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Abstract

- Grasslands are one of Earth's major biomes and the native vegetation of up to 40 % of Earth's terrestrial surface. Grasslands occur on every continent except Antarctica, are ecologically and economically important, and provide critical ecosystem goods and services at local, regional, and global scales.
- Grasslands are surprisingly diverse and difficult to define. Although grasses and other grasslike plants are the dominant vegetation in all grasslands, grasslands also include a diverse assemblage of other plant life forms that contribute to their species richness and diversity. Many grasslands also support a diverse animal community, including some of the most species-rich grazing food webs on the planet.

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- Grasslands allocate a large proportion of their biomass below ground, resulting in large root to shoot ratios. This pattern of biomass allocation coupled with slow decomposition and weathering rates leads to significant accumulations of soil organic matter and often highly fertile soils.
- Climate, fire, and grazing are three important drivers that affect the composition, structure, and functioning of grasslands. In addition to the independent effects of these factors, there are many interactions among grazing, fire, and climate that affect ecological patterns and processes in grasslands in ways that may differ from the independent effects of each driver alone.
- Grasslands occur under a broad range of climatic conditions, though water is generally limiting for some part of the year in most grasslands. Many grasslands experience periodic droughts and a dormant season based on seasonal dry or cold conditions.
- Grasslands are sensitive to climate variability and climate changes. There are well-documented shifts in the distribution of North American grasslands in response to past droughts, and both observational data and experiments suggest that grasslands will be affected by future changes in rainfall and temperature.
- Fire is a common occurrence, particularly in more mesic grasslands, due to the large accumulations of dry, highly combustible fine fuel in the form of dead plant material. Fire affects virtually all ecological processes in grasslands, from the physiology of individual plants to the landscape-level patterns, though the effects of fire vary with grassland productivity and the accumulation of detritus.
- All grasslands are grazed or have experienced grazing as a selective force at some point in their evolutionary history. The ecological effects of grazing vary with climate and plant productivity, and the associated evolutionary history of grazers in different grasslands.
- Grasslands have been heavily exploited by humans, and many temperate grasslands are now among the most threatened ecosystems globally. Widespread cultivation of grasslands was the major land-use change that impacted grasslands historically, while multiple global changes drivers (i.e., altered fire and grazing regimes, woody plant encroachment, elevated CO₂, invasive species, fragmentation) contribute to the contemporary loss of grasslands.
- Grassland restoration aims to recover the diversity and ecosystem services that grasslands provide. While restored grasslands may attain productivity comparable to native grasslands and sequester carbon for extended periods, they typically support much less diversity than comparable native grasslands. Recovery of soil communities and properties is often very slow.

Introduction

Grasslands and other grass- and graminoid-dominated habitats (e.g., savanna, open and closed shrubland, and tundra) occur on every continent except Antarctica (though some grasses do occur there) and occupy about 30–40 % of Earth's land surface. They cover more terrestrial area than any other single biome type.

The extent and diversity of grasslands and related habitats is reflected in their ecological and economic importance at local, regional, and global scales. For example, grasslands provide critical habitat for a diverse array of plants and animals. Grassland soils store tremendous quantities of carbon and other key nutrients and play a major role in global biogeochemical cycles. There is also a long and complex relationship between grasslands and humans. Modern humans are thought to have originated in the open grasslands and savannas of Africa, and grasslands have provided the template and biological raw material for the development of modern agriculture and associated human societies. The fertile soils that developed under many grasslands have been plowed and the nutrients mined to support agricultural production. Domesticated grasses, such as corn, rice, wheat, oats, and sorghum, have become some of our most important agricultural crops, and barley was used by Neolithic humans to produce one of the first known alcoholic drinks. Grasses are not only consumed directly by humans, but they also support the production of domestic livestock for human use. More recently, several species of grasses are being widely used or considered as feedstock for biofuel production (e.g., *Panicum virgatum*, *Miscanthus* spp.). It is estimated that as many as 800 million people worldwide rely directly on grasslands for their livelihoods (White et al. 2000), and virtually everyone uses grassland products (food, fiber, fuel) in their daily existence. In total, it is clear that grasses and grasslands have played an important role in the history of humans and will continue to do so in the future.

Grasslands have also played an important role in the development and testing of ecological theory, such as assessing relationships between species richness and ecosystem function and as model systems for assessing the impacts of global changes, including responses to chronic N deposition, elevated CO₂ concentrations, and climate change. This is due, in part, to the relative ease of performing manipulative experiments in grasslands, the sensitivity of grasslands to perturbations, and the relatively rapid responses they often exhibit to these manipulations. In fact one of the longest running field experiments in the world is the Park Grass Experiment at the Rothamsted Experimental Station in England. This experiment was established in 1856 with the original goal of assessing the effects of various nutrient amendments on grass yields. The experiment has since been used to address a broad range of fundamental questions in ecology and evolutionary biology (Silvertown et al. 2006).

Grasslands also include some of the most endangered ecosystems on the planet, such as the tallgrass prairies of North America and other temperate grasslands (Hoekstra et al. 2005). In addition to the historical loss of grasslands to agricultural expansion, grasslands today are threatened by a broad array of environmental changes, including climate change, elevated atmospheric carbon dioxide concentrations, increased nitrogen deposition, invasive species, habitat fragmentation, degradation due to overgrazing, change in natural disturbance regimes (e.g., fire suppression), and woody plant expansion. Conserving, and in some cases restoring, these ecosystems will require a solid foundation of ecological knowledge. This chapter focuses on the ecology of grassland ecosystems and provides the reader with an introduction to grassland plants and the major abiotic and biotic factors that

influence the structure and functioning of grassland ecosystems. Our goal is to present a sufficiently broad coverage to familiarize readers with the variation that exists in different grasslands from different parts of the globe, combined with more detailed information and specific examples of key ecological processes from a few well-studied grassland ecosystems, including the mesic tallgrass prairies of North America where the authors have extensive experience.

General Characteristics and Global Distribution of Grasslands

A simple, all-encompassing definition of grasslands is surprisingly difficult to come by, and grasslands have been defined and distinguished from other biome types in many different ways. One defining feature of grasslands is that they are dominated or codominated by graminoid vegetation, including the true grasses (family Poaceae) and other grasslike plants including sedges (Cyperaceae) and rushes (Juncaceae). Defined narrowly, grasslands are ecosystems characterized by a relatively high cover of grasses and other graminoid vegetation in an open, often rolling, landscape with little or no cover of trees and shrubs. However, the term grassland can also be used in a broader sense to encompass ecosystems with a significant grass cover interspersed with varying degrees of woody vegetation, including relatively open savannas and woodlands (e.g., the cerrados of South America) and some deserts and shrub grasslands (also referred to as steppes) that include a significant cover of grasses interspersed with succulent plants and/or shrubs. In this context, grasslands can vary in the relative abundance of grasses and other plant life forms, such as trees and shrubs. In fact, the cover of woody vegetation is increasing in many grasslands globally, as discussed later in this chapter, and there is often disagreement about how to delimit grasslands from other vegetation types that include significant grass cover mixed with other herbaceous and/or woody vegetation.

Although grasses provide the matrix in which other plant species co-occur, grasslands include other plant life forms, such as annual and perennial forbs (non-graminoid, nonwoody plants), shrubs, and trees. The matrix-forming species in most of the world's major grasslands are perennial grasses that are relatively long-lived and that can reproduce either sexually or asexually via belowground meristematic tissue (belowground buds), though a few grasslands are dominated by annual species that must reproduce from seed each year (e.g., California and other annual grasslands). Some grasslands are dominated by grass species that produce individual tillers evenly distributed across the soil and often joined by underground stems called rhizomes (i.e., rhizomatous or "sod-forming" grasses), while other grasslands are dominated by species that produce densely packed clumps of tillers that are distinct from one another and often separated by bare soil spaces (i.e., caespitose or bunchgrasses; Fig. 1).

The graminoid flora of grasslands can be quite species rich (Fig. 2). For example, the Konza Prairie Biological Station (a tallgrass prairie research site in eastern Kansas, United States) supports more than 100 species of grasses and sedges.

Fig. 1 Contrasting growth forms of grasses. The foreground is dominated by the caespitose grass *Bothriochloa bladhii*, an exotic species native to parts of Africa, Eurasia, and Australia. The more even cover of grasses in the background includes the rhizomatous native tallgrass prairie grasses *Andropogon gerardii* and *Sorghastrum nutans* (Photo by John Blair)



Fig. 2 Although grasslands are often dominated by a small number of grass species, they often co-occur with a diverse assemblage of other grasses, as well as forbs and woody plant species. As a result, high floristic diversity is characteristic of many grasslands, such as the North American tallgrass prairie pictured here (Photo by Dan Whiting)



Yet this prairie, like most other grasslands, is dominated by just a few species of grass that comprise the majority of grass cover and contribute the bulk of annual plant productivity. For example, at Konza Prairie *Andropogon gerardii*, *Sorghastrum nutans*, and *Schizachyrium scoparium* comprise about 70 % of total plant cover and up to 90 % of the aboveground net primary productivity (ANPP), particularly in frequently burned and ungrazed areas. In fact, many grassland types are described by their dominant species (e.g., bluestem prairie). However, despite the general prevalence of graminoid plant cover, different types of grasslands are surprisingly diverse in the richness and cover of non-grass species. Using the Konza Prairie example, the grasses co-occur with over 400 species of forbs and woody plants, which provide much of the floristic diversity characteristic of the prairie.

The global distribution of grasslands is extensive, with widespread representation of grasslands on every continent except Antarctica (Fig. 3). Although grasslands are

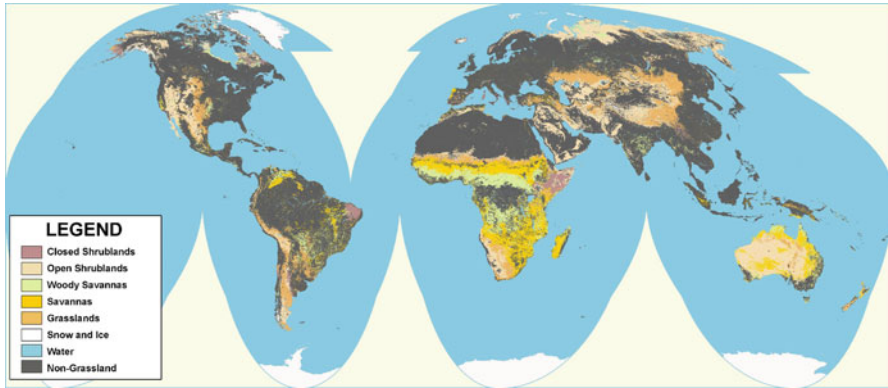
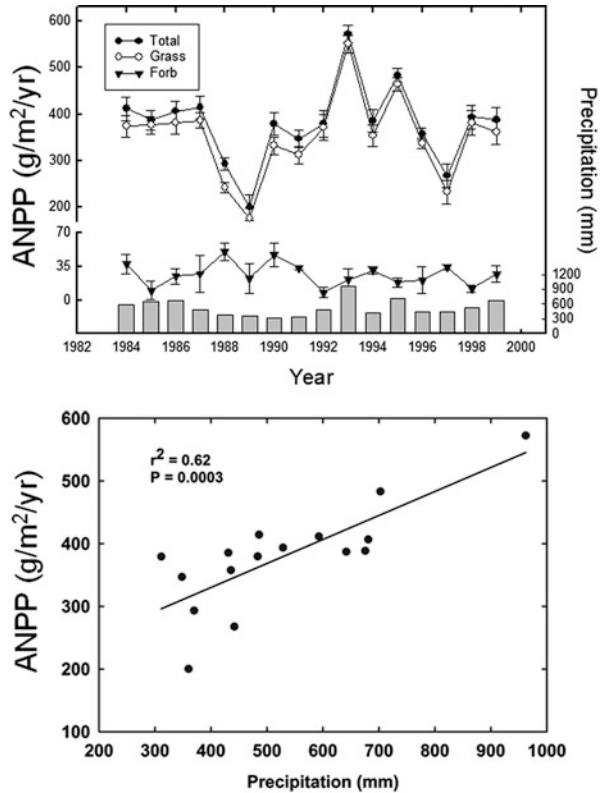


Fig. 3 Global distribution of grasslands and other ecosystem types dominated by grasses or graminoid vegetation (Reproduced from White et al. 2000)

currently absent from Antarctica, a grass species (Antarctic hairgrass, *Deschampsia antarctica*) does occur on the Antarctic Peninsula and surrounding islands surrounding, where recent warming is thought to be promoting the spread of this native grass. Major grasslands in the temperate regions of the world include the steppes of Eurasia, the velds of southern Africa, the pampas of Argentina, and the prairies of North America (Archibold 1995). Grasslands and savannas also occur within the subtropics and tropics, such as the mesic grasslands of Florida, the bushvelds of Africa, and the campos and llanos of South America, and in areas with a Mediterranean climate (dry summers and relatively warm, wet winters). Grasslands can be found in coastal areas near sea level, and in montane regions at elevations up to 4,500 m (e.g., neotropical páramos and temperate montane meadows or parks). Intensively managed, human-planted, and maintained grasslands (e.g., pastures, lawns, etc.) occur worldwide as well, though these are not discussed further in this chapter.

As might be expected with such widespread distribution, grasslands occur under a very broad range of mean annual temperature and rainfall. The climates of grasslands vary from temperate to tropical with annual rainfall ranging from about 250 mm/year in arid grasslands to well over 1,000 mm/year in mesic grasslands. Mean annual temperatures vary from near 0 °C to around 26 °C. While there are many significant correlations between mean annual precipitation and the properties of grasslands, such as aboveground net primary productivity, rooting depth, and soil organic matter accumulations, these relationships are often more complex than they might first appear. Grasslands often experience very high intra- and interannual variability in rainfall, and comparisons with other biomes indicate that grasslands are more responsive to variation in rainfall amounts than are most other biomes (Fig. 4). This may occur because the relatively high density of plants and associated meristematic tissue (growing points) in grasslands results in greater growth potential when water is available, relative to more arid

Fig. 4 *Top*: Long-term record of aboveground net primary productivity (ANPP) (mean \pm SE, $n = 20$) for grasses (primarily C_4 species) and forbs (C_3 herbaceous plants) with corresponding growing season (April–Sept) precipitation amount in an annually burned mesic grassland in NE Kansas (Konza Prairie LTER site). *Bottom*: Positive relationship between grass ANPP and growing season precipitation (mm) based on the data in *top panel* (From Nippert et al. 2006)



ecosystems, and because wetter forests and woodlands are not as limited by water availability. These results suggest that grasslands may be especially sensitive to changes in precipitation amounts or timing in an altered future climate. Seasonality of precipitation, in addition to total annual amount, is also critical in grasslands. For example, in North America the area around Washington, DC, is dominated by eastern deciduous forest, and the annual precipitation is ~ 102 cm, which is very similar to the annual precipitation amount (~ 100 cm) near Lawrence, KS, which is dominated historically by tallgrass prairie. In spite of similarities in total rainfall amount, the seasonal distribution of rainfall is very different with over 60 % of the rainfall occurring in the growing season (April to September) and with drier late summer months in Lawrence, KS, whereas the precipitation is more evenly distributed throughout the year in Washington, DC. The importance of seasonal patterns of rainfall in grasslands is apparent in the numerous studies that have used climatic data and concurrent measurements of ecological processes to identify specific times of the year (critical climate windows) when precipitation has the greatest effect on processes such as plant productivity or grass reproductive effort. There are also significant interactions between rainfall amounts and temperature, and the ratio of precipitation to the potential evapotranspiration (PET) is often a better predictor of

ecological properties and process rates than is mean annual precipitation alone. Of course, the ability of soils to hold and supply water is also critical, and soil water dynamics are affected not only by rainfall quantity and intensity but also by physical characteristics of the soil, such as soil texture and porosity. At local scales, soil water dynamics in grasslands are often highly correlated with plant physiological processes, plant productivity, and soil microbial activity.

Climatically determined grasslands are those that result from prevailing climatic conditions, as opposed to planted grasslands (pastures or lawns) or those that represent intermediate successional stages. A characteristic feature of climatically determined grasslands is that they are subject to periodic droughts, which contributes to the accumulation of highly flammable plant detritus and the occurrence of periodic fires. Many of the world's most extensive grasslands occur in the interior regions of the continents, where annual rainfall amounts are relatively low and irregularly distributed across the year. Some of these grasslands lie between more arid deserts and more mesic forests and woodlands, while others occur in the rain shadows of major mountain ranges. The continental climates of these regions are often marked by extremes in seasonal temperatures (hot summers and cold winters), to which the plants and animals living there are adapted. For example, at Konza Prairie in the Central United States, the mean monthly temperature varies from a January low of -3°C to a July high of 27°C . In temperate grasslands with such continental climates, a significant proportion of annual rainfall often coincides with the warm growing season, and plant dormancy is a mechanism for surviving low winter temperatures. Many grassland animals also become dormant or migrate to avoid harsh winter conditions. In grasslands with a Mediterranean climate, such as those in the Central Valley of California, dormancy is driven by summer droughts, and the growing season coincides with seasonal rainfall that occurs in the relatively warm winter months. Tropical grasslands also exhibit distinct seasonality based on cyclic annual rainfall patterns, though annual temperatures vary less than in temperate grasslands. Dormancy still occurs, but in this case it is a response to annual dry seasons that alternate with the rainy growing season as a result of annual movement of tropical low pressure system boundaries. Soils of tropical grasslands may also be less fertile than comparable temperate grassland soils as a result of faster weathering rates under warm year-round temperatures and soils that are much often much older than in temperate grasslands. Many tropical grasslands also have a greater density of woody shrubs and trees than do temperate grasslands.

Although many climatically determined grasslands experience seasonal water deficits and periodic droughts that preclude the establishment of forests in those regions, some mesic grasslands, such as the tallgrass prairies of North America or the sourvelds of South Africa, occur in regions where the climate could support woodland, shrubland, savanna, or even forest vegetation. In these cases, the persistence of grasslands often depends on recurring disturbances, such as fire and grazing. Such grasslands may be best thought of as disturbance-dependent communities, where periodic fires, droughts, and the activities of grazers are necessary to keep grasslands from transitioning to other ecosystem types.

In fact, it is generally recognized that climate, fire, and grazing are three key factors that are responsible for the origin, maintenance, and structure of the most extensive natural grasslands on Earth. Although the relative importance of fire in structuring grassland communities tends to be greatest in the most mesic and productive grasslands, which also burn at more frequent intervals and with greater fire intensities do to large accumulations of fine fuel in the form of aboveground grass litter, fires do occur at varying frequencies in most grasslands, including shortgrass steppe and even desert grasslands. In addition, most grasslands coevolved with large grazers, and herbivory is an important process affecting ecological processes at levels ranging from the physiology of individual plants through population and community dynamics to ecosystem processes and landscape patterns. Although there are some similarities with respect to the effects of fire and grazing (i.e., both can be considered disturbances that remove aboveground plant biomass and free up resources), there are importance differences in their effects on soil resources and plant communities, as well as some important interactions between fire and grazing in grasslands. The effects of fire and grazing, and their interactions, are discussed in more detail in later sections of this chapter.

A final characteristic feature of grasslands is a relatively high allocation of plant biomass belowground (a high root to shoot ratio) and proportionally large inputs of plant root litter relative to surface litter. Relatively high belowground plant inputs coupled with relatively slow decomposition rates due to periods of water limitation can lead to large accumulations of organic matter and nutrients in the soil. In addition, the limited rainfall characteristic of most grasslands reduces the rate of weathering and leaching of critical plant nutrients from the rooting zone of grassland soils. The resulting high fertility of grasslands soils is one of the reasons they have been so widely exploited for agricultural purposes. The accumulation of soil organic matter is generally positively correlated with water availability, which stimulates plant productivity more so than decomposition, such that the most productive grasslands also tend to store the most organic matter and nutrients in the soil. Although grasslands can occur on a variety of different soil types, the archetypal dark, rich soils characteristic of many grasslands are known as Mollisols in the US Soil Taxonomy system or as a Chernozem in the World Reference Base for Soil Resources. These are the dark, rich soils that formed under the prairie of North America and the steppes of Europe and that have now largely been cultivated for use in agricultural production. Grasslands can also occur on other soil types, too. Many tropical and subtropical grasslands occur on soils that are geologically much older and therefore more highly weathered than most temperate grassland soils. These soils may be more depleted in cations and have lower phosphorus availability than temperate grassland soils. One unique association between soils and grasslands are the serpentine grasslands. Serpentine soils have a unique chemical composition due to the type of parent material from which they formed. Serpentine soils generally have high levels of magnesium and other metals and low concentrations of calcium. The flora growing on these soils is often very different from surrounding soils growing on more typical soils. In many cases, serpentine grasslands include species that are uncommon in other habitats.

Basic Biology and Ecology of Grasses

Grasslands are species-rich ecosystems with a variety of life forms including annual, biennial, and perennial plant species. The defining plant species are the grasses, but these ecosystems also contain a diverse assemblage of other plant types, including forbs (herbaceous non-grasses), sedges, wetland plants, and woody plants (shrubs and trees). The high rates and amount of growth by grasses in grasslands may be attributable to their unique morphology and physiology. As noted earlier in this chapter, many grasslands are “disturbance-rich” ecosystems, existing in locations that typically experience frequent, wide swings in weather (daily, weekly, monthly), a variable climate over longer periods of time (periodic extended droughts), and forces like fire and the activities of large grazers that alter the landscape. Grasses have adapted to these forces over evolutionary time, and their unique morphology, developmental patterns, and physiology make them well suited to the grassland environment.

Morphology

The aboveground portion of grasses is organized into tillers – individual shoots growing from the base of the plant. Tillers may be vegetative or reproductive and consist of one or more repeating units called phytomers, which are the basic building blocks of all grass shoots. Each phytomer consists of a node and internode with an axillary bud, cylindrical sheath, and leaf blade (Fig. 5).

Tillers are initiated from undifferentiated cellular tissue (meristematic tissue) that typically exists just beneath the soil surface. This is an important feature in an environment that includes periodic disturbances that remove tissues above the soil surface (i.e., fire and grazing). Additional meristematic tissue in grasses is also located at the intersections where leaves attach to the tiller (intercalary meristems). Thus, the oldest portion of a grass leaf is at the tip of the leaf and the top of the plant, and the youngest portion of a leaf is nearest the stem or the soil surface. For this reason, when grass blades are eaten, the actively growing plant tissues (intercalary or basal meristems) are left to produce new growth to replace removed leaf tissue. The presence of protected meristematic tissue belowground also allows grasses to survive and regrow when grazed or when fire removes aboveground tissues. This is an important mechanism giving grasses an advantage in environments with recurring droughts and fires or high grazing pressure (Fig. 6).

An individual grass plant generally consists of multiple joined tillers, but different grass species show great variation in the way tillers are aggregated as they expand from their origin. Two general classifications of tiller aggregation apply to most grasses: bunch-forming (caespitose or tussock) forms that are common in more arid grasslands and sod-forming (rhizomatous) grasses found more commonly in mesic grasslands (see Fig. 1). Sod-forming grasses utilize stolons (aboveground stems running along the ground surface) or rhizomes (belowground stems that occur just beneath the soil surface) to expand laterally through the

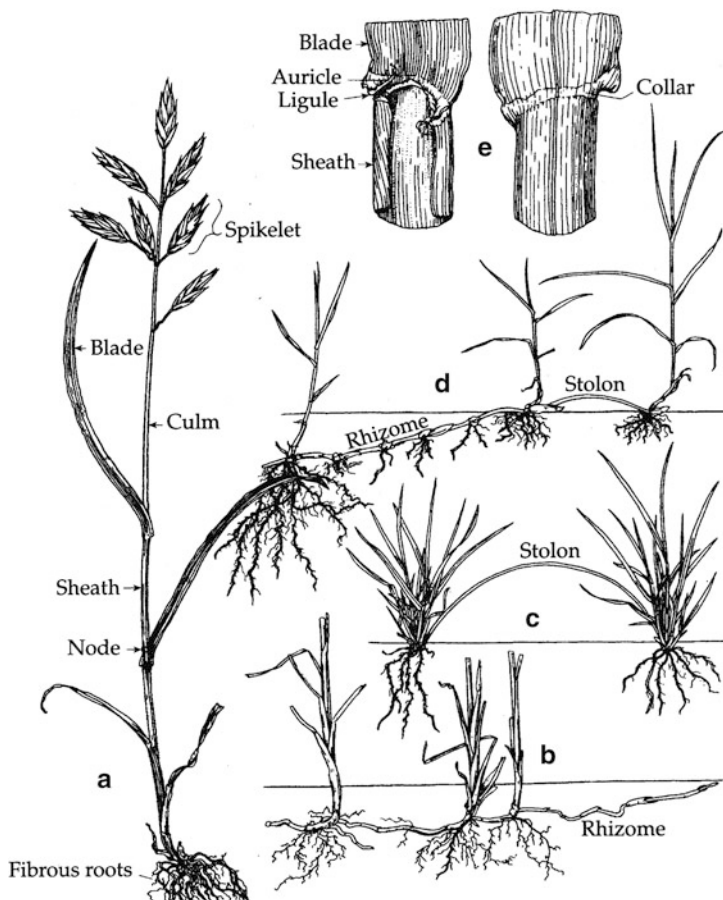


Fig. 5 Structure of the grass plant: (a) General habit (*Bromus unioloides*); (b) rhizomes; (c) stolon; (d) rhizome and stolon intergradations (*Cynodon dactylon*); and (e) the leaf at the junction of sheath and blade, showing adaxial surface (left) and abaxial surface (right) (Reproduced from *Common Texas Grasses. An Illustrated Guide* by F. W. Gould by permission of the Texas A&M University Press)

asexual production of new tillers (see Fig. 5). Bunch-forming grasses cluster the production of new tillers around a central stem without rhizome or stolon production. Annual plants and the bamboos are obvious exceptions to these two tiller classification schemes, as annual plants complete their life history within a single growing season, and bamboos can produce very large wood-like stems.

Grass leaves are narrow, parallel veined, and characterized by thick-walled cells that provide rigidity and support that allows them to remain upright despite environmental (i.e., wind) or biotic (trampling) forces. Grasses also have specialized cells (bulliform cells) that permit leaf rolling during periods of water deficit or high-light stress, and some species have specialized tissues with air channels

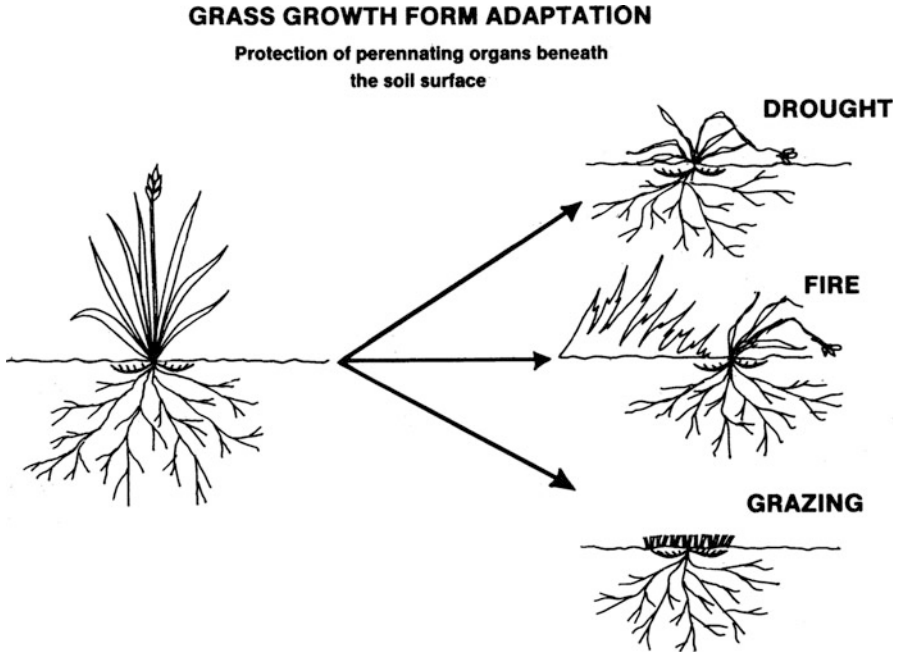


Fig. 6 Belowground location of perennial meristematic tissue contributes to ability of grasses to survive and regrow following loss of aboveground biomass (From Anderson 1990)

(aerenchyma) that facilitate growth in water-logged soils. Another feature of grass leaves is the presence of biogenic deposits of silica in structures known as phytoliths, which provides structural rigidity and contributes to defense against herbivores. The physical structure of a phytolith is typically distinct within a species or taxonomic group (Fig. 7), and phytoliths recovered from soils and buried sediments have been used to determine the historic presence of grasses and to reconstruct past plant communities. Phytoliths breakdown slowly, allowing them to persist in the soil for long periods of time. For this reason, phytoliths are a useful paleo-ecological tool for assessing changes in grassland species composition over centuries and millennia.

Because biogenic silica produced by grasses may weather at rates different from soil silica pools, the presence of large amounts of biogenic silica in soils can alter weathering rates (Blecker et al. 2006). In addition to its role in structural rigidity of plant parts, silica deposits within grass tissues wear down an herbivore's teeth over the lifetime of the animal. It is now generally accepted that the evolution of abrasion-resistant teeth in many modern grazing animals was an evolutionary response to tooth-wearing effects of a diet high in grass. This also suggests that the grasses and their megaherbivore grazers are highly coevolved. In fact, grass phytoliths have been found in fossilized dinosaur dung from the Late Cretaceous (65–70 MYA), indicating that a long evolutionary relationship of grasses and their herbivores (Prasad et al. 2005).

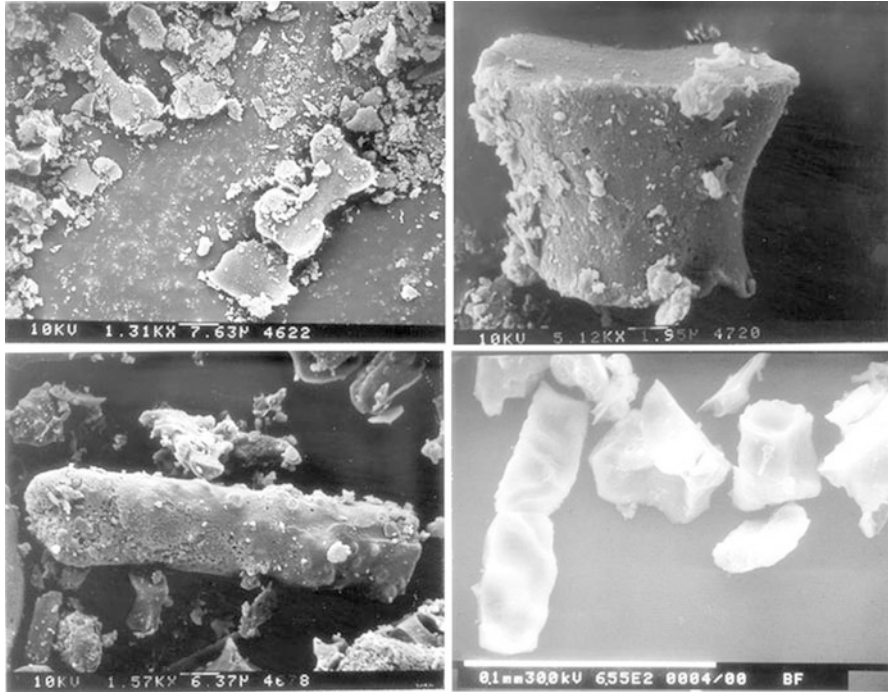


Fig. 7 Scanning electron micrographs of phytoliths. *Upper left, Andropogon gerardii*; *Upper right, Bouteloua gracilis*; *Lower left, Festuca sp.*; *Lower right, Stipa comata* (Photos from E.F. Kelly)

Population Dynamics

Population dynamics of grassland plants are the product of the demography of the species living there, including life-history traits such as reproductive effort, germination and survivorship, and patterns of mortality. Temperate grasslands can be divided into two main types based on the life-history characteristics of the dominant grass species – the annual grasslands (i.e., California grasslands) and the perennial grasslands (i.e., tallgrass prairie). All grasses are flowering plants (Angiosperms) and nearly all are wind pollinated with a (relatively) simplified floral structure. Within the annual grasslands, recruitment of new individuals from year to year is based exclusively on sexual reproduction and germination of seeds by annual (i.e., monocarpic) grass species. Seed production and viability are critical parameters affecting population dynamics, and the soil seed bank is an important reservoir of new individuals. Annual grass species vary in the longevity of seeds in the soil seed bank, germination cues, rates of growth, and generation time. In contrast, recruitment of new individuals and population dynamics of perennial grasses are influenced much less by sexual reproduction and seed dynamics (production, viability, germination, and growth), but rather are a product of asexual

reproduction, and the recruitment of new “individuals” (really new tillers) is via clonal stems from existing tillers (Benson and Hartnett 2006). For these perennial grass species, rhizomes and associated belowground buds are the primary means of reproduction, and recruitment of individuals from seeds tends to be very low, except under specific circumstances such as large soil disturbances. Belowground “bud banks” in perennial grass species can be very responsive to changing environmental conditions or to disturbances such as fire and grazing, and this may be an important mechanisms underpinning spatial and temporal variability in the population dynamics and productivity of grasses (Dalgleish and Hartnett 2009).

Physiology

In addition to the morphological adaptations outlined above, grasses possess a suite of physiological traits that facilitate growth in environments that experience periodic or episodic drought, high light intensity, extremes in temperature, and pulses in nutrient availability. One of the most fundamental physiological characteristics of different grass species is the type of photosynthetic pathway used, and this is another way to distinguish between major grassland types. Throughout the world today, tropical, subtropical, arid, semiarid, and warm temperate grasslands are typically dominated by grasses that use a C_4 photosynthetic pathway (warm-season grasses), while grasses using the C_3 photosynthetic pathway (cool-season grasses) are more common in cooler grasslands at higher latitudes or higher elevations.

Most vascular plants (and ~50 % of all grass species) use the C_3 photosynthetic pathway. C_3 photosynthesis occurs in leaf mesophyll cells where the enzyme Rubisco catalyzes a reaction fixing a low-energy carbon source (atmospheric CO_2) to a five-carbon sugar (ribulose biphosphate), to form two molecules of a higher energy three-carbon organic acid (3-phosphoglycerate). With energy derived from the light reactions of photosynthesis, 3-phosphoglycerate is ultimately reduced to a single six-carbon sugar (glucose) that forms the metabolic template for all subsequent anabolic pathways in the plant. However, Rubisco is a nonspecific catalyst and can also catalyze the reaction of O_2 with the five-carbon backbone, ultimately resulting in a net loss of energy to regenerate ribulose biphosphate (a process termed photorespiration, which results in a net loss of fixed carbon). The affinity by Rubisco for O_2 over CO_2 , and therefore photorespiration, increases at higher temperatures and during geologic periods with low atmospheric CO_2 concentrations. These selective pressures are likely to have driven the evolution of the C_4 photosynthetic pathway.

C_4 photosynthesis is a more recent physiological and morphological modification of the C_3 pathway, having evolved over 50 different times and in many locations on Earth (Strömberg 2011). C_4 photosynthesis provides a growth rate advantage in the high-light and high temperature environments typical of many grassland regions worldwide. In C_4 photosynthesis, CO_2 is initially captured by the enzyme phosphoenolpyruvate carboxylase (PEP-C) in leaf mesophyll cells to form a four-carbon acid (oxaloacetate). Oxaloacetate is transported into specialized morphological tissues

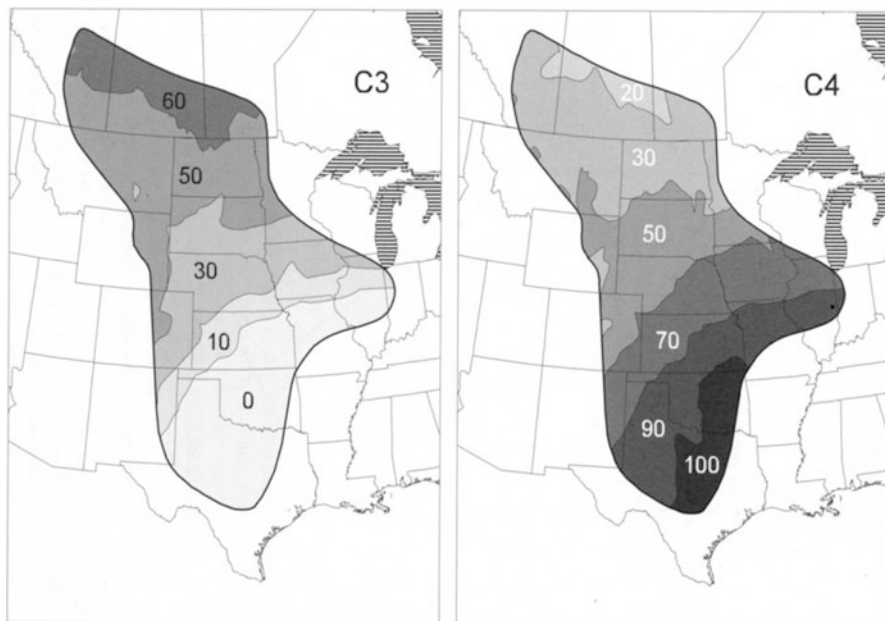


Fig. 8 Grasses with the C_4 photosynthetic pathway are more abundant in warmer grasslands of central US grasslands, whereas C_3 grasses show the opposite pattern. Similar patterns occur on other continents, indicating that differences in biochemical pathways of C fixation play a strong ecological role in the distribution and success of grasses (From Lauenroth et al. 1999)

named bundle sheath cells that typically surround the leaf conductive tissue. Once in the bundle sheath, oxaloacetate is decarboxylated, releasing CO_2 for Rubisco to fix and sugars to be formed using the C_3 photosynthetic pathway. The primary benefit of the C_4 photosynthetic pathway is the ability to concentrate CO_2 within the bundle sheath essentially eliminating the likelihood of photorespiration and maximizing the reaction kinetics of carboxylation by Rubisco. As such, the efficiency of energy capture and conversion into carbohydrates is maximized, and efficient photosynthesis can be performed in environmental conditions that otherwise would have high photorespiration (i.e., dry, hot, high-light environments). The advantage of C_4 grasses in warmer climates is evident in the proportions of C_4 versus C_3 grass species across latitudinal gradients (Fig. 8).

The C_4 photosynthetic pathway has multiple secondary benefits for the grass species that use this pathway. C_4 photosynthesis results in a higher instantaneous water use efficiency (ratio of CO_2 gained to water lost) because PEP-C has a higher affinity for CO_2 than does Rubisco. This allows grasses using the C_4 pathway more flexibility in regulating stomatal openings to reduce water vapor lost from the leaves via transpiration while maintaining adequate internal CO_2 concentrations for photosynthesis as soils dry down, relative to C_3 grasses. The high affinity of PEP-C for CO_2 also allows C_4 plants to photosynthesize at higher levels than

C₃ plants when atmospheric CO₂ concentrations are low. As a result, it has been hypothesized that the C₄ photosynthetic pathway may have evolved in response to declining atmospheric CO₂ concentrations during glaciation events of the Earth's history. Finally, because the efficiency of Rubisco is maximized in the high CO₂ environment inside the bundle sheath, less total Rubisco is required to maintain a given rate of carbon assimilation compared to C₃ photosynthesis. For this reason, the photosynthetic nitrogen use efficiency (PNUE) (ratio of C gained per unit N mass) is higher in C₄ plants, allowing for greater productivity in N-limited environments, including many temperate and tropical grasslands.

Roots

As noted previously, most grasslands are characterized by a large investment in root biomass and a high root to shoot ratio (Fig. 9). However, the root systems of different grasslands are highly variable in terms of species-specific patterns, total biomass invested, types of roots produced, and distribution throughout the soil profile. Many grass species share similar characteristics – fine roots that are highly branched, fibrous in nature, and concentrated in the upper soil profile (top 20–50 cm).

In contrast, the coexisting woody and herbaceous forb species in grasslands have root types that vary widely in terms of root types (fibrous, taproots, etc.), root depth distribution, and root to shoot biomass allocation. For this reason, most of our ability to generalize on the drivers of root structure and function in grasslands has been focused on the grasses. However, it is important to note that differences in rooting systems between the grasses and many forbs and woody plants may allow for differential use of soil resources, such as water and nutrients, and these differences can contribute to coexistence of different life forms in grasslands, as well as changes in the relative abundance of grasses and other plant life forms under changing environmental conditions. This concept of niche differentiation among grasses and woody plants was first described by Heinrich Walter and is known as “Walter’s two-layer hypothesis” (Walter 1971). This hypothesis was originally intended only for the semiarid savannas of the Southern Hemisphere, but the main concepts tend to apply to grasslands worldwide; grasses have a relatively fixed strategy of water uptake focused on surface soils, while woody plants have more plastic water uptake strategies and typically use considerably more water from deeper soil depths compared to grasses (Nippert and Knapp 2007).

The amount of root biomass varies markedly among grass species in different grassland types (mesic – semiarid – annual grasslands) as well as within a single site according to interannual variability in climate, topography, soil type, site management (fire and grazing frequency), and by depth in the soil profile. For many grassland types, the dominant grass species have very high root to shoot ratios (>3) illustrating a greater allocation of carbon to growth belowground versus aboveground. While nearly all grasslands are characterized by relatively large investments in belowground versus aboveground growth, this is typically greatest

Fig. 9 Exposed root biomass along an eroded stream bank at the Konza Prairie Biological Station (Photo by Jesse Nippert)



in grasslands with high water or nutrient limitation. In general, dry years (or adverse environmental conditions) tend to reduce overall grass growth including a reduction in root production. However, adverse environmental years tend to reduce the growth of shoots more than the growth of roots in most grasslands, though studies in the montane grasslands of Yellowstone National Park suggest that roots may be more sensitive to drought than shoots in some grasslands (Frank 2007). Changes in root production in response to disturbance tend to be mixed, varying according to ecosystem type and disturbance legacies. In tallgrass prairies that have been grazed or recently burned, root production can decrease by ~25 %, as grasses tend to allocate growth towards new leaf and stem production aboveground. The greatest reduction in root biomass production in these scenarios is in the uppermost soil layers (top 10 cm). In some other grasslands, increases in root turnover in the presence of grazers have been reported.

In addition to high relative belowground biomass (around 700–1,000 g m⁻² in mesic grasslands), the roots of many grasses extend deep into the soil profile (>2 m deep in mesic grasslands such as tallgrass prairie). Most grasses do not possess a tap root, but rather have long fibrous roots that taper with depth. The average depth distribution of roots in grasslands is generally correlated with mean annual precipitation and the depth distribution of water in the soil profile. Thus, the roots of grasses in arid grassland are much shallower than those in mesic grasslands (Fig. 10). Despite the presence of deep roots in some grasslands, the distribution of root biomass generally declines with soil depth, and majority of the biomass and total root length is concentrated in the upper soils.

The presence of grass roots at significant depths within the soil led early grassland ecologists to hypothesize that these roots served as a mechanism for drought avoidance. This hypothesis presumed that during periods of drought, deep roots would facilitate water uptake from deep soil zones recharged by infiltration from winter precipitation and maintain plant growth despite low water availability in surface soils. A closer examination of the unique physiology and morphology of

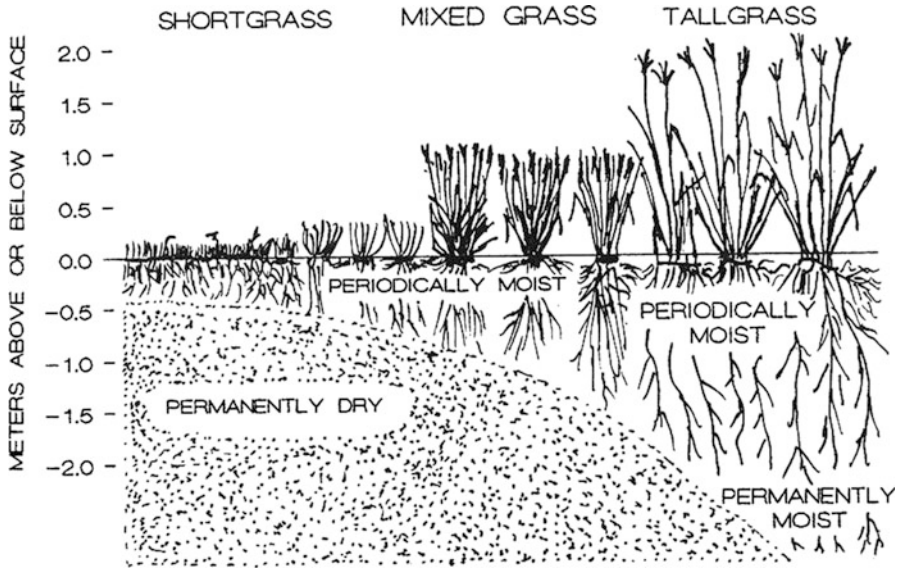


Fig. 10 Regional gradients in rainfall affects the distributions of major grassland types as well as mean root depth and root productivity, which in turn affect soil organic matter storage and other soil properties and processes (From Seastedt 1995)

grass roots has shown that drought tolerance is a more likely strategy used by many grass species (Nippert et al. 2012). For example, in soils with very low soil moisture, grasses can maintain carbon uptake despite tremendous negative physical pressures within the vascular tissues of the roots, stems, and leaves (up to -14 MPa, or nearly 58 times the pressure of automobile tires!). The ability to withstand these pressures without collapse is facilitated by vascular tissues with a greater number of vessels each with a smaller diameter. Thus, while many grasses can be deeply rooted, the small vessel number and diameter limits the total amount of water that can be transported from deeper soil depths, compared to the high root biomass and total root length present in surface soils. The unique physiology, morphology, and distribution within grassland soils provide a significant advantage for grass roots compared to forbs and woody plants to tolerate long periods of low water availability during drought.

Grasslands, Drought, and Climate Change

Despite the adaption of many grassland species to periodic water deficits, grasslands are sensitive to both short-term climatic variability (e.g., variability in rainfall patterns within and between years) and longer-lasting changes in climate (e.g., multiyear droughts or directional changes in prevailing climate). One of the most well-documented grassland responses to severe drought comes from the Central

Plains region of North America in the early twentieth century. The early 1930s marked the beginning of a series of successive droughts that resulted in very little rainfall over much of the Central Plains and extreme reductions in soil moisture in the top meter of soil. This period, known as the Great Drought, was characterized by low precipitation (persistent reduction by ~50 % than average), higher wind speeds, low humidity, and maximum air temperatures that were ca. 5–6 °C above average maximum values during the summer months (Weaver 1968). The combination of extended severe drought conditions and widespread unsustainable agricultural practices led to the Dust Bowl and the widespread loss of top soil throughout much of the southern and central Great Plains. Prior to the Great Drought, Prof. John E. Weaver at the University of Nebraska-Lincoln spent 5 years surveying the community composition of 60,000 sq. miles throughout the central Great Plains (Weaver and Fitzpatrick 1934). This survey provided the basis for assessment of changes imposed by the continued drought later in the decade, and Weaver provided the most detailed assessment of the role of drought on grassland community structure ever performed.

Initially, the first stages of the drought (1930–1931) resulted in little change in grassland community composition (Weaver 1968). However, as the drought continued from 1934 to 1940, it had profound consequences for grassland productivity and community composition. In the eastern areas dominated by tallgrass prairie, the initial and most dramatic response to the drought was the desiccation and widespread mortality of the dominant species, primarily big bluestem, *Andropogon gerardii* (then classified as *Andropogon furcatus*); little bluestem, *Schizachyrium scoparium* (then classified as *Andropogon scoparius*); Indian grass, *Sorghastrum nutans*; and Kentucky bluegrass, *Poa pratensis* (Weaver and Albertson 1939). The loss of cover of the dominant species resulted in the exposure of much bare ground (estimates range from 36 % to 100 % reductions in basal area of plant cover in the permanent quadrats studied by Weaver (1968)). The drought eventually impacted the entire grassland community, with high rates of mortality for forbs, woody species, and ruderal species. An increase in cover was reported by those species adapted to drier grasslands to the west (mixed-grass and shortgrass prairie – including western wheatgrass, *Agropyron smithii*; side-oats grama, *Bouteloua curtipendula*; and needlegrass, *Stipa spartea*). Changes in the relative cover of species (from tallgrass to shortgrass prairie species) did not occur by immigration of individuals or seeds, but rather by changes in cover of species that were present, but less abundant (<1 % of cover), prior to the drought (Weaver and Albertson 1939). In all, the replacement of “true prairie” (i.e., tallgrass prairie) by mixed-grass and shortgrass prairie species occurred over an extensive range (~150 mile wide band) and within a period of 7 years. While community replacement did occur (from bluestems to xeric species), large reductions in basal cover (>50 %) persisted. The dramatic changes recorded during the Great Drought are best expressed by Weaver (1944, pp. 128–129):

The drought has shown clearly that nature has richly endowed True Prairie with many species, some of which are best adapted to cover the soil, enrich it, and hold it against the forces of erosion during moist climatic cycles. Others which are then found in such small

amounts that they seem almost a non-essential part of grassland rapidly increase to great abundance and become of great importance when a severe drought cycle occurs. This is what happened in the 1934–1940 drought and must have occurred many times in the historical and geological past, although no written record has been made.

Once the long period of drought ended, bare ground was colonized by ruderal (i.e., early successional) species common to disturbance (Weaver 1944). Stands of western wheatgrass, needlegrass, and buffalo grass (*Buchloe dactyloides*) that had increased during the drought remained resistant to immediate invasion for the first few years after drought (although species composition and cover ultimately returned to pre-drought conditions in the decades to follow). In regions where the bluestem cover was reduced, but not lost altogether, recovery to pre-drought abundance occurred within several years via rhizome extension into bare patches. Finally, for many of the original dominant perennial grasses (bluestems) as well as the forb species, recovery occurred via dormant rhizomes, root crowns, bulbs, and corms that persisted in the soil for the duration of the drought (without production of aboveground stems or leaves). Originally classified as “dead” years before, these individuals reinitiated growth 2–3 years following the drought from their decade of belowground “dormancy” [term used by Weaver – 1944]. Thus, the recovery of the tallgrass prairie was spatially and temporally varied – with quick recovery (~years) in locations where species persisted at low abundance but slow recovery (~decades) in locations where bare patches allowed the development of new grassland communities or replacement by mixed-grass or xeric prairie species.

The responses of grasslands to historic droughts may provide some insights into possible responses to future climate changes. Many climate change predictions for regions currently occupied by grasslands include more extreme weather patterns and increased temperatures, which may combine to reduce soil water availability and increase plant stress. Past responses to drought suggest that such climate changes may result in mortality and reduced cover of species adapted to wetter climates and possible replacement of those species with other adapted to drier conditions. Such changes in climatic conditions and species distributions would also be accompanied by changes in a suite of ecological processes, such as primary productivity, decomposition, nutrient cycling, soil formation, and species interactions. The degree to which species distributions and community boundaries shift in under a future climate may depend on the rate at which climate changes occur, the severity of those changes, and whether those changes are transient or represent a more permanent shift in prevailing climates.

Fire in Grasslands

Grasses produce shoots that when senescent or dormant leave behind fine combustible fuel in the form of surface plant litter (detritus) and standing dead grass biomass. The accumulation of highly flammable plant litter coupled with periods of drought, relatively open landscapes, and windy conditions is highly conducive to large-scale fires (Fig. 11). As a result, fire is (or was) an important force in many

Fig. 11 Although fire can be a destructive force in some ecosystems, fire is an important natural disturbance in many grasslands. Historically, fire was particularly important in moist, productive grasslands, such as North American tallgrass prairie, and it remains an important tool for the preservation of these grasslands today (Photo by Eva Horne)



grasslands around the world, though the frequency and intensity of fire varies as a function of precipitation (or soil water availability) and aboveground productivity. Historically, many grassland fires originated as a result of lightning strikes or due to the activities of aboriginal humans. Once ignited, fire could sweep relatively unimpeded through large areas of open grassland that lacked natural fire breaks, and fires are generally thought to have been widespread and common in many of the extensive grassland regions around the world. The higher productivity of more mesic grasslands would have promoted more rapid and larger accumulations of combustible fuel, and so fires were likely more frequent in mesic than arid grasslands. However, even desert grasslands can burn once sufficient fuel accumulates, and some arid grasslands are more often now as a result of introduced annual grasses that promote more frequent fires.

The intensity of grassland fires vary, depending on such factors as fuel load (accumulated biomass), fuel condition (compaction, moisture content, etc.), relative humidity, wind speed, and topography. Grassland fires can be very intense and can generate sufficient heat aboveground to damage the aboveground shoots of woody plants (“top kill”) or even kill entire trees. However, because these fires tend to move rapidly and much of the fuel is above the ground, most of the heat is concentrated aboveground and temperatures peak quickly as fire passes. Heat transfer into the soil is generally small, and soil heating into the range that is biologically damaging ($>60\text{ }^{\circ}\text{C}$) occurs only at the surface. Thus, the belowground buds and meristematic tissues of the grasses and many other grassland plants are well protected against even the most intense grass fires. This is an important contrast to other ecosystems (e.g., forests and woodlands), where the effects of fire are often associated with an immediate negative impact on plant mortality and even the effects of soil heating on loss of soil organic matter and nutrients and changes in soil microbial communities. For grasslands, many of the most significant effects of fire are indirect and result from changes in the postfire environment, rather than the effects of the fire per se. Recovery from a fire event in grasslands in

terms of new plant growth and accumulated aboveground biomass is generally very rapid, especially for mesic grasslands. Recovery in more arid or desert grasslands may take considerably longer.

Changes in natural regimes and/or fire suppression have been implicated as one of the major drivers of contemporary land-cover change in many grasslands worldwide. In many instances, this is a function of a reduction in the frequency or intensity of fires relative to their historical occurrence and subsequent increases in woody plant cover or, in some cases, the conversion of grasslands to shrublands, woodlands, or forest. However, there are also cases where increasing fire frequency is the driver of land-cover change, such as the positive feedbacks between grass cover and fire associated with the spread of invasive fire-prone grasses into ecosystems that were historically less susceptible to fire (e.g., the spread of cheatgrass (*Bromus tectorum*) throughout Western US shrublands). Prescribed fire has also become an important management tool in many grasslands, such as tallgrass prairies where it is used to limit the growth of woody plants and to promote the growth and vigor of the dominant C₄, or warm-season, grasses. Because of its importance in the development and persistence of tallgrass prairie, research on the effects of fire has been a major emphasis of the Konza Prairie Long-Term Ecological Research Program. Fire alters many aspects of prairie ecosystem structure and functioning. At Konza Prairie, over 20 years of data on the effects of different fire regimes, including annual spring burning and infrequent burning (every 10–20 years), has been amassed. Below examples from these studies have been used to illustrate some of the ecological effects of grassland fires.

Although fires can occur at anytime of the year, dormant season fires are generally most common in grasslands. In tallgrass prairie, burning at the end of winter dormancy (i.e., early spring) is a common management practice. Spring burning generally increases total plant productivity by stimulating growth of the warm-season grasses, particularly in times (wet years) or locations (deeper soils) with adequate soil water available. This is due primarily to the removal of the large amount of plant detritus (up to 1,000 g m⁻²) that accumulates in the absence of the fire and the changes in microclimate and soil resource availability induced by the removal of detritus (Knapp and Seastedt 1986). This detritus acts as a mulch layer, insulating the soil surface and greatly limiting light availability for emerging plants. The removal of this accumulated surface detritus and standing dead biomass alters the energy environment and microclimate of the soil. Direct solar inputs to the soil increases soil temperatures as much as 20 °C in the early spring, relative to comparable unburned grasslands. The warmer temperatures promote earlier emergence and more rapid spring growth, especially for the dominant warm-season grasses. In most years, these changes in the soil microclimate promote the growth of the dominant warm-season grasses, as long as there is adequate water in the soil profile. However, removal of the detrital layer also enhances evaporation from the soil surface, and in dry years or shallow soils, this can reduce productivity following fire. This is also a reason that the effects of fire on plant productivity vary across precipitation gradients, with positive effects in wetter grasslands and neutral or negative effects in drier grasslands.

In tallgrass prairie and other mesic grasslands, the enhanced growth of the grasses also increases their ability to compete for limiting resources with other plant species, leading to another effect of frequent fires – a reduction in overall plant species richness and diversity due to reductions in the abundance and cover of many subordinate species, including the cool-season graminoids and the forbs that provide much of the biodiversity in tallgrass prairie. Thus, frequent burning generally increases plant productivity, but lowers plant diversity, at least in ungrazed prairie. The presence of grazers that preferentially graze on warm-season grasses can offset this effect and changes the relationship between fire and plant diversity, as discussed in the next section.

In addition to its more apparent effects on prairie vegetation, fire alters nutrient cycling processes in these grasslands (Blair et al. 1998). The most important effects involve changes in the cycling of nitrogen. Nitrogen (N) is an essential plant nutrient which often is in short supply relative to plant demand, and the availability of N limits plant productivity in many ecosystems. Based on fertilizer studies, N availability has been shown to limit plant productivity in tallgrass prairies. However, N limitation is not a universal characteristic of tallgrass prairie and, in fact, depends on management practices, such as fire and grazing, and on other external factors, such as climate and topography. In addition to its effects on plant productivity, N availability can alter competitive interactions among plant species and, therefore, plant community composition. Nitrogen availability is a major determinant of plant nutritional quality for herbivores, and the N content of plant litter influences rates of litter decomposition and therefore the storage of organic matter in tallgrass prairie soils. Understanding how N cycling processes are altered by different land-use practices, such as burning, is an important prerequisite to understanding and predicting grassland ecosystem responses to these practices.

When plant detritus burns, some nutrients are lost with the smoke and gases, while others are released and deposited in the ash. Much of the nitrogen contained in surface detritus and plants is volatilized, or converted to gaseous forms, in the heat of a prairie fire, while other heavier elements such as phosphorus and many cations are simply deposited in the ash. The volatilization of nitrogen by fire is the major pathway by which nitrogen is lost from the prairie (especially ungrazed prairie), and frequent fires represent a substantial loss of the prairie's nitrogen capital. Nitrogen cycling in frequently burned prairie is further altered by the responses of the grasses, which produce more root biomass and produce plant tissue which is lower in N content, or which has a higher C/N ratio. The increased input of organic matter with a wider C/N ratio stimulates nitrogen immobilization by soil microbes, leading to even greater N limitation under frequent burning regimes. Thus, the loss of N, along with the increased growth of the grasses, greatly reduces the amount of available N in the soil and increases N limitation for the plants growing in frequently burned prairie. An important question is how a frequently burned prairie can maintain higher productivity than unburned prairie, in spite of increased N limitation. This appears to be, in part, to the increased abundance of warm-season grasses and the high efficiency with which these grasses utilize N, giving them a competitive advantage over other coexisting plant types.

Grazing in Grasslands

Grazing is a form of herbivory in which herbaceous plants (grasses and forbs) are consumed by herbivores (Fig. 12). This process differs from browsing in which the leaves and woody twigs are consumed from trees and shrubs. Grazing is, or was historically, an important process in nearly all grasslands and is considered a key factor affecting species composition and biomass production in grassland ecosystems. The relationship between grazers and grasslands has developed over millions of years, and it is likely that grazers and grasslands ecosystems coevolved. Grazers promote heterogeneity in grasslands by selectively consuming some species while leaving others, through trampling, soil compaction, soil tunneling, and redistribution of nutrients.

Grazing occurs both aboveground (leaves and stems) and belowground (fine roots and root hairs) by a wide variety of animal herbivores from microscopic invertebrates to the large mammalian megafauna. In general, while a relatively low density of the largest grazers (e.g., bison, wildebeest, zebra) can consume a significant proportion of plant biomass, many small rodents or numerous invertebrates can have comparable impacts within the same grassland when their densities are high enough. Grazers can have a tremendous impact on grasslands through their effects on plant populations and community composition, on energy flow and nutrient cycling in grassland ecosystems, and on landscape-level heterogeneity and movement of materials (McNaughton 1985; Knapp et al. 1999). Although some grasslands (the tallgrass prairies of North America or the Serengeti grasslands of Africa) appear to be well adapted to relatively high grazing intensities, other grasslands can be quickly degraded by overgrazing. When managed in an unsustainable fashion (e.g., overgrazing), large ungulates can significantly impact grassland health and sustainability.

Spatial and temporal patterns of activity by grazers can be greatly affected by fire and grazing by large herbivores and, in turn, can greatly alter the effects of fire in grasslands (Fig. 13). These interactive effects of fire and grazing are especially important in mesic temperate and tropical grasslands. Many large grazers are attracted to recently burned areas, as the removal of detritus and the emergence of new grasses provides a high-quality grazing areas. Intensive grazing in these areas can lead to selection for high-quality grazing tolerant grasses and the formation of a “grazing lawn.” At the same time, increased grazing intensity in burned areas removes aboveground biomass that would otherwise accumulate and serve as fuel for future fires. As a result, fire and grazing in extensive grasslands can be spatially and temporally dependent on each other and can transform the grassland landscape into a dynamic mosaic of shifting patches that vary in time since fire, grazing intensity, and fuel accumulation (Fuhlendorf and Engle 2011). This spatiotemporal interaction of fire and grazing has been referred to pyric herbivory, a term that highlights the codependence of fire and grazing in many natural grasslands. This same principle is the basis of a proposed alternative management practice called patch-burn grazing, which is designed to mimic the interaction of fire and grazers to promote greater heterogeneity and habitat for wildlife in grasslands managed for production of domestic grazers (i.e., cattle).

Fig. 12 Large vertebrate grazers, such as these North American bison (*Bison bison*), can modify the plant species composition and the flow of energy and resources within grassland ecosystems (Photo by Matt Whiles)

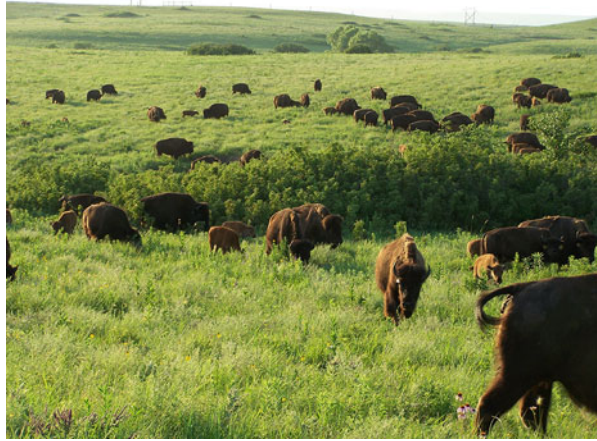
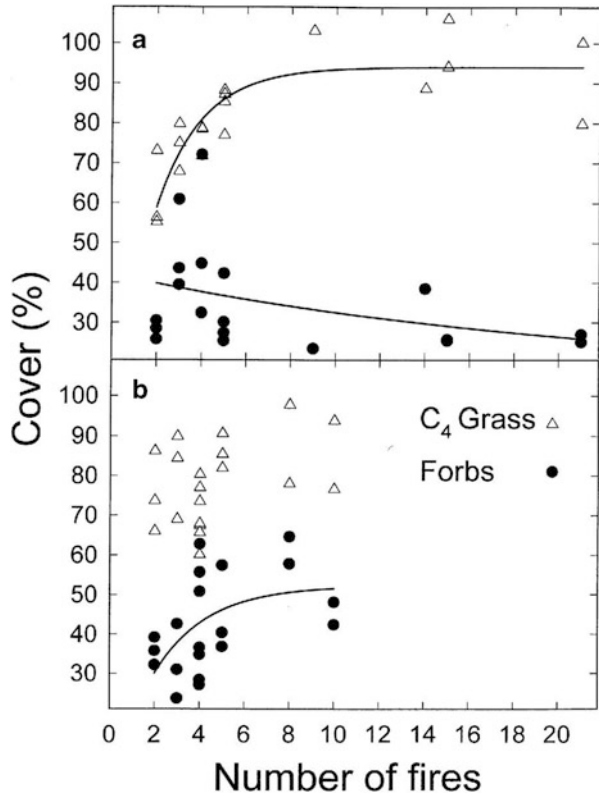


Fig. 13 There are often significant interactions between fire and the activities of grazers, as illustrated by the patchy nature of fire in areas that are grazed by bison. Grazers are often attracted to fresh grass regrowth in areas that were previously burned, but the activities of grazers can reduce fine fuel to carry future fires resulting in a mosaic of burned and unburned patches, as shown here (Photo by John Briggs)



As noted in section “[Fire in Grasslands](#),” fire in ungrazed mesic grasslands often reduces heterogeneity and lowers species diversity by removing detritus, reducing woody plant cover, and promoting the dominance of grasses that respond positively to fire. However, large ungulate grazers selectively feed on many of these same grasses.

Fig. 14 Effects of fire frequency on the abundance (cover per 10 m²) of warm-season (*C*₄) grasses and forbs in ungrazed tallgrass prairie (A) and in tallgrass prairie grazed by bison (B). In ungrazed prairie, more frequent fire greatly increases the abundance of the dominant *C*₄ grasses and decreases the abundance of forbs, which results in lower overall plant diversity. However, the presence of grazers offsets these effects and increases the relative abundance of forbs even with more frequent fires (From Collins et al. 1998)



Thus, grazing can offset the reduction in species diversity that results from frequent burning of productive grasslands such as tallgrass prairie by reducing grass dominance and increasing plant species diversity in areas that have been burned (Fig. 14). In xeric grasslands, on the other hand, grazing may lower species diversity particularly by altering the availability of suitable microsites for forb species. These effects are strongly dependent on grazing intensity. Overgrazing may rapidly degrade grasslands to systems dominated by weedy and nonnative plant species.

Most grazers are highly selective in the plants they consume. This selectivity results in a landscape with heterogeneous species composition and patchy nutrient distributions. Plants that lose tissues to grazing must use assimilated carbon and nutrients to regrow leaves (or roots), leaving less palatable species to grow taller and increase in number. Many large grazers such as African buffalo, North American bison, or domesticated cattle primarily consume the grasses, allowing less abundant forb species to increase in abundance and new species to colonize the space that is made available. In more productive grasslands adapted to the activities of grazers, grazing can be an important management tool to increase biodiversity when managed at appropriate stocking rates.

Grazers also accelerate the conversion of plant nutrients from forms that are unavailable for plant uptake to forms that can be readily used. Essential plant nutrients, such as nitrogen, are bound for long periods of time in unavailable (organic) forms in plant foliage, stems, and roots. These plant parts are slowly decomposed by microbes, and the nutrients they contain are only gradually released in plant-available (inorganic) forms. This decomposition process may take several years. Grazers consume plant tissues, process this material inside the gut, and excrete nutrients that are available for uptake by plants back onto the landscape. This nutrient processing happens rapidly compared to the slow decomposition process, and nutrients are excreted in high concentrations in small patches. Thus, grazers may increase the availability of potentially limiting nutrients to plants as well as alter the spatial distribution of these resources.

Some grasses and grassland plants can compensate for aboveground tissue lost to grazers by growing faster after grazing has occurred. Thus, even though ~50 % of the grass foliage may be consumed by large grazers, when compared to ungrazed plants at the end of the season, the grazed grasses may be only slightly smaller, the same size or even larger than ungrazed plants. This latter phenomenon, called “overcompensation,” has not been shown in all grassland ecosystems, but the ability of grasses to compensate partially or fully for foliage lost to grazers is well established. Compensation occurs for several reasons including an increase in light available to growing shoots in grazed areas, greater nutrient availability to regrowing plants, and increased soil water availability (because less water is being lost via leaf transpiration compared to an ungrazed dense plant canopy).

As with fire, the impact of grazing on grasslands and the ability of grasslands to tolerate heavy grazing depend upon where the grassland occurs (usually more mesic grasslands can recover more quickly than arid grasslands) as well as the growth form of the grasses within the system: caespitose (bunch-forming grasses) versus rhizomatous grasses. But another key factor determining the ecological responses of grasslands to grazing is the evolutionary history of the grassland (Fig. 15). In general, grasslands with a long evolutionary history of grazers, as in Africa and North and South America, are very resilient to grazing. The evolution of this resilience may reflect the migratory nature of most herds of large grazing mammals. Historically, herds of thousands (and up to millions) of grazers moved across African and North American landscapes in response to seasonal cues and availability of resources. While the impact of these large herds has (or had in the case of North America) a tremendous impact on the grasslands, the animals spend only a small period of time within a given location, allowing for periods of recovery before the next grazing event.

Due to the ability of grasses to cope with high rates of herbivory, many former natural grasslands are now being managed for the production of domestic livestock, primarily cattle in North and South America and Africa, as well as sheep in Europe, New Zealand, and other parts of the world. Grasslands present a vast and readily exploited resource for domestic grazers. However, if not managed properly, grasslands can be easily overexploited with subsequent land degradation, nutrient loss, and susceptibility to invasion by undesirable plant species.

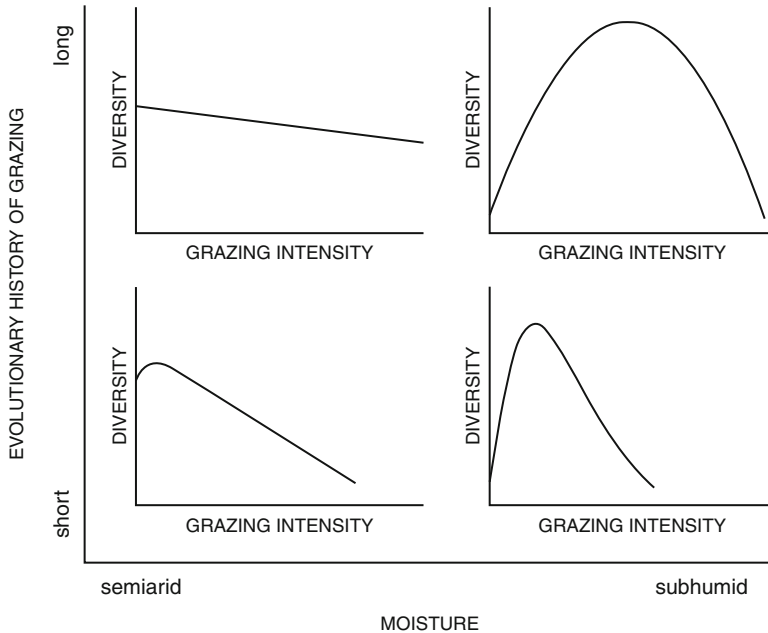


Fig. 15 Response of grassland plant communities to grazing intensity as a function of moisture gradients and grazing evolutionary history (From Milchunas et al. 1988)

Potential Threats to Grassland Conservation

Although grasslands are the natural vegetation of much of the Earth's terrestrial surface, many grassland communities and ecosystems are among the most impacted and endangered in the world. Why is this? In many parts of the world, grasslands are the natural vegetation on some of the most ecologically productive lands with high levels of soil nutrients and an open rolling topography conducive to cultivation or ranching. Consequently, many grasslands around the globe have been cultivated and converted to agriculture use or are intensively managed for the production of domestic livestock. As a result, both the spatial extent of native grasslands and the quality of remaining grasslands is declining. This is due primarily to human-induced modifications such as agriculture, excessive or insufficient fire, livestock grazing, fragmentation, and invasive plants and animals. Precise estimates of the areal extent of these changes are difficult to come by as there is no international organization tracking grasslands and because of the difficulty in identifying what is grassland and what is not. In addition, it is known that all croplands were developed from either forests or grasslands. In that respect, since areas of cropland are expanding, it can be assumed that on the whole, grassland areas are continuing to decline. On the other hand, large areas of tropical rainforests are being cleared to

provide pasture for livestock. Therefore, grasslands – at least in the form of pastures – may be expanding in some localized areas.

Recent estimates suggest that a large percentage of the Earth's total grazing land has been degraded to the point that it has lost some of its animal carrying capacity. Even though the damage from overgrazing is spreading, the world's livestock population continues to grow in step with increases in the human population and a growing demand for meat that accompanies increased wealth; thus, grasslands will continue to deteriorate. As world population increased from 2,500 million in 1950 to over 7 billion, the world's cattle, sheep, and goat populations have also grown exponentially. As a result of overstocking and overgrazing, grasslands in much of Africa, the Middle East, Central Asia, the northern part of the Indian subcontinent, Mongolia, and much of northern China are deteriorating. While grazing was once a pastoral activity that involved people moving with their herds from place to place, it has become a far more sedentary undertaking. The result is an increase in grassland degradation worldwide.

In addition to grazing, grassland environments are the basis for major agricultural areas worldwide. Historically, the major threat to the mesic grasslands of the United States (and world) was cultivation of soils and conversion to row-crop agriculture. Although the conversion of grasslands to agriculture continues today (especially with increased demand for biofuels; Fargione et al. 2008), some of the most significant losses of grasslands now are related to changing land management coupled with other global change phenomena. Temperate grasslands are important from both agronomic and ecological perspectives. As mentioned earlier, many of the most productive temperate grasslands in North America and elsewhere are considered to be endangered ecosystems. For example, in the United States, up to 99 % of native tallgrass prairie ecosystems in some states have been plowed and converted to agricultural use or lost due to urbanization. Similar but less dramatic losses of mixed and shortgrass prairies have occurred in other areas.

While the loss of native grasslands due to agricultural conversion and urbanization is ongoing in many locations around the world, another major threat is the dramatic increase in shrubs and trees (many of them native species) now occurring in many grasslands (Briggs et al. 2005). Increases in the abundance and cover of native woody plant species in areas that were historically grass dominated can occur as a result of expansion of woody plant cover within grasslands as well as encroachment of woody species into grasslands from adjacent ecosystems. In many cases, these are tree species that were historically present in grasslands, but at a relatively low abundance. In other cases, grasslands are being invaded by nonnative woody plants. Recent increases in cover and abundance of woody species in grasslands and savannas have been observed worldwide, with well-documented examples from North America, Australia, Africa, and South America. In North America, this phenomenon has been documented in mesic tallgrass prairies of the eastern Great Plains, in subtropical savannas of Texas, in desert grasslands of the southwest, and in shrub steppes of the upper Great Basin. Some of the purported drivers of increased woody plant cover include changes in climate, increased

atmospheric CO₂ concentrations, elevated nitrogen deposition, altered grazing pressure, and changes in disturbance regimes, such as the frequency and intensity of fire. Although the drivers of woody plant expansion may vary for different grassland types, the consequences for grassland ecosystems are strikingly consistent. In most areas, the expansion of woody species increases above ground biomass and thus aboveground carbon storage, but at the same time reduces biodiversity of native grassland fauna and flora. However, the full impact of woody plant encroachment on grassland environments remains to be seen.

Another contemporary threat to native grasslands is the increase of nonnative grass species. For example, in California it is estimated that an area of approximately 7,000,000 ha has been converted to grassland dominated by nonnative annuals primarily of Mediterranean origin. Conversion to nonnative annual vegetation was so fast, so extensive, and so complete that the original extent and species composition of native perennial grasslands are unknown. In addition, across the Western United States, invasive exotic grasses are now dominant in many areas and these species have a significant impact on natural disturbance regimes. For example, the propensity for annual grasses to carry and survive fires is now a major element in the arid and semiarid areas in western North America. In the Mojave and Sonoran deserts of the American Southwest, in particular, fires are now much more common than they were historically which may reduce the abundance of many native cactus and shrub species in these areas. This annual-grass-fire syndrome is also present in native grasslands of Australia and managers there and in North America are using growing season fire to try to reduce the number of annual plants that set seed and thus reduce the population, usually with very mixed results.

Grassland Restoration

Given the ecological importance and extensive loss or degradation of grasslands globally, it isn't surprising that grassland restoration has become increasingly important and widespread, especially in locations where substantial areas of native grasslands have been lost as a result of land-use or land-cover change. Grassland restoration often takes place on formerly cultivated lands and involves reintroduction of native species characteristic of grasslands in that particular region. However, there are other types of grassland restoration, including restorations that target reductions in woody plant cover in areas that have experienced woody plant encroachment or those that target the removal of invasive species and their replacement with native grassland species. The motivation for these restoration efforts varies from restoring native plant biodiversity, to restoring ecosystem processes that provide environmental benefits (e.g., limiting soil erosion and improving water quality, sequestering carbon), to providing suitable habitat for regional native fauna. There are multiple difficulties associated with restoring grassland communities and ecosystems, fragmentation of historically extensive areas of intact grassland, loss of genetic diversity of grassland plant and animal populations, and insufficient area to include some of the drivers that were historically important in

shaping grasslands, such of landscape-level patterns of fire and grazing. Nevertheless, there are widespread efforts to restore native grassland diversity and ecosystem functioning.

Much research has focused on restoring temperate grasslands in North America, particularly in the tallgrass prairie region where the cover of native tallgrass prairie has declined 82–99 % since the 1830s, primarily as a result of cultivation for agricultural use. Dispersal of native grasslands plants into abandoned agricultural fields is very limited, and many areas targeted for grassland restoration are isolated from potential native seed sources. As a result, restoration of these grasslands typically begins with the introduction of seeds or transplants of native plant species. One of the earliest attempts to restore tallgrass prairie on ex-arable land began in the 1930s at the Curtis Prairie in Madison, WI. Since then numerous prairie restorations have been initiated at a range of spatial scales, and recent decades have seen a sharp increase in efforts to restore prairie for both conservation and research purposes. In fact, restored grasslands are being used to address a variety of basic and applied ecological questions, such as the relationship between species diversity and ecosystem function, the role of resource heterogeneity in structuring plant communities, or the role of dominant species in community assembly (Baer et al. 2003, 2005). It has even been suggested that restoration can serve as an “acid test” of our understanding of community assembly.

Reestablishing the dominant grass species in restored grasslands is relatively easy. However, it is difficult to establish and maintain many of the less common species that provide the majority of biodiversity in native prairies. As a result, restored grasslands generally have much lower diversity than comparable native grasslands. Even when initial seed mixtures include a diverse assemblage of subdominant and rare forbs, establishment of these species may be poor. In addition, the cover of the dominant warm-season grasses tends to increase over time in many restored grasslands, with a concurrent loss of rarer species, such that diversity declines over time. Overseeding (adding additional seeds to restored grasslands) is sometimes used in an effort to overcome potential dispersal limitations and enhance recruitment of new species in older restorations. However, the underlying reasons for loss of diversity are unclear, and additional studies are needed to assess the relative importance of dispersal limitations, interspecific competition, resource heterogeneity, herbivory, or other factors on limits to diversity in restored grasslands.

The restoration of grasslands on former agricultural soils can provide other benefits, including reduced soil erosion, greater nutrient retention, and providing a sink for atmospheric CO₂. One of the well-documented effects of cultivation is the loss of a significant proportion of carbon stored in the form of soil organic matter. Cultivation of grasslands reduces inputs of plant-derived new organic matter and the disruption of soil structure coupled with improved aeration greatly increased microbial mineralization of stored soil carbon. As a result, grasslands can lose from 20 % to 50 % of their organic carbon content within a few decades of cultivation. Eventually, these cropland soils come to a new equilibrium soil C content that is much lower than the grassland soils they replaced. However, if these fields are

removed from cultivation and restored with perennial grasses and forbs, the soil carbon pools will increase as new perennial root systems redevelop, new C inputs are added to the soil, and soil structure begins to reform. Several studies have documented significant rates of carbon accrual, generally in the range of 20–60 g C m⁻² year⁻¹, and suggested that these rates could persist for decades until a new equilibrium is reached. It is important to point out, however, that although some soil C (and N) pools in restored prairie may approach those of native prairie within a few decades, it may take much longer for other soil properties (e.g., soil aggregate structure or soil microbial communities) to recover.

Future Directions

Below are a few suggestions regarding future research directions that are particularly relevant to grassland conservation and management. This is not an exhaustive list, but rather meant to stimulate further discussions about the scope and directions of future research required for an improved understanding of grassland ecology and the maintenance/conservation of these ecosystems around the world.

- It is essential to develop a mechanistic understanding of how grasslands are responding and will respond in the future, to multiple global change phenomena, including changes such as enhanced N deposition, altered climate, and elevated CO₂ changing land use and land cover. Additional multifactor experiments are needed to address the interactions of global changes driver that occur in combination. Better forecasting of potential responses to environmental changes will improve both conservation goals and the sustainable use of grassland resources.
- A better understanding of the factors that affect the success of grassland restoration efforts is needed. While many studies have focused on deterministic factors, such as site preparation, seed sources, and seeding rates, additional studies that address the relative importance of stochastic factors (e.g., climatic variability, in establishment years) are also needed. This information will be critical for designing more effective methods of restoring grassland in areas where they have been degraded or extirpated.
- Effective management and conservation of grasslands will require a better understanding of social and economic drivers. One example of a newly emerging threat is the increase in restrictions on the use of grassland fires for management and conservation due to human health concerns. There is a need to explore other methods to minimize the negative effects of burning (e.g., impacts of smoke on air quality) in areas where fire is essential for maintaining grassland flora and fauna or perhaps ways to “simulate” some of the major ecological effects of fire to achieve desired management goals.
- Understanding the abiotic and biotic conditions that result in variable responses to grazing in different grasslands has both basic and applied significance. Many studies report contrasting effects to grazing, for example, with respect to root productivity and belowground carbon allocation. Similar conflicting results have been reported to for a suite of other responses. The occurrence of grazing in most

grasslands, and increased reliance on rangelands as a source of food for a growing human population, increases the importance of understanding grassland-grazer interactions and designing more sustainable means of managing grasslands for multiple goals in a changing environment.

- Linking theory to conservation, grasslands may serve as the first terrestrial ecosystem in the development of “warning signs” that signify a pending transition to an alternate ecosystem attractor (state shift). These warning signs would allow land managers and conservationists to employ adaptive management techniques to avoid the rapid conversion of grassland to shrubland or grassland to degraded states.

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