance from southwestern communities.

The Fort Stanton Experimental Ranch in south-central New Mexico is west of the shortgrass steppe but within the Great Plains geomorphic province. The grassland at this site is dominated by blue grama, with wolftail, sideoats grama, ring muhly, sand dropseed, and other important grasses. Although dominant, blue grama is roughly half of the grass biomass and a third of the total biomass. The open grassland sites are found between surrounding pinyon-juniper communities. Precipitation is about 400 mm/yr, with 60 percent falling during the June through September growing season. Pieper and others (1978, 1991) compared moderate, "proper" stocking rates to a 25 percent greater heavy stocking rate for seven years. Blue grama, other grasses, and forbs were lower on the heavily compared to moderately grazed treatment for all of years 2 through 7. The reductions in blue grama under the heavy grazing treatment were often large, with half as much biomass compared to moderately grazed. The differences were not due to consumption, since sampling occurred under temporary cages that were moved each year. A drought near the middle of the study did not greatly affect relationships between the two treatments. Similar treatment effects were observed for basal cover of all species and blue grama, except that differences did not appear until the fourth year of study. Larger grazing treatment effects were observed between moderate and heavy grazing at this site than were observed between ungrazed and heavy grazing at the shortgrass steppe site above.

Five exclosure-grazed paired grasslands were among the large number of sites compared between 1940 and 1964 by Krenetsky (1971). The sites were considered the shortgrass association due to the dominance by blue grama, but they spanned a wide geographic range in three different National Forests, a precipitation range from 300 to 500 mm/yr, and were sometimes closely associated with pinyon-juniper or ponderosa pine communities. Averaged over the five sites, there was little difference between grazing and protection in the percentage change between 1940 and 1964 of grasses, forbs, browse, or total vegetation basal cover. The largest difference was for grasses, which increased 15 percent over time in the ungrazed compared to an increase of 11 percent on the grazed sides of the fences. There were large differences among sites, but the differences among sites in the temporal changes were greater than differences due to grazing. Blue grama did not respond to grazing treatment at three of the five sites, showed small relative increases with protection at one site, and showed large relative increases at another. Blue grama generally increases with grazing throughout Great Plains grasslands (Lauenroth and Milchunas 1991), so this is a rather unusual response, but one that is not uncommon in the southwest as shown in this review. The latter site was in Gila National Forest in western New Mexico. Other unusual dynamics at the Gila-8 site were the loss of a number of forb species on both treatments between 1940 and 1964 and the appearance of mesquite in the exclosure. Krenetski concluded that there was little difference between grazed and protected sites except for some differences for the two at lower elevation. New species of grasses did not come into the exclosures. From Krenetski's tables, understory species richness averaged 8.4 in ungrazed exclosures compared to 8.0 in the adjacent grazed areas.

Orodho and others (1990) studied an Indian ricegrass/fourwing saltbush community in northwestern New Mexico. Grass biomass alone at this productive site was 187, 261, and 235 g/m^2 for upland, slope, and swale topographic position, respectively. Communities protected from grazing for about 50 years within Chaco Culture National Historical Park were compared to adjacent heavily grazed sites. The response to grazing treatments differed with topographic position. The density of Indian ricegrass was greater on protected slope and swale, while the opposite was found on the upland. Similar treatment effects were observed for other grasses, except for no difference with grazing on the slope community. Forb density was greater only on swales. Fourwing saltbush is a valuable forage plant for livestock, especially in winter, and this species increased with protection. No differences in grazing treatments were observed for biomass of Indian ricegrass, other grasses, or forbs when plots on the grazed sites were protected during the year of study.

Natural geologic refuges that have never been grazed can provide interesting comparisons with adjacent grazed areas, although there are other potential confounding effects of their isolation (Milchunas and Noy-Meir 2002). A study of a "park" isolated by steep surrounding walls in southeastern Utah's Canyonlands National Park is included here because of climate and soils that are reasonably similar to nearby northern New Mexico and Arizona (Kleiner and Harper 1972, 1977). Because of the nature of isolation, abiotic conditions are similar at the protected and grazed sites with 250 mm/yr precipitation. Relative frequencies of plant and cryptogram species in galleta/needle-and-thread grass

Table 5—Species relative abundance index for ungrazed natural geologic refuge and grazed communities in Canyonlands National Park. Adapted from Kleiner and Harper (1972).

	Relative abundance index *	
Species	**Ungrazed**	**Grazed**
Galleta	5,206	3,553
Needle-and-thread	3,626	4,902
Wooly Indian-wheat	3,304	516
Six-weeks fescue	1,876	2,890
Prickly pair	1,377	39
Indian ricegrass	1,141	1,343
Sand dropseed	663	1,530
Desert tansy mustard	588	48
Rosy gilia	538	0
Blueburr stickseed	476	6
Hoary tansyaster	465	296
Nodding wild buckwheat	312	138
Downy chess	183	9
Praire pepperweed	163	64
Aster spp.	36	230
Small wirelettuce	36	4
Plains hiddenflower	27	105
Sego lily	18	0
Desert false-yarrow	17	0
Blue grama	16	522
Green joint-fir	3	360
Winterfat	3	90
Pale evening-primrose	1	15
Russian thistle	0	24
Silvery globe mallow	0	1,463
Floral characteristic		
Average number of species/stand (species richness)	22	13
Average number of vascular species/stand	15	11
Average number crytogam species/stand	6	2
Average number of species/quadrat	7	3
Vegetational characteristic		
Average total living cover (percent)	55	22
Vascularplant living cover (percent)	17	17
Crytogamic cover (percent) (½ moss - ½ lichen)	38	5
Average number of hits/stand on living vascular tissue	23	26
Litter cover (percent)	12	10
Contribution of annual to the total vegetation (percent)	12	16

* constancy times frequency, with a possible range from 0 to 10,000.

communities displayed very large differences between species composition and richness. Sixteen species were significantly more abundant in the refuge and 12 were more abundant in the grazed site (Table 5). The average number of vascular species per stand was 15 and 11 for ungrazed and grazed sites, respectively, and was 6 and 2 for cryptogram species. Vascular plant cover was similar between ungrazed and grazed sites (17 percent), but cryptogram cover was much higher with protection (38 vs. 5 percent). Annuals were more abundant on the grazed site, primarily due to six-weeks fescue grass. The exotic cheatgrass was more abundant in the refuge, while the naturalized exotic Russian thistle was more abundant in the grazed site. Of the dominant grasses, galleta was more abundant in the refuge and needle-and-thread more abundant in the grazed site. These very large differences existed even though the grazed site was utilized lightly to moderately during winter due to lack of adequate water, and was ungrazed for five years prior to sampling. Kleiner (1983) assessed successional trends in the grazed site 10 years later and reported continued directional change towards the relict ungrazed condition. The recovery of cryptogramic crust was more rapid than earlier believed.

Primary Production, Root, and Soil Responses

Aboveground primary production for the shortgrass steppe site described above was greater in ungrazed than grazed treatments in two out of three years of study (Sims and others 1978). Average values were 257 and 225 g/m^2/yr for the ungrazed and very heavily grazed treatment, respectively. However, these values may not be statistically different, and the method used for calculating production was the sum of individual species peaks through the growing season. Although this was chosen as the best out of more than 30 methods of calculation at the time (Singh and others 1975), the summation of peaks method can generate large biases whereby peak-standing crop of temporarily caged vegetation gives more reliable estimates with less bias (Milchunas and Lauenroth 1992). Peak-standing crop estimates of aboveground production from the same data yield estimates of 103 and 179 g/m^2/yr for the ungrazed and grazed treatments, respectively, which is opposite treatment direction to the sum of peaks estimate. Similarly, estimates of root and crown production based on summation of peaks should be viewed with caution, but in this case only an estimate of biomass is valid for peak standing crop values since crown and root turnover takes many years. Estimates of crown, near-surface root, and total root biomass were greater in grazed than ungrazed southern shortgrass steppe (Table 4). Very little difference in crown and root biomass between heavily grazed and 47-year ungrazed treatments have been observed in northern shortgrass steppe (Milchunas and Lauenroth 1989).

Estimates of total herbage production for the Fort Stanton Ranch study described above were greater for the moderate compared to heavy grazing treatments in all eight years but two, and the two were drought years. For the non-drought years near the end of the study, aboveground production was greater in the ungrazed compared to grazed treatment by as little as 12 g/m^2/yr to as much as 50 g/m^2/yr.

Primary production did not differ with grazing treatment at the Indian ricegrass/fourwing saltbush community described above (Orodho and others 1990). However, soil bulk density was 8 percent greater at the grazed compared to long-term protected site. The largest difference between grazing treatments was for an upland site, and the least for a swale site. Bulk density did not differ at the Canyonlands site in Utah, but soil organic matter was 1.33 percent for the refuge compared to 0.88 percent for the previously grazed site. Soil potassium and phosphorous were also slightly higher in the ungrazed communities, but nitrogen did not differ with grazing.

Grazing Management

Two grazing systems were evaluated at the Fort Stanton Experimental Ranch. While comparing the moderate and heavy continuous grazing treatments described above, Pieper and others (1978, 1991) also assessed a four-pasture, one-herd rotation system stocked at the same level as the heavy continuous pasture. The rotation system resulted in greater primary production than the continuously grazed pasture in five out of eight years. Grasses other than blue grama showed the greatest increase in response to rotational grazing, and forbs showed declines. There was no advantage of the rotation system in terms of cattle performance.

A short-duration seven to nine cell rotation system was compared to a continuously grazed pasture. However, the short duration pasture was stocked from 1.1 to 2 times more heavily than the continuous pasture and received generally less precipitation as well. Blue grama increased production and basal cover in the short duration pasture. However, no other species significantly increased under the short duration system, and basal cover of both total grasses and total forbs decreased. Average total production over growing periods were only slightly greater on the continuously grazed pasture.

As mentioned above, grazing intensities for the shortgrass type are generally higher than for other southwestern communities. Of nine native communities, Holechek and Pieper (1992) recommended 40 to 50 percent utilization of shortgrass steppe and southern mixed-grass prairie of the Great Plains, compared to 20 to 30 to 30 to 40 percent utilization for other southwestern communities. This reflects the relative tolerance to grazing of these systems that have a long history of grazing by native large herbivores.

There are a limited number of studies given the diverse nature of plant communities in the broad general type. A true shortgrass steppe community displayed a high tolerance to relatively very high grazing intensity. Magnitude of responses to grazing appeared to increase over a gradient of shortgrass steppe, short grass communities within pinyon-juniper range but within the Great Plains grassland Province (see Fig. 2, 3), to grasslands of the Colorado Plateau Shrub-Steppe associated with the Great Basin. The response of blue grama also changed across the history of grazing gradient, from increases with grazing to a mix of decreases or no effect. The large and important belowground component of the southern shortgrass system also appears highly tolerant of heavy grazing; although based on only one study, the data are supported by similar studies in the northern shortgrass steppe. At the other extreme of evolutionary history of grazing, a never-grazed natural geologic refuge shows very large effects of grazing.

Mesquite Savanna

Mesquite savanna communities receive from 200 to 500 mm/yr of precipitation, and there is a major west - east gradient in the seasonal distribution (Martin 1975). The percent of annual precipitation occurring April through September is only 45 percent in western Arizona, increases to 65 percent in western New Mexico, and peaks at 75 percent in western Texas. As mentioned above, Mediterranean climates are conducive for annual and/or shrub dominance, and the degree of a Mediterranean climate has important implications for the success of these life-forms and their potential response to disturbance. Another important aspect of the climate that drives vegetation composition is the high variability of precipitation and the periodic cycling of drought periods. Mesquite savanna, which includes what is commonly called desert grassland and semi-desert grasslands, has undergone more change over the past hundred years than possibly any other non-wetland community type in North America. Large-scale shrub invasions (mesquite, creosote-bush, tarbush, snakeweed, burroweed, cholla) into grassland coincided with the historic period of very heavy grazing by domestic livestock, which led to a century of debate concerning mechanisms associated with livestock grazing that may be responsible for such drastic shifts in communities. This will be discussed in the Shrub Invasion, Livestock Grazing, Fire, Small Mammals, and Climate section below, along with other hypotheses about contributing factors. In many cases, what is now a Chihuahuan Desert mesquite dominated shrubland used to be a mesquite savanna grassland. This transition is still ongoing. Therefore, there is some ambiguity concerning classification and an overlap between this section and the Chihuahuan Desert section below.

There are possibly more studies of grazing in the mesquite savanna type than all others combined. This is because mesquite savanna occupies large areas of several long-term research sites and because livestock grazing is an important landuse in the community. The sites include the Jornada Experimental Range and the nearby Chihuahuan Desert Range Research Center College Ranch (231 mm/yr precipitation) near Las Cruces, New Mexico, in the Jornada Del Muerte Basin, the Santa Rita Experimental Range south of Tucson, Arizona (384 mm/yr precipitation), the Page-Trowbridge Experimental Ranch in southern Arizona (394 mm/yr precipitation), and the Appleton-Whittel Research Ranch in southeastern Arizona (430 mm/yr precipitation, half in July and August). Some of these research sites provide long-term monitoring of controlled grazing treatments through periods of drought and favorable growth and spanning shrub invasions. These long-term data sets are particularly valuable in disentangling the complexity of interacting factors involved in community shifts. The following section on species composition is organized by research site and plant community, from earliest to latest study for sites with a history of research.

Species Composition

Jornada black grama and dropseed communities—Interactions between drought and grazing on black grama communities were noted by Campbell and Bomberger (1934). Severe drought and some very heavy grazing had large effects on the basal cover of black grama and snakeweed. Black grama is a primary component of the late seral stage and is a valuable forage species. Black grama does not often reproduce by seed but spreads by stolons. Recovery of black grama is therefore often slow. Snakeweed is a shrub sometimes toxic to cattle and was thought to represent deteriorated range condition (Jardine and Forsling 1922). These authors had previously shown that very heavy grazing leads to loss of black grama and establishment of snakeweed. Drought and heavy grazing were believed to also result in movement of the mesquite sand dune shrub association into black grama grassland. Campbell and Bomberger showed that with above-average precipitation and light grazing, black grama basal cover increased nearly five to six times after six years of recovery from heavy grazing and drought, while snakeweed was only two to three times greater.

Nelson (1934) studied black grama communities over 13 years that spanned two drought periods. Early grazing studies often used distances from water, together with exclosures, to obtain grazing intensity gradients. Conservative grazing was considered to be 75 to 80 percent utilization of black grama, whereas too intense grazing pressure was considered complete use of black grama and a range that appeared trampled after the grazing season (see below for more recent definitions of conservative grazing intensities). Drought alone was found to have extremely large effects on black grama. In plots protected from grazing, black grama basal areas declined 42 percent during the first drought, nearly recovered after two favorable growing seasons, declined to 11 percent of the original cover after an additional two years of drought, and then recovered again. Conservative grazing resulted in similar average basal covers to that of complete protection. However, the recovery from drought cycle was faster under conservative grazing than it was under no grazing. Increased tillering from a greater number of, but smaller more evenly distributed, tufts in conservative compared to ungrazed areas was thought to better utilize spatial distribution of soil water. Heavier grazing intensities prevented full development of black grama following drought, and allowed other species to increase. Very heavy grazing resulted in almost complete disappearance of black grama during drought and lead to unstable soil conditions. Height growth of black grama under very heavy grazing was 20 percent of that on ungrazed treatments during dry years and 75 percent during favorable years.

An additional early report of responses of black grama communities to grazing was provided by Paulsen and Ares (1961, 1962) for 1916 through 1952. By this time, definitions for grazing intensities had changed. Heavily grazed sites were considered to have more than 55 percent utilization of black grama, intermediate 40 to 55 percent, and conservative less than 40 percent. These authors reinforced Nelson's (1934) conclusions. The prolonged dry period between 1916 and 1926 reduced basal cover of black grama to approximately the same level regardless of grazing intensity or initial cover conditions. However, basal cover declined the most in protected plots after the severe drought of 1923, with other treatments declining in proportion to pre-drought covers. Recovery during favorable periods was more rapid in protected and conservatively grazed plots than intermediate and heavily grazed plots (3 times greater cover compared to 2 times, respectively). Low rainfall during 1935 again resulted in large declines in black grama on all grazing treatments. After recovery in 1937, basal cover of black grama increased 20, 68, 62, and 42 percent on ungrazed, conservatively, intermediately, and heavily grazed plots, respectively. Previously high basal areas were reached only on conservatively grazed plots. Associated less drought tolerant species declined even more than black grama during drought periods but then recovered more rapidly than black grama during favorable growth periods. Another dry period ensued and by 1956 black grama had disappeared from all ungrazed plots, 67 percent of heavily grazed, 62 percent of intermittently grazed, and only 30 percent of the conservatively grazed. Recovery was slower when losses were extensive. Tobosa communities responded similarly to dry/wet conditions but were less sensitive to grazing intensities (see below). Paulsen and Ares do not report on temporal trends in shrub covers under various grazing intensities because their data were from small quadrats. They do, however, mention that the number of mesquite plants increased 125 percent from 1936 to 1951 on even conservatively grazed range. Hennessy and others (1983) analyzed data from transects spanning over 2000 m that were sampled between 1935 and 1980 on the Jornada Experimental Range. Changes that occurred over the 45 year time period did so both on areas grazed and ungrazed by livestock. Mesquite attained complete dominance, while black grama and 25 percent of forb species had completely disappeared by 1980. Species capable of inhabiting the inter-dune areas were mesa dropseed, fluffgrass, and broom snakeweed.

Rodents and rabbits are native herbivores that can have significant effects on plant communities and may interact with livestock if the domestic large herbivore has an influence on abundance of the small herbivores. Norris (1950) conducted one of the early studies of the relative effects of these herbivores in both black grama grassland and mesquite-snakeweed communities. Rodent and rabbit populations are relatively low in the black grama communities compared to mesquite type (3 ½ times greater), whereby the small mammals had little effect on basal area or standing crops of perennial grass plants in the grassland community. Similarly, Havstad and others (1999) found only small effects of long-term rabbit exclosure on black grama grassland, and effects were only apparent after 50 years of protection. In contrast, standing crop in the shrub type was four to five times greater when protected from rodents and rabbits together (note, Norris [1950] often uses the term production when grazed-standing-crop was actually measured). Crown cover of snakeweed shrubs were somewhat greater in plots open to rodents or to both rodents and rabbits, but data was variable. The author suggests, however, that small herbivore grazing tends to favor shrub increases and prevent restoration of perennial grasses. Similar large effects of rodents on grass biomass was reported for the nearby College Ranch (Knox and others 1951, cited in Paulsen and Ares 1962). Gibbens and others (1993) reported similar shrub canopy cover to grass basal cover ratios in shrublands grazed or protected from rabbits for 50 years. However, changes in species composition were evident due to rabbit grazing. Although there was no difference in creosotebush, mesquite and tarbush decreased in grazed areas compared to exclosures, probably due to both browsing of the canopy and seedlings. Spike dropseed was 30-fold greater in exclosures, while fluffgrass was more abundant in grazed areas. Black grama and bush muhly did not respond to the long-term rabbit grazing treatments. Perennial grasses showed only small increases in basal cover 30 yrs after shrub removal treatment, similar to findings of Beck and Tober (1985). The potential role of small mammals in shrub invasions are discussed in the section below.

Buffington and Herbel (1965) described the shrub changes in a large 640 acre exclosure built across a mesquite sand dune / grassland transition zone in 1931. Even though grazing had been excluded, the mesquite expanded completely across the exclosure and out into grazed grassland on the other side. Based on visual observations, Hennessy and others (1983) indicated no difference in 1980 between grazed and ungrazed sections of the transect crossing through this exclosure.

Controlled grazing intensity studies of the recovery of "deteriorated" black grama range ("deteriorated" = areas where there were some remaining individuals) were undertaken in 1954 through 1963 at the College Ranch (Valentine 1970). The most severe drought in 350 years occurred from 1951 to 1956. At each of three pastures at deteriorated locations near watering points, light, moderate, "proper", and heavy grazing intensity treatment plots were established with goals of 20, 35, 50, and 65 percent utilization of black grama herbage weight, respectively. Actual intensities averaged over 10 years were 26, 35, 49, and 60 percent utilization. Light and moderate uses were generally similar and different from proper and heavy uses in terms of black grama seed-stalk height (a measure of "vigor"), average number and length of stolons, number of rooted buds (tillers initiating from stolons), and cover. Cover of black grama averaged 38 percent of that for "good-condition range" under both light and moderate use compared to 26 percent for proper and heavy use treatments. Recovery was just as rapid under moderate grazing as under light grazing. An interesting finding was that soil conditions at a particular site had large effects on grazing treatments. Recovery of black grama cover was 57 percent of that for good condition range where soils were a moderately deep sandy loam compared to only 8 percent recovery where soil was a shallow sandy loam with surface wind-scour, and 21 percent recovery where the soil was a very deep sandy loam.

An additional study of the extreme drought of the 1950s was done at the adjacent Jornada Experimental Range (Herbel and others 1972). The importance of soil characteristics was again clearly seen, although the study did not address grazing as a factor. Prior to the drought, cover and yield of black grama did not differ among deep sandy, sandy flat, shallow sandy, low hummocky, flood plain, heavy sandy flat, or slope sites, and no site-location was particularly favored by precipitation during the drought. A direct relationship between drought damage to grasses and depth of soil was observed. Cover and biomass of grasses during the drought remained greater on shallow sandy sites and there were greater losses on the deep sandy and low hummocky sites. It was hypothesized that deep roots during a drought when moisture is primarily near the surface may be more susceptible to drought damage, and a shallow caliche layer holds more available moisture in a more readily obtainable depth. Black grama was so reduced on the deep sandy and low hummocky sites that there were not enough residual plants to provide a base for increase shortly following the drought. Many grass plants were killed by being covered by blowing sand, and erosion was greatest on sandy sites. The drought had greater impact on dropseeds and threeawns than on black grama, but those species do not have the constraint on recovery by seed like black grama does. Tobosa and burrograss on the flood plain sites were little affected by the drought. Possibly most important was that the drought favored mesquite at the expense of grasses. A later follow-up on this study reporting data through the late 1970s (Herbel and Gibbens 1996) showed that perennial grass cover remained low on deep sandy soils but increased on shallow soils over indurated caliche. A large response to protection from rodents, rabbits, or cattle was not observed. Mesquite cover was greater in areas protected from grazing, but grazing did not prevent an increase in mesquite.

Gil (1975) studied an extreme case of very heavy grazing compared to 12 years of exclosure to grazing. The exclosure had been built and grazed as a treatment during 1954 to 1963 in the Valentine (1970) study discussed above, but then left ungrazed. The exclosure was within 300 m of a stock tank. Therefore, the exclosure prior to 1954, and the adjacent grazed area, had been a "sacrifice" area. Areas near water are not only grazed heavily, but they are constantly trampled by animals coming to water and are also areas of very high nitrogen enrichment due to fecal and urine deposition (Senft 1983). While Atwood (1987) discounted the Gil study, it should simply be noted that the study does not represent general-area range conditions but a very heavily disturbed condition and the potential for recovery. Black grama was less than 1 percent of the grazed plant community compared to 64 percent of the ungrazed. Threeawns and dropseeds were 6 and 14 percent of the grazed and ungrazed communities, respectively. The

Table 6—Plant density of ungrazed (Ungz) and grazed (Gz) plant communities at New Mexico mesquite savanna sites where the ungrazed treatment was protected for 17, 22, 32, or 48 years. Adapted from Atwood (1987).

	Density (individuals/m²)							
	17-Year		**22-Year**		**32-Year**		**48-Year**	
Species	**Ungz**	**Gz**	**Ungz**	**Gz**	**Ungz**	**Gz**	**Ungz**	**Gz**
Black gramma	13.7	12.8	11.7	25.8	33.1	22.8	15.3	22.1
Dropseed spp.	0.8	9.5	1.8	4.4	0.3	0.3	1.1	3.4
seedlings	0.5	9.8	0.4	1.5	0	0	0.3	0.5
Other perennial grasses	0.2	0.8	0.9	11.4	0.8	17.6	1.0	1.2
seedlings	0	0.3	0.5	0.2	0	0.3	0	0.1
Annual grasses	8.7	34.9	1.6	9.0	2.0	1.6	8.4	3.8
seedlings	0	0	0.1	0	0	0	0.3	0
Perennial forbs	1.9	3.7	15.6	14.5	8.6	14.8	43.4	44.6
seedlings	0.3	1.7	6.6	13.3	0.1	0.4	37.9	34.8
Annual forbs	47.9	52.1	84.3	90.1	147.7	166.2	30.4	19.8
seedlings	9.8	14.4	42.5	50.4	1.9	4.1	37.2	21.7
Shrubs	1.9	1.4	1.3	1.5	0.8	0.7	1.2	1.8
seedlings	0.3	0.2	0.3	0.5	0.1	0	1.1	2.9

majority of the heavily disturbed site was the half-shrub snakeweed (89 percent), while it was only 20 percent of the ungrazed community. Total biomass at the sites was 75 and 59 g/m^2 for the ungrazed and grazed community, respectively, and bare ground cover was 69 and 90 percent.

Comparisons were made between grazed and ungrazed treatments among 10 grasslands during the International Biological Program, with the Jornada being one of the sites (Sims and others 1978; Sims and Singh 1978 a, b; Grant 1971). More detailed information of the three years of sampling (1970 to 1972) specific to the Jornada site was published by Pieper and Herbel (1982) and Pieper and others (1983). Only one exclosure was sampled, but it was 10 ha. Sampling of shrubs by small quadrat methods was highly variable, but means across all years for mesquite and for yucca were higher in ungrazed than grazed treatment. Grazed areas were considered light to moderate at about 40 percent utilization. Based on peak live standing crop, black grama was the most abundant species on the ungrazed treatment, followed by Russian thistle. Russian thistle was the most abundant species on grazed treatments, followed by snakeweed. It is interesting to note that Russian thistle (tumble weed) is an exotic (but naturalized) annual forb that can be considered a colonizing ruderal species. Perennial grasses contributed 50 percent of the biomass of the ungrazed treatment compared with less than 30 percent for the grazed.

A sequence in years of protection from grazing, and adjacent grazed sites, was sampled by Atwood (1987) by using exclosures at both Jornada experiment stations. Exclosures represented 17, 22, 32, and 48 years of protection from grazing. The 17-year site was the same one sampled during IBP (see previous paragraph), but sampling then was by standing biomass and this study used density (see Introduction for interpretation of methods). Years previous to and during the study had good rainfall, except for the 17-year site. Sites were far enough apart as to introduce a spatial factor into the temporal comparison, and there was only one site per duration of protection. The study does, however, provide one of the few temporal comparisons where sampling occurred at the same point in time, and sites were sampled for three years. Comparing grazed and ungrazed treatments within exclosure age, the density of black grama was equally abundant in the grazed and ungrazed 17-year site, greatest in the grazed 22- and 48-year site, but greater in the ungrazed 32-year site (Table 6). The lack of a temporal pattern in black grama abundance suggests that differences among sites in local precipitation, soils, or initial conditions are more important than a 17 to 48 year range in duration of protection. Dropseeds were generally favored by grazing. There were no consistent trends in forb, shrub, or annual species densities that could be attributed to grazing. Annuals were often greater on one treatment in one year or season and the other treatment in another year or season. Atwood concluded that properly managed grazing was sustainable in black grama communities. Again, however, the lack of a consistent temporal trend in direction of response may possibly be attributed to important interactions of grazing treatment with factors such as local precipitation, soils, or initial conditions.

The permanent quadrat data for grass basal cover and forb density collected at the Jornada Experimental Range was summarized over a 64-year period by Gibbens and Beck (1988). Early years were reviewed above. For the black grama community type, long-term changes in perennial grass cover were similar for grazed and protected plots. Regardless of grazing treatment, however, perennial grass cover had not recovered by 1976 following the very severe drought of the 1950s. Highest cover of perennial grasses was recorded in the late 1920s to early 1930s at about 10 percent, fluctuated around 5 percent up to the 1950s drought, and then declined to below 5 percent for the rest of the recorded time. Black grama disappeared from 77 percent of the original quadrats by 1961 and was no longer the dominant perennial grass through the 1970s. Perennial forbs, annual grasses, and overall plant species richness declined through the 64 year period. Shrubs dominated 42 percent of the quadrats by 1981 (Gibbens and Beck 1987). Similar results were recorded for quadrats in the poverty threeawn community type, except losses of perennial grasses and plant species richness through time were even more distinct. The loss in perennial grasses was not only due to drought, but also because mesquite had invaded and dominated the area, including the plot protected from grazing. Temporal patterns were not the same for tobosa or burroweed communities (see below).

A study of five exclosures (37 years old or greater) and adjacent grazed sites spanning both the Jornada Experimental Range and the College Ranch showed reduced perennial grass cover on the grazed sites but no effects of grazing on forb or shrub cover (Kerley and Whitford 2000). Black grama showed the largest decreases with grazing from 31 to 8 percent canopy cover. Fluffgrass was the only grass to increase with grazing, from 0.1 to 0.4 percent cover. Annuals were not affected by grazing treatments. No differences between grazing treatments were found for diversity or richness of either annuals or perennials. Nash and others (1999) also found only small effects of grazing on annual plant communities. Although there were no differences in shrub cover between treatments, Kerley and Whitford (2000) still suggest that grazing moves the plant community towards one more similar to a shrub community. Evidence is based on a DCA analysis showing some movement of ungrazed to grazed sites along axes towards shrub space. Additional evidence is cited from the Gibbens and Beck (1988) long-term study, but the material presented by these authors (reviewed above) indicates no difference in grazed and ungrazed quadrats in invasion by mesquite. Kerley and Whitford (2000) appear to imply that there is a sequence from long-lived black grama to short-lived dropseeds and threeawns and then to mesquite, but neither papers actually show this and neither show differences in mesquite between grazed and ungrazed treatments over reasonably long periods of time.

Herman (1988) sampled 15 exclosure and adjacent grazed areas that ranged in age of protection from 6 to 74 years old. Only a few species showed time trends with increasing age of protection, and none were consistent among the 15 sites. Although some minor differences between grazed and ungrazed comparisons were evident, no differences between grazed and ungrazed treatments were observed for the four “problem shrubs” in the region. Similar results were observed for six mixed-brush grazed-ungrazed comparisons where the exclosures ranged from 5 to 52 years of protection.

Two other studies on the College Ranch (Nelson and others 1997; Winder and others 2000) are not considered here due to experimental design constraints in interpreting grazing intensity or grazing systems effects for the purpose of this review, although valid comparisons may be possible for other purposes. Sites previously in good condition were stocked lightly and pastures previously in fair condition were stocked more heavily, whereby site versus current intensity are confounding in comparisons. Additional studies at the College Ranch by Tembo (1990) and Holechek and others (1994) also have experimental design problems and unclear interpretation of results. Two different grazing systems were crossed during sampling of the moderately grazed site and the two grazing intensity treatments were past intensities, not current intensities as implied.

Jornada tobosa/burrograss community—Seral stages on various clay soils of the Jornada were studied from 1915 to 1929 by Campbell (1931). Basal cover was assessed after four years of above average precipitation, thereby representing species composition under favorable conditions for growth. A sodgrass, tobosa grass is the late seral-stage dominant or sub-dominant of clay soils on the Jornada. When not dominant it is often still the most important forage species. Tobosa is palatable to livestock only when green, and therefore, this plant community is often grazed during the growing season. This allows for deferment of grazing on black grama communities, which increases black grama because of its sensitivity to grazing during reproductive stages, and higher palatability during the dormant season. Campbell presents species composition and palatability of the four main seral stages but does not quantitatively address grazing treatments. A burrograss association is the second lower stage after the tobosa stage. Drought and too heavy of a grazing intensity reduce basal areas of both species, but tobosa recovers more slowly. Campbell suggested that tobosa could be grazed to 60 percent utilization without injury or lowering of seral stages in adjacent recovering communities. This high rate of utilization would suggest that previous very heavy grazing during the uncontrolled grazing of the late 1800s to early 1900s must have been extremely heavy to push communities to an annual, ruderal-weed stage.

Common, periodic cycling of tobosa grass through drought and relatively wet periods is similar to that for black grama described above, but fluctuations were reported as less pronounced by Paulsen and Ares (1961, 1962) as well as Gardner (1950, see below). Somewhat different conclusions were reached by Herbel and others (1972) during the extreme drought of the 1950s. Tobosa and burrograss were reported to be little affected by the drought on flood plains sites. They indicate a capacity of tobosa to become completely dormant as soil moisture approaches the wilting point.

The Paulsen and Ares (1961, 1962) data showed highest basal cover of tobosa on intermittently grazed plots rather than conservatively grazed plots as for black grama. Average basal areas were 191, 461, 718, and 294 cm^2/quadrat for protected, conservatively, intermittently, and heavily grazed plots, respectively. Protection from grazing resulted in accumulation of old-dead plant material in the clumps that resulted in "stagnation," whereas heavy grazing resulted in thinning of the stand and increases in bare ground cover. Less palatable dropseeds were a larger proportion of the community under heavy grazing, and lower seral-stage burrograss was a larger proportion during dry cycles.

The 64-year permanent quadrat data for the Jornada Experimental Range included quadrats in tobosa and burroweed (Gibbens and Beck 1988). Although only one quadrat per type was located in an exclosure, no differences between grazing treatments were noted. Unlike the effect on the black grama or poverty threeawn type (see above), the severe drought of the 1950s did not result in an apparent permanent reduction in perennial grass basal cover in either type. Tobosa remained on all but three of the original 22 quadrats over the 64-year period, and shrubs became dominant on one. Tobosa retained reasonable cover during the drought and recovered rapidly after the drought. Burrograss maintained more cover through the drought than other perennial grasses and recovered rapidly following the drought. Of 12 quadrates, burrograss remained present on all but two over the 64 year period, and shrubs became dominant on only one. The tobosa and burrograss communities of heavier soils were more tolerant of drought and recovered more rapidly than the black grama or poverty threeawn types on the sandier soils. Herman (1988) sampled two 11-year-old, and a 29-year-old, exclosures in lowlands and found no difference in species frequency or richness with adjacent grazed areas.

Santa Rita Arizona mesa mesquite grassland—These plant communities occupy sandy loam soils receiving an average of 343 mm/yr precipitation, and are the lower elevation, drier of the two grassland types on the experimental range (Canfield 1948). Shrub invasion into these grasslands has also been very extensive (Brown 1950; Mehrhoff 1955). The Santa Rita Experimental Range is located in southeastern Arizona, south of Tucson.

Before focusing specifically on the quantitative data from the Santa Rita Range, we summarize the qualitative descriptions of range condition provided by Humphrey (1960) for sites in the same general area as the Santa Rita. Humphrey considered the extensive invasion of mesquite, burroweed, and cholla and prickly pear cactus into grasslands to be a result of too heavy of a grazing intensity and fire control. Three distinct sites were differentiated as valley-bottomlands, high-potential sites, and medium-potential sites. For valley-bottomlands, a decline from excellent to good condition was displayed by decreases in blue grama, sand dropseed, bluestems, and cane beardgrass with increases in Rothrock grama. Annual grasses such as six-weeks needle grama and six-weeks threeawn, and burroweed shrubs, are indicative of fair condition range. Erosion is evident, and even more so on poor condition range where even annual grasses are sparse. An excellent condition high-potential site supported sideoats, slender, hairy, and black gramas intermixed with mid-grasses like Arizona cottongrass, plains beardgrass, and plains lovegrass. Density of these grasses declines on good condition range and are replaced with increasing amounts of Rothrock grama, Santa Rita threeawn, burroweed, mesquite, and cholla. Poor condition range has only annual grasses and a well developed shrub component. The sequence of declining condition on medium-potential sites is somewhat similar, except the shrub component is made up of guajilla, various cacti, ocotillo, and desert hackberry.

On the Santa Rita, examples of general composition of plant communities with different grazing treatments based on extensive sampling of a large number of exclosures and grazed sites were presented by Canfield (1948). Although grazing intensities were not provided, large differences in species composition were observed between heavily grazed sites and those either conservatively grazed, protected for five years, or protected for 25 years (Table 7). The dominant species on heavily grazed sites was Rothrock grama, while black

Table 7—Grass species composition and shrub cover for mesa-type mesquite savannas heavily grazed, conservatively grazed for five years, and protected for five or 25 years. Adapted from Canfield (1948).

	Heavily grazed	Conservatively grazed 5 years	Protected 5 years	Protected 25 years
Grass species		**Composition (percent)**		
Threeawn species	10	23	24	14
Slender grama	5	11	0	1
Black grama	15	8	16	26
Rothrock grama	64	8	7	7
Sideoats grama	trace	3	2	2
Tanglehead	3	2	7	3
Arizona cottongrass	2	22	19	26
Bush muhly	trace	12	16	11
Other grasses	1	11	9	10
Shrub species		**Cover (percent)**		
Mesquite		4.7	9.8	9.2
False mesquite		0.1	0.2	2.1
Burroweed		8.2	9.0	6.6
Cacti species		1.5	0.7	2.7
Other shrubs		3.8	2.0	2.8

grama, and Arizona cottongrass shared dominance on long-term protected sites. The most uniquely different community among the four was the heavily grazed treatment. Black grama did not respond exactly the same as in the Jornada grasslands, where greatest covers were often found under conservative grazing and least under heavy grazing. It is not clear as to whether this was just because data are presented as composition and not absolute cover, but Canfield comments that black grama's greater composition on heavily rather than conservatively grazed sites was because it was less susceptible to either very heavy grazing or drought. The highest composition of black grama was on long-term protected sites. Black grama was considered to increase after heavy grazing at greater rates under protection than under conservative grazing. At the Jornada black grama grasslands, the species was able to withstand drought better under conservative grazing compared to complete protection. Canfield does conclude that other species do almost as well under conservative grazing as under complete protection. The very high composition of Rothrock grama on deteriorated ranges was attributed to high seedling establishment during conditions of either high precipitation and/or low levels of competition from longer-lived, better competitor species of later seral stages. Arizona cottongrass was considered a good indicator of range condition, becoming depleted and confined to shrub canopies when range is very heavily grazed, and conspicuously increasing under conservative grazing or protection. A low abundance of bush muhly was another indicator of very heavy grazing. Shrubs were not considered a good indicator of range condition because of their lack of response to protection. Among Canfield's conclusions were 1) rates of recovery are approximately equal under conservative grazing or protection if the range has not been abused for a long time and erosion is not excessive; 2) the tall grasses such as Arizona cottongrass, sideoats grama, and black grama are major components of "climax" communities; and 3) deep-rooted shrubs that have invaded the grassland may be slow to respond to conservative grazing or protection. Once established "they become a relatively permanent part of the plant cover," even though the grass understory improves with the protection. However, field observations suggested a more rapid invasion under heavy grazing.

The extreme expansion of shrubs into grasslands of the Santa Rita prompted a study of the effects of protection from cattle as well as protection from both cattle and rabbits-rodents (Brown 1950). The rodent exclosure was for rabbits and larger rodents, since chicken wire was used as fencing. The densities of 12 shrub or cacti species were sampled initially (in 1931), 10 years and 18 years after fencing. Mesquite increased under all three treatments. However, the rate of increase was greater in the grazed community, and similar under cattle only and cattle plus rodent protection. Over the 18 year period, burroweed increased 248 percent in the grazed community, increased 189 percent under protection from cattle, and decreased 42 percent under protection from both cattle and rodents. Brown concluded: "The increase of all shrubs except burroweed under all treatments are at variance with the theory that grazing has directly affected the spread and increase of noxious plants in the desert grassland through breakdown of sod and release of shrubs from grass competition. Instead, it would seem that the shrubs, rather than the grass, were natural dominants of the area, and that the grass was present because of some factor that was unfavorable to the shrubs." Brown suggested studies to determine whether fire was the factor missing from the current system. Even burroweed can eventually become dominant over large areas of grassland. The Santa Rita was ungrazed from 1903 until 1915, and burroweed spread over large portions of grassland during that period (Griffiths 1910, cited in Mehrhoff 1955).

A similar study to that of Brown (1950) above was conducted by Glendening (1952) on apparently different sites (two replications instead of one, slightly lower elevation and precipitation, sampling in 1932, 1935, and 1949). In this study, mesquite more than doubled on treatments grazed moderately year-long, ungrazed by cattle for 17 years, and ungrazed by cattle, rabbits, and rodents for 17 years. However, increases in mesquite were slightly greater in both types of exclosures than in the grazed treatment. Since all shrubs were mapped on all plots, the establishment and mortality of individuals could be distinguished, rather than just density or increases in crown cover of the same individuals, thereby providing information concerning reproduction from seed. Cattle consume some mesquite seeds, and these could be transported to uninhabited grassland and germinate after passage through the animal. Small rodents could potentially cache seed that would then establish new individuals. New mesquite individuals were recorded on 70 percent of the grazed treatment and 79 percent of each of both exclosure treatments. Death loss overall was only 0.3 percent. The higher establishment under the two grazing exclosure treatments suggest that cattle were not an agent of dispersal in this case, but some very small rodents may have been able to get through or over chicken-wire-mesh size material. Glendening comments that the Merriam kangaroo rat is of a small enough size to get through the fencing and that it is known to bury seeds in a pattern whereby seedlings emerge in clusters of 2 to 10 or more individuals. Many such clusters were observed on all treatments, suggesting the kangaroo rat may be an important means of dispersal. Initial perennial grass densities differed among treatments, and a drought during 1935 thinned all stands. Differences in the percent loss in density due to the drought among the treatments would be difficult to attribute to treatments, since initial densities differed, and studies reported above for Jornada grasslands (Paulsen and Ares 1961, 1962) indicated drought reduced basal covers to similar levels regardless of grazing treatment. Sampling was done only during the 1935 drought and again in 1949, so the immediate post-drought conditions are not known. Interestingly, however, densities remained low long after the drought. This is similar to the lower perennial grass cover reported for the Jornada after the 1935 drought (see above Gibbens and Beck 1988). Glendening speculated that the increases in mesquite and/or grazing by rodents may have been responsible for the continued low levels of grasses. Rothrock grama was initially the dominant grass at the start of the experiment, but it was not at the end in the protected sites. Increases in cactus accompanied the increases in mesquite and decrease in grass abundance. Grass density at the final sampling was 9.5, 5.2, and 14.3 cm^2/m^2 for the grazed, cattle exclosure, and cattle plus rabbit/rodent exclosure, respectively, from initial values of 287, 214, and 146 cm^2/m^2. Glendening concluded that mesquite increases regardless of grazing treatment, and moderation in grazing would not prevent loss of grass cover.

Martin and Cable (1974) assessed effects of different seasons of grazing on grasslands of the Santa Rita (see management section below). Some sampling was also done in relation to a distance from water grazing intensity gradient. Sampling distances ranging from only 1/4, 5/8, and 1 mile did not result in large differences in utilization (48, 44, and 43 percent), but some differences in community species composition were noted. Jumping cholla and Rothrock grama were more abundant nearest water, while black grama was twice as abundant distant to water. Cholla is a tall cactus that can establish from branches that are knocked off and transported by cattle.

Santa Rita mixed-grama grassland—This grassland is generally similar to mesa mesquite grassland, but cacti and half-shrubs are rare, cover of grasses is double, and the relative composition of the grass species changes (Canfield 1948). Precipitation (470 mm/yr) and elevation is higher than for mesa mesquite grassland, and soils are darker with higher organic matter content.

Changes in this community type with heavy grazing, conservative grazing, and short-term or long-term protection are somewhat similar to that described above for mesa mesquite grassland (Canfield 1948; Reynolds and Martin 1968). Differences include the dominance of

Table 8—Grass species composition and shrub cover for foothills-type mesquite savannas heavily grazed, conservatively grazed for five years, and protected for five or 25 years. Adapted from Canfield (1948).

	Heavily grazed	Conservatively grazed 5 years	Protected 5 years	Protected 25 years
Grass species		**Composition (percent)**		
Threeawn species	5	11	15	9
Slender grama	49	44	27	15
Black grama	5	5	10	7
Hairy grama	2	3	3	3
Rothrock grama	12	3	2	2
Sideoats grama	6	14	18	10
Curlymesquite	13	4	2	1
Tanglehead	1	2	2	5
Arizona cottongrass	6	6	11	31
Other grasses	1	8	10	17
Shrub species		**Cover (percent)**		
Mesquite		6.63	8.28	6.42
False mesquite		4.06	4.95	5.92
Burroweed		2.81	2.10	0.38
Cacti		0.54	0.09	0.88
Other shrubs		0.51	4.31	4.93

depleted heavily grazed communities by slender grama, although long-term protected mixed-grama grassland also has a large component of slender grama (Table 8). Deteriorated range is in general characterized by short-lived grasses that reproduce abundantly by seed or short, sod-like grass that avoid herbivory because of the prostrate morphology. Long-term protected grassland is characterized by a dominance of Arizona cottongrass and also by a diversity of a number of other grass species that comprise small amounts of the composition on their own. A difference between this type and the mesa mesquite grassland is the difference between community species composition of short-term conservatively grazed and short-term protected sites. While there was little difference between the two treatments for mesa mesquite grassland, rates of recovery were greater under protection than under conservative grazing for the mixed-grama type. Mesquite did not respond to protection from grazing, although values for the heavily grazed treatment were not presented. There was some indication that burroweed declines with long-term protection. Canfield concluded that shrubs respond little to grazing management or protection once established, but he stated that field observations suggested a more rapid invasion of mesquite and burroweed under heavy grazing. Later consideration of a long-term data set for the Santa Rita indicate that burroweed and cactus abundance appear to be independent of cattle grazing intensity, and fire influenced only short-term dynamics (McClaran 2003).

Grazing intensity at the Santa Rita has declined through time, as perceptions of what was "conservative grazing" changed. When grazing intensities declined after 1942 to 52 to 58 percent utilization, and to 42 to 49 percent utilization from 1962 to 1966, a substantial increase in perennial mid-grass composition was observed (Rivers and Martin 1980). The increases ranged from 14 to 35 percentage units, depending on site elevation/precipitation. Short grasses were the component that decreased, particularly for the short-lived Rothrock grama which showed up to a one-third reduction. Based on previous studies and additional more recent data, McClaran (2003) concluded that "grass dynamics appear to be more sensitive to varying intensities of livestock grazing and neighboring plants than the dynamics expressed by mesquite, burroweed, and cactus. The spread of the exotic sweet resin bush (hawk's eye) was also not related to light to moderate grazing or ungrazed treatments (Howery and others 2003). Excellent reviews, more detailed than can be provided here, of the long-term monitoring of vegetation on the Santa Rita are found in McClaran (2003) and Ruyle (2003). The impact of rodents on vegetation is considered in the following section on Mesquite Savanna Conversion to Chihuahuan Desert, and in a review wildlife research on the Santa Rita (Krausman and Morrison 2003).

Lehmann lovegrass communities—Lehmann lovegrass is an exotic from South Africa introduced to southern Arizona in 1932 to prevent erosion during road construction and to provide forage for livestock after loss of native grasses to drought or very heavy grazing (McClaran and Anable 1992; Robinett 1992). The species is well adapted to the environment and has more than doubled in area from that originally seeded. The species utilizes moisture stored in soil during winter more effectively than native species (Cable 1971) and produces large amounts of seed and maintains a large soil seed bank. The species provides an early spring forage, is very productive through the summer, and recovers rapidly from drought, fire, and grazing. Seeds are too small to be utilized effectively by small mammals and germinate profusely after canopy removal by fire or grazing. Diversity of birds and small mammals is lower in the near-monocultures of Lehmann lovegrass compared to native grassland (Bock and others 1986). Lehmann lovegrass is perceived as a major threat to native grasslands because it displaces natives and heavily dominates areas, but it may also be the only perennial grass capable of inhabiting areas invaded by shrubs and providing soil cover and forage for domestic and native consumers (Robinett 1992).

Robinett (1992) described the response of Lehmann lovegrass and native species to a drought in southern Arizona during winter 1988 to spring 1989. One-third to one-half of the area had dead patches of grass, particularly where the surface sandy loam soils were shallowest over a clayey subsurface. Utilization of Lehmann lovegrass and black grama appeared similar, and did not seem to affect mortality that also was similar between the two species. A transect read after rains fell indicated high germination of Lehmann lovegrass seedlings in the dead grass patches, and no germination of native species. One year after the drought, Lehmann lovegrass completely dominated the former dead patches. The native black grama, red threeawn, mesa threeawn, hairy grama, and sprucetop grama all declined at the expense of Lehmann lovegrass, with only aparejograss unaffected by the drought. Similar displacements were observed on the Santa Rita Experimental Range in response to fire (Cable 1965, 1971; reviewed by McClaran 2003). The fire killed 98 percent of the Lehmann lovegrass and 90 percent of the black grama, but only Lehmann lovegrass germinated immediately following the fire. Once established, Lehmann lovegrass soon became the dominant on the site.

The relationship between grazing intensity and Lehmann lovegrass abundance and rate of spread was assessed at the Santa Rita Experimental Range by McClaran and Anable (1992). Distance from water as a grazing intensity gradient, and ungrazed exclosures, were used to monitor native grass and Lehmann lovegrass density from 1972 to 1990. Lehmann lovegrass increased over time equally under all distance-from-water grazing intensities or protection from grazing. Although grazing had no effect on Lehmann lovegrass, native grasses decreased at higher grazing intensities, whereby the relative proportion of natives to exotics decreased. Angell and McClaran (2001) reported on the same study but after another 10 years (1972 to 2000). They also examined differences between grazing management of frequent summer rest versus grazing every summer and at a heavier stocking rate (see Grazing Management section below). Although native grass density declined with increasing grazing intensity after 18 years, there was no relationship with grazing intensity and native grass density after 28 years. Lehmann lovegrass showed no relationship to grazing intensity. There was no evidence that the faster, preemptive establishment of Lehmann lovegrass after drought or fire had changed over time. Some self-thinning had occurred, but the dominance by this species was expected to continue.

At the Page-Trowbridge Experimental Ranch in southern Arizona, Schmutz and Smith (1976) found greater basal cover of Lehmann lovegrass in areas protected from grazing for 28 years than areas “closely” grazed. In contrast, Brady and others (1989) reported greater canopy cover of Lehmann lovegrass in grazed compared to ungrazed communities at Appleton-Whittell Research Ranch in south-central Arizona. However, Lehmann lovegrass was only a minor component of the plant community at both of these study plots. Bock (J. H., personal commun.) notes that lovegrass more permanently occupies sites following disturbance, compared to native, short-lived, bare-ground colonizers that play an important role in stabilizing a site after disturbance yet readily give way to natives of the next seral stage.

The invasion of native grasslands by Lehmann lovegrass does not appear to be affected by grazing intensity or whether a site is protected from grazing, or by specific grazing management systems (see Grazing Management section below).

Page-Trowbridge Experimental Ranch—Grazing at the Page-Trowbridge Experimental Ranch in southern Arizona was conservative from 1923 to 1941 and was ungrazed after that time (Schmutz and Smith 1976). An adjacent property was “overgrazed” at the time of Haskell’s (1945) first sampling in 1941. The “severely-grazed” site showed more erosion to the point that its runoff water deposited soil on a part of the conservatively grazed area. Both areas were pure grassland at one time, but by 1941 supported a community with mesquite, burroweed, and snakeweed. Large differences in

Table 9—Plant community characteristics for an Arizona mesquite savanna that had been lightly grazed from 1923 to 1941 and the same area ungrazed from 1942 through 1969 or still heavily grazed through 1969. Adapted from Schmutz and Smith (1976).

	Basal cover (percent)				**Composition (percent)**			
	1941		**1969**		**1941**		**1969**	
Grass species	**Light**	**Heavy**	**Ungz.**	**Heavy**	**Light**	**Heavy**	**Ungz**	**Heavy**
Arizona cottontop	0	0	0.07	0.08	0	0	23.3	7.1
Sideoates grama	0.12	0	0.53	0.01	7.9	0	17.7	0.9
Cane beardgrass	0.18	0.02	0.27	0.02	11.8	16.7	9.0	1.8
Poverty threeawns	0.15	T	0.37	0.32	9.9	T	12.3	28.6
Rothrock grama	0.30	0.06	0.35	0.52	19.7	50.0	11.7	46.4
Red threeawn	0.65	T	0.34	0.07	42.8	T	11.3	6.2
Lehmann lovegrass	0	0	0.30	0.01	0	0	10.0	0.9
Others	0.12	0.04	0.14	0.09	7.9	33.3	4.7	8.1
Total	1.52	0.12	3.00	1.12	100.0	100.0	100.0	100.0
Shrub species	**Crown cover (percent)**				**Composition (percent)**			
Velvet mesquite	0.66	0.76	3.80	5.32	17.4	8.9	47.7	55.0
Burroweed	1.96	1.69	1.69	2.30	52.1	74.9	21.2	23.8
Wright buckweed	0.64	0.02	2.48	0.16	16.8	0.2	31.1	1.6
Sticky snakeweed	0	0.84	T	1.10	0	9.9	T	11.4
Others	0.52	0.52	T	0.79	13.7	6.1	T	8.2
Total	3.80	8.52	7.97	9.67	100.0	100.0	100.0	100.0

species composition were observed between the two areas. Perennial three-awns comprised 45 percent of the basal cover of the conservatively grazed site and only a trace on the overgrazed site. Conversely, Rothrock grama comprised 38 percent of the overgrazed site and 17 percent of the conservatively grazed, and respective values for the non-palatable fluffgrass were 13 and 1 percent. Even though a greater proportion of the heavily grazed community, Rothrock grama attained greater cover on the conservatively grazed site. Once established, burroweed did not respond to a change to conservative grazing and remained at similar crown covers on the two sites. Mesquite was approximately the same density on both sites. Smith and Schmutz (1975) and Schmutz and Smith (1976) re-sampled the same sites in 1969. Actual grazing intensities were not provided but described as still conservative on the Research Ranch and "closely" grazed on the adjacent land. Some of the 1941 data from Haskell were included, but differences in values suggests that only a portion of the original 8 blocks were sampled. Total cover increased on both sites from 1941 to 1969 (Table 9). Differences between the treatments that changed since 1941 included the appearance of Arizona cottontop and the exotic Lehmann lovegrass with a much greater cover and composition on protected sites and a greater composition of poverty threeawns on grazed than on protected sites. With the exception of the exotic Lehmann lovegrass and possibly Arizona cottontop, differences between years may be due to temporal trends or to abiotic conditions during or just prior to the years of sampling, because only one year was sampled by each author.

Appleton-Whittell Research Ranch grama grass—The Appleton-Whittell Research Ranch in southeastern Arizona has been an ungrazed National Audubon sanctuary since 1968 (Bock and Bock 2000). Adjacent moderately grazed sites are available for comparative purposes and are generally grazed moderately (Bock and Bock 1993). Precipitation is higher at this site compared with those above. Canopy cover is high at 86 percent in ungrazed grassland, with a large amount of grass cover of 68 percent (Brady and others 1989). The flora of the site is mostly comprised of Madrean and Apachian elements similar to floras to the southeast in Mexico and southwestern Texas, even though the area has previously been classified as Plains and Great Basin Grasslands (McLaughlin and others 2001). Only 7.4 percent of the flora are exotics, over half of which are grasses.

A comparison of initial conditions at the time of the removal of livestock from the sanctuary with conditions 16 years later, as well as a cross-fence grazed versus ungrazed comparison after 16 years of protection, was conducted by Brady and others (1989). Total vegetation cover more than doubled over the 16 year period, and species richness tripled. However, neither cover nor species richness differed when compared across the fenceline in the same year. The very high current values on both grazed and ungrazed sites suggests that factors other than grazing were also responsible for the temporal changes. Blue grama increased the greatest over the period, and cover was similar on grazed and ungrazed areas along the fenceline. The relatively tall plains lovegrass increased greatly in both areas. Shrubs increased over time but were a small component of total cover and did not differ between the grazed and ungrazed sites. Based on the fenceline comparison, differences solely attributable to grazing were the increase in mid-grass cover (primarily plains lovegrass) and changes in forb composition.

Total vegetative cover in 1981 to 82 was 106 percent in the ungrazed compared to 73 percent in grazed sites (Bock and others 1984). Species composition did not vary greatly between treatments, but there were 10 species that differed significantly with grazing (Table 10). The dominant on both grazing treatments was blue grama, but it did not significantly differ with grazing. Sideoats grama was the second most abundant species on both sites and did not differ between treatments. This is contrary to most studies elsewhere showing increases in blue grama with grazing, but consistent with the Brady and others (1989) study at the same ranch. The cover of total grasses and total forbs was significantly greater on the ungrazed side of the fences, with values for forbs more than double that on the grazed portion of the study area. Total shrub cover did not differ between grazed and ungrazed sites. Separate measurements of shrub densities, heights, and maximum canopy widths did show some differences with grazing. Three out of five shrub species attained greater heights and canopy widths in ungrazed treatments. However, there were no significant differences between treatments in density, height, or width of mesquite, which occurred at an average of only 1 individual/400 m^2. Burroweed was also not significantly different between grazed and ungrazed sites, although individual plants were larger in the ungrazed site. Bock and Bock (2000) indicated that burroweed population dynamics is much more related to fire and weather than to livestock grazing. Bock and others (1984) commented that the lack of response to grazing by the dominant grama grasses may be due to their co-evolution with large native herbivores (Mack and Thompson 1982; Milchunas and others 1988), but that other species were able to co-exist within the grazing resistant matrix of grama grasses within the sanctuary.

Eight cross-fence sites were intensively sampled for canopy cover by Bock and Bock (1993) in 1990, after 22 years of protection from grazing in the sanctuary. Canopies were well developed at the time of sampling, and cattle were not yet present on grazed sites, whereby measurements were not confounded by current consumption (see Introduction section on methods). Total grass canopy cover was again greater without grazing. Out of ten grasses, the two stoloniferous grasses showed the greatest cover on grazed sites and the three tallest bunchgrasses showed the greatest increases with protection from grazing. A good relationship between “grazing release ratio” (ungrazed canopy cover divided by grazed canopy cover) and culm height (an index of undisturbed plant height) was observed for the 10 main species, indicating that taller species responded more to grazing than short species. While in agreement with global analyses (Milchunas and Lauenroth 1993), this is at the same time unusual because the species that increased was the generally grazing intolerant black grama. Blue grama, a general increaser with grazing in the Great Plains, was greater in ungrazed than grazed sites, although it was a greater composition of the grazed. Some very interesting points were raised by the

Table 10—Basal cover (percent) of grama grassland in southeastern Arizona ungrazed for 14 years or grazed moderately. Adapted from Bock and others (1984).

	Basal cover (percent)	
	Ungrazed	Grazed
Grasses-total	80.4**	55.6
Cane bluestem	1.3	1.3
Reverchon three-awn	1.0	0.3
Purple three-awn	7.4**	2.1
Spider grass	4.6*	2.5
Sprucetop grama	1.5	3.1*
Sideoats grama	14.0	15.6
Hairy grama	3.5	4.5
Blue grama	22.0	20.1
Plains lovegrass	6.1**	0
Curly-mesquite	0.4	2.0*
Common wolfstail	8.1*	2.4
Vine mesquite	3.6**	0.6
Arizona cottontop	4.3*	0.1
Herbs-total	12.0**	5.6
Field bindweed	1.4	0.5
Leatherweed	3.5	2.0
Trailing fleabane	1.3	1.1
Silver dwarf morning-glory	1.6*	0.1
Woody plants-total	13.5	11.5
Yerba de pasmo	2.0	1.0
Cooley’s bundleflower	6.0*	3.6
Rayless tansyaster	1.0	1.9
Shrubby false mallow	3.0	3.3
Bare ground	17.6**	34.6

* Significantly greater than other treatment ($P<0.05$)
** Significantly greater than other treatment ($P<0.001$)

Bocks. First, they questioned the classification of this area as a grama grassland but as being an "artifact of over 100 years of livestock grazing." Only one of five taxa that was a grama grass increased in response to release from grazing, and the study site is in a location that was not subjected to 10,000 years of grazing by bison that occurred in adjacent grasslands of the Great Plains. Second, they commented on the differences in response of their Arizona grassland with blue grama as a dominant and the shortgrass steppe of the Great Plains that is also dominated by blue grama. Changes in plant species composition were much greater for this study compared with that found in the Colorado shortgrass steppe by Milchunas and others (1989). This is confirmed by calculation of dissimilarity indices for the two studies. The average community dissimilarity (Whittaker 1952) for the eight sites in the Bocks study is 32 percent, compared with an average of 10 percent dissimilarity between ungrazed and grazed sites for the Milchunas study. The Bocks considered one possibility for the greater responsiveness of the Arizona site to protection from grazing was the greater precipitation (430 vs. 310 mm/yr), whereby tall and mid-height species were more capable of increasing with protection at the Arizona site compared with abioticly maintained short grasses at the shortgrass steppe site. The Bocks also considered the possibility that, although the same species, blue grama responds differently to grazing in areas where it was not subjected to bison grazing for 10,000 years compared with areas where it was subjected to bison grazing. This is a very important consideration that will be examined in greater detail in the conclusions section below, based on responses of blue grama from studies throughout this review. Third, the Bocks raised the question as to whether protected areas may respond differently when they are large areas such as the sanctuary (3160 ha) compared to the generally small size of exclosures. Bock and Bock (2000) suggest that changes may still be taking place on the ungrazed sanctuary and that eventually taller grasses may displace blue grama and other shorter grasses.

Other locations—As with the Appleton-Whittell Research Ranch, black grama and blue grama co-occur at the Sevilleta National Wildlife Refuge Long-Term Ecological Research site, located in central New Mexico at a biome transition zone between Great Plains grasslands, the Chihuahuan Desert, and the Colorado Plateau shrub-steppe (Gosz and Gosz 1996; see Fig. 2). Precipitation averages only 222 mm/yr in grassland communities. Domestic grazers were removed from this site when it was established as a refuge in 1973, and black grama has been increasing compared with cross fence visual observations and five years of data. Increases in blue grama were also observed, but they were not as great as that for black grama. A controlled clipping, burning, and native herbivory experiment demonstrated that black grama was more sensitive to all three factors than was blue grama in terms of plant height growth and production. Native herbivores did not, however, significantly affect productivity. The data suggested that the absence of both burning and grazing on the refuge could be attributed to the increases in black grama. Black grama also responded more to wet-dry conditions than did blue grama.

A study established in 1976 and resampled in 1986 and 1996 at the Sevilleta also showed very large temporal dynamics in plant communities, especially in the black grama communities (Ryerson and Parmenter 2001). Although landscape-scale analyses showed no differences between inside and outside refuge boundaries between 1976 and 1996, site specific analyses inside the refuge showed stable perennial plant cover and increases in annual forb and litter cover while communities outside the refuge showed declines in perennial plant cover. However, changes in community similarities of the black grama communities from 1976 to 1996 inside the refuge ranged from just under 80 to nearly 100 percent different (5 sites), while those outside displayed a greater than 95 percent change over time. Temporal dynamics were extreme compared to herbivore regulated dynamics. The authors noted a very interesting black grama - blue grama relationship. Sites dominated by blue grama in 1976 were dominated by black grama in 1996, and this occurred outside the refuge in the presence of livestock grazing. Blue grama, the ubiquitous increaser with grazing throughout the Great Plains, and a grazing tolerant species in the southwest, and the grazing intolerant black grama, must have responded more to climate or some other factor than to the presence of grazers. Perennial plant cover in the black grama community decreased over time in the presence of herbivores, while remaining the same in the absence of the grazers. In contrast, Burrograss communities increased in perennial grass cover outside the refuge and decreased inside the refuge. Short-term protection from grazing showed few effects, but these effects increased in importance with longer-term protection.

Blue grama also dominated at an upland site in southwestern New Mexico that had been protected for 28 to 30 years or very heavily grazed (Gardner 1950). Precipitation at this site was approximately 370 mm/yr. Blue grama, ring muhly, and total grass basal cover (not density as the author calls it) in the protected area

Table 11—Basal cover of herbaceous and canopy cover of shrubs (percent) and number of forbs/30.5 m transect in ungrazed and very heavily grazed grama grassland in southwestern New Mexico. Pre-drought was 28 years after protection and post-drought 31 years after. Adapted from Gardner (1950).

	Pre-drought		Post-drought	
Grasses	**Ungrazed**	**Heavily grazed**	**Ungrazed**	**Heavily grazed**
Red threeawn	0	0.23		
Sideoats grama	0	0		
Black grama	0.16	0.24	0.32	0.11
Blue grama	7.48	3.30	1.92	0.66
Hairy grama	0	0		
Tobosa	0.51	0.79	0.03	0.19
Ringgrass	1.15	0.02	0.04	0.01
Other grasses	0.34	0	0.03	0.05
Total grasses	9.64	4.58	2.34	1.02
Half-shrubs	0	0.1	0.1	0.3
Shrubs	2.9	0	0.3	0.4
Forbs	0	0	0.33	0.17

were at least twice as much as in the heavily grazed area (Table 11). Black grama, tobosa, and red threeawn were slightly greater in the grazed site. Although cross-fence tobosa lowlands in a grazed area were not available for direct comparison, swales in the grazed areas were cut by steep-sided arroyos while those in the protected area had some plant cover stabilizing the soils, but were predicted to require much more than 28 years to heal. Two years later after a drought in 1947, resampling of the same area showed a decline in total grass basal cover of 75 percent inside the exclosure compared to 78 percent outside. Although declines in cover due to drought were similar with either protection or very heavy grazing, some changes in species distributions were evident post-drought. Black grama became more abundant in the protected site and forbs increased greatly everywhere and were also greater in the protected site. The decrease in cover due to drought in the tobosa community was only about 50 percent. The greater resistance to drought of lowland tobosa communities compared to uplands agrees with those reported above for Jornada tobosa/burrograss communities.

Only one of the Potter and Krenetsky (1967) plots was in mesquite savanna. Although they report two in desert grassland, one was a site dominated by mesquite. Both sites showed an increase in grass cover and a decrease in shrub cover with protection. This is one of the few examples where mesquite was reported to increase greatly under grazing while decreasing under protection. Species richness increased over the 25 years in the exclosure, as did the cover of black grama. Total cover increased 60 percent and grass cover increased from 23 to 70 percent of the vegetation in the exclosure.

Navarro and others (2002) estimated range condition during seven years spanning 1952 to 1999 at 41 BLM sites in six counties across southwestern New Mexico. Average grazing intensity at the sites was a conservative 34 percent utilization, and average precipitation ranged from 260 to 350 mm/yr. Range condition fluctuated greatly with fluctuations in precipitation but did not differ significantly between beginning and end of the sampling period. Cover of black grama, tobosa grass, and mesquite was not different between beginning and end of the sampling period, except mesquite increased dramatically on one of the 41 sites and creosote-bush on another site. The authors concluded that conservative grazing was sustainable in this part of New Mexico. Of the 41 sites during the 1998, 1999, and 2000 period, the percentage of sites grazed severely, heavily, moderately, conservatively, and lightly and ungrazed were 1, 12, 35, 19, 28, and 5 percent, respectively, which is an approximately 50:50 split between what was considered sustainable and not.

Dutchwoman butte in central Arizona supports the only relict, geologic refuge for mesquite savanna available for this review. Precipitation was estimated at 432 mm/yr, with 60 percent falling during the winter (Ambos and others 2000). Precipitation during the two-year study period was above normal, but a long-term period of below average precipitation preceded sampling. The site is at the cool/moist end of the semiarid grassland gradient and is also at the transition between grassland and higher elevation woodlands of redberry juniper and turbinella oak. Dramatic differences were found between the plant community on the butte and surrounding grazing allotments on Tonto National Forest

Table 12—Canopy cover (percent) of plant species and basal cover of ground components of a cental Arizona grassland never grazed by livestock (geologic refuge, mesa), protected from grazing for ~50 years, and a grazed allotment in Tonto National Forest. Adapted from Ambos and others (2000) and Ambos (unpublished data, personal communication).

		Canopy cover (percent)		
Trees/shrubs/half-shrubs		**Never grazed relict**	**Exclosure built 1934**	**Grazed**
White-ball Acacia	*Acacia angustissima*	0.1		
Catclaw Acacia	*Acacia gregii*	1.0		
Agave	*Agave parryi*	1.2		
False Mesquite	*Calliandra eriophylla*	10.8		
Hedgehog Cactus	*Echinocereus* spp.	0.2		
Wright Buckwheat	*Erigonum wrightii*	4.7	14.1	7.3
Redberry Juniper	*Juniperus erythrocarpa*	2.0	T	T
Englemann Pricklypear	*Opuntia phaecantha*	1.7	3.8	3.0
Banana Yucca	*Yucca baccata*	3.1		
Broom Snakeweed	*Gutierrezia sarothrae*		T	6.1
Littleleaf Ratany	*Krameria parvifolia*		T	0.4
Mimosa	*Mimosa biuncifera*		T	2.1
Velvet Mesquite	*Prosopis velutina*			T
Scrub Oak	*Quercus turbinella*		T	T
Total Trees/Shrubs/Half Shrubs		24.8	17.9	18.9
Forbs				
Aster	*Aster* sp.	T		
Sunflower	*Helianthus* sp.	T		
Deer-vetch	*Lotus rigidus*			
Wright's Thimblehead	*Hymenothrix wrightii*		3.0	0.4
Plantain	*Plantago* sp.		0.3	0.6
Total Frobs		T	3.3	1.0
Grasses				
Threeawn	*Aristida* sp.	1.2		
Cane Beardgrass	*Bothriochloa barbinodis*	0.3		
Sideoats Grama	*Bouteloua curtipendula*	13.9	0.4	0.1
Hairy Grama	*Bouteloua hirsuta*	8.6		
Plains Lovegrass	*Eragrostis intermedia*	5.9		
Tanglehead	*Heteropogon contortus*			
Curly Mesquite	*Hilaria belangeri*	1.8	T	15.8
Prairie Junegrass	*Koeleria pyramidata*	3.9		
Green Sprangletop	*Leptochloa dubia*	0.8		
Bull Muhly	*Muhlenbergia emersleyi*			
Bottlebrush Squirreltail	*Sitanion hystrix*	2.7	17.7	T
Sand Dropseed	*Sporobolus cryptandrus*	0.2		
Total Grasses		39.3	18.1	15.9
Ground cover components			**Basal cover (percent)**	
Grass Basal Area		7.9	3.3	9.9
Tree/Shrub/Half-Shrub Basal Area		1.8	1.4	1.7
Litter > 1.2cm		20.7	20.9	5.8
Rock Fragments > 0.2 cm		32.8	14.0	10.0
Bare Soil		36.1	63.8	71.5

(see below for productivity and soils). Sideoats grama, hairy grama, and plains lovegrass comprised 70 percent of the grass canopy on the butte (Table 12). The heavily grazed ranges were dominated (90 percent) by curly mesquite, which was only 5 percent of the grass canopy on the butte. This represents a complete change in dominant species on the butte compared with thousands of acres of adjacent rangeland. Sideoats grama (0.1 percent cover vs. 13.9 percent on butte) was the only other grass species to occur on the grazed area in more than trace amounts. In contrast, 12 species occurred on the butte in an abundance greater than 0.1 percent canopy cover. Canopy cover of palatable forage species was 55 percent on the butte compared to 23 percent on the grazing allotment. Abundant in the grazed areas, snakeweed was observed on the butte but not recorded in the sampled transects. There were 21 species encountered in sampling the relict compared to 12 in the exclosure and 13 on the grazed area. Species sampled in the exclosure were generally the same species sampled in the grazed area, but a very different set of species was sampled on the butte. Basal cover of grasses was greatest on the grazed area due the sod-like structure on grazed areas compared with bunchgrass structure on the butte. Litter cover was similar in the butte and exclosure communities, which were three times greater than in the grazed area.

Primary Production

Primary production in mesquite savanna is highly variable from year to year, depending on precipitation. Paulsen and Ares (1962) estimated a 15 year average of perennial grass production of about 50 g/m^2/yr in black grama grassland at the Jornada Experimental Range, with a minimum of 15 and a maximum of 80 g/m^2/yr. Tobosa type range produced 112 and 168 g/m^2/yr for two years of measurement. At the nearby College Ranch, Holechek and others (1999) reports a 30-year average of 22 g/m^2/yr forage production, with a range from near zero to over 80 g/m^2/yr. Perennial plus annual grass production at the Santa Rita Experimental Range over a 10 year period averaged 22 g/m^2/yr, with a minimum of 4 and a maximum of 33 g/m^2/yr (Martin and Cable 1974). Grass production was greater on coarse than on fine soils, although black and Rothrock gramas produced more on fine soils. Mesquite-free plots produced an average of 26 g/m^2/yr compared to 18 g/m^2/yr for mesquite-infested plots. Annual grasses comprised 71 percent of the total grass production, and this did not vary with mesquite cover. The annual grass component varied greatly among years compared to the relatively more stable perennial grass component. Production on low elevation, low rainfall sites heavily dominated by annuals can vary from 0.4 to 107 g/m^2/yr in consecutive years, while values for productive sites with a good perennial grass component for the same two years were 50 and 95 g/m^2/yr (Martin 1975). While annual fluctuations are evident, previous as well as current-season precipitation was important in controlling perennial grass production.

Martin and Cable (1974) also estimated grass production over the 10 year-period for pastures grazed November to April, May to October, and year-long. Percentage differences for the last three years of study compared to the first three years indicated significant increases in perennial grass production for the year-long grazing treatment with little change in the two seasonally grazed pastures. Concomitantly, annual grasses tended to decrease in pastures grazed year-long to a greater extent than those grazed in November to April or May to October. Fifteen different grazing systems involving different periods of seasonal or year-long rest of 1 year rest over 3 years, 2 years rest over 3 years, 3 years rest over 4 years, rested every year during winter, or never rested were tested over eight years at the Santa Rita (Martin 1973). Of the 15 treatments, only spring-summer rest 2 out of 3 years resulted in significantly greater production of perennial grasses compared to all other treatments. Weather greatly overrode any grazing management system. Rest schedules of the various treatments gave deferment percentages (time not grazed) of from zero to 67 percent. Density of perennial grasses other than Rothrock grama (a short-lived perennial) did, however, increase with the 44 and 67 percent rest schedules. None of the treatments involving periods of rest during the year improved production of annuals or Rothrock grama.

Valentine (1970) assessed different grazing intensity effects on yields of black grama at the College Ranch adjacent to the Jornada Experimental Range. Percent utilization of black grama during the dormant season averaged 26, 35, 49, and 60 percent over the 10 year study for what was considered light, moderate, proper, and heavy grazing. The sites used for the study were previously deteriorated due to proximity to water, and the objective of the experiment was to assess recovery of black grama. Average production of black grama was 22, 21, 13, and 9 g/m^2/yr, with plant production under light - moderate grazing being significantly greater than that under proper - heavy and not different within either of the two. Yield as an average of that for good-condition black grama range was 46 percent for the lighter grazed treatments. Light grazing compared to proper or heavy grazing resulted in greater seed-stalk height, stolons per plant, length of stolons, and rooted stolon buds per plant, while moderate grazing was greater than the heavier treatments only in length of stolons.

In a 10 to 11 year field clipping study, Canfield (1939) estimated production in both black grama and tobosa types. Clipping black grama at a height of one inch drastically lowered production to 9 to 11 g/m^2/yr regardless of clipping intervals of 2, 4, 6 weeks, or once at end-of-season. Clipping at a two-inch height resulted in average 11 year mean production of 20, 21, 32, and 34 g/m^2/yr black grama production for clipping intervals of 2, 4, 6 weeks, or once at end-of-season, respectively. Similar results were not obtained for the tobosa type until the last three years of treatment, at which time tobosa began to decline dramatically under severe clipping. Plots

Table 13—Grass, forb, and shrub composition (percent) and aboveground primary production (g/m^2/yr) of a New Mexico (Jornada) mesquite savanna ungrazed or moderately grazed by livestock. Adapted from Pieper and Herbel (1982).

	Composition (percent)	
	Ungrazed	Grazed
Warm season grasses	43.9	18.1
Warm season forbs	23.7	30.5
Cool season forbs	3.7	5.1
Warm season shrubs	22.2	40.3
	Production (g/m^2/yr)	
Total aboveground	148	109

clipped weekly at four inches height produced 11 times as much biomass as plots clipped at two inches. A four week clipping interval represents very heavy defoliation, and production was 87 and 127 g/m^2/yr for the two inch and four inch height clipped plants, respectively.

Total primary production was estimated in grazed and ungrazed grassland for three years at the Jornada during the International Biological Program (Sims and others 1978; Pieper and Herbel 1982; Pieper and others 1983). Total primary production over the three years averaged 74 percent greater on ungrazed compared to grazed treatment (about 40 percent utilization), with significant differences in two out of three years (Table 13). Warm-season grasses were always a greater percentage of the production of ungrazed treatment, and warm-season shrubs were always a greater proportion of the grazed. Holechek and others (2000) report 16 and 13 g/m^2/yr production for conservatively compared to moderately grazed treatments at the College Ranch, but there were experimental design layout problems for making this comparison (see Species Composition section).

At the relict, never grazed butte examined by Ambos and others (2000) (see Species Composition section above for description), herbage production was 127 g/m^2/yr in a good year and 53 g/m^2/yr in a drought year. These authors indicate primary production on the butte was about four times that as similar grazed areas.

Root and Soil Responses

Although there is a considerable amount of research concerning aboveground plant responses to grazing on mesquite savannas, surprisingly very little research has been done belowground. Sims and others (1978), Pieper and Herbel (1982), and Pieper and others (1983) observed greater root biomass in ungrazed compared to grazed treatments at the Jornada in the 0 to 10 cm depth increment, and no effects of grazing at deeper depths to 30 cm. Average root biomass over the three years of study and all depths were 168 and 143 g/m^2 for the ungrazed and grazed treatment, respectively (old estimates of root production based on various means of summation of peaks produce very biased values [Milchunas and Lauenroth 1992] so are not reviewed here). Other comparisons between grazed and ungrazed conditions involve extreme examples. Gill (1975) estimated 12 and 6 g/m^2 root biomass for ungrazed and grazed sites. However, the values are extremely low, possibly because the sites were established in "sacrifice" areas very close to water. The only conclusion from these data may be that relative root biomass does not recover from denuded areas after 12 years of protection from grazing. Ambos and others (2000) reported six-times the root biomass in surface horizons of the relict, never-grazed butte compared to similar nearby grazed allotments.

Soil compaction was compared by Ambos and others (2000) at the relict butte site, a long-term exclosure since 1934, and a grazed site, all of which were heavy-loams. Soil bulk densities were 0.93, 0.98, and 1.33 for the butte, long-term exclosure, and grazed site respectively. Organic carbon contents of the butte site were very high relative to Arizona soils in general. Gil (1975) found no significant difference in bulk densities between ungrazed and grazed sites, but some improvement in soil organic matter after 12 years of recovery. Gardner (1950) found "no critical differences" in soil nutrients or organic matter between areas grazed or protected from grazing for 30 years.

Grazing Management

The free-range policy in the late 1800s to early 1900s represented a period of extremely heavy grazing. Early researchers thought that grazing systems with periods of rest would lead to improved range condition. Griffiths (1901, 1904, cited in Martin 1975) suggested that three year periods would be sufficient for improving condition to acceptable levels. This was based on observations that protected range recovered more rapidly than range where stocking rates were reduced (Wooton 1916, cited in Canfield 1948; Canfield 1948). Humphrey (1960) recommended rest during every July to August growing season for southern Arizona range in poor condition to allow palatable perennial grasses to grow and set seed. Rest every third year was thought to be adequate once the range reached good condition. Rest and particular periods of rest were thought to be important means by which range managers could devise grazing systems that would do more towards improving range condition than just regulating year-long grazing intensity. A number of systems were devised that involved various, and sometimes complicated, combinations of deferment or rest and rotations among various numbers of pasture units.

Martin (1973) tested 15 different season/frequency of rest combinations on replicated but small plots at the Santa Rita Experimental Range for an eight year period. Seasonal or year-long rest for one year in three, two years in three, three years in four, and every year were compared to year-long grazing. Increases in the densities of long-lived perennial grasses occurred only when rest periods were 44 or 67 percent of the time (Fig. 6). Rest period totaling 33, 25, 22, or 11 percent of the time did not provide a significant increase over season-long grazing with no rest. A system with spring-summer rest in two years out of three showed the greatest increases in perennial grasses. Increases in perennial grasses other than Rothrock grama occurred after four years under this system, but this did not continue after additional years. None of the systems increased production of annual grasses or Rothrock grama. Martin concluded that rest for only a part of the year provided little increase in production over year-long grazing. In other studies at the Santa Rita, rest in some cases was shown to decrease perennial grasses and increase burroweed (Martin and Cable 1974). This occurred for annual rests from November through April and particularly May through October compared to year-long grazing. Martin and Ward (1976) further tested some of the promising treatments found for previously very heavily grazed sites (Martin 1973) on an additional three sites less intensely grazed. Four different alternate-year rest schedules, one seasonal every-year rest treatment, and continuous year-long grazing was compared for seven years. Year-to-year variability in perennial grass production was so great as to mask any treatment effects. The authors concluded that perhaps alternate-year rest did not provide sufficient periods of growing-season recovery. Based on the studies, however, Martin proposed a three-year, three-pasture system of spring-summer and winter rest two out of three years that would become known as the Santa Rita grazing system.

Grazing under the Santa Rita system would average the same 40 percent level over time as that for year-long grazing, but would be heavier in a pasture being grazed that year to make up for the amount not grazed when the pasture was rested. The heavy grazing followed by rest is the basis for a number of grazing systems that attempt to obtain more uniform utilization across species of different palatability and across the landscape, thereby more uniformly spreading the burden of defoliation. A 13 year test of the Santa Rita system alongside year-long grazing at three sites representing low-, mid-, and high-elevations resulted in no significant differences in grass, forb, or shrub densities or in shrub cover (Martin and Severson 1988). The lack of response to the rest-rotation grazing system was attributed to the good initial conditions of the study sites, and the moderate grazing intensities. The authors speculated that different results may have been found if the sites had been in a poor condition initially. In contrast, distance to water, in other words grazing intensity, resulted in significant differences in perennial grass production, particularly black grama.

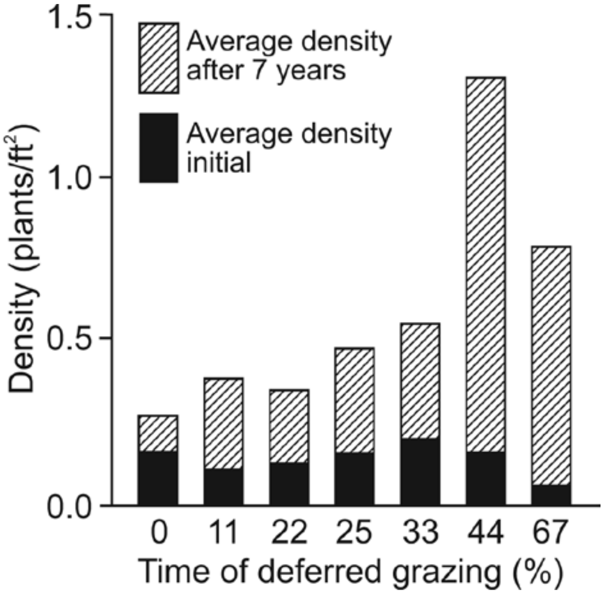

Figure 6—Density of perennial grasses other than Rothrock grama in relation to the percent of time grazing had been deferred over a seven year period in a mesquite savanna community. A total of 15 different season/frequency of rest combinations were examined on replicated but small plots at the Santa Rita Experimental Range. Adapted from Martin (1973).

Another long-term, 28-year study at the Santa Rita Experimental Range assessed some of the same pastures used previously by Martin and Severson (1988) that continued in the Santa Rita system compared to some of the previous pastures that had been switched to year-long heavier grazing than that used in the Santa Rita system pastures (Angell and McClaran 2001). The switch in grazing practices was for 15 years, but there was only one replicate per treatment. Results did, however, confirm those reported originally by Martin and Severson. Grazing every summer compared to frequent rest during the growing season resulted in a decreased density of only one perennial grass (bush muhly). The lack of difference between grazing intensities/rest - no-rest treatments in density of the exotic Lehmann lovegrass was consistent with a previous study showing no effects of complete protection on the lovegrass.

On the Jornada, Paulsen and Ares (1962) recommended deferment of grazing on ranges with a high percentage of black grama. This was suggested as a means to allow black grama stolons to establish new plants. Grazing could be shifted to lowland tobosa communities, since tobosa could withstand moderate grazing, and was palatable during the growing season while black grama was palatable at any time of the year and more so during the dormant season. Based on three pastures with different percentages of grazing during winter-spring, land-area requirements decreased with increasing percentage of use during the non-growing season. Black grama increased with summer deferment in only one of three pasture replicates at the Santa Rita (Martin and Severson 1988), but the sites had only minor amounts of black grama. Paulsen and Ares also recommended placing salt one to four miles from water to obtain a more uniform distribution of pastures. Martin and Ward (1970) found lighter use near water if access to water was rotated in large pastures lightly or moderately stocked. While this may increase potential stocking rates, the heterogeneity of grazed to less grazed sites may be important to wildlife diversity.

Martin (1975) suggested there may be some advantage to grazing sheep and/or goats with cattle to balance pressure on forbs, shrubs, and grasses, based on some research in Texas. However, browsing by sheep or goats was not considered a likely means to reduce growth and spread of shrubs.

In general, the current view of range managers is that "various rotation grazing systems cannot overcome the rangeland degradation associated with chronic overstocking." Grazing intensity is the overriding factor in range condition, although periods of rest longer than seasonal can be beneficial. Hughes (1980) suggested that low to moderate utilization rates were necessary for grazing systems to work in northwestern Arizona, but stocking rates were the only factor varied at the sites that were assessed. Martin (1975) suggested that, theoretically, there should be some advantage to rest in bunchgrass grasslands compared to sodgrass grasslands, simply because the former more often reproduce by seed and the latter by vegetative spread. Seed production is generally, but not always, reduced by current-year grazing (Obeso 1993). Longer-term rest-rotation systems may also better provide a diversity of community physiognomies across the landscape, which may be important for wildlife populations. An important aspect of management is the ability to reduce herd size during drought without seriously affecting the breeding herd, thereby protecting from overutilization when production is low (Paulsen and Ares 1962). Additional grazing systems studies in mesquite dominated systems are examined in the Chihuahuan Desert section below.

Mesquite Savanna Conversion to Chihuahuan Desert: Shrub Invasion, Livestock Grazing, Fire, Small Mammals, and Climate

The invasion of grassland by shrubs has been extensive in many areas, and not extensive in other areas, although encroachment continues. For example, Mehrhoff (1955) and Humphrey and Mehrhoff (1958) indicate that three-quarters of the Santa Rita Experimental Range was at one time grassland, but that at the time of writing less than one-fifth of the site remained in grassland. McClaran (2003) reviewed early studies at the Santa Rita and showed recent data that indicates cover, but not density, continues to increase through 2000. At the Jornada, a 107 percent increase was observed in mesquite-dominated areas between 1915 and 1946, while grasslands declined 28 percent (Branscomb 1956, 1958; Buffington and Herbel 1965). In contrast, mesquite increased dramatically between 1952 and 1999 on only one of the 41 sites, and creosote-bush on a single site, of the 41 sites assessed by Navarro and others (2002). Bahre (1991) suggested that the changes may not have been as extensive as some researchers have implied. However, the review above clearly indicates that 1) where shrubs have invaded, there have been changes in understory species composition, 2) the shrub invasions occur regardless of whether sites are currently grazed or not, 3) however, early studies and observations suggest that grazing can be a factor under conditions of very heavy grazing intensities now considered abusive, and 4) in some cases, light grazing may dampen post-drought effects on shrub increases. We here focus on mesquite/creosote when speaking of shrub invasion. Shrub invasion regardless of grazing management does not mean grazing is not a factor, since interactions such as grazing effects on fire and/or previous grazing may still be an operating explanation. A patchy spatial distribution of the phenomenon would perhaps suggest that no one single factor may be responsible, and/or there may be thresholds associated with particular or interacting factors, or there is a seed limitation or some other factor associated with a moving front of shrubs. Factors other than current direct effects of grazing that have been suggested to potentially be involved include: 1) previous very heavy grazing during the late 1800s to early 1900s, 2) current grazing effects on reducing fire fuel-loads and fire suppression practices, 3) grazing by small mammals, and 4) climate change or climate fluctuations and/or a reoccupation of sites that were previously a shrubland community. Soil types can provide the patchy framework for interactions with fire and climate, through productivity/fuel load relationships or precipitation use efficiency and infiltration depth dynamics. Before exploring how grazing may interact with the above factors, we first return briefly to the primary possibility that current grazing directly influences shrub invasion. We do this because there are recent authors that imply or suggest current grazing is still a factor in shrub invasions (Schlesinger and others 1990; Bahre 1991; Bahre and Hutchinson 2001; Kerley and Whitford 2000). From the standpoint of "what can be done now?" and "what are the current management implications?", it is important to differentiate between past effects of grazing, current direct effects of grazing, and current effects of grazing as an interaction factor. Residual effects of past grazing events without current effects of grazing become academic and do not have a bearing on the two questions.

The Schlesinger and others (1990) model of desertification was a high-impact publication in the journal Science and was further elaborated in Whitford (2002). It is an eloquent and logical formulation of a hypothesis for the formation and maintenance of the alternate-stable-state shrub condition. The model is based on local landscape distribution of soil nutrients and water. The homogeneous distribution of soil resources under grassland are disrupted when livestock grazing lowers black grama cover, resulting in erosional redistribution of soil and runoff redistribution of water. Some local areas receive increased water that percolates deeper and favors shrubs over shallow rooted grasses, while other areas receive less water and loose soil. Once established in microsites of increased soil water depth percolation, shrubs reinforce the heterogeneous pattern of soil nutrients and water because infiltration is greater under the litter of shrubs, and wind- and water-moved soil further accumulates under the shrubs over time creating "islands of fertility" that are commonly observed in shrublands throughout the world. The model is conceptually sound, and probably reflects the real world in many instances. However, 1) the model was presented as a hypothesis for the renewal proposal for the Long-Term Ecological Research program at the Jornada site, not as a statement of fact for the site in general. 2) past or current very heavy grazing could very well fit conditions necessary for the model to operate. However, some of the strongest data indicating that shrub invasion into grassland exclosures is comparable to grazed grassland comes from the same site. That does not detract from proposing to study processes that maintain the shrub stable state, or the conditions under which grazing could initiate such dynamics. Once established due to whatever cause, the Schlesinger and others model provides a good description of the dynamics helping to maintain the shrub dominated system (Martin and Cable 1974; Gibbens and others 1993). Very heavy grazing could very possibly be a cause, but very heavy grazing is not the current situation at the Jornada or other research sites and is obviously not the current situation in exclosures. Based on the data reviewed above, grazing as practiced at these sites or protection from grazing does not differentially affect invasion outcomes. Similarly, the Kerley and Whitford (2000) data show only a slight directional shift in community trajectory towards an ordinated shrub space that requires a large extrapolation across Euclidian space to reach the shrub domain, while their own shrub data and the Gibbens and Beck (1988) and Gibbens and others (1993) long-term data do not support such an extrapolation. In a review of shrub encroachment in the southwest, Allred (1996) also questioned the emphasis the model placed on grazing, given the data from that site. Bahre (1991) and Bahre and Hutchinson (2001) do not clearly differentiate among historic past very heavy grazing, current grazing practices, and grazing interactions with other factors. There is no doubt that current heavy grazing and past very heavy grazing can and has had large effects on southwestern grasslands, but the evidence reviewed above indicates that current grazing intensities, or even protection from grazing, does not influence shrub invasion. This does not rule out other potential effects of various grazing intensities versus no grazing on understory plant species composition and structure. Because previous grazing intensities could very possibly lead to conditions described in Martin and Cable (1974) and the Schlesinger and others (1990) model, there is the potential for previous or current heavy grazing effects on soils to manifest with long time lags (Grover and Musick 1990). Soil formation is a long-term process, whereby loss or redistribution of soil can have very long-term consequences, all of which may not occur immediately. This topic will be discussed further, after reviewing other potential factors and interacting factors in shrub invasions.

A grazing effect on fuel loads resulting in reduced fire frequency or intensity is always a potential factor that may alter plant communities. While an extensive review of fire effects will not be attempted here, a few contrasting points of view should be mentioned. Some authors were of the view that productivity in these, or some of these communities, was low enough to reduce the importance of fire even under pristine conditions, and the potential for fire to reduce abundance of black grama (Reynolds and Bohning 1956 - "seriously damaged" and did not recover after 4 years; Cable 1965 - 90 percent mortality) is another factor arguing for a relatively lower importance of fire in some of these communities. Gosz and Gosz (1996) suggest that "the increased dominance of black grama reflects the absence of burning and grazing" on the Sevilleta National Wildlife Refuge. On the other hand, Kaib and others (1996) and Kaib and others (1999) indicate a fire frequency of 4 to 8 years that is more frequent than previously thought. Bock and Bock (1996) report that fires on the ungrazed Appleton-Whittell Research Ranch have been somewhat regular. Black grama is not a component of that grassland, where fire was not a factor in grass mortality. For two or three growing seasons, fire reduced grass canopy cover, resulting in increased forb abundances for the same period, but had no negative long-term effect on shrub abundance except for burroweed. Mesquite resprouted from their bases. Importantly, changes in community physiognomy and seed production for the 2 to 3 years post-fire had some large effects on bird, rodent, and insect communities. Unfortunately, there are few large sanctuaries such as the Appleton-Whittell where fire frequencies may more closely resemble past conditions. The role of Indians in setting fires and affecting fire frequencies would be another aspect of debate. Would these be considered natural fires, and did these change through ecological time or did populations and social conditions remain constant enough and long enough to be considered an endogenous disturbance? While the Bocks found few long-term effects of fire, the observed short-term effects could historically be significant if fire return frequencies were short, whereby a patchy distribution of unburned and recently burned habitats was created across the landscape. Fire does have significant effects on grass and forb compositions for three to four years after the burn (Reynolds and Bohning 1956; Bock and Bock 1996).

The difficulty of killing mesquite with fire has led some researchers to question the role of fire in its distribution (Wright and others 1976). Some of the densest honey mesquite areas in Texas are in areas most subject to recurring fires (Allred 1949). Young velvet mesquite less than 1.3 cm (half inch) are more susceptible to mortality by fire in Arizona, but fire may kill only 10, 30, to 60 percent of even the young (Glendening and Paulsen 1955; Reynolds and Bohning 1956; Cable 1965). Even seedlings survive fire, although only one-third of one-year-olds survive (Cable 1961). Greater intensity fires kill more individuals, but even with over 500 g/m^2 grass fuel the mortality of young shrubs was low and black grama mortality was high under even less intense fire (Cable 1965). Fire on the Santa Rita significantly reduced burroweed, cholla, and prickly pear, but only reduced mesquite 9 percent (40 percent of young shrubs) and did serious damage to black grama (only 37 percent recovery four years post-fire). Densities of mesquite on burned and unburned treatments do not differ 3 years (Martin 1983) or 13 years (Cable 1967) after prescribed fire or 8 years after wildfire (Gottfried and others 2003). Ffolliott and others (2003) reviewed evidence from the Santa Rita and concluded that the effects of fire on grasses lasts only a couple of years and shrubs and cacti come back quickly unless other control measures are also implemented, but the authors also concluded that the effects of fire are season and site specific. Fires that were not very hot and extensive have not been successful in controlling mesquite expansion, but fires hot enough to kill mesquite would also kill grass and forage species. On upland sites in Texas, seedlings of honey mesquite up to 1.5 years old were easily killed with moderate fires, severely damaged at 2.5 years of age, and very tolerant of fire after 3.5 years of age. Short fire return intervals of 4 to 8 years (Kaib and others 1996; Kaib and others 1999), therefore, would have an effect on mesquite canopy cover, but would not be frequent enough to prevent invasion. This is counter to early perceptions of the role of fire and grazing-fire interactions (Humphrey and Mehrhoff 1958; Branscomb 1958).

Rodents have often been cited as a potential factor in shrub invasions. Their very large effect on plant communities in the southwest has been well documented (Norris 1950; Brown and Heske 1990; Heske and others 1993; Curtin and others 1999; review in Fagerstone and Ramey 1996). Where grassland and shrubland sites have been compared, smaller effects of small mammals have been observed in grassland compared to shrubland (Norris 1950). This is probably because most rodents prefer the shrublands, where they are 3 ½ times more abundant. In the shrublands, small mammals can have large effects on grass abundance. Reynolds and Glendening (1949) and Wood (1969) showed that Merriam kangaroo rats prefer the shrub habitat and cache seeds that would later sprout. Wood found an average of nearly one kilogram of food stored in wood rat dens, much of which was mesquite beans. Further, Paulsen and Ares (1962) state that mesquite invasion occurs most rapidly in the transition zone between the shrubland and grassland. Therefore, a reasonable hypothesis can be generated whereby a front of shrub invasion is generated by rodents foraging out from the shrubland into the grassland border, consuming grass that reduces competition, and planting seed at the same time. Curtin and others (1999) and Curtin and Brown (2001) found that shrub cover increased from 1979 to 1995 at an Arizona site, but the increase did not differ among kangaroo rat exclosures, all rodent exclosures, and control plots open to native mammals, even though rodents altered other components of vegetation composition. There are insufficient data from small mammal exclosures to reject this hypothesis as at least a potential contributing factor in shrub encroachment. However, Curtin and others (1999) and Curtin and Brown (2001) demonstrated a role of small mammals in vegetation patch-size dynamics, but the rodents countered the temporal increase in patch size associated with the temporal increase in shrubs. Gibbens and others (1992) observed a 79 percent mortality of marked mesquite seedlings due to lagomorphs or other small mammals, which suggested a role of these herbivores in limiting establishment. Based on kangaroo rat exclosures, Valone and Thornhill (2001) also observed a greater negative effect of herbivory on mesquite seedling establishment than the potential positive effects of seed-caching. The alternate hypothesis that small mammals inhibit spread of shrubs may also be posed. There are other shrubs and tree encroachment situations in many other southwestern communities in addition to the mesquite example. Rodents would need to be implicated in these as well for this to be a primary rather than a potential contributing factor. Although rodents other than kangaroo rats may also influence shrubland and grassland dynamics (Curtin and others 1999), it is interesting to note that Merriam kangaroo rats increase with grazing and fire (Bock and Bock 1996). Livestock can also consume and scatter mesquite seed. Hansen (1976) suggested that feral horses may also spread mesquite seed in their feces, because diets in southern New Mexico were 53 percent seed-pods in September. If there is a positive effect of livestock on seed planting rodent numbers and if both rodents and livestock are dispersal agents, both of these particular effects do not appear large enough to show significant differences in shrub encroachment between livestock exclosure sites and adjacent grazed sites. Reynolds (1954) observed that kangaroo rats consumed 98 percent of the seed they buried and transported seed a maximum of 32 m, suggesting that this would result in a dispersal rate of only 1.6 km in 500 years.

Climate change has many facets, some of which can have potentially important bearing on shrub encroachment in the southwest. Some aspects of climate change act at local and regional scales, and others at global scales. Changes include elevated concentrations of atmospheric CO_2, increases in temperature, and alterations in precipitation amounts, seasonal patterns, and temporal cycles. Because of differences in CO_2 saturation points of the C_3 versus C_4 photosynthetic pathways, C_3 plants can potentially increase growth with CO_2 enrichment to a greater extent than C_4 plants (Wand and others 1999). Atmospheric CO_2 has been increasing since the industrial revolution (Crowley 2000), which coincides with shrub invasions in the southwest. This led to considerations of a possible link between the encroachment of the C_3 shrubs into the C_4 grass dominated communities (Polly and others 1996a, b). There is no direct evidence to support or reject this hypothesis, but the results of experiments in nearby semiarid systems have some implications. Although western wheatgrass (C_3) biomass increased more in response to elevated CO_2 than blue grama (C_4) when grown in pots, there was no difference in their response to elevated CO_2 when grown in the field at a semiarid shortgrass steppe site treated for five years (Morgan and others 2004). Needle and thread grass (C_3) did, however, increase in biomass and community species composition in the elevated CO_2 field experiment, where CO_2 treatment also resulted in better soil water relationships. How plants respond competitively to the soil water conservation effects of CO_2 in semiarid and arid systems can be more important than the relative carbon gain effects through photosythetic pathways. The results from the shortgrass steppe do, however, demonstrate that CO_2 can change plant community species composition over short periods of time. Gill and others (2002) found that increases of CO_2 from pre-industrial time levels to current-day levels altered plant communities in Texas, indicating that changes in plant community species compositions could already have occurred in response to CO_2. Further, a recent study by Polley and others (2002) using a two-step correlative experimental approach showed that increased soil water with CO_2 and reductions of grass roots or water addition could result in increased survival of mesquite seedlings. There are infinite possibilities for plant-herbivore interactions to alter the outcome of CO_2 induced competitive relationships, but the evidence showing no differences in shrub encroachment with long-term grazing treatments and protection from grazing in the southwest suggests that interactions with grazing are not important in this situation. Similar arguments could be made for increases in temperature if they do occur in the southwest.

Climate changes involving both temperature and precipitation have been proposed as causes of the community shifts from C_4 grasses to C_3 shrubs in the southwest (Neilson 1986). Although older simple assessments of annual precipitation did not show relationships with shrub encroachment (Humphrey and Mehrhoff 1958), new meteorological techniques and a focus on winter versus summer precipitation patterns coupled with plant-life form life cycles provides a general hypothesis describing shifts from C_4 grasses to C_3 shrubs. Neilson indicates that prior to 1900 there was a period characterized by cool weather and relatively dry winters and wet summers. The end of the "little ice age" about 1900 and a shift in climate to warmer conditions with relatively wetter winters coincided with shifts from grasses to shrubs. After 1940, years with favorable winter precipitation became more common. Warm season C_4 species would be favored by summer precipitation and cool season C_3 species by winter precipitation. C_4 grasses would be photosynthetically more efficient in summer when temperatures were warm and relatively less efficient during winter and spring. C_3 shrubs would be photosynthetically active in warm winters with favorable precipitation, and shut down during dry summers. Very heavy grazing in the late 1800s and early 1900s resulted in sufficient erosion and inhibited asexual reproduction by perennial grasses, without which there may have been sufficient "biological inertia" (sensu Harper 1977) to overcome the subtle changes in climate. There are some strengths and some weaknesses in this argument, but there are also some important points not presented by the author that support the hypothesized link between the changes in climate raised in the analysis and the grass-shrub shifts in plant community structure. The shifts in temperature are counter to what may be expected to favor cool versus warm season species, in other words, cooler conditions prior to 1900 would possibly favor the cool-season shrubs rather than the warm season grasses. However, the overriding factor in Mediterranean climates favoring the dominance by shrubs and annuals is the timing of precipitation in relationship to the larger annual amplitude in winter-summer temperatures. Any smaller oscillation in longer-term temperature would be minor in comparison to summer-winter oscillation, and the seasonal timing of precipitation on soil water dynamics would be the overriding factor. Greater precipitation falling during cooler seasons would not only photosynthetically favor cool-season species (including many Eurasian opportunistic species) but would also be less subject to rapid evaporative loss, percolate deeper into the soil profile, and favor deeper rooted shrubs regardless of their photosynthetic pathway. Temperature optimums occurring in spring would favor the cool season species, often before warm season species even become active. Fast growing annuals and relatively faster growing perennials and cool season shrubs utilize winter-stored water before warm season species become fully active. Sandy soils would accentuate the greater penetration into the soil profile of winter precipitation. It is interesting to note that sandy soils are preferentially invaded by shrubs (Gibbens and others 1983). Soil texture/rooting depth arguments were not invoked by Neilson, but further support his hypothesis. Rooting depths also explain the increase in shrubs after droughts. Years of drought and years of high moisture favor shrubs, as shrubs can access deep stored water to maintain longer through a drought and can access the deep water that percolate deep during years of high rainfall. On the other hand, years of moderate or frequent light rains favor grasses. Leopold (1951) and Cooke and Reeves (1976) reported that an analysis of precipitation from the latter quarter of the 1800s showed that large rainfall events were more frequent and small events less frequent, even though total precipitation was not changing.

Some evidence supporting climate change as an important factor in shrub invasion has been provided by Brown and others (1997) in a long-term study in southeastern Arizona near the transition between desert shrubland and arid grassland. A study site was fenced from livestock grazing in 1977, and adjacent areas remained grazed. At that time the area was largely an open grassland with only widely scattered large shrubs. Much higher winter precipitation occurred across the area in most years through 1995, which coincided with large increases in shrubs. Aerial photos of the ungrazed research site and adjacent grazed sites in 1979 and 1995 indicated a 3-fold increase in shrubs on all sites regardless of whether it was grazed or protected from grazing.

The shrub increase could not be attributed to drought as well. The rodent and ant populations that were being monitored at the site showed large effects of the shrub invasion. Large increases in shrubs did not occur in many other areas, some as close as 20 km from the research site, even though the large increases in winter precipitation occurred over a much wider area. The authors considered this as supporting Neilson's (1986) hypothesis of shrub increases during periods of winter precipitation, but other factors must be operating that either produce changes through positive feedback or dampen changes through negative feedback. However, current grazing was found not to be the direct factor. McClaran (2003) provides long-term data on burroweed cycles that correlates abundance with wet winters.

While there may be many different factors interacting with short-term climate variability, fire has been shown to be one of the interacting factors associated with shrub invasion (Swetnam and Betancourt 1998). Decadal variability in climate is linked to fire occurrence across the southwest, and is associated with amplitude of the Southern Oscillation during the past three centuries. Fires are most likely to occur during drought, and rapid switches from wet to dry periods further enhances the fire potential. Plant mortality during drought was followed by pulses of shrub invasions not only in grasslands, but in shrublands and woodlands as well. The occurrence of these oscillations is further substantiated by independent tree-ring width, ice core, and coral isotope reconstructions.

Interactions between climate change and livestock herbivory were investigated by Curtin and Brown (2001) in association with the climate and rodent/climate interactions described above. Woody vegetation was assessed in the same region where increased winter precipitation was linked to shrub increases at the smaller study site, but was done at a larger landscape scale in 1) higher elevation oak savanna areas ungrazed since 1960 or continuously grazed, and 2) by comparisons across U.S. - Mexican borders where the Mexican side shows much more intensive grazing based on aerial photos. Aerial images showed no difference in shrub cover between grazed - ungrazed sides of the fence in 1946, 1957, or 1976, the latter being after 17 years of protection from grazing. Aerial photos from 1992 indicated an increase in shrubs associated with the increased winter precipitation, as was also observed at the lower elevation rodent exclosure research site (discussed above). However, the increase in shrubs was not the same in grazed and ungrazed areas. Shrubs increased two-fold in the grazed area compared to six-fold in the ungrazed area. The contrast in shrub abundance across the international border also showed increases in shrubs between the 1979 and 1992 photos, and the increases were similar for upland and lowland sites. In this case, however, no differences were observed in shrubs between the more heavily grazed Mexican and the lighter grazed U.S. sides of the boarder. Curtin and Brown concluded that increased bare ground and decreased herbaceous understory cover with heavier grazing was not associated with increased shrub density.

Chihuahuan Desert

Chihuahuan Desert communities can be dominated by a variety of shrubs, two of which are mesquite species (see Plant Community Descriptions in Appendix 1). Some of what may be said about mesquite dominated systems is contained in the Mesquite Savanna and the Mesquite Savanna Conversion to Chihuahuan Desert sections above. Chihuahuan Desert communities dominated by shrubs other than mesquite and long-term mesquite dominated systems are examined in this section. These shrub dominated communities produce less herbaceous understory vegetation in comparison with mesquite savanna, although mesquite savanna areas with low and moderate shrub cover may not show such reductions. However, dry grassland that has been invaded by shrubs actually store greater amounts of carbon in soil under the shrub condition than the grass condition, particularly in deeper depths (Jackson and others 2002). The shrub condition appears to be a self-perpetuating stable state (Schlesinger and others 1990, Whitford 2002). Although the above section focused on mesquite invasion into grassland, creosote bush and tarbush have also encroached into areas of what was previously grassland (Gardner 1951).

Species Composition

Much of the San Simon valley in southern Arizona was grassland in the late 1800s but had been heavily converted to mesquite-catclaw-greasewood shrub dominated communities by the early 1900s. Precipitation averages 350 mm/yr in a bimodal distribution, resulting in emergence of a winter annual group and a summer annual group of species. In this context, Kelt and Valone (1995) assessed the effects of a 16 year old livestock exclosure compared with adjacent grazed sites on annual plant communities composition. Total density of winter annuals was significantly greater in ungrazed compared to grazed treatment (166 versus 112), but only one species was significantly greater in the ungrazed treatment and there was no treatment effect on plant species diversity. No significant effects of grazing treatment were observed for total summer annual plant density or diversity. Six species were more abundant in the exclosure, but only one was significantly more abundant with grazing. A less conservative statistical approach would have resulted in additional significant effects of grazing, but the authors conclude that the few effects of protection from grazing suggest a very slow response in this community. The authors cite a personal communication with Chew as support for this, because he observed that it took 25 years of protection from grazing to see significant changes in perennial grass species at a site 10 km from this study site. Valone and Kelt (1999) compared fire treatments with the grazing treatments. Fire had greater, and independent, effects compared to grazing. These authors point out that summer annuals responded positively to fire and did not respond to grazing, and this group has affinities with communities to the east that more likely evolved with grazing and fire. In contrast, winter annuals displayed mixed and complex responses to the grazing and fire treatments, and this group has greater affinity with communities to the west in the Sonoran and Mojave Deserts.

The Chew (1982) study site mentioned above was in a creosote bush and a tarbush community. The exclosure was 170 m from a watering point, so grazing was often heavy although stocking rates varied with year. Eighteen to 19 years of protection did not alter the directional change in vegetation that started in this area in the late 1800s. In the creosote bush community, large increases in canopy cover of perennial understory species occurred from 1958 to 1977 in both grazed and protected sites. Only fluffgrass differed with grazing treatment, and it was greater inside the exclosure. Species diversity as estimated by H' (an index of incorporating both richness and evenness components of diversity) was greater outside the exclosure due to the greater dominance of fluff grass inside. In the tarbush community, large increases in snakeweed occurred from 1958 to 1977, but this happened both inside and outside the exclosure. Some grazing treatment differences were observed: fluffgrass increased over time outside but not inside the exclosure, and the opposite was seen for "other" perennial species. Black grama had large increases through time inside the exclosure but was not found in quadrats outside. Overall, changes with protection from grazing in these communities were considered very minor, even after 18 to 19 years of protection. Some increases in palatable perennials occurred, particularly in shallow washes. Based on general observations, Martin and Cable (1974) also commented that "mesquite could greatly retard or prevent improvement of deteriorated perennial grass stands…and mesquite effects might override the effects of other variables."

More recently, however, a resampling of both the Kelt and Valone (1995) and Chew (1982) study sites showed that recovery in these systems is possible, but only after very long periods of time (Valone and others 2002). The site that had been ungrazed for 39 years (Chew's site) now showed significantly greater cover of perennial grasses than the adjacent grazed site, with most changes occurring in the latter 20 years. The other site (Kelt and Valone's site), that had at the resampling been ungrazed for 20 years, showed no indication of recovery compared to the adjacent grazed area. The difference in recovery between the 39 year old exclosure and the 20 year old exclosure was apparently a length-of-protection and not a spatial phenomenon, because the two study sites were only 6 km apart. Further, the latter 20 years did not receive above average summer precipitation, which could have potentially explained the greater recovery of perennial grasses. The authors argue that these arid systems respond very slowly to changes in grazing pressures, because conditions conducive to seed production and establishment of particular species are rare and episodic.

In an early study of creosote bush communities of the Rio Grande Valley, Gardner (1951) also commented on the very slow recoveries after protection from grazing, especially in areas where grasses were previously nearly eliminated due to historically uncontrolled very heavy grazing. A comparison of areas lightly grazed and heavily grazed showed very similar species composition. While no grasses were observed in heavily grazed areas, small amounts were found in the lightly grazed areas. Gardner suggested that recovery after protection was somewhat more rapid on north facing slopes and in areas where water concentrates. Throughout the valley, areas where gullies and arroyos had developed showed some increases in grass cover after only 10 years. An increase in half-shrubs was also noted as a first sign of recovery in areas devoid of grasses.

Beck and Tober (1985) assessed the effects of protection from cattle and rabbits and shrub removal after 22 years at three creosote bush sites in southern New Mexico. Precipitation at the sites varied with averages of 207, 234, and 243 mm/yr, but the majority fell during the growing season at all sites. The treatments were established just after a drought. Responses to removal of cattle, rabbits, or shrubs was variable among sites, although there was a general increase for all herbaceous

Table 14—Increase (+), decrease (-), or no change (0) in plant cover over a 21 year period in response to removal of rabbits, cattle, or shrubs from a Chihuahuan Desert site in southern New Mexico. Adapted from Beck & Tober (1973).

	Site stocking rate								
	Low 80 ha/animal unit, then ungrazed 11 yrs			Low initially, then 20 ha/ animal unit continuous			Low initially, then 26 ha/animal unit		
				Organism removed					
	Rabbit	Cattle	Shrubs	Rabbit	Cattle	Shrubs	Rabbit	Cattle	Shrubs
Grasses				Plant species response					
Threeawn spp.	+	–	+	–	–	+			
Black grama				+					
Fluffgrass				+	0	+	+		
Tobosa grass				–	–	–			
Bush muhly	–	+	–	–	+	–	+		
Burrograss	+	+	+	–	–	+			
Alkali sacaton							–	+	+
Other grasses	–	+	+	–	–	+			
All Forbs	+	+	+	–	–	–	+	+	+
All Herbaceous Species	+	+	+	+	+	+	+	+	+
Half shrub									
Broom snakeweed	–	+	+	–	–	+			

species combined (Table 14). The increases in cover were low for most species after removal of any of the three. The authors concluded that "range improvement will be a slow process" for most ranges dominated by creosote bush. Gibbens and others (1993) arrived at similar conclusions based on a 30 year shrub removal study, where perennial grasses showed only limited increases. Shrub to grass cover ratios did not change with rabbit grazing compared to 50 years of rabbit exclosure, but there were some large changes in species composition (see Species Composition of Jornada black grama and dropseed communities section above).

An additional three sites were studied by Roundy and Jordan (1988) in southeastern Arizona. Precipitation at the two Chihuahuan Desert sites averaged 248 and 284 mm/yr, with most occurring in the summer. Changes in species composition or in life-form composition were small (Table 15). Native perennial grasses were not significantly different at one site protected from grazing for 19 years and were greater in the grazed treatment at the other site where the exclosure was 16 years old. Total overstory shrub cover did not differ between treatments at either site. These authors concluded "there is no evidence that exclusion from grazing alone or even in association with rootplowing will encourage reestablishment of native perennial grasses."

In contrast to studies above indicating little or very slow change with protection from grazing, Potter and Krenetsky (1967) reported decreases in mesquite under protection and increases in grazed areas. Their one site in the Chihuahuan Desert type was dominated by mesquite and tarbush. The grazed area is, however, an example of very heavy grazing, since it is crossed with a frequently used cattle trail. After 25 years of protection from grazing, new species were found in the exclosure, while species were eliminated in the grazed area. Only fluffgrass remained in the grazed area, while black grama increased in the exclosure.

Minor influences of native mammalian folivores (cottontail rabbits, jackrabbits, mule deer, and collared peccaries) was observed after 11 years of exclosure in a southern Arizona site dominated by acacia, tarbush, and joint-fir (Guo and others 1995). In contrast, birds had a strong effect on both winter and summer annuals, rodents had a relatively weak effect compared to birds, and mammals had the least effect. Effects were primarily on large-seeded annuals. Excluding each of the bird and rodent groups did not produce the same combination of effects produced by excluding both at the same time; in other words, effects were not additive. The effects of mule deer on plant communities is generally not large in semiarid communities of the west (see Ponderosa Pine section), although there are situations where impacts are great (see Pinon-juniper section, Kaibab Plateau). Based on numbers in Wallmo and others (1981) and Teer (1996), assuming average deer densities of 4 to 8 animals/km^2 and consumption of 1 kg/day then deer would only consume 1.5 to 3.0 g/m^2/yr of forage, which

Table 15—Density of plants on Chihuahuan Desert sites in southeastern Arizona ungrazed for 16 or 19 years or grazed by domestic livestock. The 16-year site was formerly desert grassland. Data from Roundy & Jordon (1988).

	16-year site (San Simon)		**19-year site (Bowie)**	
Species	**Ungrazed**	**Grazed**	**Ungrazed**	**Grazed**
Native perennial grasses		**Density (number/60 m^2)**		
Threeawn spp.	0.1	0	T	O
Arizona cottontop	T	0	N	N
Fluffgrass	8.8	16.0	0	0
Bush muhly	15.8	15.1	0.9	0.2
Total native perennial grasses	24.7	31.1	0.9	0.2
Full-shrubs				
Whitethorn acacia	0	0	N	N
Fourwing saltbrush	5.8	5.0	N	N
Longleaf jointfir	0.1	T	N	N
American tarwort	6.3	7.9	N	N
Creosote-bush	4.3	2.7	28.7	27.8
Desert-thorn spp.	0.4	0.1	T	0
Honey mesquite	11.0	13.3	0.4	0
Total full-shrubs	27.9	29.0	29.1	27.8
Half shrubs				
Rayless goldenhead	N	N	N	N
Broom snakeweed				
Juveniles (<20 cm height)	128.7	159.8	3.4	0.1
Mature	N	N	N	N
Burroweed				
Juveniles (<20 cm height)	0.1	0.7	T	0
Mature	N	N	N	N
Mariola	3.0	1.8	N	N
Desert zinnia	11.1	4.9	0.2	0.1
Total half-shrubs	183.0	208.0	3.8	0.2
Total shrubs	210.9	237.0	32.9	28.0
Perennial forbs				
Desert globemallow	2.2	2.8	0	0
Succulents				
Walkingstick cactus	N	N	N	N
Devil cholla	N	N	T	0.2
Purple pricklypear	0.2	T	N	N

0 = observed in area but not in transects
T = trace amount
N = none even observed in sampling area

is very low given even the low productivities for many southwestern plant communities. Water often restricts use of the landscape, as deer will generally not forage more than 2.4 km from water. In contrast, very high densities of white-tailed deer from 15 to 47 deer/km^2 have been reported in Texas (Teer 1996), and the Kaibab herd at the eruption peak would have averaged 34 deer/km^2 (Rasmussen 1941). While there is generally not a lot of overlap in deer and cattle diets, deer are sensitive to drought in the Chihuahuan Desert and competition with cattle can increase under drought conditions. This then would be the period when one or both animal species may have a greater impact on the plant communities.

Rodents, especially *Dipodomys* sp., have been considered "keystone" species in these systems (Brown and Heske 1990 reviewed above; Samson and others 1992). Seed consumption of large seeded winter annuals reduced this group of plants and allowed persistence of small seeded annuals, thereby greatly influencing species diversity (Samson and others 1992). Ants also had impacts on the plant community, consuming smaller seeds than rodents. Ants and rodents affected each other differently and together produced large effects on densities of winter annuals (Davidson and others 1985). Reynolds (1958) observed that seed weight and plant height influenced preference for seeds by Merriam kangaroo rats, with short plants and large seeds favored. Some exceptions occurred because some small seeded species within reach of the rats were utilized by harvesting entire seed heads rather than individual seeds, and the seeds of some tall shrub species were harvested from the ground. Kangaroo rats were favored by shrub habitat, avoided habitat with large amounts of perennial grasses, and therefore increased with grazing by livestock. Reynolds (1950) reported that perennial grass, shrub, and cactus seeds were preferred, and the greatest impact of the kangaroo rats were found on these plants when comparing rodent grazed and ungrazed treatments. Small seeded perennial grasses were not affected by rodent grazing treatment. Chew and Chew (1970) estimated that rodents consumed over 85 percent of seed production and only 1.1 percent of shoot production. Reynolds (1958) notes that re-seeding of small areas of rangeland in often unsuccessful due to the ability of rodents to easily locate large seeds planted up to one inch deep in the soil. In some cases, the seed catching activity of heteromyid rodents increases the probability of successful germination of seeds, even though many others are consumed. McAdoo and others (1983) found that germination of about 50 percent of seeds of Indian ricegrass in caches were greatly enhanced by rodent removal of the indurate lemma, palea, and pericarp. This was thought to be the primary means of stand renewal, since seeds of this species require some extreme form of treatment to break dormancy. The caching and shucking of mesquite seed by rodents acts as a burying, which improves vigor and survival relative to seeds on the surface of the soil (Reynolds 1958; Chew and Chew 1970). Browsing by lagomorphs and wood rats is another component of herbivory in these communities. Chew and Chew (1970) estimated that lagomorphs and wood rats kill about 4 percent of the shrub food resource, but consume only about 2 percent of it. However, this level of pruning and utilization has a large impact on some shrubs, reducing volumes of particular species up to 56 percent. Additional discussion of the role of small mammals in this system is covered in the section above on Mesquite Savanna Conversion to Chihuahuan Desert: Shrub Invasion, Livestock Grazing, Fire, Small Mammals, and Climate.

Although the number is small, the consensus of studies in shrub dominated Chihuahuan Desert communities is that recovery after even complete protection from mammalian grazing is a slow process, and the shrub dominance may place a limit on the extent of recovery. Small mammals, birds, and ants can have large influences on the plant communities.

Management

There are large declines in herbaceous production after conversion of mesquite savanna to shrub dominated Chihuahuan Desert communities. An extremely large body of literature exists on shrub control practices but will not be reviewed here. Interactions of grazing and mesquite control by other means is assessed below. The effects of fire on mesquite is briefly covered in the Mesquite Savanna Conversion to Chihuahuan Desert section above. However, fuel loads in moderate to dense stands of shrubs are often too low to carry a sufficiently intense fire for shrub control (Paulsen 1975). Paulsen also mentions that many perennial grasses associated with mesquite savanna of Chihuahuan Desert communities are sensitive to fire. While acknowledging this sensitivity as a consideration, Allen (1996) comments that experience in the Malpai area suggests that burning of black grama stolons is not as detrimental in this area of higher rainfall as it is in lower, drier desert elevations.

A couple of studies have assessed interactions between mesquite control and grazing systems. In Texas, Scifres and others (1974) studied herbicide spraying of mesquite with continuous, year-long heavy grazing and a moderately grazed deferred rotation system. Eight years after spraying, reinfestation of mesquite was greater in the moderately grazed deferred rotation system than with year-long heavy grazing. At the College Ranch adjacent to the Jornada, McNeely (1983) found reduced mesquite cover 20 years after herbicide treatment and greater herbaceous understory production even though basal area did not differ. Year-long grazing had greater herbaceous cover and cover of black grama than did a seasonal grazing system. While some differences in pastures could have confounded results, the author concluded that conservative grazing intensity was the most important factor in maintaining and improving range condition.

Great Basin Sagebrush Shrubsteppe

Much of the research on grazing in this community has been done at more northern sites. A couple of studies in southern Utah where climate is somewhat similar to northern New Mexico and Arizona are used in this review. A review of earlier research in the northern communities indicated that changes in grazing intensities resulted in changes in sagebrush abundance as well as herbaceous understory species, which tends to be a somewhat different situation than for many other shrub or woody communities discussed above (Ellison 1960). Grazing in northern communities commonly 1) reduces palatable grasses and increases the sagebrush component, particularly when grazing is in the spring, 2) promotes the spread of sagebrush into other communities, and 3) promotes spread of pinyon and juniper into sagebrush communities in locations where they occur in proximity. On the other hand, Ellison indicates that grazing in the sagebrush type in the fall reduces sagebrush and improves palatable herbaceous species, whereby "this is one of the few instances known to the reviewer where grazing pressure can be applied under range conditions to achieve improvement of the forage." More recent assessments of grazing management in northern sagebrush communities support the capacity of fall grazing by sheep and complete protection to reverse the shrub dominance when the site has a good grass understory (Laycock 1987). However, sites heavily dominated by sagebrush with very little grass and herbaceous cover recover slowly or may not recover at all after complete protection for up to 46 years (Sanders and Voth 1983). West and others (1984) concluded that many sagebrush dominated sites are successionally stable. Laycock (1987) concluded that any system or season of grazing would not improve highly depleted sagebrush range. For ranges in fair or better condition, Laycock notes that various authors in different parts of the sagebrush range have come to different conclusions concerning positive and negative aspects of different grazing systems, and that different responses to grazing may occur in different sagebrush communities. Below are findings for southwestern communities. Grazing effects on a similar community type are presented above in the Great Basin Juniper-Sagebrush section.

Species Composition

Upland and lowland big sagebrush communities were studied using a 22-year-old exclosure in north central New Mexico (Holechek and Stephenson 1983). The site received 250 to 350 mm/yr precipitation and was grazed by cattle in late winter and spring at a 30 to 50 percent utilization level. Big sagebrush cover was greater inside the exclosure on the upland site and lower on the lowland site, although initial conditions were not known. The only other significant effect of grazing treatment on species was an increase in blue grama with grazing on both uplands and lowlands, and a decrease in western wheatgrass on grazed lowlands. The greater grass cover outside the exclosure on both sites was considered a positive effect of grazing at this particular site. The authors concluded that dominance of sagebrush and very low understory cover after 22 years of protection suggests similar slow to nonexistent recovery of depleted ranges as reported above for northern Great Basin sites.

Similar conclusions were reached by Hughes (1980) studying three 25-year-old exclosures, which included railed and seeded areas. The adjacent sites were grazed during the June-to-November growing season, which is considered to be the most detrimental period for grazing. Sagebrush increased over time both inside and outside the exclosures. The railed and seeded areas showed the largest increase in shrubs, from 10 percent after treatment to 80 percent after 25 years. Grass cover showed the opposite temporal trend. Only one of the three exclosures "maintained a better species composition," but this is not described. The authors concluded that "grazing systems (rest-rotation, deferred) in arid sagebrush zones by all appearances seem to be a waste of money unless land treatment (chaining, burning, and so forth) is a recurring event with the grazing system to keep the sagebrush canopy very open and patchy."

Measuring only grass and forb cover, Bonham and Trlica (1985) found very little difference in forb cover between a 48-year-old ungrazed and an area grazed at 40 percent utilization in a sagebrush community. The site was in the New Mexico Four Corners area receiving 200 mm/yr precipitation. Grass cover of galleta and sideoats grama was only slightly greater in the ungrazed compared to the moderately grazed area. Total grass cover was 1.4 and 0.9 percent for the ungrazed and moderately grazed sagebrush communities, respectively, and total herbaceous cover differed by only 11.3 compared to 11 percent, respectively. However, heavy grazing at 60 percent utilization resulted in greatly reduced grass and forb cover, with total cover only 1.8 percent compared to the 11.3 percent in the ungrazed area. Similar ungrazed, moderately, and heavily grazed fourwing saltbush community comparisons showed total herbaceous covers of 19.9, 13.6, and 15.4 percent, respectively. This again suggests little effect of long-term protection. However, two species showed significantly different covers between long-term ungrazed and heavily grazed communities: galleta increased and bottlebrush threeawn decreased with grazing. A third winterfat community showed little difference in total cover between ungrazed and heavily grazed communities but an increase in blue grama with grazing and a decrease in sideoats grama and bottlebrush threeawn. However, data in this study appeared highly variable.

Short-term ungrazed exclosures (6 years) and longer-term ungrazed (30+ years) Canyonlands National Park in southeastern Utah were compared to adjacent grazed sites under a deferred system in fourwing saltbush communities. Canopy cover of perennial grasses was significantly greater in both the short- and long-term ungrazed compared to grazed communities, and annual forbs were greater in the grazed. Shrub density or cover did not differ between protected and grazed communities for either short- or long-term ungrazed sites.

A relict area on the north rim of the Grand Canyon receiving 305 mm/yr precipitation was studied by Schmutz and others (1967). Although isolated, a bridge allowed sheep to cross to Boysag Point between 1920 and 1943 when weather and water availability permitted, with grazing generally occurring in March to April or April to May. The relict site was slightly lower in elevation than the grazed mainland site, and exposure and windswept conditions may have also caused differences in temperature and precipitation, while fire had not occurred at either site since the late 1800s. Large differences were observed in species richness and composition. A total of 88 species were found on the relict compared to 38 on the grazed mainland. The ungrazed relict had grass cover of 36 percent and an overstory cover of 60 percent, compared to the grazed site's 6 and 90 percent, respectively. Total vegetative cover did not differ at 23.5 and 21.5 percent for the ungrazed and grazed sites. Actual grass cover was 8.6 and 1.3 percent for the relict and grazed site, respectively, and shrub covers were 14.1 and 19.5 percent. Species increasing with grazing included blue grama and squirreltail, and those decreasing included black grama, galleta, muttongrass, and needlegrasses. Sagebrush was more than twice as abundant on the grazed site. Sagebrush in northern Arizona is able to maintain good levels of production with up to 80 percent simulated deer browsing of current annual growth (Sheperd 1971, cited in Carpenter and Wallmo 1981).

Primary Production

Over the entire range, West (1983a) gives total aboveground standing crop values of from 200 to 1,200 g/m^2 for the Great Basin sagebrush shrubsteppe, and a range in aboveground primary production from 50 to 150 g/m^2/yr. Belowground biomass is similar to aboveground values, and litter is about half the standing aboveground biomass.

Dense stands of sagebrush produce little understory forage, so early attempts at improving sagebrush range involved brush control efforts (Vale 1974). Grazed sagebrush in northwestern New Mexico at the southeastern edge of the community averaged 12 g/m^2/yr of usable livestock forage, with a range from 7 to 17 g/m^2/yr (Francis 1990 cited in Vincent 1992). Degraded sagebrush/grass range in this area produce only 10 to 15 percent of the potential forage, but removing livestock from range in this condition for 12 years resulted in only minor reductions in sagebrush cover compared to areas with continued use by cattle (Dahl and others 1976, cited in Vincent 1992). Sagebrush is not considered a palatable forage for livestock, but some is utilized. Deer will browse up to 50 percent in their diet (volatile oils in large amounts can lower rumen microbial activity), and a mix of grass, forbs, and shrubs are considered good for both deer and pronghorn antelope (McEwen and DeWeese 1987). While early management efforts were focused on sagebrush eradication, current practices attempt to provide a mix of forage and browse for both livestock and wildlife.

Actual production estimates are available only for little-grazed relict and heavily grazed mainland sites from the Schmutz and others (1967) study. As mentioned above, differences between treatments may be due to site differences, and methods of clipping are not described but are called "annual production" and not standing crop. Values were 46 compared to 32 g/m^2/yr for the ungrazed and grazed communities, respectively. Grass production was 50 and 13 percent of the total for the ungrazed and grazed communities, respectively, while shrub production was 45 and 77 percent. Snakeweed and sagebrush were the shrubs producing more on the grazed site, whereas cacti and more palatable shrubs were more productive on the ungrazed site.

Management

Studies in Idaho, Utah, and Nevada all indicate that grazing too heavily or too early in the spring can result in loss of herbaceous understory and favor sagebrush (Laycock 1987). Vincent (1992) suggests this is true for New Mexico sagebrush communities as well, and grazing should occur only in the non-growing season. In degraded range in contrast, Hughes (1980) considered any grazing system to be ineffective since shrubs increased in abundance even in exclosures. However, one of the exclosures did show improvement in abundance of herbaceous species. Holechek and Pieper (1992) recommend 30 to 40 percent utilization of key forage species as a moderate level of grazing for sagebrush grassland. For the entire region, West (1983a) indicated stocking rates were originally 0.83 AUM/ha, declined to 0.27 AUM/ha in the 1930s due to loss of perennial grasses, and were 0.31 AUM/ha by 1970.

Because of the cheatgrass invasion throughout much of the inter-mountain west, fire is not considered beneficial in sage control, since it highly favors the annual cheatgrass (Vincent 1992). In situations where cheatgrass is not a problem, Schmutz and others (1967) suggested that ungrazed relicts in the Great Basin juniper-sagebrush type (see above section; Jameson and others 1962) burning eliminates the pinyon and juniper and increases big sagebrush, whereas at his study site the absence of fire and grazing favored grasses and reduced shrub and tree composition. Considering the region from Navada and Utah to the southwest, West (1983a) suggests controlling wildfires in sagebrush communities because of the susceptibility of perennial grasses relative to annuals, loss of litter and nutrients, and a resulting decline in productivity.

In the Great Basin, a greater pressure on the shrub component in sagebrush shrubsteppe occurred during the Pleistocene by browsers such as camels and ground sloths (Martin 1970). While pronghorn antelope can consume relatively large amounts and deer up to 50 percent, shrub intake by all present day ruminants are limited by the volatile oils that can inhibit rumen microbial activity when present in high amounts. West (1983a) suggested that reintroduction of a browser such as the saiga antelope may provide more efficient utilization than that obtained by livestock and native large herbivores. Although often in reference to more northern communities, early accounts of the herbaceous component in this system suggest a very sparse cover existed even before large numbers of livestock were in the area. West (1983a) comments that Jedediah Smith had difficulty finding forage for his horses in this community type during the 1820s and 30s. Livestock were first brought into sagebrush areas in Utah in the late 1840s, and livestock depletion of the more northern upland communities began in the late 1800s.

There are few data to base conclusions concerning the effects of grazing in Great Basin sagebrush shrubsteppe when restricted to the southwestern region. The limited amount of data suggests very slow or no recovery in terms of lower shrub abundance even after long-term complete protection of more arid sites that were previously degraded by very heavy grazing. Weak (due to potential site differences) and limited data suggest relatively greater herbaceous and lower shrub cover on sites with little historic grazing and continued decline in condition on heavily grazed communities. Grazed versus protected sites can possibly show differences in herbaceous species composition.

Shinnery Oak/Sand Sage

No studies were found concerning grazing of this community type. Note that the Kleiner and Harper (1972, 1977) studies covered under the Temperate Grasslands section has a sand sage component and is considered by West (1983d) to be a Utah galleta-three-awn shrub steppe community.

Great Basin Temperate Desert

Very little research is available for these arid, low productivity communities. For blackbrush communities in southeastern Utah and northeastern Arizona, West (1983c) gives an average annual precipitation value of 160 mm, with most occurring in late summer. In pristine sites never grazed by livestock, aboveground primary production ranges from 30 g/m^2/yr in stands of nearly pure blackbrush to 169 g/m^2/yr where soils allow a good understory of grasses. Grazing value of these communities is considered very low, and blackbrush itself is spiny, of low quality, and contains secondary compounds. Navajo Indians use this range for mixed herd goat and sheep grazing. Desert bighorn sheep were the primary native large herbivores utilizing the community. Aboriginal people made little use of the community, and livestock use as winter rangeland was confined to the more accessible areas with available water.

Similarly, much of the research in shadscale communities has been done far north of Arizona and New Mexico (West 1983b). Sheep grazing was the primary use, since there was little grass forage for cattle in these communities. As in the blackbrush type, shadscale type has never been suitable for livestock grazing and was little used by aboriginals. Based on research primarily in northern communities, West concluded that recovery from very heavy grazing is very slow with “progressive livestock management, and little can be done otherwise to accelerate improvement.” Intensive livestock management is not practical in this community type due to the very low primary production.

The limited number of studies in more southern communities are reviewed below.

Species Composition

Blackbrush communities—Thirteen years of grazing management at a demonstration ranch in southern Nevada, where intensity and season of grazing were controlled, resulted in no improvement in understory herbaceous production in a blackbrush community. Halliday (1957) reported "practically no forage produced" at the start of the study in 1938 and no change in production by 1955. At an associated grassland community, protection from summer grazing improved production of warm-season grasses, but April grazing was still preventing improvement in cool-season grasses.

A series of ungrazed and grazed sites were studied by Jeffries and Klopatek (1987) in northern Arizona and southern Utah with annual precipitation of about 163 mm/yr. A relict (ungrazed by domestic livestock) on a mesa represented the pristine condition, although it was also inaccessible to wild ungulates as well as livestock. Another site experienced little or no grazing by livestock until 1981, due to lack of water, and light to moderate winter grazing after water development. A third site in the Navajo Indian Reservation was continually and heavily grazed by cattle horses, sheep, and goats since the 1880s. A fourth site represented a recovery from heavy grazing after it was isolated by the creation of Lake Powell in 1974, an island, similar to a 10 year exclosure from grazing. Total herbaceous cover was four-times or more greater on the never-grazed geologic refuge than on any other site and tended to be higher on the long-term lightly grazed site than either heavily grazed or the 10-year protected site (Table 16). There was a general shift in grass species composition from Indian ricegrass in the relict site to galleta in the heavily grazed sites, although absolute amounts of galleta were similar among sites. Extremely large differences were found in cryptogram cover, where the relict or lightly grazed sites had at least 23 times the cover of the heavily grazed site or the site excluded from heavy grazing for 10 years. Shrub cover was also greater on the relict and lightly grazed site than the heavily grazed or recovering site. The authors concluded that recovery of cryptogram cover on sandy soils of the blackbrush type is much longer than that found for some heavier soils, that blackbrush is able to survive heavy grazing but is also the natural dominant climax on relict sites, that even light grazing impacts herbaceous vegetation in this community, and that recovery of the herbaceous community is also a slow process.

Very heavy grazing by feral burros in Grand Canyon National Park was reported to reduce cover and density of total vegetation, seed production, and diversity in both richness and evenness components (Bennett and others 1980). Grasses were particularly heavily utilized and affected by burro grazing. At the same site, Carothers and others (1976) found canopy cover of 80 percent in an ungrazed site compared to 20 percent in the grazed site and a 30 percent increase in species richness on the ungrazed. Increased mistletoe infestation of mesquite appeared correlated with heavy grazing. The effects on vegetation translated into effects on small mammal communities, with much greater abundance and diversity on control compared to burro-grazed site. Douglas and Leslie (1996) provide a review of feral burro grazing in the western United States and the interaction of burros with desert bighorn sheep.

Shadscale communities—Three exclosures were studied by Hughes (1980) in Arizona that were built in grassland at the edge of a shadscale shrub community. Twenty-eight years later shadscale and snakeweed dominated the area. However, at one of the exclosures, shrubs attained a greater dominance outside than inside the exclosure. Snakeweed was twice as abundant outside as inside the exclosure, even though it also increased inside. Galleta and blue grama decreased at the expense of the shrub increase. At a second site, shadscale increased from nearly nothing to 80 percent of the species composition outside, replacing galleta and alkali sacaton. Galleta remained the dominant inside the exclosure even though shadscale invaded there as well. Conclusions from a third exclosure were confounded by contour furrowing outside the exclosure, but shrubs invaded this altered and grazed area while the exclosure remained nearly devoid of vegetation. These results in general may suggest differences in the response of shadscale communities compared to blackbrush communities, but may also just be due to invasion/expansion dynamics versus responses of long established communities.

Management

West (1983c) thought there was a low potential for grazing systems to effect change in blackbrush communities and that fire should not be used in management. Shrub control at a Nevada site resulted in much more erosion and instability in primary production. West considered feral burros as a threat to remote communities where livestock grazing had not previously depleted grasses. Halliday (1957) suggested that April grazing appears detrimental to cool-season species in an associated grassland community type, particularly Indian ricegrass, but there were no grazing management effects on the blackbrush type. Mixed-herd grazing would seem to be an area where future research may be useful.

The very limited number of studies in this community type in the southwest suggest that areas not previously grazed or only lightly grazed should remain ungrazed or lightly grazed. Recovery from grazing is

Table 16—Vegetation cover in a Great Basin temperate desert community dominated by blackbrush in northern Arizona/southern Utah in a never grazed geologic refuge (mesa), lightly grazed, heavily grazed, and an island ungrazed for 10 years after a dam caused formation of Lake Powell. Adapted from Jeffries and Klopatek (1987).

	Grazing treatment			
Cover categories	**None**	**Light**	**Heavy**	**Ungrazed 10 years**
Total shrub cover (m^2/ha)	3645a*	2874b	1405c	1372c
Blackbrush cover (percent of total shrub)	87a	83a	92a	95a
Total herbaceous cover (m^2/ha)	1047a	256b	102b	127b
Indian ricegrass cover (percent total herbaceous)	80a	22b	3b	76a
Galleta cover (percent total herbaceous)	2b	11b	32b	76a
Total cryptogamic cover (m^2/ha)	2129a	1196a	70b	50b
Total cover (m^2/ha)	6821a	4326b	1576c	1549c

* Values within a row not sharing the same letter are significantly different.

slow. The relationship of grazing to shrub cover is not clear, although in some situations at least, high shrub dominance is the natural climax, while in others grazing may increase shrub abundance.

Sonoran/Mohavian Deserts

Precipitation in the Sonoran Desert lies between that for Mojave and Chihuahuan Deserts in both the quantity and the percent that occurs during winter (MacMahon and Wagner 1985). Mean annual precipitation ranges from 75 to 300 mm/yr for the Sonoran Desert and 50 to 275 mm/yr for the Mojave Desert, compared to 175 to 425 mm/yr for the Chihuahuan Desert. The percentage of precipitation that occurs in winter is greatest for the Mojave, intermediate for the Sonoran, and least for the Chihuahuan Desert. MacMahon and Wagner (1985) illustrate good relationships between decreasing variability in precipitation with increasing amounts of precipitation, and increasing amounts of precipitation with increasing elevation. Shrub cover and standing biomass increases with increasing precipitation, with 231 g/m^2 standing live-plus-dead at a Mojave Desert site with 138 mm/yr and 747 g/m^2 at a Sonoran Desert site with 279 mm/yr. Primary production at the same Mojave Desert site in southern Nevada ranged from a low of 20 $g/m^2/yr$ for perennials and near zero for annuals to about 60 $g/m^2/yr$ for each. Production at a Sonoran site in Arizona over eight years ranged from 2.4 to 71.3 g spring grass/m^2, 0.9 to 84 g spring forbs /m^2, 3.6 to 39.2 g autumn grass /m^2, and 12.5 to 30.8 g autumn forbs /m^2 (Smith and LeCount 1976, cited in Wallmo and others 1981).

There is a wide variety of plant communities in both the Sonoran and Mojave Deserts, and within a site the Sonoran Desert is particularly diverse in terms of both floristics and physiognomy (MacMahon and Wagner 1985). Temperature determines the appearance of the two distinct summer and winter species. The evolutionary origin of the summer species was Mexico and Central America, while winter species were primarily from the Pacific coast of California. Consumption by native herbivores is not a large proportion of primary production. MacMahon and Wagner speculate that consumption by livestock is also low because much of the vegetation is woody, allelopathic, or spinescent.

Humphrey (1960) also commented on the low potential for livestock utilization of Sonoran Desert communities because of the low grass production and unpalatability of the larger shrub component of production. As a result, there is little change in plant community species composition under long, continued use, little improvement in range condition under light use, and little noticeable deterioration under heavy grazing. On the more alkaline soils, saltbush can provide some good forage, but creosote bush has no forage value. Humphrey considered it difficult to classify this type into range condition classes. Sites heavily dominated by creosote bush or by paloverde and triangle bur-sage produce very little forage and cannot be converted to useful rangeland even with shrub control and seeding of herbaceous species. Thin soils with an indurated caliche layer may hold more moisture near the surface and produce some forage.

While the large pool of unpalatable perennial woody and cacti species may not be altered much with grazing, Shreve (1929) reported that the effects of grazing on small perennials may be large in some cases. A study of vegetation change after a 21-year period of protection indicated no consistent successional trend but an increase in small perennial plants from 33 to 164 percent on level sites and a gain of 7 percent to a loss of 16 percent on hill slopes. However, the measurement of only two points in time, without adjacent grazed sites also being monitored, makes it difficult to separate grazing from climate effects. Climate effects in ungrazed refuge communities can be large. In a crater refuge site in Sonora, Mexico, Turner (1990) found that drought and unusually high periods of precipitation can profoundly affect community species composition. Creosote bush and paloverde populations declined by more than 50 percent during the first half of the century, mesquite increased 200-fold in the playa-like center of the crater, and there were only three major peaks in recruitment of saguaro cacti over 170 years.

Prolonged periods of drought are common in the southwestern deserts, and grazing may interact with these periods of stress. Robinett (1992) reported no visible effect of grazing on drought mortality at a southern Arizona Sonoran Desert site in a grassland-desert transition zone receiving 305 mm/yr precipitation. However, recovery after a drought appeared to be promoted by the presence of litter that may have trapped seeds and lowered evaporative losses. This author recommended that ranchers grazing these communities be particularly aware of the need to de-stock during droughts whereby litter is left on the soil surface for subsequent recovery of the plant community.

Some unpalatable species may be susceptible to herbivores during the seedling stage. In the Sonoran Desert, the conspicuous and representative saguaro cactus and paloverde can be limited by herbivores to establishment in biotic or geologic refuges. Paloverde establishment is apparently limited by native mammalian herbivores to locations under unpalatable shrubs or among rock outcrops (McAuliffe 1986). Similarly, saguaro cacti mortality due to rodents and insects is much lower in rock outcrops, even though microenvironmental conditions are more unfavorable (Steenbergh and Lowe 1969). McAuliffe (1984) found that tree cacti protected two species of barrel cacti from rodents in the Sonoran Desert. While these studies were in areas ungrazed by domestic livestock and livestock find all unpalatable, trampling can be a factor restricting even unpalatable cacti species to refuges from large herbivores in other communities (Rebollo and others 2002). Abouhaidar (1992, cited in Wilson and others 1996) observed that young saguaro were much more abundant in areas where cattle had been excluded.

Some quantitative studies of the effects of grazing on Sonoran Desert communities have been reported. Blydenstein and others (1957) compared plant communities protected inside the Carnegie Desert Laboratory in southern Arizona for 50 years to an area outside that was grazed only lightly. Only minor differences in species composition were found, but the density of plants was significantly greater in the protected area (Table 17). Increases in density with protection were primarily due to perennial grasses and one palatable shrub. The only species to increase on the grazed sites was a bursage. The dominant creosote bush showed no response to the different grazing regimes. Annuals did not appear to respond to protection, but the timing of sampling and climatic conditions at that time did not permit a good evaluation. Although the author commented that no invasions of new species occurred, there were 11 species sampled in the protected area that were not sampled in the grazed area, and only one sampled exclusively in the grazed area.

A decline in diversity with increasingly recent grazing was also observed by Waser and Price (1981) at sites inside and outside Organ Pipe Cactus National Monument in southern Arizona. The communities were dominated by creosote bush. The cover composition of winter annuals was sampled after 2 and 3 years of protection, after 16 and 17 years of protection, and on two adjacent heavily grazed sites. The decline in diversity with grazing was primarily due to loss of less common species. Total cover or the cover of the three most abundant species did not differ consistently among grazing treatments between years and replicates.

One of the three sites studied by Roundy and Jordan (1988) was considered Sonoran Desert. The site received an average of 222 mm/yr precipitation, and both the grazed and an area protected for 14 to 18 years were dominated by half-shrubs and large Ephedra and mesquite shrubs. Half-shrubs were slightly more abundant in the grazed area, and compositional differences were also somewhat small. Full-shrubs densities did not differ, but there were some compositional differences. Mesquite and Ephedra were more abundant in the protected area, and an Acacia was more abundant in the grazed. Perennial grasses and forbs were very low in abundance in both grazed and protected treatments. Annual forbs were greater in grazed than ungrazed areas, and there was no difference in annual grasses. Root-plowed treatments also showed only small increases in perennial and annual grasses. The authors concluded that "there is no evidence that exclusion from grazing alone or even in association with root-plowing will encourage reestablishment of native perennial grasses."

A study of the effects of feral burro grazing on Mojave desertscrub communities found reductions in palatable perennial grasses, total plant cover and density, and plant diversity (Bennett and others 1980). These authors noted, however, that the abundance of

Table 17—Relative frequency (Raunkaier's frequency index) of a Sonoran Desert site in southern Arizona protected from grazing for 50 years or grazed lightly by livestock. A * represents a significant difference between the two treatment means. Adapted from Blydenstein and others (1957).

	Frequency Index	
Plant species or catagory	**Protected**	**Grazed**
Whitethorn acacia	9	8
Annuals	316	332
Threeawn spp.	13	9
Spider grass	3	---
Dense ayenia	8	12
Red grama	29 *	2
Fairyduster	15 *	4
Saguaro	1	1
Yellow paloverde	2	7
Woody crinklemat	22 *	9
Condalia spp.	1	---
Prairie clover spp.	---	1
Silver bush spp.	1	---
Candy barrel cactus	1	---
Ocotillo	13 *	3
Triangle burr ragweed	252 *	324
Slender janusia	2	---
Sangre de cristo	9	4
White ratany	147 *	93
Creosote bush	73	64
Berlandier's wolfberry	2	---
Graham's nipple cactus	1	---
Rough menodora	2	---
Bush mulhy	14 *	3
Prickly-pear cactus spp.	17 *	6
Cactus apple	24	19
Whiplash pappusgrass	1	---
Mariola	2	---
Paperflower spp.	18 *	5
Slim tridens	49 *	19
Low woollygrass	210 *	131
Zinnia spp.	1	---
No Vegetation	57 *	91

species of low palatability that burros ignore tends to obscure impacts on the smaller palatable plants.

Deer densities in Sonoran and Mojave Desert habitat tend to be lower than for many other communities (Urness 1981). A review of diet studies showed that plants such as Wright buckwheat, mistletoe, cactus fruits, catclaw acacia, mesquite beans, and fairy duster leaves were important in deer diets in Sonoran Desert, and paloverde, desert ironwood, mesquite, and catclaw acacia important in Mojave Desert. The effects of deer browsing on the plant communities have not been reported.

Merriam's kangaroo rats consumed nearly 7 percent of primary production at a Mojave Desert site in California (Soholt 1973). While this is a high level of consumption for a rodent population, it is small relative to the amounts generally consumed by livestock. However, the small mammals are much greater dietary specialists, consuming 75 percent seed material, and can therefore have relatively large impacts on plant communities. Redstem stork's bill was a preferred food for kangaroo rats at this site, where utilization was over 95 percent. Seed consumption was great enough to reduce density of that species by 30 percent. In southeastern Nevada, rodent consumption of seeds accounted for 30 to 80 percent of losses, but no more than 25 percent of germination (Nelson and Chew 1977). These authors concluded that it takes "an exceptional coincidence of events…to cause a severe depletion of seeds reserves" and reported only slight evidence for decreases of large-seeded species due to rodent consumption.

Interactions of grazing with fire in these communities has in the past been considered as probably not important. Fuel loads are generally too sparse to carry fires over large areas (Schmid and Rogers 1988). These authors estimated that it would take 274 years for fires to affect the entire 391,000 ha desert portion of Tonto National Forest in Arizona. Allen (1996) considers the Sonoran Desert to be a system that did not evolve with frequent fires and many of the grasses associated with this community to be susceptible to fire injury and mortality. However, fuel loads can be high after periods or years of unusually high precipitation (McLaughlin and Bowers 1982), and the additional fuel load from introduced grasses and human-caused fires have increased the frequency of fires in many areas (Rogers 1985; Wilson and others 1996). Rogers (1985) suggests that saguaro cactus may be endangered over portions of its range when fire frequency is less than the 30 years necessary for them to reach reproductive maturity. Saguaro cacti are important to many cavity nesting birds, bats, and other wildlife and are the symbol of the southwestern desert, although they are of restricted distribution. Saguaro mortality after fires is related to age/size class, with younger classes displaying very high mortality rates of up to 100 percent (Cave and Patton 1984). Some large saguaros that survive fires and others that display delayed post-fire mortality provide a much diminished seed supply for regeneration (Cave and Patton 1984; Rogers 1985; Wilson and others 1996). Grazing can interact with fire in regeneration of saguaros because of its negative effect on seedling establishment (reviewed above).

The very limited number of studies in Sonoran/Mohavian Deserts does not allow for strong conclusions to be drawn. Plant diversity appears to decline with grazing, although overall changes in species composition are relatively small. Grazing does not appear to have large effects on the major woody components, but impacts the less abundant and smaller species. Regeneration of saguaro cacti in areas of the Sonoran Desert can be negatively impacted. Recovery of a perennial herbaceous understory may be site dependent, and it is not clear whether the difference in recovery is due to site potential to support a herbaceous understory or due to the intensity of historic grazing.

Riparian and Wetland Communities

Riparian and wetland communities represent a very small percentage of the land area in the southwest but are areas of high plant and animal diversity and productivity. Regulation of water flow and the elimination of winter-spring flooding, lowering of water tables due to irrigation, clearing, and wood cutting, as well as livestock grazing have and are currently resulting in large losses of all types of these habitats (Minckley and Brown 1982). Riparian areas and wetlands provide water and cover to animals that may be more associated with adjacent upland communities, including livestock, as well as many species that are obligate to these communities for part or all of their life cycle. These areas are probably more important to animals more associated with uplands in arid and semiarid regions because of the refuge from the harsh environment they can provide. Artificially built watering areas are often known as "sacrifice areas" because of the high trampling and utilization of forage near them. Resting grounds and watering areas are known to be centers of high nutrient concentration due to the deposition of feces and urine. Natural watering areas with greater production, a shaded favorable microenvironment, and scratching posts are most probably even more utilized by livestock than are artificial watering areas. Livestock impacts due to trampling effects on soil compaction are often evident on sparsely stocked unproductive upland communities so would be expected to be much greater in a heavy-use area, and wet soils are more susceptible to cutting and compaction than are dry soils. Unlike shrub invasion problems in upland communities, riparian zone overstories are often reduced by livestock grazing (Kauffman and Krueger 1984), and this strata provides cover and nesting for many land vertebrates and affects water temperatures for aquatic organisms. Stream-side vegetation exerts a large influence on bank and channel morphology through effects on flow velocities, cutting during flood conditions, and erosional inputs from uplands. There is a potential for these productive areas to be impacted by livestock to a relatively greater degree than adjacent less productive communities, but there is also the potential for more rapid recovery from disturbance because of faster growth rates of the vegetation.

Narrowleaf Cottonwood

Two narrowleaf cottonwood community types, in addition to two Broadleaf cottonwood community types, along the Mimbres River in southwestern New Mexico were examined by Boles and Dick-Peddie (1983). Early accounts of the appearance of the river in 1846 described a 4.6 m wide by 0.9 m deep river. Current conditions observed by Boles and Dick-Peddie were of a river with similar water course width, but much shallower water course and a much wider riverbed. This suggested that vegetation along the river bank had been reduced, because an effect of vegetation is to constrict and deepen a river channel. Vegetation along a river can be altered by grazing by livestock and/or changes in the historical water flow patterns and levels. Although no controlled grazing studies were accomplished, the authors present observations that suggest livestock grazing may be a primary cause of change along the river. Changes included factors that are commonly attributed to livestock grazing in other controlled studies: erosion, absence of reproduction by woody components of the vegetation, large cottonwoods uprooted by floods, and absence of moist alluvial microsites for seed germination. Although irrigation use could lower water tables, no permanent dams occurred on the river and signs of flooding were evident and substantiated by long-time residents. Data were collected showing an even-age-class distribution of obligate riparian woody species, and observations indicated severe grazing and browsing of most new woody shoots. However, this occurred primarily for obligate riparian species that included two broadleaf cottonwoods but not the narrowleaf cottonwoods. A much higher density of facultative riparian species (pines and junipers that also occur in the dry uplands) are associated with narrowleaf cottonwood communities than with broadleaf communities. This would suggest that the less mesic communities may have been favored. The Mimbres is a canyon-type drainage compared to the more broad, flat flood-plain type. Thus, while the authors report a wider riverbed, the vegetation favored is a canyon type. This would suggest that flash-flooding may be more common and a more favorable mesic flood plain condition less common than in the past, or that narrowleaf cottonwood is just less susceptible to grazing. Controlled grazing experiments would be needed to differentiate mechanisms, and to also clearly separate grazing from potential lower water-table influences on population structure and composition. The extreme grazing pressure observed on cottonwood sprouts, their emergence within biotic refuges (logs preventing access by grazers), and evidence of erosion would all point to grazing as at least a major factor.

Experimental evidence for some of the observations of Boles and Dick-Peddie (1983) were obtained by Skartvedt (2000). This author sampled 17 sites along the upper Mimbres River in what appears to be primarily narrowleaf cottonwood communities (dominants across all sites in decreasing order were ponderosa pine, alligator juniper, and narrowleaf cottonwood). Six of the 17 sites had been ungrazed for at least 10 years. Sites were not paired grazed-ungrazed, but varied with elevation, stream direction, channel type, as well as grazing history. It is not clear from the authors description how confounded the various variables were, but principal component analyses were used to partition variance. Only one out of three graphs of PCA axes plotted against grazing showed any discernable correlations, where ungrazed sites showed a higher cover of less dominant woody species. Dominant constraints on plant communities were climate, hydrology, and elevation, with grazing a secondary factor. However, plots of the cover of four woody obligate riparian species showed extremely low values for grazed compared to ungrazed sites. Unfortunately, the degree of confounding factors due to other site differences was not discussed by the author, but two of the six protected sites were at a lower elevation Nature Conservancy site.

A 10-year exclosure was compared to a lightly grazed site in a narrowleaf cottonwood - gambel oak - ponderosa pine - Arizona walnut community along McKnight Creek in southwestern New Mexico (Medina and Martin 1988). Protection from grazing did not prevent channel erosion, a decline in herbaceous vegetation cover, or decreasing tree cover over time. No differences between grazing treatments was found for channel morphology or species composition of the plant community. The cause of high sediment transport, stream channel aggradation, and loss of plant cover was a large wildfire in the headwater section of the stream 24 years prior to erecting the exclosure and 34 years prior to the last reported measurements and subsequent storm events. Although grazing was very light and treatment differences minimal, the study demonstrates the very long-term nature of changes that can be brought about by an event associated with surrounding communities. While the authors considered the events to have "upset the dynamic equilibrium of the stream," Asplund and Gooch (1988) considered flash flooding and stream degradation and aggradation to be the natural dynamics of cottonwood, disturbance-based communities (see below). Medina and Martin (1988) did comment that establishment of willows was greatest during years of greatest change in channel morphology. The disturbed or unstable condition of the streambanks was more conducive to establishment than were other soils. Unstable conditions of aggradation may be necessary for periods of establishment and disruption of even-aged conditions (Asplund and Gooch 1988).

Broadleaf Cottonwood Forest

No information within the Arizona - New Mexico area was found specific to broadleaf cottonwood forest community type 21 in Appendix 1. Information below pertains to broadleaf cottonwood forest community type 22.

In contrast to adjacent Madrean woodland and pinyon-juniper communities that displayed very slow recovery to protection from grazing, cottonwood-sycamore-alder riparian areas protected from grazing for 10 years displayed significant increases in tree, shrub, and forb diversity compared to when the area had been grazed (Tolisano 1995). Additional measurements of areas where grazing continued indicates that regeneration of overstory riparian species was rare to nonexistent. Cottonwood and sycamore trees in the grazed areas were all 24 inches in diameter or greater compared to all size classes being represented in the ungrazed areas. Boles and Dick-Peddie (1983) also observed an even-age structure in Freemont cottonwood and lanceleaf cottonwood in two broadleaf community types along the Mimbres River (see Narrowleaf Cottonwood section above). A similar even-age structure of the narrowleaf cottonwood population was not observed. Boles and Dick-Peddie cite personal communications with Hilderbrant and Ohmart, and with Spellenberg, for similar observations along the Salt and Verde Rivers in Arizona and for sycamores in the Guatalupe Canyon in New Mexico, respectively. Based on visual observations along the same rivers, Davis (1982) suggested that the Santa Rita four-pasture rest-rotation grazing system with proper stocking management was favorable for cottonwood reestablishment goals, even though many authors in other parts of the country and Ames (1977) suggest that only complete protection is effective. Sponholtz (1997) observed 60 percent less vegetation, 50 percent greater channel width, 85 percent lower flow velocity, and 50 percent lower fish density at a grazed compared to ungrazed section of the Verde River.

The Sonoita creek in southeastern Arizona supports a broadleaf cottonwood-willow-ash-sycamore community that is surrounded by an oak-mesquite-juniper community (Glinski 1977). Measurements of the number and size-class of cottonwoods and sycamores were made in a segment of the stream ungrazed by livestock for eight or more years and in four areas grazed by cattle and horses, cattle, or horses. The ungrazed site was at the highest elevation, followed by the grazed sites sequentially downstream. Sycamore sprouts were the main form of reproduction, and cattle did not appear to inhibit reproduction by sprouting. In contrast, cottonwood reproduces only by seed, and trampling and grazing of seedlings by cattle appeared to severely limit reproduction. Horses did not graze seedlings but trampled some and stripped the bark from some saplings.

In contrast to the above studies showing a deleterious effect of grazing on cottonwood establishment, Asplund and Gooch (1988) found that recruitment of Fremont Cottonwood was a function of stream geomorphologic features and refugia from flood damage rather than on the absence of livestock grazing. Recruitment was found to be low in a "virgin" ungrazed canyon, and competition with mature trees was thought to be a factor. The authors conclude that recruitment primarily occurs where aggradation of materials was from upstream degradation and erosion. Flash flooding and stream degradation and aggradation were considered to be the natural dynamics of this disturbance-based community. Uncontrolled correlative studies of the effects of grazing on recruitment need to consider tree distributions over a long stretch of the watershed before eliminating the lack of natural geomorphic processes as the cause for the lack of recruitment. The authors argue that high sediment loads and upslope erosion are natural factors necessary for community persistence, and that management practices that emphasize stabilization of channels and floodplains are ignorant of the necessary natural processes required for recruitment.

An exclosure and an adjacent grazed plot in cottonwood-willow riparian areas along the southern Arizona-New Mexico border were sampled the year after establishment and over the subsequent 10 years (Hayward and others 1997). The area was at one time an 8 km long marsh until irrigation projects lowered the water table, so vegetation change due to this was overlaid on both grazing treatments. The primary objective of the study was to monitor small mammal populations, so vegetation data was limited and no description of the grazing regime was provided. Height of vegetation was greater in the exclosure in 13 of 18 measurement periods, and vegetation visually appeared more dense.

Minckley and Brown (1982) provide some general descriptions of understory plant community species composition changes that may be associated with grazing of Sonoran broadleaf cottonwood forest. Historically ungrazed communities would support a variety of native annual and perennial grasses, forbs, and several species of saltbushes in more saline areas. Grazed or otherwise disturbed communities would be likely to have an exotic component that can include filaree, mustards, red brome, and in open places Schismus and Bermuda grass. Other invasion problems also occur in overstory species, where saltcedar and tamarisk replace native vegetation. This has been linked to intermittent flooding during the growing season, which may or may not be indirectly associated with livestock grazing. Saltcedar is highly flammable, and fire can maintain a saltcedar disclimax scrub community.

One of the few studies measuring herbaceous understory vegetation as well as shrub and tree abundance and size distributions was conducted along Little Ash Creek in central Arizona in a Fremont cottonwood, velvet ash, Gooding willow community (Szaro and Pase 1983). An area protected from grazing for four years showed "extremely limited" recovery compared to an adjacent grazed area. This conclusion appeared to be based on no significant grazing effects on overstory canopy cover or tree growth (average radial growth). There were large differences in size distributions of Fremont cottonwood between grazing treatments. No cottonwoods under 22.5 cm dbh were found on the grazed site while 48 percent of the trees on the ungrazed site were less than 22.5 cm. However, this would suggest there were initial differences in the sites prior to establishment of the exclosures. Size distributions of 7.5 and 15 cm dbh were found on the ungrazed but not on the grazed site, yet it would not be possible for a tree to grow to a 15 cm diameter over four years. Total basal area of cottonwoods increased 10 percent in two years on the ungrazed treatment compared to 5.7 percent on the grazed treatment. Understory cover after four years of treatment was 5.2 and 2.2 percent for the ungrazed and grazed treatment, respectively. Differences in herbaceous understory species composition and diversity were also apparent. Ten species (one in trace amounts) were sampled in the ungrazed exclosure compared to seven (four in trace amounts) in the grazed treatment. Unfortunately, pre-treatment conditions were not sampled, and the possibility of prior differences based on cottonwood size distributions makes interpretation of understory responses difficult as well.

Table 18—Plant density (#/464 m^2) and cover (percent) along Trout Creek, Arizona, broadleaf cottonwood riparian communities in never grazed geologic refuges and grazed sites. The refuges were formed by granite rubble that prevents livestock entry (area for density represents smallest site). Values are an average of three sites/treatment. Adapted from Reichenbacher (1984).

	Ungrazed refuge		Grazed	
Plant	**Density (#/464m^2)**	**Cover (percent)**	**Density (#/464m^2)**	**Cover (percent)**
Shrubs and herbs				
Mule's fat	37	0.60	4,951	5.84
White clover	984	4.99	39	0.09
Salt cedar	26	0.01	144	0.02
Singlewhorl burrobrush	48	2.97	48	0.87
Sweetbush	0	0.00	39	0.64
Desert false indigo	32	0.53	0	0.00
sub total	1,127	9.14	5,220	7.46
Emergent aquatics				
American bulrush	41,248	8.20	880	0.00
Pale spikerush	0	0.00	368	0.00
sub total	41,248	8.20	1,248	0.00
Trees				
Green ash	5	1.46	3	3.23
Black willow	62	48.79	11	10.68
Fremont cottonwood	16	1.15	1	3.70
Soapberry	26	8.61	0	0.00
sub total	108	60.12	15	17.61
Total vegetation	42,483	69.25	6,483	25.07

Ohmart (1996) provides photographic evidence for very large changes in vegetation structure along a portion of the San Pedro River in southeastern Arizona before and four years after livestock removal to create a National Riparian Conservation Area. Similar dramatic photos are shown of not-managed compared to 24-year-managed sections of Date Creek in Arizona. Willows and cottonwood had developed along the creek in the managed section, and trees and herbaceous vegetation in this area survived a flood much better than in the not-managed section. However, the management regime was not described. Additional qualitative and quantitative data for the San Pedro River are presented in Krueper (1993, 1996), U.S. Fish and Wildlife Service (2002), and Krueper and others (2003). Herbaceous, shrub, and low and tall tree components of the vegetation was estimated as foliage height density prior to cattle removal, and two, five, and eleven years after cattle removal in Fremont cottonwood/Gooding willow riparian, mesquite grassland, and Chihuahuan desert communities. Herbaceous plant density doubled after two years in both riparian and grassland communities. Increases in herbaceous vegetation density continued from year two to year five after removal of livestock at lesser rates for low strata but at similar rates for upper strata, then remained similar from year five to year eleven. The shrub and tree components in both riparian and grassland communities showed little response over the period of study, and no significant responses to removal of livestock were ever observed for the Chihuahuan desert communities.

Only one other study assessed both understory and overstory vegetation responses to protection from grazing, and this study included three replicates along Trout Creek in Arizona (Reichenbacher 1984). The ungrazed treatments were geologic refuges formed by granite rubble, making this unique for riparian grazing studies. Reichenbacher describes the pristine ungrazed sites as "remarkable riparian luxuriance" unlike anywhere along the grazed stretches of the river. Understory species composition was drastically different between grazing treatments (Table 18). Ungrazed sites had dense stands of American bulrush, cattail, sweet clover, and tree saplings, while grazed sites were heavily dominated by the shrubby, opportunistic seepwillow. Total vegetative cover was nearly three-times greater, and density nearly seven times greater, on ungrazed compared to grazed areas. Diversity (calculated as H', which incorporates both richness and evenness components of diversity) was nearly three-times greater in ungrazed compared to grazed sites (2.83 vs. 1.0, respectively). The high density of trees in ungrazed refuges was due to large numbers of seedlings and saplings.

Riparian Scrub

No information was found specific to this type. However, willow and alder are components of narrowleaf and broadleaf cottonwood forest types, and some species found there are also found in the riparian scrub type (see Appendix 1). General management considerations for riparian habitat are covered below in the Grazing Management section.

Other Riparian

Arizona willow is an imperiled species that has a very restricted range, from southern Utah, on one mountain in northern Arizona, and recently found in New Mexico (NatureServe Explorer 2002). Cattle and elk grazing in particular, and timber harvest and off-road vehicles are considered primary threats to this species. The importance of cattle versus native ungulate grazing of Arizona willow was assessed by Strohmeyer and Maschinski (1996) and Maschinski (2001) by exposing planted individuals to no grazing, open to cattle grazing only, or open to native grazers only for a one year period. Both native and domestic herbivores reduced mean plant height, number of branches, branch length, and total shoot length. Elk in particular selected for the willows, while similar evidence of deer or antelope herbivory were not observed. While having a similar effect, cattle selected for grasses amongst the willows and consumed willows only after other herbaceous forage had been consumed. The studies were conducted in both artificial and natural community settings and demonstrated that willow damage can be attributed to both wild and domestic herbivores additively. Maschinski (2001) noted that this species of willow is sensitive to herbivory and that it requires years to recover from defoliation. Stein and others (1992) also reported very heavy use of arroyo willow by elk, but this was of the nutritious resprouts after fire.

Rinne (1985, 1988) sampled some structural characteristics of the vegetation along the Rio de la Vacas in Sante Fe National Forest in conjuction with a study of fish populations in grazed and ungrazed sections of the third-order montane stream. No plant species descriptions were provided, but stream-bank vegetation cover averaged 8.4 and 1.0 percent for ungrazed and grazed treatments, respectively, and overhanging vegetation cover was 17 and 0 percent, respectively. An index of bank instability for grazed sections of the stream ranged from 20 to 100 percent, with an average of 64 percent, compared to 0 percent for all six ungrazed plots.

A riparian area along the Paria River in north-central Arizona, southern Utah, had been fenced from grazing for six to eight years with no establishment of new cottonwoods, even though a seed source was available (Bezanson and Hughes 1989). No description of the plant community was provided, but surrounding vegetation included saltbush - Indian ricegrass communities. Heavy grazing and flash-floods had previously degraded much of the vegetation. A grazing system whereby grazing occurred during November through January for two years, followed by a year of rest (6 months grazed, 30 months rested), allowed cottonwood recovery after four years. The lack of sprouting of cottonwood during the protected period prior to implementing the grazing system would suggest that years suitable for reproduction of cottonwoods were not frequent, but this particular grazing system may have allowed for recovery when conditions were favorable. This was not a controlled experiment and no data were provided, but photographs indicate much improved conditions.

Another non-experimental observation was reported by Grette (1990) in an unidentified plant community along McCoy Gulch in south-central Colorado surrounded by pinyon-juniper communities. Woody riparian vegetation at the site was described as nonexistent due to unregulated winter grazing, and uplands were in poor condition even though stocking was moderate. When the grazing season was changed from winter to spring, cattle use shifted from willows to grass, resulting in an increase in willows. Although improving, the riparian area was fenced to allow better control of grazing. A grazing objective was established whereby willow leaders were allowed to be grazed only once (removing about 12 cm), thereby acting like a mild pruning. Utilization limit of preferred grasses was set at 80 percent, and supplemental protein was provided in the uplands. Photographs indicate good recovery of riparian woody species, and perennial grass and forb cover increased.

Tamarisk is a woody plant that was introduced into the United States in the early 1880s as an ornamental (Horton 1977). The plant spread throughout flood plains of the southwest and became a permanent vegetation type. Tamarisk uses more water than native species and also supports a less diverse faunal community. The plants can grow as much as 3.5 m in a year, and grazing of 50 percent of the foliage does little to prevent stands from becoming very dense.

Vegetation along streambanks can affect water flow and, therefore, sediment transport rates. A series of 1- to 3-year-old exclosures was studied along the Rio Senorito in north central New Mexico, focusing on solute transport and retention (Sewards and Valett 1996). Even with short-term exclosure from livestock grazing, channel widths were restricted by vegetation growth in the exclosures, and channel depth was greater. These differences in channel structure resulted in a greater linear flow velocity in exclosed compared to grazed areas, but lateral areas with dense vegetation allowed for a four to five times greater retention time. The authors hypothesized that the lateral areas of increased residence time are important for biological processing of incoming material and could also influence sediment transport and deposition. Grazing of riparian areas could thereby increase occurrence of flash-flooding, and subsequent grazing of vegetation could slow recovery.

In contrast, Thibault and others (1999) measured greater nutrient retention in grazed sections of four streams in New Mexico due to greater in-stream vegetation. Greater in-stream vegetation and wider widths of streams slows water flow and allows for greater utilization of passing nutrients. However, ungrazed portions of the streams generally had greater cover of riparian vegetation. Two of the four streams had greater cover of herbaceous vegetation in ungrazed sections compared to grazed, one had greater in the grazed section, and one did not differ with grazing treatment. Two of the four streams had greater woody plant cover in the ungrazed sections. Implications of the differences in nutrient dynamics in streams due to grazing have not been investigated.

Dry Washes

Only four reports of grazing effects on dry wash communities were located, two of which were of feral burro grazing. Chew (1982) reported much greater response to protection for wash communities than for adjacent creosote bush or tarbush communities. Differences in standing biomass between inside versus outside exclosures (after adjustment for grazing loss) were about 2, 4, and 73 g/m^2 for creosote bush, tarbush, and dry wash communities, respectively. Differences between ungrazed and grazed washes were also large for density and basal cover of total vegetation excluding fluff grass. Chew concluded that washes, like riparian areas, have a potential production much greater than their area and than adjacent uplands, and recovery following protection from very heavy grazing can be much greater in these productive sites. Gardner (1951) also reported large grazing intensity effects on washes in the Rio Grande valley, New Mexico, although not as great as those reported by Chew. Gardner compared uncontrolled grazing with light grazing, and the lesser differences between this and a completely protected site can be due to heavy grazing of preferred washes even under general light stocking of the entire area. Grasses were common in lightly grazed areas and rare under uncontrolled grazing (0.06 percent vs. trace basal cover, respectively). Total shrub and forb covers did not differ much between grazing treatments, although species composition differences were evident. Creosote bush was a high proportion of shrubs in areas with uncontrolled grazing, and with two other species-dominated sites. Lightly grazed areas had more even proportions of seven to eight shrub species.

Grazing by feral burros in Grand Canyon National Park was observed to impact mesquite riparian scrub communities much greater than three other community types because of the relatively greater use (Bennett and others 1980). Plant cover, density, and diversity declined in burro impacted compared to control areas. Grazing by burros in secondary washes of Sonoran Desert ranges in Arizona was found to decrease total canopy cover from 8.6 to 2.8 percent, and of white bursage (burrobush) from 2.26 to 0.04 percent (Hanley and Brady 1977). Secondary washes were the most utilized plant community in the area, with some areas receiving 100 percent utilization of current-year's growth. No species were observed to increase or invade under the heavy grazing.

Wetlands

The amount of wet meadows or cienagas in New Mexico and Arizona National Forests has been estimated at about 17,700 ha (Patton and Judd 1970). These communities occur within coniferous forests and may be important to wildlife populations because of their high productivity, even though they represent only 0.2 percent of the area. Productivity averaged approximately 300, 150, and 20 g/m^2/yr for the wet meadow, transition zone, and surrounding dry forest, respectively. Protein contents of meadow/transition community species were also greater than dry forest species. Arnold (1954, cited in Patton and Judd 1970) estimated that wet meadows produced four times the amount of herbaceous vegetation than associated ponderosa pine communities. Patton and Judd found the greatest plant species diversity in transition communities, with only 20 species recorded in the wet meadow compared to 43 in the moist transition and 28 in the dry forest communities.

However, deer use of the forest edges was much greater than for wet meadow/transition communities, and elk displayed similar but less pronounced preferences. This was thought due to predator avoidance behavior, but also because the pellet count method of utilization probably underestimated the actual importance of the time spent foraging in meadows. In contrast, cattle use of the meadow/transition communities was from 4 to 10 times more than for forest edge communities. Turkeys and ducks were observed to also preferentially use the meadow/transition communities during certain periods of the year.

At the site described above for Broadleaf Cottonwood Forest (Hayward and others 1997), an additional paired ungrazed-grazed plot was established in a cienaga dominated by sacaton grass. Height of vegetation was greater in the exclosure in 18 of 20 measurement periods, and vegetation visually appeared more dense.

In White Mountain riparian meadows dominated by *Carex*, *Cyperus*, and *Juncus* species, Neary and Medina (1996) found that trampling and grazing of native and domestic animals resulted in disruption of aggradation processes. Tearing of the root-soil matrix leads to loss of fine materials and down-cutting riffles. Grazing of aboveground material reduces the filtering and deposition of sediment. Introduced grasses such as Kentucky bluegrass, wheat grasses, or orchard grass do not have the same fibrous, thick root mats like native grasses, and break down easier under trampling. Eventually, down-cutting of the channel can lead to changes in stream bank vegetation from aquatic to more mesic species.

Grazing Management

Kovalchik and Elmore (1992) provide a good review of grazing systems and management effects on northern, colder climate, willow dominated communities. A good review of grazing management of riparian habitat based on studies from throughout the western United States can be found in U.S. Fish and Wildlife Service (2002). Clary and Webster (1990) recommend spring grazing for intermountain ranges, as described above by Grette (1990). Differences between riparian and upland vegetation lushness and quality, and microhabitat differences (temperature, and so forth), are least during spring. Fall is recommended as a second-best option, while mid- to late-summer grazing should be avoided in most areas because the hot dry conditions make riparian habitat more preferred. A stubble height of grasses of 10 to 16 cm should be left to entrap sediment and protect streambanks during high flow. Other recommendations of Clary and Webster include: 1) limit use of herbaceous forage to 65 percent and remove animals while plants are still in a vegetative stage (this seems very high utilization compared to even use-levels of uplands reviewed above; note that Kovalchik and Elmore 1992 indicate that livestock start utilizing willows when herbaceous forage use reaches about 45 % in Oregon), 2) utilization should be less if grazed in summer, because of lower regrowth potentials, 3) fall grazing levels should be closely monitored, because no regrowth will occur, and use should be even lower at 30 to 40 percent, 4) relatively sensitive habitat will require even more conservative use, 5) provide salt and alternative water away from riparian areas, and 6) rest of heavily degraded streambanks and/or woody vegetation may require from 1 to 15 years for recovery, followed by the above to maintain a good condition. Along the Verde River in Arizona, seasonal differences in use-preference by livestock described above were observed on an annual basis (Tonto National Forest unpubl. data cited in U.S. Fish and Wildlife Service 2002). Use of riparian areas was greater during dry winters, when upland vegetation was relatively less available than in good winters. In this case, use of woody vegetation by livestock increased after bud break in late February to early March. The above recommendations seem based on reasonably sound logical concepts in terms of proposed mitigation practices but, unfortunately, there is little hard scientific evidence to support them.

It seems rather surprising that, given the volumes of literature written on riparian systems in the southwest, such little actual research has been accomplished. This appears the general case for riparian research throughout the western United States (Larsen and others 1998). Some research is available on tree regeneration, with very little on understory vegetation. There are problems with statistical design and replication in riparian communities that are more difficult to overcome than in upland communities, due to the linear and elevational aspects of stream flow. Initial pre-treatment background measurements need to be considered of even greater importance in riparian systems than in upland communities due to especially high levels of variability in physical conditions along streams. Because of natural, continual aggradation/degradation processes that change in location along stream lengths where flooding and catastrophic events are common, there is an extreme need to consider sufficient length and replication of treatment areas. Although the congregation of livestock in riparian areas undoubtedly causes severe alterations in plant community species composition and structure in communities that historically have not experienced a grazing force by large herbivores, the experimental evidence showing the effects is weak. Based on a number of reports and a number of visual observations, cottonwoods that reproduce by seed are reduced by grazing, while root sprouting species are less affected. Channel morphology is altered, and the potential implications are great. Unfortunately, very little substantial work has been accomplished specific to southwestern riparian understory plant communities, but what information is available shows much greater effects of grazing than for upland, non-riparian communities (see also Comparison of Southwestern Community Types section below).

Relative Effects of Grazing Among Southwestern Community Types, and Comparison of SW with Great Plains Community Responses: Does Evolutionary Grazing History Matter?

The detailed assessments of plant community response to grazing examined above to some extent relies on each study author's interpretation of their results. The compilation of these accounts within a particular community type to some extent depends on a reviewers interpretation, and a broader perspective of comparing among community types can be complex, qualitative, and difficult. Quantitative comparisons among community types using community-wide variables and indices often provide insight into relative sensitivities of different communities to controlled conditions or treatments and into factors contributing to the different sensitivities. A meta-analysis-like approach may sometimes bring order to what at first appears to be complex and unassociated responses. Even though methods and experimental designs differed, an assessment of 236 pairs of ungrazed-grazed treatment comparisons yielded explanations of factors that explained 54 to 69 percent of the variance in grassland or shrubland plant community species composition responses to grazing across communities throughout the world (Milchunas and Lauenroth 1993). Explanatory variables included evolutionary history of grazing, aboveground productivity or precipitation, intensity of grazing and years of protection and grazing treatment (see The Importance of Evolutionary History section above).

The objectives in this section are to examine all ungrazed-grazed comparisons reviewed in the sections above to see whether there are any discernable differences among community types in response to grazing, and then compare southwestern communities with short histories of grazing to communities in the adjacent Great Plains of North America with a long evolutionary history of grazing by native, large, generalist herbivores (bison).

Convergent selection pressures of herbivory and aridity in systems with a long evolutionary history of grazing and frequently low soil water availability are predicted to result in communities least responsive to grazing by introduced livestock. In contrast, divergent selection pressures of herbivory and an ability to compete for light in the canopy in more productive, subhumid environments are predicted to result in communities most responsive to grazing (Milchunas and others 1988, and History of Grazing by Native and Domestic Large Herbivores section above). Rapid switching from short species adapted to grazing to tall species adapted to competing in the canopy, and visa-versa, may occur with temporal and spatial changes in herbivore abundance in the latter. Intermediate in responsiveness are communities with a short evolutionary history of grazing. Productive communities with a short history of grazing by large herbivores do not have a suite of species capable of withstanding heavy grazing, whereby local species losses can occur and/or a few weedy ruderals eventually increase in abundance. Unproductive communities with a short history of grazing have some degree of tolerance/avoidance of herbivory due to adaptations to aridity but have not developed in the presence of the large herbivores. Therefore, the order of plant communities from least to most responsive to grazing can be hypothesized as unproductive/long history < unproductive/short history < productive/short history < productive/long history. The responsiveness does not possess a "good or bad" component, other than invasion of exotics or opportunistic species from outside the community would be most likely in the productive/short history situation followed by the unproductive/short history situation, and least likely in the communities with a long history of grazing.

Table 19—Examples of dissimilarity values calculated using the Whittaker Index of Community Association, and percent change in total species abundance, for comparisons of hypothetical ungrazed versus grazed communities. These hypothetical community examples may aid in interpretation of data for real ungrazed versus grazed community comparisons in figures that follow.

Comparison	**Example A**		**Example B**		**Example C**		**Example D**		**Example E**		**Example F**	
Community	**Ungrazed**	**Grazed**	**Ungrazed**	**Grazed**	**Ungrazed**	**Grazed**	**Ungrazed**	**Grazed**	**Ungrazed**	**Grazed**	**Ungrazed**	**Grazed**
Species 1	50	50	50	0	90	90	90	900	98	91	98	5
Species 2	40	40	40	0	9	1	1	10	55	61	55	13
Species 3	30	30	0	50	1	9	9	90	10	13	10	61
Species 4	20	20	0	40	0	0	0	0	7	5	7	91
Total	150	150	90	90	100	100	100	1000	170	170	170	170
Percent dissimilarity	0		100		8		8		5		79	
Percent change abundance	0		0		0		900		0		0	

Below, the Whittaker (1952) index of community association is used as a community-wide dissimilarity metric. A comparison of an ungrazed to an adjacent grazed community that yields a value of zero indicates that all species present in the ungrazed community are also in the grazed community, and every species is present in the same proportion (Table 19 example A). A dissimilarity value of 100 percent means there is not even one single species that was sampled in both communities (Table 19 example B). Index values are based on the proportions of all species in the two communities being compared and do not indicate differences in abundance but indicate proportional differences (Table 19 example C compared to D). The percent difference in total vegetative cover is used as a second metric, to evaluate differences in abundance between the ungrazed and grazed communities being compared, since differences in abundance do not affect dissimilarity indices when proportions are similar. For example, differences in abundance between the ungrazed and grazed communities in example C in Table 19 are 0+8+8 divided by a total abundance of 90+9+1+90+9+1 which equals 8 percent. This is the same as the dissimilarity index of 8 percent because abundances are the same. However, the same calculation of difference in abundance for example D in table 19 is 810+1+89 divided by 90+9+1+900+10+90 equals 82 percent which is not the same as the dissimilarity value of 8 percent. The dissimilarity measures do not place a value on particular species and quantitatively provide an overall index of change in community species composition between two treatments/sites based on all species but do not account for differences in abundances of the species.

Some information emerges for a simple comparison of community types for the southwest, without taking any other factor into consideration (Fig. 7). One possible conclusion may be that riparian community species compositions are consistently and very drastically affected by grazing (average dissimilarity of 84 percent), although there are only four riparian comparisons from two studies. Grassland, shrubland, and forest communities averaged approximately the same differences in plant species composition between grazed versus ungrazed treatments, but desert communities were relatively less responsive to grazing. Great Basin temperate desert communities also have a high average dissimilarity, but there is very high variability within this community type. The two very high dissimilarity sites were both shallow-upland Bigelow sagebrush/galleta grass/blue grama sites where the ungrazed site had been protected for 73 years. Chihuahuan Desert, Sonoran/Mohavian Desert, interior chaparral, and Great Basin juniper/sagebrush communities appear particularly unresponsive to grazing/protection treatment. This may be due to the high shrub/non-forage component that varies little with grazing. Very small differences between ungrazed-grazed Chihuahuan Desert sites were also observed. Sites in Fig. 7 were sorted by increasing precipitation within a particular community type. Only pinyon-juniper and mesquite savanna community types have enough data to assess effects of increasing precipitation on grazing responses within a community type. No relationship of increasing effects of grazing with increasing precipitation was observed for the mesquite type (r^2 = 0.02). A slightly negative relationship was found for pinyon-juniper communities (r^2 = 0.34, slope -0.002), possibly indicating an overriding effect of overstory control on the response to grazing.

Differences among communities in grazing response with respect to total vegetation abundance are less clear than that for species composition (Fig. 8). This may be due to the fact that method of measurement in the

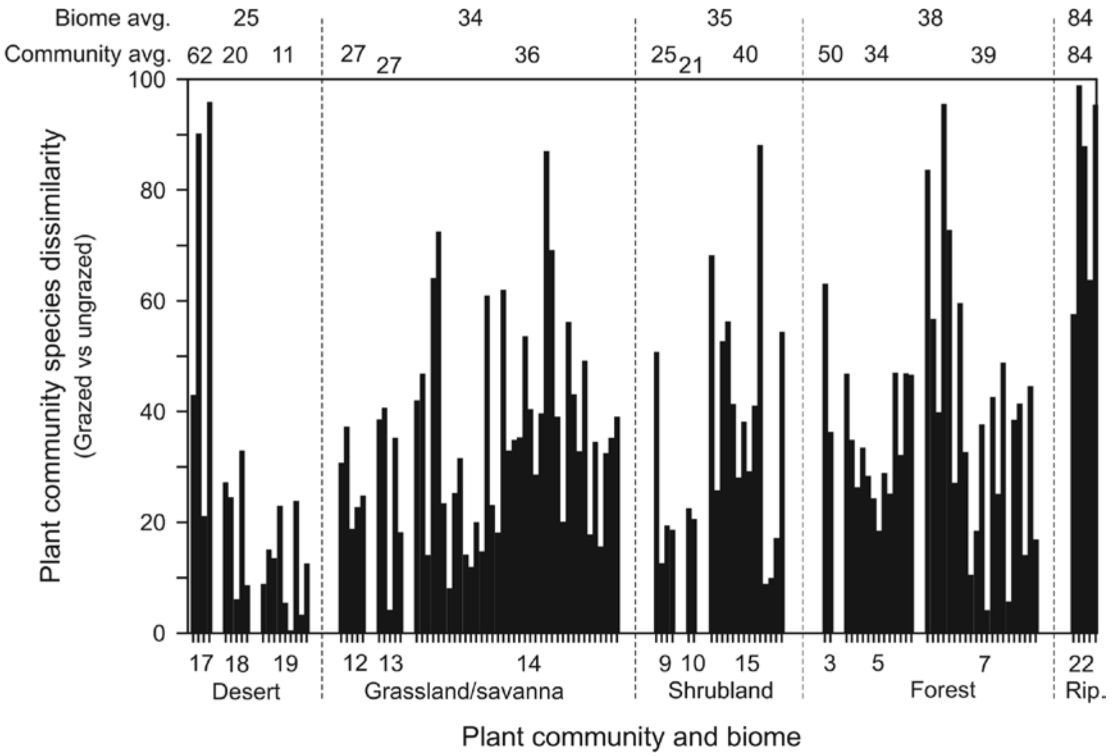

Figure 7—Plant community species dissimilarity (grazed versus ungrazed percent) for plant community types for which ungrazed and grazed sites have been compared. Dissimilarity values calculated using the Whittaker (1952) index of community association. Community types are: 3 = mixed conifer forest, 5 = ponderosa pine, 7 = pinyon-juniper, 9 = Great Basin juniper/sagebrush, 10 = interior chaparral, 12 = montane meadow, 13 = temperate grassland, 14 = mesquite savanna, 15 = Great Basin sagebrush, 17 = Great Basin temperate desert, 18 = Sonoran/Mohavian Desert, 19 = Chihuahuan Desert, 22 = Broadleaf cottonwood forest (M) riparian, 24 = dry washes. Community numbers correspond to the numbering system for community descriptions in Appendix 1.

studies would likely have more influence on this variable. Estimates based on canopy cover or grazed, non-temporary-caged biomass versus ungrazed biomass would by definition of consumption due to grazing more likely show reductions. Estimates based on basal cover, productivity, density, or frequency may also show reductions, but not just due to current-year grazing unless immediate mortality occurs. Regardless of method, reduced plant abundance has implications for habitat structure for other consumer populations, even if it does not for long-term plant population dynamics (see Introduction section for additional interpretive definitions). In general, most studies and most community types showed declines in total vegetation abundance with grazing. Although limited by the number of studies, large and/or mostly reductions in abundance were observed in riparian (with one exception), temperate grassland, and Great Basin sagebrush, ponderosa pine, and pinyon-juniper types. Although only two comparisons, montane meadows showed increases in plant abundance with grazing. The most notable conclusion that can be drawn from Fig. 8 is the preponderance of negative values (67 negative, 28 positive). This is not the general direction of response for Great Plains grasslands (Milchunas and others 1989; Lauenroth and others 1994) or in other systems with long evolutionary histories of grazing (Milchunas and others 1988), where increases in cover of prostrate, grazing adapted species often occurs. Interestingly, blue grama consistently increases in Great Plains grasslands but does not always do so in southwestern communities (studies reviewed above). Blue grama actually decreased in two out of 13 community types assessed by Dahl and others (1976).

How do responses differ between plant communities of the southwest and Great Plains? Are there different multiple variables that may better explain variability in responses shown in Fig. 7, and do they differ between southwestern and Great Plains communities? First, over a low precipitation to similar high precipitation cutoff for Great Plains communities, average dissimilarity between ungrazed versus adjacent grazed communities was greater for Great Plains communities compared to southwestern communities (Fig. 9). The difference between ungrazed versus grazed communities increased with increasing precipitation for Great Plains

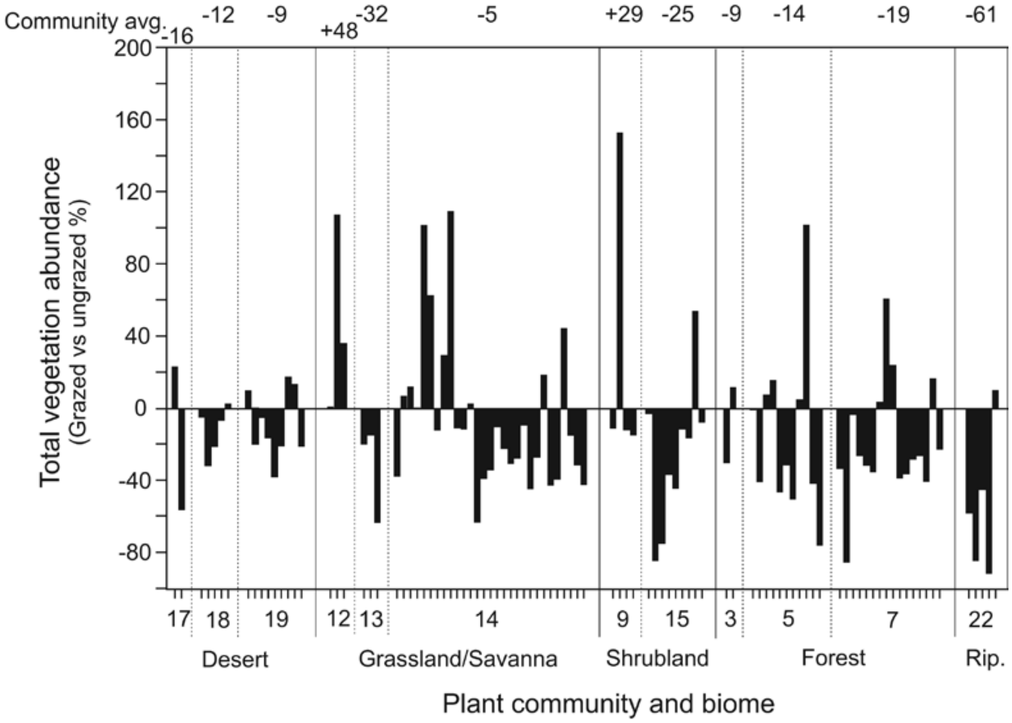

Figure 8—Plant community total vegetation abundance (grazed / ungrazed percent) for plant community types for which ungrazed and grazed sites have been compared. Community types are: 3 = mixed conifer forest, 5 = ponderosa pine, 7 = pinyon-juniper, 9 = Great Basin juniper/sagebrush, 10 = interior chaparral, 12 = montane meadow, 13 = temperate grassland, 14 = mesquite savanna, 15 = Great Basin sagebrush, 17 = great Basin temperate desert, 18 = Sonoran/Mohavian Desert, 19 = Chihuahuan Desert, 22 = Broadleaf cottonwood forest (M) riparian, 24 = dry washes. Community numbers correspond to the numbering system for community descriptions in Appendix 1.

communities and explained 22 percent of the variance among sites even though study methods, grazing intensities, and years of protection differed. In contrast, precipitation explained only eight percent of the variance for southwestern communities. The relationship between precipitation and change in species composition with grazing for the two regions can possibly better be seen by dividing studies into four groups and doing an analysis of variance. Large differences between arid and subhumid communities in the effects of grazing on plant species composition were seen in the Great Plains, with subhumid communities being very responsive and arid ones least responsive (Fig. 10). Also as predicted, southwestern communities were intermediate to the two types of Great Plains communities. However, subhumid southwestern communities were only slightly more responsive to grazing than arid southwestern communities, and arid southwestern communities only tended to be more responsive to grazing than arid Great Plains communities. The increase in change in species composition with increasing community productivity predicted by the Milchunas and others (1988) theoretical model, the Milchunas and Lauenroth (1993) quantitative global-community model, and various other studies relating increasing productivity to increasing response to grazing pressure (Milchunas and others 1989; Proulx and Mazumder 1998; Osem and others 2002, 2004) tended to hold within southwestern communities, but differences were not significant. Southwestern communities were more variable in response to grazing within each community type than were Great Plains communities.

There was a relationship between years of protection from grazing and plant community dissimilarity of grazed versus protected sites for Great Plains communities, but not for southwestern communities (Fig. 11). Even though the maximum years of protection from grazing for the studies available was 47 years for Great Plains grasslands compared to 73 years for southwestern communities, the r^2 values were 0.29 for the Great Plains compared to 0.03 for the southwest. As above, average dissimilarity between ungrazed versus grazed communities was greater for Great Plains communities (43 percent) compared to southwestern communities (33 percent), while average years of protection was greater for southwestern communities. Extremely

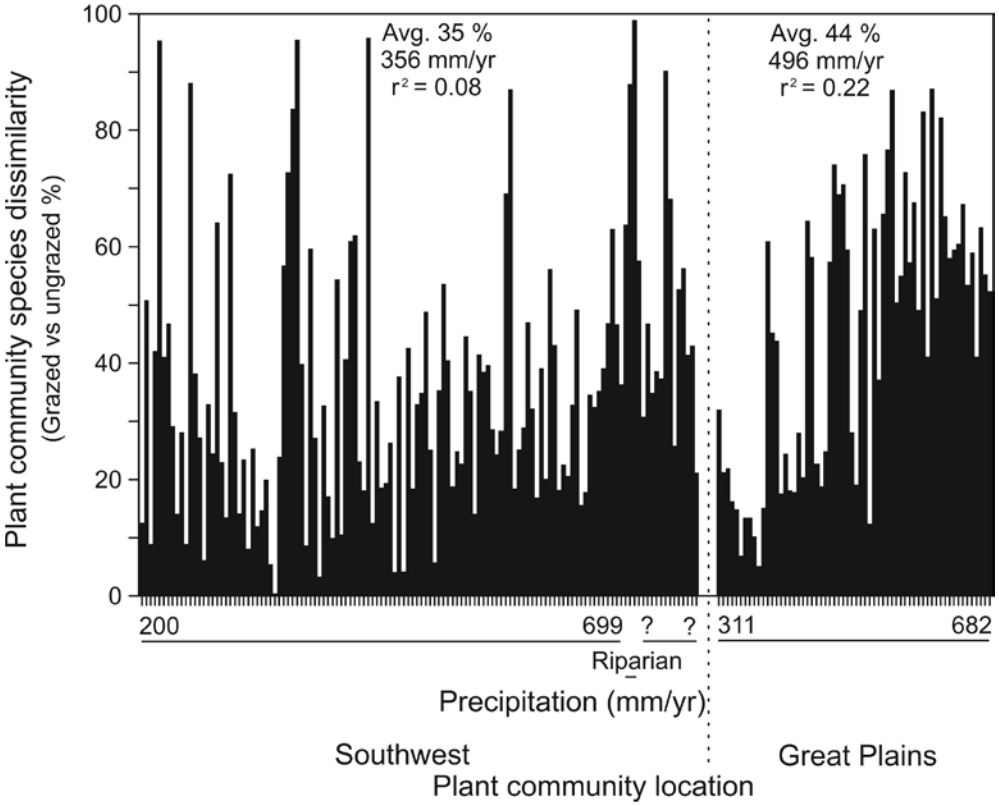

Figure 9—Plant community species dissimilarity (grazed versus ungrazed percent) in relationship to increasing precipitation (productivity) within southwestern and Great Plains plant communities for which ungrazed and grazed sites have been compared. Dissimilarity values calculated using the Whittaker (1952) index of community association. Values at the top of figure are average dissimilarity, average long-term precipitation at the study sites, and r^2 for dissimilarity versus precipitation regression within geographic location.

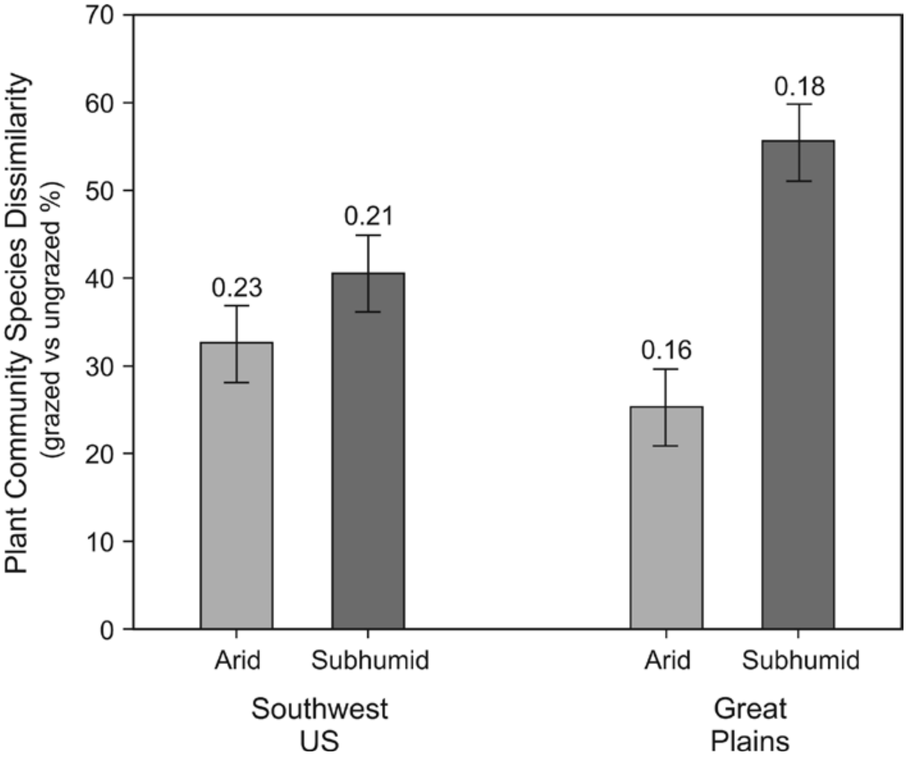

Figure 10—Plant community species dissimilarity (grazed versus ungrazed percent) for all studies categorized into four groups based on southwestern United States versus Great Plains plant communities and arid versus subhumid environments. Arid versus subhumid communities were those above or below 410 mm/yr precipitation, which is used as a surrogate for level of primary productivity because of greater availability of precipitation than productivity data. Number of observations for each bar from left to right is 78, 35, 25, 44. Value above each bar is the standard deviation of that mean and represents individual differences in variance. See text for description of similarity data.

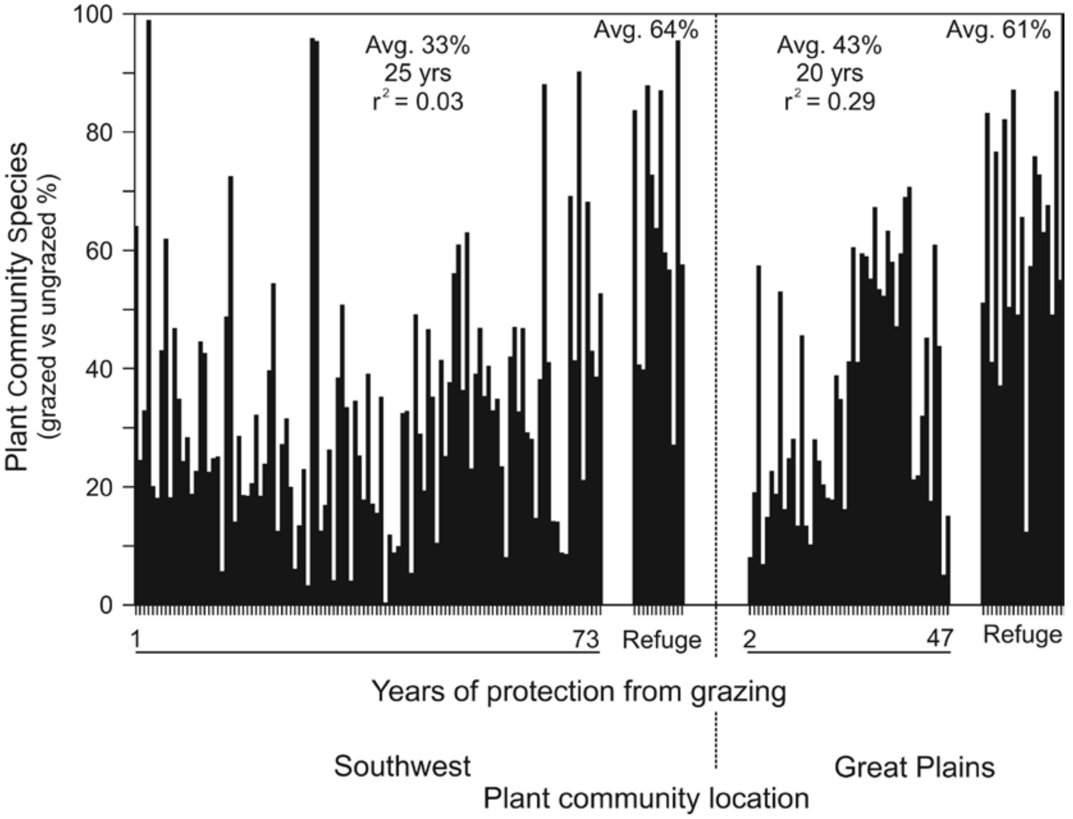

Figure 11—Plant community species dissimilarity (grazed versus ungrazed percent) in relationship to increasing years of protection from grazing within southwestern and Great Plains plant communities for which ungrazed and grazed sites have been compared. Dissimilarity values calculated using the Whittaker (1952) index of community association. Values at the top of figure are average dissimilarity, average years of protection from grazing at the study sites, and r^2 for dissimilarity versus years of protection regression within geographic location.

interesting was the difference between natural geologic, relict, never-grazed refuges compared to human-made, shorter-term, previously grazed exclosures. This was true for both Great Plains and southwestern communities. The average spread between exclosure versus relict comparisons was greater for southwestern communities than for Great Plains communities. However, an average dissimilarity in ungrazed versus grazed community species composition of 33 percent for human-made exclosures versus 64 percent for never grazed versus grazed communities for the southwest, and similarly 43 percent versus 61 percent for the Great Plains, were very large differences due to type/length of protection. This may in some part be due to micro-climatic effects of refuges, but differences between never-grazed refuges and grazed communities that appear greater than for recent human-made exclosures are seen worldwide and in many cases cannot be attributed to micro-climate (Milchunas and Noy-Meir 2002). Separating micro-climatic effects from historical grazing effects of relict sites would seem to be a potential interesting avenue of investigation, but only a few studies (partially published comparison Ambos and others 2000 and Ambos and others unpublished data Table 12 personal communication, Milchunas and Noy-Meir 2004) attempt to compare or differentiate between natural refuges and human-made exclosures.

Averaged over all studies, grazing intensity effects on plant community species dissimilarity between ungrazed versus grazed communities shows a trend of increasing dissimilarity with increasing grazing intensity from light to moderate to heavy grazing for both southwestern and Great Plains plant communities (Fig. 12). Communities in both geographic locations seem to in general show increasing differences between ungrazed versus grazed communities as grazing intensity increases from light, light/moderate, moderate, to moderate/heavy. Regression analyses for southwestern communities indicated grazing intensity explained 16 percent of the variance over all communities. When the analyses was confined to grasslands alone, the r^2 increased to 0.2. Grazing intensity was not related to

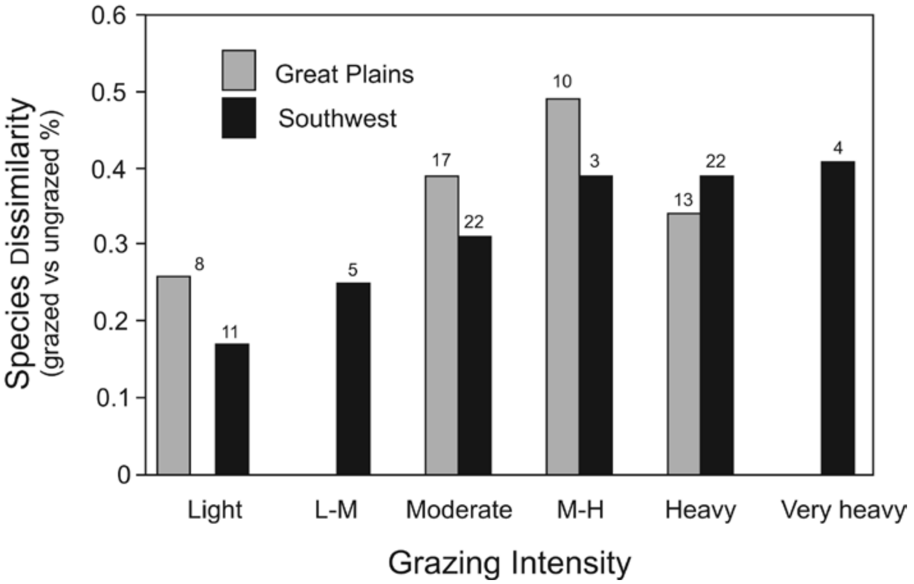

Figure 12—Plant community species dissimilarity (grazed versus ungrazed percent) in relationship to increasing grazing intensity within southwestern and Great Plains plant communities for which ungrazed and grazed sites have been compared. Dissimilarity values calculated using the Whittaker (1952) index of community association. Values at the top of bars are the number of studies the value is based upon.

total vegetative abundance differences between ungrazed - grazed comparisons.

None of the single-factor models explained much of the variance associated with southwestern communities, although better relationships were observed for Great Plains communities. This could be due to other interacting factors, so multiple regression analyses were preformed on data for both the southwest and the Great Plains. For the southwest, analyses included both grassland and all communities combined. There were not enough data to examine shrub/forest communities separately. Great Plains communities were primarily grasslands. All models were run on dissimilarity data in coefficient form, not as percentages, so slopes reported below are based on dissimilarity values ranging from 0.0 to 1.0, not 0 to 100 percent. A good multivariate model could be developed for dissimilarity between ungrazed-grazed comparisons for Great Plains communities. Three factors (precipitation, grazing intensity, and years of grazing treatment/protection) together explained 48 percent of the variance among studies. Dissimilarity in species composition between grazing treatments was most influenced (greatest slope) by grazing intensity (0.09), followed by years of grazing treatment (0.0025), and precipitation (0.0006), with a model intercept of -0.17.

Models for southwestern communities were not at all as capable of explaining variance in the data as for the Great Plains. The most successful model for plant community species dissimilarity between grazing treatments was a single factor model for grasslands only. Twenty-three percent of the variance in grassland plant dissimilarity with grazing could be explained by years of grazing treatment/protection. The relationship was positive, where increasing years of protection resulted in greater dissimilarity between ungrazed and grazed sites (slope = 0.0033). Grassland plant community dissimilarity increased with increasing grazing intensity (slope = 0.063) and explained 20 percent of the variance.

Other models assessed percent change in total vegetative cover for grasslands and for all communities combined. For grasslands alone, only 15 percent of the variance could be explained by precipitation (slope = 0.021) and years of grazing treatment/protection (slope = 0.005). For all communities combined, only 11 percent of the variance could be explained by precipitation (slope = 0.04) and years of grazing treatment/protection (slope = 0.0057).

It is interesting that good models can be produced for Great Plains plant community species composition response to grazing but not for southwestern communities given an even larger data set for the latter. One possible conclusion is simply that southwestern communities are just not very predictable. Large variability in response to grazing appears to occur both within and between community types relative to Great Plains plant communities (Fig. 9). The shrub invasions into some areas and not others reviewed in sections above, independent of grazing treatment, is another example of the more "random" southwestern phenomenon that are less clearly explained by grazing. Factors contributing to the response of Great Plains plant communities to grazing are twice as predictable as for southwestern communities. Alternatively, factors not considered here in analyses and not commonly reported in grazing studies may be explanatory variables. However, intensity of grazing and years of protection from grazing would be thought to be important within a

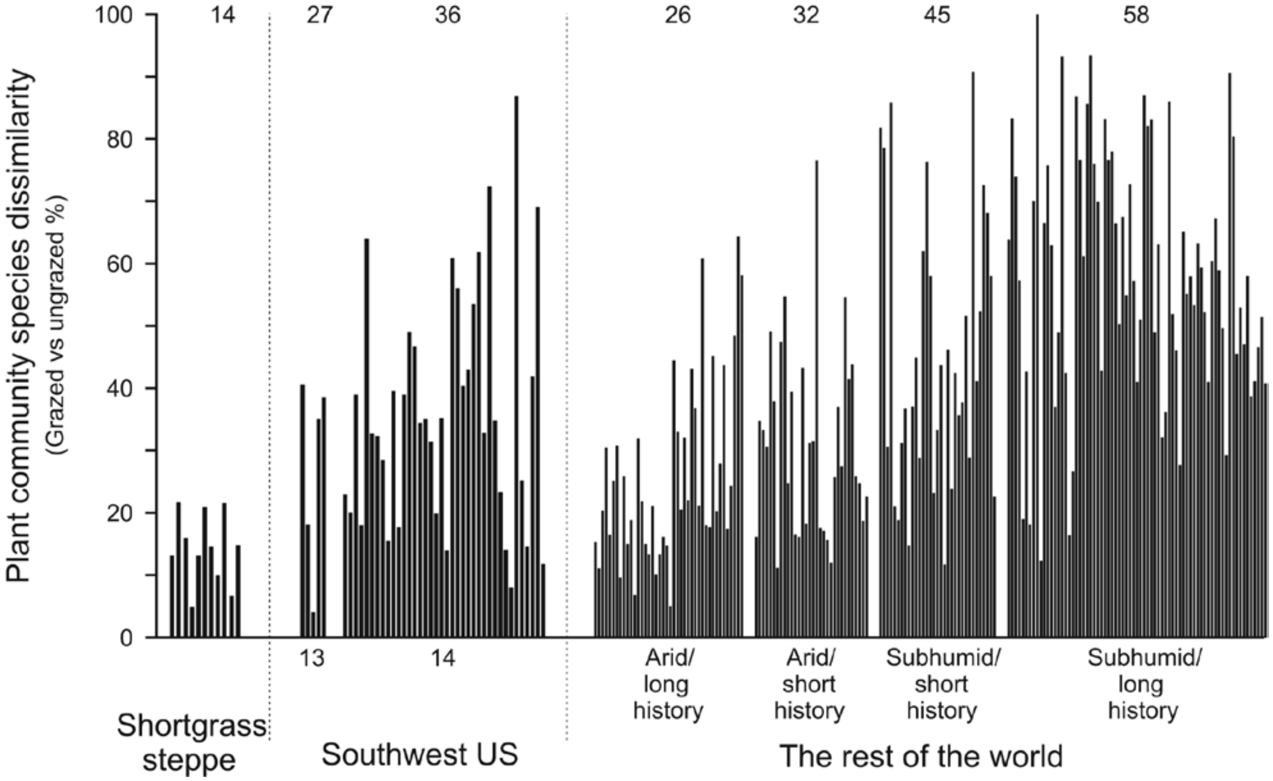

Figure 13—Plant community species dissimilarity (grazed versus ungrazed percent) for studies conducted in the shortgrass steppe with a long evolutionary history of grazing, contrasted with dissimilarity for southwestern temperate grasslands (13) with a mixed history of grazing and mesquite savanna (14) communities with a short evolutionary history of grazing, and communities from around the world based on data in Milchunas and Lauenroth (1993). Value above bars are the average for that particular community or group. Dissimilarity values calculated using the Whittaker (1952) index of community association.

region, even though precipitation/productivity and evolutionary history of grazing are more important explanatory variables across global regions (Milchunas and Lauenroth 1993).

How does the southwest compare to the highly grazing-resistant shortgrass steppe, and to the rest of the world, with respect to change in plant community species composition with grazing? The shortgrass steppe has some species in common with some southwestern grasslands, and possibly the most closely related community types would be temperate grasslands (which includes some southwestern shortgrass steppe) and mesquite savanna. In general, the shortgrass steppe is among the most grazing tolerant of plant communities in the world, averaging nearly three times less change in plant community species composition than the rest of the world (Fig. 13). Temperate grasslands and mesquite savannas of the southwest were more responsive to grazing than shortgrass steppe but were near the mean dissimilarity for semiarid/arid communities with a short history of grazing in the rest of the world. Further, the mean dissimilarity between grazed and ungrazed sites for all arid southwest communities (Fig. 3, 33 percent dissimilarity) was very close to the global mean for other semiarid/arid communities with a short evolutionary history of grazing (Fig. 4, 32 percent dissimilarity). In contrast, the mesquite savanna community type averaged 36 percent dissimilarity between grazed versus ungrazed sites, which is slightly higher than for other semiarid/arid communities with a short evolutionary history of grazing. However, precipitation for mesquite savannas averaged 374 mm/yr compared to 293 mm/yr for the other communities. On the more productive side, subhumid southwestern communities averaged 41 percent dissimilarity (Fig. 10) compared to a slightly higher 45 percent global mean for other subhumid communities with a short evolutionary history of grazing (Fig. 13). In general, southwestern communities were much more sensitive to grazing than the adjacent shortgrass steppe, but were similar in response to other semiarid/arid and subhumid communities with a short evolutionary history of grazing.

Conclusions

All ecosystems are pulsed through time by many different forces, and the living components of the system are continually reacting to those disturbances. Because of their predictability and the adaptations of the species within a community, some disturbances become an integral part of the system. These types of disturbances stabilize the system and become a part of our management of the system should the historic natural source or frequency of that disturbance be altered by human activities or encroachment. For example, the removal of fire from southeastern longleaf pine communities would mean the loss of that community. Controlled burning of some communities may not exactly replicate historical patterns and frequencies but is generally a better approximation than no fire at all. Other disturbances are not within the genetic "memory" of the systems' components and can cause changes in states that may or may not be permanent. Margalef (1968) termed these two types of pulses endogenous and exogenous disturbances. While conceptually appealing, defining what is an internal, stabilizing disturbance to a system and what is an external, destabilizing disturbance is most often very subjective. However, differentiating between these two classes of disturbance is what we attempt to do with respect to our approach to management. Usually it is not an either/or situation, but a matter of at what point does a particular disturbance become exogenous? If the disturbance is exogenous, then management strictly for conservation purposes would dictate its removal, unless the alternative results in an equal or greater exogenous disturbance. If the disturbance is exogenous and it remains, it may be considered "sustainable" only if an alternate state is not the permanent end state. If an alternate stable state is reached through deflection by some other force, then the previous reference point is no longer valid for evaluating the subject disturbance. What type of a disturbance is grazing in southwestern plant communities?

Some level and type of herbivory is endogenous to any ecosystem. However, the review of the evolutionary history of grazing of southwestern communities above indicates grazing by herds of large generalist herbivores is not an endogenous disturbance in southwestern communities, with the exception of the shortgrass steppe communities of far eastern New Mexico. That was based on geographic occupation by bison, but two lines of evidence presented in this review support that conclusion with respect to adaptations of species in the communities. First, dissimilarities in plant community species composition of ungrazed versus grazed treatments are greater for southwestern comparisons than for Great Plains comparisons (above section). This is predicted by the generalized model of Milchunas and others (1988), and differences are greater than the quantitative global comparison between semiarid systems with short versus long evolutionary histories of grazing (Milchunas and Lauenroth 1993). Second, the response of a species common to both Great Plains communities and some southwestern communities is not the same in the two locations, even under similar community productivities. Blue grama is a species that increases with grazing in abundance and composition throughout Great Plains plant communities with a long history of grazing by bison. When a component of the plant community, blue grama is also known as relatively tolerant to grazing in southwestern plant communities. However, decreases of this species were noted in 9, and increases in 8, of 23 reports in the community response sections above. The "grazing lawn" (sensu McNaughton 1984, see Milchunas and Lauenroth 1989 for shortgrass steppe) structure of very heavily grazed communities was not noted above; rather, heavy grazing was often noted to result in relatively bare, non-vegetated conditions. Short grasses commonly evade grazers more effectively than taller bunch grasses (Milchunas and Lauenroth 1993; Diaz and others 2006), particularly those with large proportions of crown organs. Blue grama and other short grasses avoid excessive losses to grazers to some extent in southwestern communities as well, but there does not appear to be a similar capacity to increase under very heavy grazing. Blue grama is a genetically diverse species, and populations in mixed-grass prairie do not respond to defoliation treatments similar to even shortgrass steppe populations (Kotanen and Bergelson 2000). Blue grama in the shortgrass steppe forms sod-like "grazing lawns" (Milchunas and Lauenroth 1989) while it appears as a bunchgrass under grazing in Arizona (J. H. Bock pers. commun.). While bison and blue grama co-occurred in eastern New Mexico, it is the edge of the range for bison, and the smaller southern bison may have been a more selective grazer than its large northern counterpart (see Evolutionary History of Grazing section). The species that provide the high degree of grazing tolerance of Great Plains communities do not appear to provide a similar degree of tolerance to southwestern ecotonal communities. To the degree that they do, the introduction of large domestic grazers into the southwest would only artificially expand the boundary of Great Plains associations. Thus, Bock and Bock (1993) questioned whether Appleton-Whittell Research Ranch site was a grama grassland, or a community created by grazing since the 1800s. Grazing by large generalist herbivores may be considered an exogenous disturbance in most southwestern communities.

Does livestock grazing lead to alternate stable states in plant communities of the southwest, or is it sustainable at some level? Although declining with periods of drought, the widespread increases in woody vegetation across many community types in the southwest, coincident with the very heavy grazing of the late 1800s and continuing through present, has for a long time been blamed on grazing by domestic livestock. From the review above, it is clear that the majority of evidence indicates that the encroachment occurs into ungrazed sites as well as grazed sites. There are four possibilities that could still invoke livestock grazing as a factor in this conversion of communities: 1) previous very heavy grazing during the unregulated grazing of the late 1800s resulted in redistribution of soil in a fashion favorable for mechanisms described in the Schlesinger and others (1990, see review above) and Whitford (2002) grazing/desertification model (this has been proposed by Grover and Musick [1990]), 2) grazing interacts with fire, favoring woody encroachment, 3) there are highly erodible areas (see discussion of Davenport and others 1998, pinyon-juniper section) where long-term studies have not been in place, where current grazing could initiate the mechanisms described in the Schlesinger and others model, and 4) grazing interacts with some other factor such as climate or rodents. All of these and some alternatives have been addressed in the review above but are briefly summarized here. The first is a remote possibility based on some relict, never-grazed geologic refuge studies reviewed above. Due to dispersal limitations of woody species, a time lag in occupation of local sites favorable and unfavorable to deep water penetration could eventually result in conditions described in the Schlesinger model. Based on exclosure studies reviewed above, current grazing does not result in dynamics described in the model in the locations studied. No management or policy options could alter outcomes if present dynamics were set in motion a century ago, and a century time-lag in dispersal would not seem realistic. Second, reductions in fuel loads due to removal by grazers, and fire suppression, would influence results of exclosure studies because both grazed and ungrazed treatments would be affected by the absence of fire. Very large ungrazed areas adjacent to grazed areas are needed to adequately test this possibility (Bock and Bock 1993). In some situations, however, a fire return interval shorter than the predicted natural interval would be necessary to cause enough mortality to prevent encroachment (see Mesquite Savanna Conversion to Chihuahuan Desert section). While a more frequent fire return interval in some southwestern communities may more closely mimic the endogenous fire disturbance, this may be a separate issue to the shrub encroachment one. Third, highly erodible soils are always more prone to irreversible vegetation change due to grazing. It is possible that the long-term study sites and the US/Mexican border analyses reviewed above were not in highly erodible areas. This is an area of comparison that would also make an interesting test of conditions necessary to initiate mechanisms in the Schlesinger and others model. However, given the number of study sites reviewed above, it would seem unlikely for this to on its own explain the extent of conversion that has been reported. Fourth, grazing can interact with other factors, and both climate and small mammals have been implicated as a potential factor in vegetation change in the southwest. Grover and Musick (1990) argue that all factors (grazing, fire, small mammals, and climate) interact complexly with positive feedbacks that can have long time-lags in producing the shift to shrublands. With respect to conversion of community types, however, changes in climate do not differ across fenceline comparisons. Further, climate interactions with livestock grazing and native herbivores can, in at least some situations, mitigate the effects of climate as a cause of shrub expansion (Curtin and Brown 2001, and see review above). There is an increasing amount of evidence implicating changes in the seasonal proportions of precipitation as a primary cause of community change in the southwest (reviewed above). Why only in the southwest, and what are the implications for assessing the impacts of livestock grazing in the southwest?

There are two reasons why the seasonal distribution of precipitation may affect community conversion in the southwest. Semiarid and arid Mediterranean plant communities have climates where precipitation falls in greater proportions in the winter and are characterized by a dominance by shrubs and annuals. In dry regions, deep rooted shrubs are favored by deep storage of winter precipitation. In contrast, relatively shallow rooted grasses are favored by precipitation falling when they are active and capable of intercepting the moisture. Annuals are capable of rapid utilization of moisture in spring, yet they do not require a season-long supply for survival, and remain as seed through dry summer periods. The southwestern United States is not a true Mediterranean climate, but much of the area does receive a relatively more equally proportional amount of winter/summer precipitation than a strictly continental climate. A second factor in the distribution of southwestern communities is the relatively diverse local topography, which plays an important role in the proximity of shrubland-grassland communities. Given these two factors, it would be easy to propose a teeter-totter hypothesis of expansion or contraction of shrub-grassland interfaces with only minor changes in the seasonal distribution of precipitation. Soil texture and rainfall event size distributions, as they influence the depth of percolation of soil moisture, could create the patchy, unpredictable spatial pattern of woody expansion that has been reported. Past very heavy grazing and current grazing of highly erodible soils could also be a factor in the spatial distribution of community conversion. A complication with this hypothesis is that shrub expansion also occurs in many parts of Texas (Archer 1994), where the climate is relatively more continental that it is in the far west. No one factor alone appears to adequately explain the complex spatial pattern of community change throughout this region, but progress has been made in correlating local changes to climate. Regardless of changes in community types, seasonal and annual fluctuations in weather often have a greater influence on plant community species composition than do different grazing regimes. Based on long-term studies, annual fluctuations in weather have much larger effects on plant community species composition and production than do extreme differences in grazing pressures in shortgrass steppe of the Great Plains (Klipple and Costello 1960; Milchunas and others 1994). It is the author's perception that the temporal variability in plant community species composition due to weather is much greater in southwestern than in Great Plains communities, based on long-term data sets such as those reported above from sites such as the Jornada and Santa Rita compared to long-term sites in the Great Plains such as the Central Plains Experimental Range. This may be due to the large influence in this area of El Niño and La Niña conditions and to greater orographic effects producing annual to decadal oscillations in amounts and seasonality of precipitation (Neilson 1986; Swetnam and Betancourt 1998), but the high temporal variability points to a particularly important need for long-term studies in this region for understanding the dynamics of vegetation within and among communities.

The implications of climate change/community conversion in assessing the effects of livestock grazing on plant communities are twofold. First, a different end-point for "recovery" with protection from grazing would need to be recognized; in other words, the previous reference point is no longer valid for evaluating the subject disturbance. Exclosures, and preferably large areas of ungrazed controls, are necessary to evaluate grazing effects. Grazing is simply overlain on changing communities. While the woody/grassland conversion has captured much attention over the past decade, other understory changes are also ongoing, as described in the review above and emphasized by Allred (1996). Some of these are grazing related and independent of community conversion, and others are overstory controlled. Second, if grazing is not related to change to woody communities, this does not at all preclude grazing-related alternate stable states. Assessing whether this occurs is difficult when the reference state is changing. Do the differences between old exclosures and new exclosures converge? The uniquely large difference observed for natural geologic refuges never grazed by large herbivores and more recent human-made exclosures shown in Fig. 11 could be due to different abiotic conditions associated with the refuges or to divergent trajectories associated with grazing in the distant past (Milchunas and Noy-Meir 2004). Does current grazing result in the shrub state as predicted by the Schlesinger and others model even when winter precipitation is experimentally manipulated to disfavor shrubs, or when rain-event size-class distributions change? These types of questions would need to be addressed to answer questions concerning grazing-related alternate states if other factors are producing a changing reference state. This would appear difficult given the fact that there are few or no controlled studies of the effects of grazing for many of the broad community types covered above. Often the goal simply becomes managing to best maintain a resemblance to previous conditions. The even greater changes that may come with predicted future climate change will possibly push management decisions beyond even that baseline. Waiting for protected areas to return to some initial condition to demonstrate recovery is impractical/will never happen if the reference point is changing. We need to develop alternate bases for management guidelines.

Intense non-selective grazing is an exogenous disturbance in most southwestern communities. Changes in plant species composition between grazed and ungrazed communities are greater than in Great Plains grasslands, even when grazing at "moderate" levels is at a lower level of consumption than that considered "moderate" in the Great Plains. Grazing in the Great Plains is an endogenous disturbance to the system, both in terms of the plant community species composition (Milchunas and others 1989) and resistance to exotic invasion (Milchunas and others 1992) and in terms of endemic shortgrass fauna (Milchunas and others 1998). While grazing by cows may not be exactly like bison, they are in many ways similar in function and act as surrogates. From a conservation standpoint then, it would simply appear that there are places where grazing by livestock should be encouraged in the absence of the native grazer, and other places where livestock grazing should be discouraged or at least cautiously managed because similar grazers were not present historically. Things are never that simple, even if viewed from a purely biological perspective. The subdivision of large ranches into small acreage ranchettes throughout the western United States may be one of the largest threats to biodiversity conservation due to the land-use change it represents as well as effects through fragmentation (Curtin and others 2002). While information is still too scarce to fully evaluate the full extent of the tradeoffs, the elimination of fire, introduction of house pets, livestock pets, and exotic landscaping are just a few to consider. The fate of private lands will often closely be coupled to use of public lands, since many ranchers economically depend on grazing of public lands for their existence (Raish and McSweeney 2003). The review above clearly shows weaknesses in even basic understanding of the response of many major plant community types to grazing. For other community types, there is often contradictory results, suggesting there are factors responsible for differential sensitivities that we do not understand. However, possibly more critical at this time is the need for a consideration and an understanding of the alternatives if livestock are removed.

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Appendix 1. Synonyms for the plant community classification system of Moir (2000).

1. **Alpine tundra—**synonyms: Rocky Mountain alpine tundra, krummholz.

2. **Boreal forest—**synonyms: Engelmann spruce [*Picea engelmannii*] province, spruce-fir forest, taiga, subalpine forest, bristlecone pine woodland, Petran subalpine coniferous forest, aspen.

3. **Mixed conifer forest (C)—**synonyms: upper montane forests, white fir/douglas-fir, pine/douglas-fir (Küchler 1964), Petran conifer forest, aspen.

4. **Mixed conifer forest (M)—**synonyms: Madrean montane forest.

5. **Ponderosa pine forest—**synonyms: ponderosa pine [*Pinus ponderosa*] province, transition zone (Merriam), lower montane forest.

6. **Madrean pine forest—**synonyms: Chihuahuan pine [*Pinus leiophylla*] Series, Engelmann spruce [*P. engelmannii*] Series (Layser and Schubert 1979), Arizona pine forest (Küchler 1964), Pine-oak woodland (Marshall 1957), Madrean montane conifer forests, aspen (rare).

7. **Pinyon-juniper woodland—**synonyms: Pygmy woodland, coniferous woodland, juniper-pinyon woodland, Upper Sonoran Zone (Merriam), Mexican pine [*Pinus cembroides*] province (Daubenmire 1978), Juniper savanna (Dick-Peddie 1993).

8. **Madrean woodland—**synonyms: encinal, open encinal, oak-juniper woodland, pine-oak woodland, cypress woodland on mountain slopes.
   1. Gray Oak (*Quercus grisea*) woodland.
   2. Arizona white oak (*Quercus arizonica*) woodland.
   3. Emory oak (*Quercus emoryi*) woodland and savanna.

9. **Great Basin juniper-sagebrush savanna—**synonyms: Juniper steppe woodland, juniper savanna, Great Basin conifer woodland - juniper series.

10. **Interior chaparral—**synonyms: chaparral, evergreen chaparral, turbinella oak chaparral, turbinella oak scrub, oakbrush, Great Basin montane scrub.

11. **Subalpine grassland—**synonyms: Rocky Mountain montane grassland, forest steppe, high elevation parks, Thurber fescue meadows, subalpine meadows, mountain bunchgrass - Thurber fescue.

12. **Montane meadow—**synonyms: montane parks, forest steppe, mountain meadow, meadow, grasslands associated with ponderosa pine.

13. **Temperate grassland—**synonyms: shortgrass prairie, shortgrass steppe (Lauenroth and Milchunas 1991), grama-buffalo grass (Küchler 1964), mixed prairie, grama-galleta steppe (Küchler 1964), Galleta-three awn shrubsteppe (Küchler 1964), foothills grassland, plains-mesa grassland, tallgrass prairie (rare in the SW), mid-grass prairie, cold temperate grassland.

14. **Mesquite savanna—**synonyms: desert grassland, semi-desert grassland, mesquite-acacia savanna, grama-tobosa shrubsteppe (Küchler 1964), Upper Sonoran (Merriam), Trans-Pecos shrub savanna (Küchler 1964), warm temperate grassland.

15. **Great Basin sagebrush shrubsteppe—**synonyms: Great Basin sagebrush, sagebrush-steppe (Küchler 1964), Western intermountain sagebrush steppe, Great Basin desert grassland.

16. **Shinnery oak/sand sage—**synonyms: Plains-Mesa sand scrub, shinnery scrub, shin-oak scrub.

17. **Great Basin temperate desert—**synonyms: cold temperate desert, Colorado Plateau semidesert, Great Basin desert scrub.

18. Sonoran/Mohavian deserts—synonyms: Lower Sonoran Zone (Merriam), hot desert, creosote bush [*Larrea divaricata*] province of Daubenmire 1968.

19. Chihuahuan desert—synonyms: Lower Sonoran Zone (Merriam), hot desert, creosote bush [*Larrea divaricata*] province of Daubenmire 1968.

20. Narrowleaf cottonwood forest—synonyms: montane Cottonwood-Willow.

21. Broadleaf cottonwood forest (C)—synonyms: cold temperate cottonwood forest, flood plain-plains riparian forest, lowland plains broadleaf deciduous forest, Great Basin broadleaf deciduous forest, gallery forest, cottonwood-willow forest.

22. Broadleaf cottonwood forest (M)—synonyms: warm-temperate riparian forest, lowland interior southwestern broadleaf deciduous forest, Sycamore forest, Cottonwood forest, bosques, mesquite bosques, saltcedar, tamarisk, floodplains-plains riparian forest, Arizona walnut woodland.

23. Riparian scrub—synonyms: cold-temperate and Arctic-boreal riparian scrub, montane scrub, willow-alder shrub riparian, coyote willow shrub riparian.

24. Dry washes—synonyms: arroyo riparian, riparian scrub, desert riparian washes.

25. Wetlands—synonyms: wet meadows, herbaceous wet meadows, emergent wetlands, marshes, cienegas, strands, seeps, bogs (rare in the Southwest), playas.

Appendix 2. List of scientific and common names of plants used in text.

Acacia	*Acacia* spp.	
Agave	*Agave* spp.	
Agoseris	*Agoseris* spp.	
Alderleaf mountain mahogany	*Cercocarpus montanus*	Raf.
Alkali sacaton	*Sporobolus airoides*	(Torr.) Torr.
Alligator juniper	*Juniperus deppeana*	Steud.
American bulrush	*Scirpus americanus*	Pers.
American tarwort	*Flourensia cernua*	DC.
Annual dropseed	*Muhlenbergia minutissima*	(Steud.) Swallen
Antelope bitterbrush	*Purshia tridentata*	(Pursh) DC.
Apache pine	*Pinus engelmannii*	Carr.
Apache plume	*Fallugia paradoxa*	(Don) Endl. ex Torr
Aparejograss	*Muhlenbergia utilis*	(Torr.) A.S. Hitchc.
Arizona alder	*Alnus oblongifolia*	Torr.
Arizona cottongrass	*Trichachne california*	(Benth.) Chase
Arizona cottontop	*Digitaria californica*	(Benth.) Henr.
Arizona cypress	*Cupressus arizonica*	Greene
Arizona fescue	*Festuca arizonica*	Vasey
Arizona pine	*Pinus arizonica*	Engelm.
Arizona ponderosa	*Pinus ponderosa* var. *arizonica*	(Engelm.) Shaw
Arizona sycamore	*Platanus wrightii*	Wats.
Arizona threeawn	*Aristida purpurea*	Nutt.
Arizona walnut	*Juglans major*	(Torr.) Heller
Arizona white oak	*Quercus arizonica*	Sarg.
Arizona willow	*Salix arizonica*	Dorn.
Arkansas rose	*Rosa arkansana*	Poter
Arroyo willow	*Salix lasiolepis*	Benth.
Aspen	*Populus tremuloides*	Michx.
Banana yucca	*Yucca baccata*	Torr.
Bearberry	*Arctistaphylos uva-ursi*	(L.) Spreng.
Beautiful fleabane	*Erigeron formosissums*	Greene
Bebb willow	*Salix bebbiana*	Sarg.
Berlandier's wolfberry	*Lycium berlandieri*	Dunal
Big sagebrush	*Artemisia tridentata*	Nutt.
Bigelow sage	*Artemisia bigelovii*	Gray
Bigtooth maple	*Acer grandidentatum*	Nutt.
Bindweed spp.	*Calystegia* spp.	
Black dropseed	*Sporobolus interruptus*	Vasey
Black grama	*Bouteloua eriopoda*	Torr.
Black sagebrush	*Artemisia nova*	A. Nels.
Blackbrush	*Coleogyne ramosissima*	Torr.
Black willow	*Salix nigra*	Marsh.
Blue grama	*Bouteloua gracilis*	(H.B.K.) Lag.
Blue paloverde	*Cercidium floridum*	Benth. ex Gray

Blue spruce	*Picea pungens*	Engelm.
Blueburr stickseed	*Lappula redowskii*	(Hornem) Greene
Border pinyon	*Pinus discolor*	Bailey & Hawksworth
Bottlebrush squirreltail	*Sitanion hystrix*	(Nutt.) J.G. Smith
Boxelder	*Acer negundo*	(L.)
Bristlecone pine	*Pinus aristata*	Engelm.
Brittle pricklypear	*Opuntia fragilis*	(Nutt.) Haw.
Broadleaf cattail	*Typha latifolia*	L.
Bromegrass	*Bromus* spp.	
Broom snakeweed	*Gutierrezia sarothrae*	(Pursh) Britt. & Rusby.
Buffalograss	*Buchloe dactyloides*	(Nutt.) Engelm.
Bull muhly	*Muhlenbergia emersleyi*	Vasey
Burrobush	*Ambrosia dumosa,* *Franseria dumosa*	(Gray) Payne
Burrograss	*Scleropogon brevifolius*	Phil.
Burroweed	*Isocoma (Haplopappus) tenuisecta*	Greene
Bush muhly	*Muhlenbergia porteri*	Scribn.
Cactus apple	*Opuntia engelmannii*	Salm-Dyck
California pine	*Pinus californiarum*	D.K. Bailey
Cane beardgrass	*Amphilophis barbinodis*	(Lag.) Nash
Cane bluestem	*Bothriochloa barbinodis*	(Lag.) Herter
Candy barrel cactus	*Ferocactus wislizeni*	(Engelm.) Britt. & Rose
Canyon grape	*Vitis arizonica*	Engelm.
Carruther's sagewort	*Artemisia carruthii*	Wood ex Carruth.
Catclaw acacia	*Acacia greggii*	Gray
Catclaw mimosa	*Mimosa biuncifera*	Benth.
	Mimosa aculeaticarpa	Ortega var. *biuncifera* (Benth.) Barneby
Ceanothus	*Ceanothus* spp.	
Cheatgrass	*Bromus tectorum*	L.
Chihuahuan pine	*Pinus leiophylla*	Schiede & Deppe
Chokecherry	*Prunus virginiana*	L.
Cholla spp.	*Opuntia* spp.	
Columbia needlegrass	*Achnatherum nelsonii*	(Scribn.) Barkworth
Common dandelion	*Taraxacum officinale*	Weber ex Wiggers
Common sotol	*Dasylirion wheeleri*	S. Wats.
Common wolfstail	*Lycurus phleoides*	Kunth
Condalia spp.	*Condalia* spp.	
Cooley's bundleflower	*Desmanthus cooleyi*	(Eat.) Trel.
Creeping muhly	*Muhlenbergia repens*	(Presl) Hitchc.
Creosote-bush	*Larrea tridentata*	(DC.) Coville
	Larrea divaricata	auct. Non Cav.
Crested wheatgrass	*Agropyron desertorumq*	(Fisch.) Schult.
Crucifixion thorn	*Canotia holacantha*	Torr.
Curly mesquite	*Hilaria belangeri*	(Steud.) Nash
Deergrass	*Muhlenbergia rigens*	(Benth.) Hitchc.
Deer-vetch	*Lotus rigidus*	(Benth.) Greene
Dense ayenia	*Ayenia microphylla*	Gray
Desert ceanothus	*Ceanothus greggii*	Gray
Desert false indigo	*Amorpha fruticosa*	L.
Desert false-yarrow	*Chaenactis stevioides*	Hook. & Arn.

Desert globemallow	*Sphaeralcea ambigua*	Gray
Desert hackberry	*Celtis pallida*	Torr.
Desert ironwood	*Olneya tesota*	Gray
Desert tansy mustard	*Descurainia obtusa*	(Greene) O. E. Schulz
Desert willow	*Chilopsis linearis*	(Cav.) Sweet
Desert zinnia	*Zinnia pumila*	Gray
Desert-thorn	*Lycium* spp.	L.
Devil cholla	*Opuntia stanyli* var. *stanyli*	Engelm.
Douglas-fir	*Pseudotsuga menziesii*	(Mirbel) Franco
Downy chess	*Bromus tectorum*	L.
Drummond's willow	*Salix subcaerulea*	Piper
	Salix drummondiana	Barratt ex Hook.
Eastern Mojave buckwheat	*Eriogonum fasciculatum*	Benth.
Emory oak	*Quercus emoryi*	Torr.
Emory's baccharis	*Baccharis emoryi*	Gray
Engelmann pricklypear	*Opuntia phaeacantha*	Engelm.
Engelmann spruce	*Picea engelmannii*	Perry ex Engelm.
Evergreen sumac	*Rhus choriophylla*	Wood & Standl.
	Rhus virens	Lindheimer ex Gray var cariophylla (Wood & Standl.) L. Benson
Fairyduster	*Calliandra eriophylla*	Benth.
False buffalo grass	*Munroa squarrosa*	(Nutt.) Torr.
False mesquite	*Calliandra eriophylla*	Benth.
Fendler sandwort	*Arenaria fendleri*	Gray
Fendler threeawn	*Aristida fendleriana*	Steud.
Fendler's ceanothus	*Ceanothus fendleri*	Gray
Flatsedge	*Cyperus* spp.	
Fluffgrass	*Tridens pulchellus*	(H.B.K.) Hitchc.
Fluffgrass	*Erioneuron pulchella*	H.B.K.
Fourwing saltbrush	*Atriplex canescens*	(Pursh) Nutt.
Fremont cottonwood	*Populus fremontii*	Wats.
Fremont geranium	*Geranium caespitosum* var. *fremontii*	(Torr. ex Gray) Dorn
Fringed sagebrush	*Artemisia frigida*	Willd.
Galleta	*Hilaria jamesii*	(Torr.) Benth.
Gambel oak	*Quercus gambelii*	Nutt.
Gambel x Scrub live oak	*Quercus x pauciloba*	Rydb.
Garrya	*Garrya* spp.	
Goldenhills	*Encelia farinosa*	Gray ex Torr
Goodding's willow	*Salix gooddingii*	Ball
Goosefoot	*Chenopodium* spp.	
Graham's nipple cactus	*Mammillaria microcarpa*	Engelm.
Grama	*Bouteloua* spp.	
Gray oak	*Quercus grisea*	Liebm.
Green ash	*Fraxinus pennsylvanica*	Marsh.
Green joint-fir	*Ephedra viridis*	(Cutler) L. Benson
Green Sprangletop	*Leptochloa dubia*	(Kunth) Nees
Groundsel	*Packera* spp.	
Guajilla	*Calliandra humilis* var. *humilis*	Benth.
Hairy false goldenaster	*Heterotheca villosa*	(Pursh) Shinners
Hairy grama	*Bouteloua hirsuta*	Lag.

Hairy mountain-mahogany	*Cercocarpus montanus* var. *paucidentatus*	(Wats.) Martin
Havard oak	*Quercus havardii*	Rydb.
Hawk's eye	*Euryops multifidus* or	(Thunb.) DC.
	Euryops subcarnosus	DC. ssp. vulgaris B. Nord
Hedgehog cactus	*Echinocereus* spp.	
Hoary tansyaster	*Machaeranthera pulverulehta*	(Nutt.) Greene
Honey mesquite	*Prosopis glandulosa*	Torr.
Honey mesquite	*Prosopis juliflora* var. *glandulosa*	(Torr.) Cockerell
Horse cinquefoil	*Potentilla hippiana*	Lehm.
Hymenoxys	*Hymenoxys* spp.	
Idaho fescue	*Festuca idahoensis*	Elmer
Indian ricegrass	*Achnatherum (Oryzopsis) hymenoides*	(Roemer & JA Schultes) Barkworth
James' galleta	*Hilaria jamesii*	(Torr.) Benth.
Joint-fir	*Ephedra* spp.	
Joshua tree	*Yucca brevifolia*	Engelm.
Jumping cholla	*Opuntia fulgida*	Engelm.
Junegrass	*Koeleria cristata*	(L.) Pers.
Juniper	*Juniperus* spp.	
Kentucky bluegrass	*Poa pratensis*	L.
Lacy tansyaster	*Haplopappus spinulosus*	(Pursh) DC.
Leatherweed	*Croton pottsii*	(Klotzsch) Muell.-Arg.
Lehmann lovegrass	*Eragrostis lehmanniana*	Nees
Letterman needlegrass	*Stipa lettermanii*	Vasey
Limber pine	*Pinus flexilis*	James
Little bluestem	*Schzachyrium scoparium*	(Michx.) Nash
Littleleaf ratany	*Krameria parvifolia*	Benth.
Littleleaf sumac	*Rhus microphylla*	Engelm. ex Gray
Longleaf jointfir	*Ephedra trifurca*	Torr. ex S. Wats
Longtongue muhly	*Muhlenbergia longiligula*	Hitchc.
Longtongue muttongrass	*Poa longiligula*	Scribn. & Williams
Low woollygrass	*Dasyochloa pulchella*	(Kunth) Willd.
Lupines	*Lupinus* spp.	
Mariola	*Parthenium incanum*	Kunth
Mat muhly	*Muhlenbergia arsenei*	Hitchc.
Menodora	*Menodora* spp.	
Mesa dropseed	*Sprobolus flexuosus*	(Thurb. ex Vassey) Rydb.
Mesa threeawn	*Aristida hamulosa*	Henr.
Mesquite	*Prosopis* spp.	
Mesquitilla	*Calliandra eriophylla*	Benth.
Mexican blue oak	*Quercus oblongifolia*	Torr.
Mexican pinyon	*Pinus cembroides*	Zucc.
Mimosa	*Mimosa* spp.	
Mountain muhly	*Muhlenbergia montana*	(Nutt.) Hitchc.
Mountain snowberry	*Symphoricarops oreophilus*	Gray
Mountain-mahogany	*Cercocarpus* spp.	Kunth
Mule's fat	*Baccharis salicifolia*	(Ruiz & Pavon) Pers.
Mutton bluegrass	*Poa fendleriana*	(Steud.) Vasey

Muttongrass	*Poa fendleriana*	(Steud.) Vasey
Narrowleaf cottonwood	*Populus angustifolia*	James
Narrowleaf willow	*Salix exigua*	Nutt.
Needle and thread grass	*Stipa comata*	Trin. & Rupr.
Needlegrasses	*Stipa* spp.	
Netleaf oak	*Quercus rugosa*	Nee.
New Mexico feathergrass	*Hesperostipa neomexicana*	(Thurb. ex Coult.) Barkworth
Nickleaf milkvetch	*Astragalus goniatus*	Nutt.
Nodding brome	*Bromus anomalus*	Rupr.ex Fourn.
Nodding wild buckwheat	*Erigonum cernuum*	Nutt.
Ocotillo	*Fouquieria splendens*	Engelm.
Oneseed juniper	*Juniperus monosperma*	(Engelm.) Sarg.
Orange sneezeweed	*Helenium hoopesii*	Gray
Orcutt’s threeawn	*Aristida orcuttiana*	(Vasey) Allred & Valdes-Reyna
Owl’s-claws	*Dugaldia hoopesii*	(Gray) Bierner
Pacific willow	*Salix lasiandra*	Benth.
Pale evening-primrose	*Oenothera pallida*	(Nutt.) Munz & Klein
Pale spikerush	*Eleocharis macrostachya*	Britt.
Paperflower spp	*Psilostrophe* spp.	
Park willow	*Salix monticola*	Bebb
Parry’s agave	*Agave parryi*	Engelm.
Parry’s oatgrass	*Danthonia parryi*	Scribn.
Peachleaf willow	*Salix amygdaloides*	Anderss.
Pennsylvania cinquefoil	*Potentilla pennsylvanica*	L.
Pine dropseed	*Blepharoneuron trichcolepis*	(Torr.) Nash
Pingue	*Actinea richardsonii*	(Hooker) Kuntze
Pingue rubberweed	*Hymenoxys richardsonii*	(Hook.) Cockerell
Pinyon ricegrass	*Piptochaetium fimbriatum*	(H.B.K.) Hitchc.
Plains beardgrass	*Andropogon hirtiflorus* var. *feensis*	(Fourn.) Hack.
Plains hiddenflower	*Cryptantha crassisepala*	(Torr. & Gray) Greene
Plains lovegrass	*Eragrostis intermedia*	Hitchc.
Plains prickly pear	*Opuntia polyacantha*	(Haw.)
Plantain	*Plantago* spp.	
Pointleaf manzanita	*Arctostaphylos pungens*	Kunth
Ponderosa pine	*Pinus ponderosa*	Laws.
Poverty threeawns	*Aristida divaricata*	Humb. & Bonpl.
Prairie clover spp.	*Dalea* spp.	L.
Prairie coneflower	*Ratibida columnaris*	(Sims.)
Prairie junegrass	*Koeleria macrantha*	(Ledeb.) Schultes
Praire pepperweed	*Lepidium densiflorum*	Schrad.
Prickly gilia	*Leptodactylon pungens*	(Torr.) Torr. ex Nutt.
Pricklypear	*Opuntia* spp.	
Pringle manzanita	*Arctostaphylos pringlei*	Parry
Purple picklypear	*Opuntia violacea*	Engelm.
Purple three-awn	*Aristida purpurea*	Nutt.
Pussytoes	*Antennaria* spp.	

Rabbitbrush	*Chrysothamnuns* spp.	
Rayless goldenhead	*Acamptopappus sphaerocephalus*	(Harvey & Gray ex Gray) Gray
Rayless tansyaster	*Machaeranthera grindelioides*	(Nutt.) Shinners
Red barberry	*Berberis haematocarpa*	Woot.
Red brome	*Bromus rubens*	L.
Red grama	*Bouteloua trifida*	Thurb.
Redstem stork's bill	*Erodium cicutarium*	(L.) L'Hér. ex Ait.
Red threeawn	*Aristida longiseta*	Steud.
Redberry buckthorn	*Rhamnus crocea*	Nutt.
Redberry juniper	*Juniperus erythrocarpa*	Cory
Redosier dogwood	*Cornus stolonifera*	Michx.
Redtop	*Agrostis alba*	L.
Reverchon three-awn	*Aristida purpurea* var. *nealleyi*	Nutt.
Ring muhly, ringgrass	*Muhlenbergia torreyi*	(Kunth.) Hitchc. ex Bush
Rio Grande saddlebush	*Mortonia scabrella*	Gray
Rocky Mountain iris	*Iris missouriensis*	Nutt.
Rocky Mountain juniper	*Juniperus scopulorum*	Sarg.
Rocky Mountain maple	*Acer glabrum*	Torr.
Rose pussytoes	*Antennaria rosea*	Greene
Rosy gilia	*Gilia sinuata*	Dougl.
Rothrock grama	*Bouteloua rothrocki*	Vasey
Rough menodora	*Menodora scabra*	Gray
Rubber rabbitbrush	*Ericameria nauseosa*	(Pallas es Pursh) Nesom & Baird
Rush	*Juncus* spp.	
Russian olive	*Elaeagnus angustifolia*	L.
Russian thistle	*Salsola iberica*	Semmem & Pau
Sacahuista	*Nolina microcarpa*	Wats.
Sagebrush	*Artemisia* spp.	
Saguaro	*Carnegia gigantea*	(Engelm.) Britt. & Rose
Saltbush	*Atriplex* spp.	
Salt cedar	*Tamarix chinensis*	Lour.
Sand bluestem	*Andropogon hallii*	Hack.
Sand dropseed	*Sporobolus cryptandrus*	(Torr.) Gray
Sandhill muhly	*Muhlenbergia pungens*	Thrub.
Sand sagebrush	*Artemisia filifolia*	Torr.
Sand wort	*Arenaria* spp.	
Sangre de Cristo	*Jatropha caraiophylla*	(Torr.) Muell.-Arg.
Santa Rita threeawn	*Aristida californica* var. *glabrata*	Vasey
Scarlet globemallow	*Sphaeralcea coccinea*	(Pursh)
Schott's yucca	*Yucca schottii*	Engelm.
Screwleaf muhly	*Muhlenbergia virescens*	(H.B.K.) Kunth
Scrub oak	*Quercus turbinella*	Greene
Sedge	*Carex* spp.	
Sego lily	*Calochortus nuttallii*	Torr. & Gray
Shadscale saltbrush	*Atriplex confertifolia*	(Torr. & Frem.) Wats.
Sheep fescue	*Festuca ovina*	L.
Shrubby buckwheat	*Eriogonum fasciculatum*	Benth.
Shrubby false mallow	*Malvastrum bucuspidatum*	(S. Wats.) Rose
Sideoats grama	*Bouteloua curtipendula*	(Michx.) Torr.

Silver brush spp.	*Ditaris* spp.	
Silver dwarf morning-glory	*Evolvulus sericeus*	Sw.
Silverleaf oak	*Quercus hypoleucoides*	Camus
Silvery globe mallow	*Sphaeralcea leptophylla*	(Gray) Rydb.
Singlewhorl burrobrush	*Hymenoclea monogyra*	Torr. & Gray ex Gray
Six-weeks fescue	*Festuca octoflora*	(Walt.) Rydb.
Skunkbush sumac	*Rhus trilobata*	Nutt.
Slender janunsia	*Janusia gracilis*	Gray
Slender gilia	*Gilia leptomeria*	Gray
Slender grama	*Bouteloua filiformis*	(Fourn.) Griffiths
Slender wheatgrass	*Agropyron trachycaulum*	(Link) Malte
Slenderbush eriogonum	*Eriogonum microthecum*	Hook.
Slim tridens	*Tridens muticus*	(Torr.) Nash
Small wirelettuce	*Stephanomeria exigua*	Nutt.
Snakeweed	*Gutierrezia* spp.	
Soapberry	*Sapindus saponaria*	L.
Soaptree yucca	*Yucca elata*	(Engelm.) Engelm.
Soapweed yucca	*Yucca glauca*	Nutt.
Somoran scrub oak	*Quercus turbinella*	Greene
Southwestern white pine	*Pinus strobiformis*	Engelm.
Spider grass	*Aristida ternipes*	Cav.
Spike dropseed	*Sporobolus cryptandrus*	A. S. Hitchc.
Spike muhly	*Muhlenbergia wrightii*	Vasey
Spiny hackberry	*Celtis pallida*	Torr.
Splitleaf brickellbush	*Brickellia laciniata*	Gray
Sprucetop grama	*Bouteloua chondrosioides*	(Kunth) Benth. ex Wats.
Squirreltail	*Elymus elymoides (Sitanion hystrix)*	(Raf.) Swezey
Sticky snakeweed	*Gutierrezia Texana* var. *glutinosa*	(S. Schauer) M.A. Lane
Subalpine fir	*Abies lasiocarpa*	(Hook.) Nutt.
Sugar sumac	*Rhus ovata*	Wats.
Sun sedge	*Carex inops heliophila*	(Mackenzie) Crins
Sunflower	*Helianthus* sp.	
Sweetbush	*Bebbia juncea*	(Benth.) Greene
Sweet resin bush	*Euryops multifidus* or	(Thunb.) DC.
	Euryops subcarnosus	DC. ssp. vulgaris B. Nord
Tamarick	*Tamarix* spp.	
Tanglehead	*Heteropogon conlorius*	(L.) Richt.
Tarbush	*Flourensia* spp.	
Teddybear cholla	*Opuntia bigelovii*	Engelm.
Texas beardgrass	*Andropogon cirratus*	Hack.
Thimbleberry	*Rubus parviflorus*	Nutt.
Thin paspalum	*Paspalum stramineum*	Michx.
Thinleaf alder	*Alnus tenuifolia*	(Nutt.) Breitung
Threadleaf ragwort	*Senecio longilobus*	Benth.
Threeawn	*Aristida* spp.	
Thurber's fescue	*Festuca thurberi*	Vasey
Timothy	*Pheum* spp.	
Tobosa grass	*Hilaria mutica*	(Buckl.) Benth.
Torrey joint-fir	*Ephedra torreyana*	S. Wats.
Toumey oak	*Quercus toumeyi*	Sarg.
Trailing fleabane	*Erigeron flagellaris*	Gray

Triangle burr ragweed	*Ambrosia deltoidea*	(Torr.) Payne
Trisetum	*Trisetum* spp.	
Tulip pricklypear	*Opuntia phaeacantha*	Engelm.
Tumblegrass	*Schedonnardus paniculatus*	(Nutt.) Trel.
Turbinella oak	*Quercus turbinella*	Greene
Turpentine bush	*Ericameria laricifolia*	(Gray) Shinners
Twoneedle pinyon	*Pinus edulis*	Engelm.
Utah juniper	*Juniperus osteosperma*	(Torr.) Little
Velvet mesquite	*Prosopis velutina*	Woot.
Velvetpod mimosa	*Mimosa dysocarpa*	Benth.
Vine mesquite	*Panicum obtusum*	Kunth
Walkingstick cactus	*Opuntia spinosior*	(Engelm.) Toumey
Wavyleaf oak turbinella	*Quercus x pauciloba*	Rydb. (pro sp.) gambelii ×
Western thimbleberry	*Rubus parviflorus*	Nutt.
Western wheatgrass	*Agropyron smithii*	Rydb.
Western wheatgrass	*Pascopyrum smithii*	(Rydb.) A. Love
Western yarrow	*Achillea millefolium occidentalis*	DC.
Whiplash pappusgrass	*Pappophorum vaginatum*	Buckl.
White-ball acacia	*Acacia angustissima*	Torr. & Gray
White bursage	*Ambrosia dumosa*	(Gray) Payne
White clover	*Melilotus alba*	Desr.
White fir	*Abies concolor*	(Gord. & Glend.) Lindl. ex Hildebr.
White ratany	*Krameria grayi*	Rose & Painter
Whitethorn acacia	*Acacia constricta*	Benth.
Winterfat	*Krascheninnikovia lanata*	(Pursh) Meeuse & Smit
Wolftail	*Lycurus phleoides*	H.B.K.
Woody crinklemat	*Tiquilia canescens*	(D.C.) A. Richards.
Woolly cinquefoil	*Potentilla hippiana*	Lehm.
Wooly bunchgrass	*Elyonurus barbiculmis*	Hack.
Wooly Indian-wheat	*Plantago purshii*	R.& S.
Wright buckweed	*Eriogonum wrightii*	Torr.
Wright’s thimblehead	*Hymenothrix wrightii*	Gray
Wright’s silktassel	*Garrya wrightii*	Torr.
Yellow paloverde	*Cercidium microphyllum*	(Torr.) Rose & I.M. Johnston
Yerba de pasmo	*Baccharis pteronioides*	D.C.

RMRS
ROCKY MOUNTAIN RESEARCH STATION

The Rocky Mountain Research Station develops scientific information and technology to improve management, protection, and use of the forests and rangelands. Research is designed to meet the needs of the National Forest managers, Federal and State agencies, public and private organizations, academic institutions, industry, and individuals.

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