

Grasslands

Introduction

Natural grassland ecosystems across the United States are diverse, shaped and governed by a range of floristic, edaphic, physiographic, and climatic factors. North American grasslands between 30° and 60° latitude, which include the grasslands of the American Southwest, are considered temperate grasslands. Temperate grasslands are characterized by seasonal temperature extremes, an annual dry season, and grass-dominated vegetative cover (Finch 2004, Ford et al. 2004).

Development, agriculture, and other land use practices have taken a heavy toll on temperate grasslands, fragmenting them into isolated islands and reducing their extent. Noss et al. (1995), who reviewed and summarized estimated habitat loss, degradation, and fragmentation in natural ecosystems across the United States, classified grasslands and shrublands as “critically endangered ecosystems”—ecosystems which have declined by more than 98%. Fire suppression and livestock grazing have also contributed to the decline of grasslands by facilitating further expansion of woody plants into former grasslands. The Nature Conservancy estimates that shrub en-

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croachment has affected over 8.7 million acres of grasslands nationwide (Gori and Enquist 2003).

Southwestern Grassland Types

In the Southwest, grassland types vary based on topography, soil type and precipitation. This overview considers three general grassland types: Desert grasslands and shrub-steppe, Colorado Plateau semi-desert grasslands and shrub-steppe, and Southern Plains grasslands. Because the grasslands west of the Great Plains prairies typically include a significant shrub component, this overview covers both grasslands, which are dominated by perennial grasses, and shrub-steppe communities, which are dominated by both shrubs and perennial grasses.

Desert grasslands and shrub-steppe

Desert grasslands and shrub-steppe include low elevation grass and shrub communities adjacent to the Chihuahuan, Mohave, and Sonoran deserts (Robbie 2004). Common grass species include black grama (*Bouteloua eriopoda*), tobosa



A Chihuahuan Desert shrub-steppe at Guadalupe Mountains National Park.





A Colorado Plateau semi-arid grassland at Wupatki National Monument with blue grama (*Bouteloua gracilis*) and galleta (*Pleuraphis jamesii*).

(*Pleuraphis mutica*), and curly mesquite (*Hilaria belangeri*). Prevalent shrub species include creosote bush (*Larrea tridentata*), velvet mesquite (*Prosopis velutina*), western honey mesquite (*Prosopis glandulosa* var. *torreyana*), tarbush (*Flourensia cernua*), turpentine bush (*Ericameria larcifolia*), desert ceanothus (*Ceanothus greggii*), and soaptree yucca (*Yucca elata*).

Colorado Plateau semi-desert grasslands and shrub-steppe

Colorado Plateau semi-desert grasslands and shrub-steppe occur in northern Arizona above the Mogollon Rim and in northern New Mexico (Robbie 2004), as well as in southern Utah and southwestern Colorado. These systems are found on nearly level landforms of sedimentary and igneous origin. Characteristic grass species include blue grama (*Bouteloua gracilis*), galleta (*Pleuraphis jamesii*), western wheatgrass (*Pascopyrum smithii*), needle and thread (*Hesperostipa neomexicana*), and several species of three-awn (*Aristida* spp.). Common shrubs include big sagebrush (*Artemisia tridentata*), black sagebrush (*Artemisia nova*), four-wing saltbush (*Atriplex canescens*), rabbitbrush (*Ericameria nauseosa*), broom snake-weed (*Gutierrezia sarothrae*), and several species of joint-fir (*Ephedra* spp.)

Southern Plains grasslands

Southern Plains grasslands consist of shortgrass and midgrass prairies occurring within semi-arid to subhumid climates (Robbie 2004). In contrast to semi-desert and Colorado Plateau grasslands, which include a significant shrub component,

the prairies of the southern plains are dominated by grasses. Characteristic shortgrass prairie species include blue grama (*Bouteloua gracilis*), buffalo grass (*Buchloe dactyloides*), and western wheatgrass (*Pascopyrum smithii*). Little bluestem (*Schizachyrium scoparium*), sideoats grama (*Bouteloua curipendula*), and Indiangrass (*Sorghastrum nutans*) are typical of midgrass prairies.

Influences on the Structure and Function of Grasslands

The structure and function of grassland ecosystems across the Southwestern United States are influenced by four major attributes: climate, soils, major functional groups of organisms, and disturbance regimes (Miller 2005, Ford et al. 2004). Ecosystem structure refers to the spatial arrangement of the living and nonliving elements of an ecosystem, and ecosystem function refers to the processes where the living and nonliving elements of ecosystems change and interact (Finch et al. 2004).

Climate

Precipitation regime is the most important climatic factor for determining the structure and function of southwestern ecosystems. The availability of moisture drives (or limits) basic ecological processes, such as primary production, nutrient cycling, and plant reproduction (Miller 2005). Precipitation events in arid and semi-arid southwestern grasslands and shrublands are spatially variable and punctuated by extended dry periods, creating systems with high potential for evapotranspiration and limited opportunities for soil-water recharge. Seasonality, area, intensity (amount of moisture per unit of time), and form (snow versus rain) of precipitation events



A shortgrass prairie at Capulin Volcano National Monument.

strongly influence which plant species and communities dominate grassland and shrubland ecosystems (Miller 2005).

Summer monsoon precipitation is an important source of moisture for arid and semi-arid grasslands in the American Southwest. Moist air masses originating in the Gulfs of Mexico and California are believed to be the source of the southwest monsoon, which extends north from central Mexico to portions of the southwestern and central United States. Summer monsoon storms are typically high-intensity convective storms of short duration. The intensity of a precipitation event, in combination with soil surface characteristics, determines how much infiltration will occur and how much moisture will be lost as runoff (Whitford 2002). Summer monsoons of short duration may trigger soil surface processes, but they may not be sufficient to initiate seed germination, photosynthesis, or soil-water recharge (Miller 2005). A larger proportion of precipitation is lost as surface water runoff during summer monsoon storms than during winter storms, when moisture from melting snow can penetrate to greater soil depths. In contrast to monsoon precipitation, winter storms are lower-intensity, of longer duration, and cover larger areas. Winter precipitation can recharge soil water and affect the growth of perennial, deeply-rooted plants.

A second important climatic factor—wind—affects the structure and function of grassland and shrubland ecosystems by influencing wildfire behavior and rates of evapotranspiration. Wind is also a major driver of erosion, redistributing surface soil and soil-forming materials (Whicker et al. 2002). Disturbances such as wildfire and livestock grazing can contribute to dramatically increased levels of wind erosion.

Soils

In addition to climate, soils are major determinants of grassland and shrubland ecosystem structure and function. The components of the soil—mineral nutrients, organic matter, water, and soil biota—regulate hydrologic processes and nutrient cycling (Miller 2005). In short, soils store and deliver the water and nutrients which sustain grassland and shrubland plant and animal populations. Soil development is slow in regions with arid and semi-arid climates. Low rates of weathering result in weakly-developed soils that closely resemble the rock from which they were derived. Nutrient turnover in dryland soils is surprisingly rapid, leading to little accumulation of nitrogen, phosphorus, and other plant nutrients (Schlesinger et al. 1990). Many species of arid and semi-arid grassland vegetation rely on symbiotic relationships with soil biota like fungi and bacteria to acquire nutrients and moisture in an environment where both are limited.

Major functional groups of organisms

Plant and animal biological diversity is high in southwestern grasslands, due to environmental variability (precipitation, temperature, and elevation) and interspersed of other habitat types (riparian and woodland), among other factors (Merola-Zwartjes 2004). Ecosystem-level “functional types,” as defined by Miller (2005), are groups of living organisms that have the capacity to influence the structure and functioning of entire ecosystems.

Vegetation

As photosynthesizing primary producers, soil stabilizers, and sources of organic material and habitat for above- and below-ground organisms, plants are considered the dominant functional type in terrestrial systems (Miller 2005). Vegetation influences the spatial distribution of soil resources through litter deposition, nutrient uptake, microclimate modification, and interaction with water- and wind-driven erosion (Miller 2005).

Soil biota

Soil biota, including bacteria, algae, fungi, and soil invertebrates (arthropods, nematodes, and protists), are a diverse, but under-researched group of organisms. Bacteria, the most abundant group of soil biota, play an important role in the decomposition of organic matter. Certain types of bacteria (*Rhizobium* spp.) live in nodules on the roots of leguminous plants, where they convert atmospheric nitrogen to nitrogen compounds that plants can use. Lupine species (*Lupinus* spp.), milkvetch (*Astragalus* spp.), and mesquite (*Prosopis* spp.) are examples of leguminous plants which form symbiotic relationships with nitrogen-fixing bacteria (Ford et al. 2004).

Another type of mutualistic relationship, one between plants and mycorrhizal fungi, is very common in grassland ecosystems. Mycorrhizal fungi act as an extension of a plant's root system, receiving carbohydrates from the plant in exchange for increased uptake of mineral nutrients (phosphorus, zinc, copper, nitrogen) and moisture to the plant. Mycorrhizal fungi may also confer resistance to pathogens and nematodes (Ford et al. 2004). Increased plant fitness may indirectly help plant communities resist colonization by exotic, invasive weeds. In greenhouse studies where native grasses were planted with nonnative Russian thistle, or “tumbleweed” (*Salsola kali*), plant mass and rates of stomatal conductance (the rate at which water evaporates from leaf pores) were greater in grasses inoculated with mycorrhizal fungi (Allen and Allen 1984). Grassland and shrubland plant species in Asteraceae (sunflower family), Fabaceae (legume family), Rosaceae (rose family), Poaceae (grass family), and Solanaceae (nightshade family)

are frequently colonized by mycorrhizae (Miller 2005). Symbiotic relationships with mycorrhizal fungi are less common or nonexistent among the species in Cactaceae (cacti family), Brassicaceae (mustard family), and Chenopodiaceae (goose-foot family) families (Miller 2005).

Biological soil crusts

Biological soil crusts are unique biological communities of fungi, lichens, algae, mosses, bacteria, and cyanobacteria (photosynthesizing blue-green algae) that live on the soil surface. Biological soil crusts perform a number of vital functions in southwestern grassland and shrub-steppe ecosystems. They stabilize surface soils, retain moisture, enrich the soil with nitrogen and carbon, and provide a favorable microclimate for seed germination. Rhizines (filaments) from mosses and lichens, gelatinous sheath material from mobile cyanobacteria, and fungal hyphae bind surface soil particles together, reducing wind and water erosion (Belnap et al. 2001). Windborne and waterborne dust, seeds, and other organic material are captured and retained in the uneven surface created by intact soil crusts (Ford et al. 2004, Belnap et al. 2001). Well-developed biological soil crusts also play an important role in post-fire revegetation. Biological soil crusts are a source of unburned plant seeds and propagules. Lightly-burned crust continues to stabilize the soil surface while vascular vegetation recovers (Belnap et al. 2001). The active growth period for crust organisms in southwestern arid and semi-arid grasslands and shrublands coincides with wet, cool conditions—generally late fall to early spring (Belnap et al. 2001).

Invertebrates and vertebrates

Several thousands of species of invertebrates (arthropods, nematodes, and insects) are present in arid and semi-arid grasslands. In addition to providing an important prey base for grassland wildlife, invertebrates aerate soils, pollinate plants, consume plant biomass, and assist with decomposition of organic material (Ford et al. 2004).

Native herbivores of Southwest grasslands and shrublands range from insects and rodents to large ungulates such as bison, elk, pronghorn, and mule deer. Large bison herds once extended into the Southern Plains, but were much less common in the semi-arid grasslands west of the Pecos River (Milchunas 2006). Elk currently have a wider distribution across the Southwest than they did in the past; elk historically occurred in only about half of their current range (Truett 1996). By contrast, pronghorn were historically more abundant across Arizona and New Mexico than they are today. Likely reasons for the relative scarcity of large herbivores in the Southwest include a lack of perennial water sources and hunting by late-

prehistoric peoples (Truett 1996).

Burrowing mammals, such as prairie dogs (*Cynomys* spp.) and kangaroo rats, directly and indirectly influence grasslands through their grazing and burrowing and by being a source of prey (Brown and Hesky 1990; Kotliar et al. 2006). Through their foraging and clipping of vegetation to maintain their habitat, as well as the mixing of subsoil and topsoil during excavations, prairie dogs redistribute minerals and nutrients, encourage penetration and retention of moisture, and affect plant species composition (Brown and Hesky 1990; Kotliar et al. 2006). Their excavations also provide habitat for predators such as snakes and burrowing owls (*Athene cunicularia*) (Brown 1994; Merola-Awartjes 2004).

Disturbance Regimes

Southwestern grassland and shrubland communities expand and contract in response to the frequency and intensity of natural disturbance events (Ford et al. 2004) and are also shaped by anthropogenic influences.

Natural disturbance

Major natural disturbances in southwestern grasslands include fire, extreme climate events, and herbivory and trampling by native fauna.

Fire

In many grassland systems, fire contributes to maintaining grass dominance by preventing woody trees and shrubs from establishing. It also may facilitate nutrient cycling and accelerate decomposition rates in grassland soils. Fire regimes vary greatly within southwestern grasslands and will be discussed individually for each grassland type.

Desert grasslands and shrub-steppe

Historically, fires occurred every five to ten years in desert grasslands (Mau-Crimmins et al. 2005). The absence of fire has allowed woody plants and nonnative grasses, like Lehmann lovegrass (*Eragrostis lehmanniana*), to invade (Mau-Crimmins et al. 2005).

Colorado Plateau semi-desert grasslands and shrub-steppe

In the most sparsely-vegetated semi-arid grasslands, wildfire is of limited importance as a natural disturbance. Examples of such fuel-limited grasslands can be seen in Glen Canyon National Recreation Area and Chaco Culture National Historic Park. However, wildfire can be an important natural disturbance on more productive, densely vegetated grasslands, such as those that occur at Wupatki National Monument (Miller 2005).

Southern plains grasslands

Fire is essential to maintaining the health of short-grass and mixed-grass prairie. Fire helps maintain the diversity of native species and prevents woody shrubs and trees from invading the grasslands (Perkins et al. 2006). Prior to the introduction of livestock, landscape-scale fires probably occurred every three to ten years in the southern mixed-grass prairie and less frequently in the short-grass prairie (Umbanhowar 1996). Prescribed fire can help replicate the natural fire regime; however, since only small areas of the prairie are protected from development, natural resource managers cannot create the landscape-scale fires necessary to restore a full diversity of plants (Perkins et al. 2006).

Extreme climate events

Drought, intense precipitation events and floods, and wind storms can fundamentally alter ecosystem structure and function for a long time afterwards. These climate events can cause vegetation mortality, allowing new species to establish at the site, and they can erode the soil and change the geomorphology of a site. These extreme climate events can also make ecosystems more vulnerable to fire, insect outbreaks, exotic species invasions, and human-caused disturbances (Miller 2005).

Herbivory and trampling

The potential effects of herbivory and trampling depend on the characteristics of a particular site. In general, native herbivores, such as elk, pronghorn, and mule deer, can alter plant production and population dynamics (Miller 2005). Moderate amounts of herbivory may impel plants to compensate for the lost foliage by growing new tissue—sometimes growing even more foliage than existed prior to the herbivory (Miller 2005). More importantly, herbivory can change the plant community structure; plants that are less palatable to herbivores or are able to recover from disturbance more quickly have a competitive advantage over palatable and slow-growing plants (Miller 2005). Although the amount of herbivory and trampling varies over the region, they are likely minor natural disturbances to Southwest grassland and shrubland ecosystems (Miller 2005).

Human-caused disturbance

Anthropogenic stressors in southwestern grasslands and shrub steppe include altered fire regimes, livestock grazing, the introduction and spread of exotic invasive plants, disturbance of biological crusts, and development (urban and agricultural).

Livestock grazing

In contrast to herbivory by native animals, livestock grazing can cause more extensive changes to the structure and functioning of grasslands. The response of a particular plant community to livestock grazing is largely determined by the evolutionary

History of Cattle Ranching in the Southwest

The first cattle arrived in the Southwest in 1540 with the Spanish explorer Coronado. Bred in a semi-arid environment in western Spain, these cattle were well-adapted to the Southwest (Milchunas 2006). Through the 1700s, the numbers of cattle, sheep, and goats in the Southwest increased, and by 1846, some signs of overgrazing began to appear near Sante Fe, the Rio Grande Valley, and the Rio Puerco watershed (Milchunas 2006). However, grazing generally remained a small disturbance until the cattle boom of the 1880s. The boom began when Civil War veterans from Texas began to relocate their herds of American cattle from the overgrazed Texan rangelands into Arizona (Morrissey 1950). Then the completion of a railroad through Arizona and New Mexico opened up quality grasslands and allowed for easier importing and exporting of cattle to and from the Southwest (Morrissey 1950). Cattle ranching expanded explosively, until the summer rains failed to fall during the catastrophic years of 1891 to 1893. With little grass growth, a large proportion of the livestock died and major erosion of topsoil occurred. Although overstocking of cattle continued after the drought, cattle numbers peaked in 1891 (Milchunas 2006). Grazing declined somewhat in the 1910s and 1920s as homesteading reduced the amounts of open, unfenced range and the Forest Service started to fence its land (Milchunas 2006).

history of large herbivore grazing and by its above ground primary productivity (Milchunas 2006). With their short histories of grazing, the semi-arid and desert grasslands are less tolerant to grazing than the plains grasslands. In addition, semi-arid and desert grasslands display a broader range of responses to grazing than plains grasslands (Milchunas 2006). Because grazing is more likely to decrease native plant cover in semi-arid and desert grasslands, they may be more susceptible to invasion by exotic and opportunistic native species (Milchunas 2006).

In general, livestock grazing affects overall grassland ecosystem productivity by altering vegetative cover, soil physical

properties, microbial communities, carbon cycling, nitrogen fixation, erosion, and soil hydrologic properties (Schlesinger et al. 1990). Trampling by cattle causes soil compaction, decreased water infiltration, and increased surface runoff. Increased surface runoff results in an uneven spatial distribution of moisture and plant nutrients—conditions conducive to colonization by woody plants (Schlesinger et al. 1990). Selective herbivory by livestock also facilitates woody plant invasions by favoring the establishment and growth of unpalatable plant species over palatable species (Miller 2005). Livestock grazing also facilitates the conversion from native perennial grass-dominated landscapes to landscapes dominated by exotic annual grasses, such as cheatgrass.

Altered fire regimes

The combination of extensive livestock grazing and wildfire suppression has altered fire regimes in southwestern grasslands. The reduction in fire frequency and severity has allowed shrub species, such as mesquite, fourwing saltbush, burroweed (*Isocoma tenuisecta*), snakeweed (*Gutierrezia* spp.), and juniper species (*Juniperus monosperma*, *J. scopulorum*, *J. osteosperma*), to expand into southwestern grasslands (Brown 1994).

Conversely, fire intensities and frequencies have increased in some areas where nonnative, invasive plants, such as cheatgrass (*Bromus tectorum*) and buffelgrass (*Pennisetum ciliare*), have become widespread. For example, Belnap and Phillips (2001) studied cheatgrass-invaded semi-arid grasslands on the Colorado Plateau that had been originally dominated by needle-and-thread (*Hesperostipa comata*), Indian ricegrass (*Achnatherum hymenoides*), and James' galleta (*Pleuraphis jamesii*). Cheatgrass had filled in the barren interspaces between clumps of perennial native grasses (Belnap and Phillips 2001), creating a continuous layer of dry surface fuels. Where nonnative grasses increase the continuity of fire fuels, fire can spread more easily across the landscape.

Woody plant encroachment

Over the past 150 years, woody plants have been expanding into areas once occupied by grasses in the semi-arid and desert Southwest. The causes behind this increase in density and cover of shrubs are widely debated. The most commonly cited reasons for woody plant encroachment are: climate change, overgrazing, changes in ability of grasses to compete with other plants, elevated levels of carbon dioxide, or a combination of these factors. A likely scenario (Van Auken 2003, 2009) implicates several factors, beginning with the widespread introduction of cattle to the Southwest in the 1870s. Overgrazing first left bare areas open for woody plant establishment. Then continued overgrazing interacted with other factors to perpet-



In some parts of the Southwest, the grasslands outside towns and cities are being developed into urban sprawl.

uate the expansion of woody plants. Woody plants could survive and flourish partly because grazing reduced the ground-cover and litter needed to fuel the frequent surface fires that maintain open grasslands. In addition, decreased grass cover allowed for soil erosion, leading to a loss of soil nutrients. Low soil nitrogen would have then favored the establishment of species with low-nitrogen requirements, like creosote bush. Shrubs then concentrated soil nutrients, making good sites for further establishment of shrubs.

Climate and increased concentrations of carbon dioxide in the air were likely not important factors in woody plant encroachment (Van Auken 2000, 2009). Although fluctuations in climate did induce short-term changes in vegetation composition, no conclusive evidence links changes in climate with shrub expansion across the Southwest (Bahre and Shelton 1993). Increases in carbon dioxide may have favored shrubs, which use the C_4 photosynthetic pathway, over grasses with the C_3 photosynthetic pathway. However, the arguments for why this hypothesis may not be plausible include: (1) under our current levels of carbon dioxide, C_4 plants have the same photosynthetic rate and water use efficiencies as C_3 shrubs, (2) the hypothesis does not explain why in cold deserts, C_3 shrubs are also replacing C_3 grasses; (3) woody plant encroachment was already underway before significant increases in carbon dioxide occurred (Archer et al. 1995).

Invasive, exotic plants

Introduced annual grasses now comprise 50–85% of plant cover in over two-thirds of western rangelands (Belnap and Phillips 2001). Introduced, nonnative plants can spread aggressively, out-competing native vegetation for nutrients and

water and decreasing the overall diversity of native plants. Once established, invasive, exotic plants have the potential to alter soil properties (soil moisture, temperature, and chemistry), vegetation species diversity, productivity, fire regimes, and quality and quantity of organic litter. These factors in turn affect the composition, distribution, and abundance of soil biota, and the timing of biological activity (Belnap and Phillips 2001).

Disturbance of biological soil crusts

Colonization by invasive, exotic plants, livestock grazing, foot traffic, and motorized vehicle traffic can cause a decrease in biological soil crust cover (Belnap et al. 2001). Biological soil crusts are fragile and slow to re-establish after disturbance. Because well-established biological soil crusts tend to be darker in color than bare or disturbed soils, they absorb and retain more solar radiation (Belnap et al. 2001). Lighter soils have increased surface albedo (energy reflected off of the soil surface) and cooler soil temperatures, which decrease plant metabolic processes and seedling growth rates, delay seed germination, and interfere with surface foraging of insects and small mammals (Belnap et al. 2001). Disturbance of biological soil crusts can also increase erosion and surface runoff. Of all soil types, biological soil crusts are least vulnerable to trampling by livestock when soils are frozen or protected by snow (Belnap et al. 2001).

Development

Over the past century, urban development, agriculture, and construction of power lines and roads have affected grassland ecosystems. Development has fragmented the once continuous grasslands (Merola-Zwartjes 2004), altered habitat structure for wildlife, increased water and air pollution, and facilitated the introduction and spread of exotic species (Miller 2005).

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