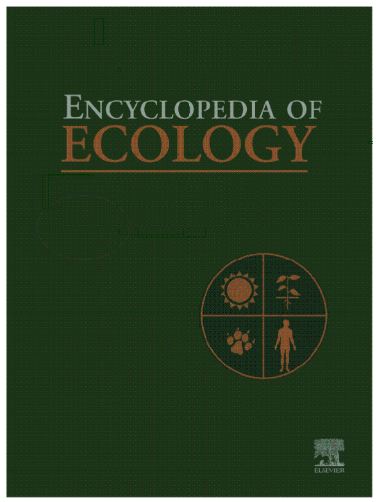

J M Briggs, A K Knapp, and S L Collins. Steppes and Prairies. In Sven Erik Jørgensen and Brian D. Fath (Editor-in-Chief), Ecosystems. Vol. [4] of Encyclopedia of Ecology, 5 vols. pp. [3373-3382] Oxford: Elsevier.

the incorporation of prior knowledge and encouraging a fuller representation of uncertainty, the Bayesian methods are especially useful for the purpose of providing support to managers and decision makers.

Ideally, the way in which data are collected and recorded should be determined by their anticipated use. However, the reality is that most modeling exercises begin only after the relevant data are already in hand. Therefore, the modeling framework often has to be chosen to accommodate the format of the data, rather than vice versa. Throughout this article, the data type used in each model has been explicitly identified. For example, **Table 1** provides an overview of how the use of discrete or continuous variables will dictate the linear regression-based modeling method that is appropriate. Similar concerns arise for nonlinear, nonregression-based frameworks as well. For example, using continuous variables in a BBN implies the use of continuous conditional probability density functions (PDFs) characterizing the relationships among nodes, while categorical variables require discrete probabilities (i.e., histograms). Different algorithms for prediction and inference have been developed for these two situations.

See also: Structural Dynamic Models.

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Steady State Models *See* Empirical Models

Steppes and Prairies

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Steppes and prairies (grasslands) are ecosystems that are dominated by grasses and to help understand grasslands, it is important to know something about grass morphology and growth forms. The remarkable ability of grasses to thrive in so many ecological settings and their resilience to disturbance is largely attributable to their growth form. Grasses are characterized by streamlined reduction and simplicity with tillers being the key adaptive structural element of the plant (**Figure 1**). Tillers originate from growing parts (meristems) typically just near, at, or below the surface of the soil. The meristems that produce tillers are generally well protected by their location near or beneath the soil surface. It is the location of the meristem that

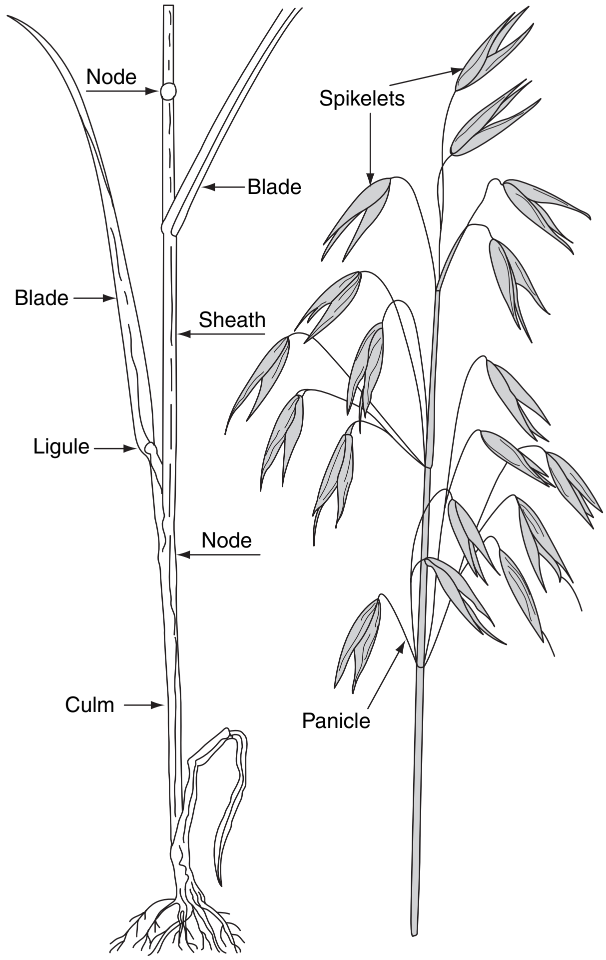

Figure 1 Common oat, *Avena sativa*, ×½. From Hubbard (1984).

explains much of the resilience of grasses and thus grasslands to disturbance.

Grass leaves are narrow and generally well-supplied with fibrous supporting tissue that has thick-walled cells. These features, along with a capacity to fold or roll the leaves along the vertical plane, permit the plant to endure periods of water stress without collapse. Another feature of grass leaves is the presence of siliceous deposits and silicified cells (phytoliths). Although silica is present in many plant families, phytoliths are characteristic of grasses. Phytoliths often have distinctive forms within taxonomic groups and since they persist in soil profiles for a very long time, they can be used by paleobotanists to determine shifts in dominance from one grass form to another. Silica also makes grass forage very abrasive and it is now generally accepted that the evolution of abrasion-resistant teeth present 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. But recent discovery of grass phytoliths in Late Cretaceous dinosaur coprolites in India suggest that grasses were already substantially differentiated and that abrasive phytoliths were present in many grasses before the explosion of grazers in the Oligocene and Miocene time periods.

Grasses show a very large variation in the way tillers are aggregated as they expand from their origin, but two general forms of grasses are recognized: bunch-forming (caespitose) and sod-forming (rhizomatous). This description captures the major features of the dominant grass species but there are some species and groups that deviate from this general pattern. The most obvious include the woody bamboos (some of which can reach tree size and for the most part are restricted to forest habitats in the tropics and subtropics).

In addition to growth form, grasses can also be roughly divided into two categories based upon their photosynthetic pathways: cool season (C_3) and warm season (C_4). C_4 photosynthesis is a variation on the typical C_3 pathway and is thought to have an advantage in high-light and -temperature environments typical of many grassland regions worldwide. Throughout the world today, tropical, subtropical, arid, semiarid, and mesic grasslands are typically dominated by C_4 grasses while in cooler high-elevation or northern climates, C_3 grasses are more common.

Grasslands

As mentioned above, ecosystems in which grasses and grass-like plants (including sedges and rushes and collectively known as graminoids) dominate the vegetation are termed grasslands. In its narrow sense, 'grassland' may be defined as ground covered by vegetation dominated by grasses, with little or no tree cover. UNESCO defines grassland as "land covered with herbaceous plants with less than 10 percent tree and shrub cover" and wooded grassland as 10–40% tree and shrub cover. Grassland ecosystems are notable for two characteristics: they have properties that readily allow for agricultural exploitation through the management of domesticated plants or herbivores, and a climate that is quite variable both spatially and temporally. They are found in regions where drought is fairly common but where precipitation is sufficient for their growth. In addition, they can also dominate wetlands in both freshwater and coastal regions. They also occur in sites where more predictable rainfall occurs and soils are shallow or poorly drained, or in areas with topography too steep for woody plants. To put it simply, grasslands usually occupy that area between wetter areas dominated by woody plants and arid desert vegetation.

Grassland biomes occur on every continent except Antarctica. It is estimated that grasslands once covered as much as 25–40% of the Earth's land surface although much of the original extent of native grassland has been plowed and converted to other grass production (corn and wheat) or other row crops such as soybeans. Indeed, grasslands are important from both agronomic and ecological perspectives. Grasslands are the basis of an extensive livestock production industry in North America and elsewhere. In addition, grasslands sequester and retain large amounts of soil carbon and thus, they are an important component of the global carbon cycle.

Indeed, because grasslands store a significant amount of carbon in their soils and they contain relatively high biodiversity, then now play a prominent role in the discussion about biofuel production. Biofuels may offer a mechanism to generate energy that releases less carbon into the atmosphere. Some energy producers recommend intensive agricultural production of corn, or other grasses such as switchgrass or elephant grass for biofuel production. However, agricultural practices have significant energy costs that may reduce the value of these fuel sources. A recent study has suggested, however, that diverse prairie communities on marginal lands are potentially 'carbon negative' because they provide significant biomass for fuel and store carbon belowground. Much additional research is needed to assess the sustainability of grasslands for biofuel production, but the prospects are certainly tantalizing to energy producers and conservationists alike.

Grassland Types

It is estimated that prior to the European settlement of North America, the largest continuous grasslands in the United States stretched across the Great Plains from the Rocky Mountains and deserts of the Southwestern states to the Mississippi river. Other extensive grasslands are, or were, found in Europe, South America, Asia, and Africa (**Figure 2**). Grasslands can be broadly categorized as temperate or tropical. Temperate grasslands have cold winters and warm to hot summers and often have deep fertile soils. Surprisingly, plant growth in temperate grasslands is often nutrient limited because much of the soil nitrogen is stored in forms unavailable for plant uptake. These nutrients, however, are made available to plants when plowing disrupts the structure of the soil. The combination of high soil fertility and relatively gentle topography made grasslands ideal candidates for conversion to crop production and thus have led to the demise of much of the grasslands across the world.

Grasslands in the Midwestern United States that receive the most rainfall (75–90 cm) are the most productive and are termed tallgrass prairies. Historically, these were most abundant in Iowa, Illinois, Minnesota, Missouri, and Kansas. The driest grasslands (25–35 cm of rainfall) and least productive are termed shortgrass prairie or steppe. These grasslands are

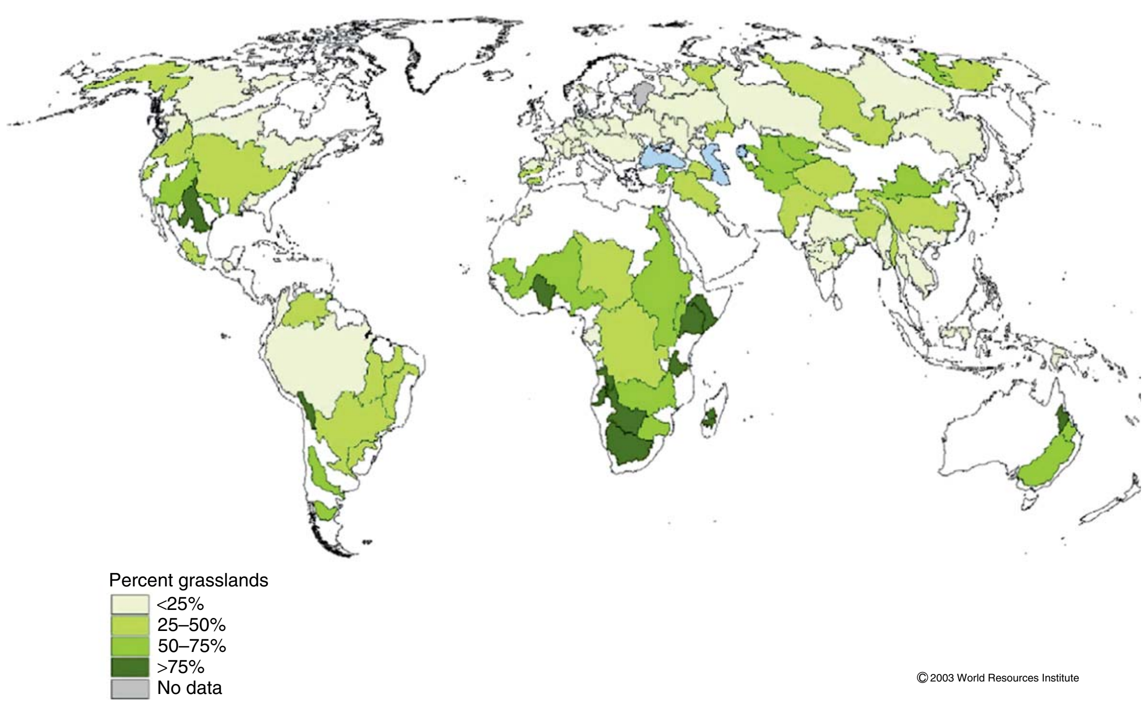

Figure 2 Map of the grasslands of the world. World Resources Institute – PAGE, 2000. Sources: GLCCD, 1998. Loveland TR, Reed BC, Brown JF, *et al*. (1998) Development of a Global Land Cover Characteristics Database and IGBP DISCover from 1 km AVHRR Data. *International Journal of Remote Sensing* 21(6–7): 1303–1330. Available online at http://edcaac.usgs.gov/glcc/glcc.html. Global Land Cover Characteristics Database, Version 1. Olson JS (1994) Global Ecosystem Framework – Definitions, 39pp. Sioux Falls, SD: USGS EDC.

common in Texas, Colorado, Wyoming, and New Mexico. Grasslands intermediate between these extremes are termed mid- or mixed grass prairies. In tallgrass prairie, the grasses may grow to 3 m tall in wet years. In shortgrass prairie, grasses seldom grow beyond 25 cm in height. In all temperate grasslands, production of root biomass belowground exceeds foliage production aboveground. Worldwide, other names for temperate grasslands include steppes throughout most of Europe and Asia, veld in Africa, *puszta* in Hungary, and the pampas in South America.

Tropical grasslands are warm throughout the year but have pronounced wet and dry seasons. Tropical grassland soils are often less fertile than temperate grassland soils, perhaps due to the high amount of rainfall (50–130 cm) that occurs during the wet season and washes (or leaches) nutrients out of the soil. Most tropical grasslands have a greater density of woody shrubs and trees than temperate grasslands. Some tropical grasslands can be more productive than temperate grasslands. However, other tropical grasslands grow on soils that are quite infertile or these grasslands are periodically stressed by seasonal flooding. As a result, their productivity is reduced and may be similar to that of temperate grasslands. As noted for temperate grasslands, root production belowground far exceeds foliage production in all tropical grasslands. Other names for tropical grasslands include velds in Africa, and the compos and llanos in South America.

Although temperate and tropical grasslands encompass the most extensive grass dominated ecosystems, grasses are present in most types of vegetation and regions of the world. Where grasses are locally dominant they may form desert (see Deserts) grassland, Mediterranean (see Mediterranean) grassland, subalpine and alpine grasslands (sometimes referred to as meadows or parks), and even coastal grassland. Most grasslands are dominated by perennial (long-lived) plants, but there are some annual grasslands in which the dominant species must reestablish each year by seed. Intensively managed, human-planted, and maintained grasslands (e.g., pastures, lawns) occur worldwide as well.

The Grassland Environment

Grassland climates can be described as wet or dry, hot or cold (typically in the same season), but on average are intermediate between the climates of deserts and forests. The climate of grasslands is best described as one of extremes. Average temperatures and yearly amounts of rainfall may not be much different from desert or forested areas, but dry periods during which the plants suffer from water stress occur in most years in both temperate and tropical grasslands. An excellent example of this comes from North America, where in the area around Washington, DC (dominated by eastern deciduous forest), the annual precipitation is ∼102 cm whereas at Lawrence, KS (dominated historically by tallgrass prairie), the annual precipitation is ∼100 cm. But the way the rainfall is distributed is notably different. At Lawrence, KS, over 60% of the rainfall occurs in the growing season (April–September), whereas at Washington, DC, the precipitation is uniformly distributed throughout the year. The open nature of grasslands is accompanied by the presence of sustained high wind speeds. Windy conditions increase the evaporation of water from grasslands and this increases water stress in the plants and animals. Another factor that increases water stress is the high input of solar radiation in these open ecosystems. This leads to the convective uplift of moist air and results in intense summer thunderstorms. Rain falling in these intense storms may not be effectively captured by the soil and the subsequent runoff of this water into streams reduces the moisture available to grassland plants and animals. In addition to periods of water stress within the growing season, consecutive years of extreme drought are more common in grassland than in adjacent forested areas. Such droughts may kill even mature trees, but the grasses and other grassland plants have extensive root systems and belowground buds that help them survive and grow after drought periods (**Figure 3**).

Fire in Grasslands

It is generally recognized that climate, fire, and grazing are three primary factors that are responsible for the origin, maintenance, and structure of the most extensive natural grasslands. These factors are not always independent (i.e., grazing reduces standing crop biomass which can be viewed simply as a fuel for fire, and biomass is also highly dependent upon the amount of precipitation). Historically, fires were a frequent occurrence in most large grasslands. Most grasslands are not harmed by fire, many benefit from fire, and some depend on fire for their existence. When grasses are dormant, the moisture content of the senesced foliage is low and this fine-textured fuel ignites easily and burns rapidly. The characteristic high wind speeds and lack of natural fire breaks in grasslands allow fire to cover large areas quickly. Because fire moves rapidly and much of the fuel is above the ground, temperatures peak rapidly and soil heating into the range that is biological damaging (>60 °C) occurs for only a short period of time and only at the surface or maybe a few centimeters into the soil. Thus, the important parts of the grasses (roots and buds) have excellent protection against even the most intense grass fires. Fires have been documented to be started by lightning and set intentionally by humans in both tropical and temperate grasslands. Fires are most common in grasslands with high levels of plant productivity, such as tallgrass prairies, and in these grasslands fire is important for keeping trees and adjacent

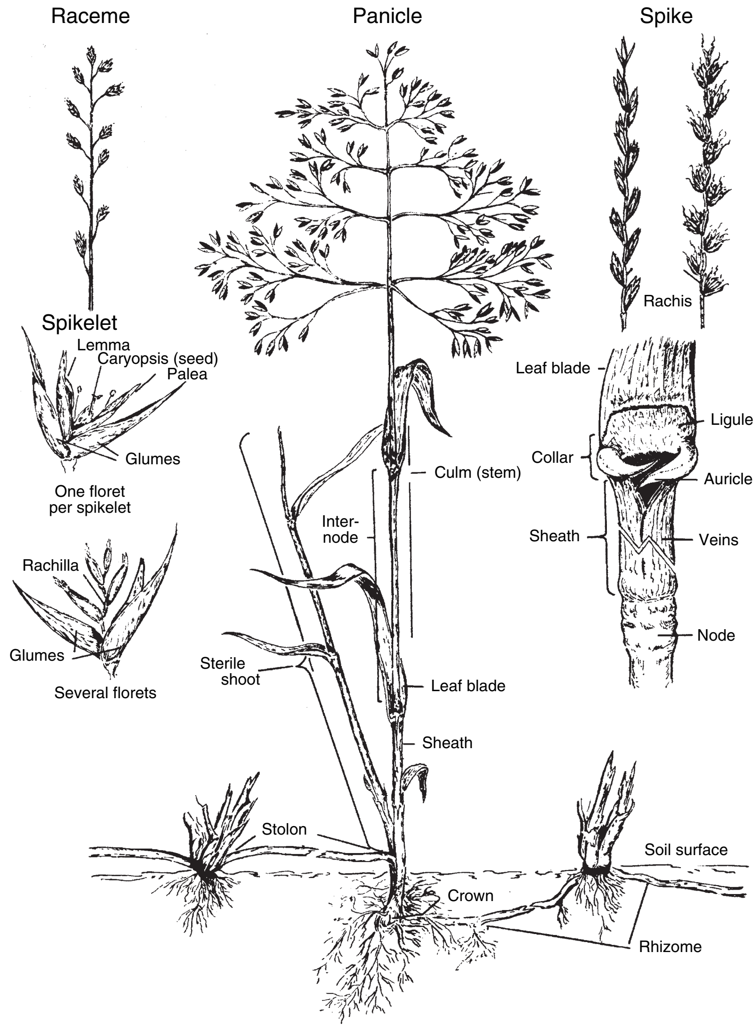

Figure 3 Structure and architecture of the grass plant. From Ohlenbusch *et al*. (1983).

forests from encroaching into grasslands. Many tree species are killed by fire, or if they are not killed, they are damaged severely because their active growing points are aboveground. Grassland plants survive and even thrive after fire because their buds are belowground where they are protected from lethal temperatures (Figure 4).

The response of grassland species to fire mostly depends upon the production potential of the grassland. In the more highly productive grasslands (e.g., tallgrass prairie), fire in the dormant season (usually right before the growing season) results in an increase in growth of the grasses and thus greater plant production or total biomass. This occurs because the buildup of dead biomass (detritus) from previous years inhibits growth; fire removes this layer. However, in drier grasslands, or even in years in productive grasslands when the precipitation is low, the burning of this dead plant material may cause the soil to become excessively dry due to high evaporation losses. As a result, plants become water-stressed and growth is

Figure 4 Photograph of a spring fire at the Konza Prairie Biological Field Station. The fire in the background is occurring ~2 weeks after the area in the foreground was burned. Photograph by Alan K. Knapp.

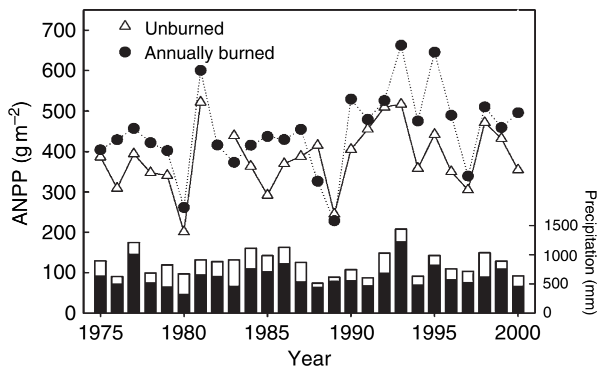

Figure 5 Long-term record (26 years) of aboveground net primary production (ANPP) at Konza Prairie Biological Field Station from unburned sites (clear triangles) and annually burned sites (solid circles). The growing season precipitation (April–September; solid bars) and annual precipitation (clear bars) is also shown.

reduced after fire, thus resulting in lower productivity. It is only with long-term data that the true impact of fires on grasslands can be determined (**Figure 5**).

So what are the mechanism(s) behind the increase in production in mesic grasslands after a fire? One of the most common misconceptions is that fire in grasslands increases productivity by increasing (releasing) the amount of nitrogen (N), a key limiting nutrient in terrestrial ecosystems. Actually, soil N decreases with burning. However, as mentioned above, the primary mechanism by which fire increases production in tallgrass prairie is through the removal of the accumulation of detritus produced in previous years. Standing dead biomass has been reported to accumulate to levels of up to 1000 g m^{-2} in tallgrass prairie and a steady state is achieved *c.* 3–5 years after a fire. The specific effects of this blanket of dead biomass on production are numerous and manifest on individual through the ecosystem levels. This detritus may accumulate to >30 cm deep, and this nonphotosynthetic biomass shades the soil surface and emerging shoots. This reduction in light available to shoots in sites without fire occurs for up to 2 months and because soil moisture is usually high in the spring, loss of energy at this time is especially critical for primary production. In concert with reductions in light available to the grasses, the early spring temperature environment is much different between burned and unburned sites, with burned sites having a higher temperature favoring the dominant C_4 grasses. All of these factors result in less production in unburned tallgrass compared to annually burned prairie (**Figure 5**). Other evidence that fire does not increase N availability in mesic grasslands comes from N fertilization experiments. Within tallgrass prairie, in annually burned sites, N fertilizer had a strong impact on production, but in sites that have not been burned for several years, additional N did not enhance production and sites with intermediate fire histories had intermediate responses to N fertilization. The results of many studies suggest that one generality regarding grasses and fire is that grasses tolerate fire extremely well and in most cases reach their maximum production in the immediate post-fire years. One qualification to this statement is that the beneficial effect of fire is not uniform across all precipitation gradients. In addition, the growth form type of the dominant grass is also very important. Highly productive grasslands on the high end of precipitation gradients show moderate to high positive response to burning whereas more arid grasslands and some bunchgrass grasslands show reduced productivity in the first few years after fire.

Most grasslands have an active growing season as well as a dormant season. Although fire can occur year-round in many grasslands, fire is most likely to occur during the dormant season and it is most rare in the middle of the growing season during normal (non drought) years. Given the fact that so many aspects of a grassland change during the yearly cycle, it seems fair to expect that a fire in different seasons would have dramatically different impacts. However, in spite of the many studies that have examined the impact of fires at different times of the year, there does not seem to be a general consensus on fire seasonality. Rather, it is probably best to say that grasslands seem somewhat sensitive to 'season of burn'. In one long-term study, it was found that the dominant grass in the tallgrass prairie (*Andropogon gerardii*) increased with burning in autumn, winter, or spring (dormant season), whereas burning in summer (growing season) resulted in an increase in many of the subdominant grasses with a reduction in *A. gerardii.*

Research indicates that community structure and ecosystem functioning in grasslands are impacted strongly by fire frequency. Plant species composition, in particular, differs dramatically between annually burned and less frequently burned sites in mesic grasslands. In tallgrass prairie, annually burned sites are dominated strongly by C_4 perennial grasses. Although C_4 grasses retain dominance at infrequently burned sites, C_3 grasses, forbs, and woody species are considerably more abundant resulting in greater diversity and heterogeneity in unburned prairie. In fact, the flora on annually burned sites is a nested subset of that found on less frequently burned areas. Thus, the differences reflect shifts in dominance between frequently and infrequently burned sites, rather than difference in composition *per se.* Again as with response of production to fire, there appears to be a gradient of response in community structure to grassland fires. In more northern prairies of North America, burning has not been shown to strongly affect community structure. However, these northern grasslands are dominated by C_3 grasses, which tend to decrease with burning, unlike the C_4 grasses that dominate prairies in warmer climates. Thus, the role of competition and fire in structuring grassland plant communities may increase along a latitudinal gradient throughout the Great Plains.

At a mesic grassland (Konza Prairie Biological Station), a clear picture of fire effects on plant community structure has emerged from the long-term (>20 years) empirical and experimental research done at the site. In the absence of large herbivores, the system is strongly driven by bottom-up forces associated with light, soil resource availability, and differential ability to compete under low-resource conditions. Although light availability increases with burning, the abundance of other critical limiting resources, N and water, declines as fire frequency increases. This is especially true in upland areas (with shallow soils) where production is likely limited by water. These changes in resource availability favor the growth and dominance of a small number of perennial C_4 grasses and forbs. As dominance by these competitive species increases, general declines in plant species diversity and community heterogeneity occur.

Impact of Fire on Consumers

Direct effects

Most grassland animals are not harmed by fire, particularly if fires occur during the dormant season. Those animals living belowground are well protected, and most grassland birds and mammals are mobile enough to avoid direct contact with fire. For example, there were few differences in the kinds and abundances of ground-dwelling beetles in frequently and infrequently burned Kansas tallgrass prairie. Insects that live in and on the stems and leaves of the plants are the ones that are most affected by fire. Fire has been shown to reduce directly the abundance of caterpillars which means fewer butterflies, which are important pollinators, in frequently burned prairies. Fortunately, most natural fires are patchy in that many unburned areas remain throughout a larger burned area. These patches serve as refugia for many insect populations. Given that these animals have short generation times these refugia often allow insect populations to recover quickly following a fire.

Indirect effects

Given the distinct effects of fire frequency on plant community structure and dynamics within and among burning treatments, it seems plausible that consumers that depend on the primary producers for food and habitat structure will be indirectly affected because fire alters food availability and habitat structure. Given that fire usually homogenizes grassland plant communities, one would predict that this would hold true for consumers. However, there does not appear to be tight linkages between changes in vegetation composition and structure animal populations. Indeed, work in an Oklahoma prairie shows that more grassland birds occur in areas with patchy burns than in areas that are uniformly burned or not burned. Much more work on how fire affects habitat heterogeneity and grassland consumers communities is needed.

Grazing in Grasslands

Grazing is a form of herbivory in which most of the leaves or other plant parts (small roots and root hairs) are consumed by herbivores. Grazing, both above- and belowground, is an important process in all grasslands. The long association of grazers and grasslands has prompted the hypothesis that grasses and their megaherbivore grazers are a highly coevolved system, but, as mentioned above, there is some more recent evidence that this might not be the case. However, there is no disagreement that large grazers have been a factor in grassland ecology since their origin. The herbivory actions of many other smaller organisms including small mammals and insects may be equally important. There is no doubt that the impact of native grazers in grasslands can be extensive and work on the East African Serengeti plains estimated that 15% to >90% of the annual aboveground net primary productivity can be consumed by ungulates. However, data from small mammal exclosures suggest that small mammals can also impact grasslands as when small mammals were excluded from plots in Kenya; biomass was 40–50% higher than in adjacent plots where small mammals occurred.

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, like many resources, grasslands can be overexploited (discussed in more detail below).

Grazing systems can be roughly divided into two main types – commercial and traditional – with the traditional type often mainly aimed at subsistence. Commercial grazing of natural grasslands is very often at a large scale and commonly involves a single species, usually beef cattle or sheep for wool production. Some of the largest areas of extensive commercial grazing developed in the nineteenth century on land which had not previously been heavily grazed by ruminants; these grazing industries were mainly developed in the Americas and Australia, and to a much less degree in southern and eastern Africa. Traditional livestock production systems vary according to climate and the overall farming systems of the area. They also use a wider range of livestock, including buffaloes, asses, goats, yaks, and camels. In traditional farming systems, livestock are often mainly kept for subsistence and savings, and are frequently multipurpose, providing meat, milk, and manure as fuel.

Grazing aboveground by large herbivores alters grasslands in several ways. Grazers remove fuel and may lessen the frequency and intensity of fires. Most large grazers such as cattle or bison primarily consume the grasses; thus the less abundant forb species (broad-leafed, herbaceous plants) may increase in abundance and new species may invade the space that is made available. Thus, fire reduces heterogeneity in mesic grassland (a few species dominate) while grazers increase heterogeneity regardless of fire frequency. In other words, grazing decouples the impact of fire in productive grasslands (**Figure 6**). As a result; grazing increases plant species diversity in mesic grasslands. 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 non-native plant species.

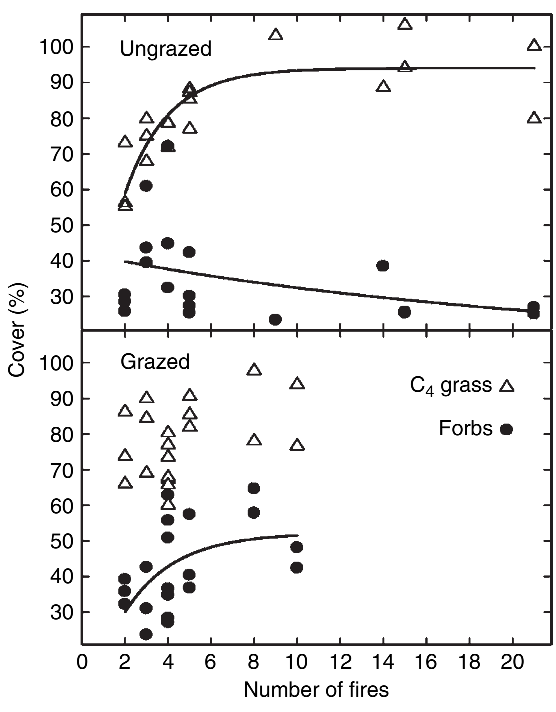

Figure 6 Aboveground biomass removal by large ungulates modulates plant community responses to fire in mesic grasslands. In ungrazed prairie (top), cover of dominant C_4 grasses increased with increasing fire frequency, while cover of forbs decreased, resulting in a loss of diversity. However, in prairie grazed by bison (bottom), the cover of forbs was positively correlated with fire frequency and the cover of grasses was unaffected, resulting in high diversity in spite of frequent fires. From Collins SL, Knapp AK, Briggs JM, Blair JM, and Steinauer EM (1998) Modulation of diversity by grazing and mowing in native tallgrass prairie. *Science* 280(5364): 745–747.

Grazers may 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 available (inorganic) forms. This decomposition process may take more than a year or two. Grazers consume these plant parts and excrete a portion of the nutrients they contain in plant-available forms. This happens very quickly 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 bison or wildebeest, 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' is controversial, yet 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. The latter occurs after grazing because the large root system of the grasses is able to supply abundant water to a relatively small amount of regrowing leaf tissue.

As with fire, the impact of grazing on grasslands depends upon where in the precipitation gradient the grassland occurs (usually more mesic grasslands can recover more quickly than arid grasslands) as well as the growth form – cespitose (bunch-forming grasses) versus rhizomatous grasses. But another key factor is the evolutionary history of the grassland. In general, grasslands with a long evolutionary history of grazers, as in Africa, are very resilient to grazing whereas grasslands with a short evolutionary history such as desert grasslands in North America can easily be damaged by even light grazing.

Threats to Grasslands and Restoration of Grasslands

Grassland environments are key agricultural areas worldwide. In North America and elsewhere, grasslands are considered to be endangered ecosystems. For example, in US Great Plains up to 99% of native grassland 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 is still occurring in some places, dramatic increases in woody shrub and tree species threatens many remaining tracts of grasslands. Indeed, across the world, the last remaining native grasslands are being threatened by an increase in the abundance of native woody species from expansion of woody plant cover originating from both within the ecosystem and from adjacent ecosystems. Increased cover and abundance of woody species in grasslands and savannas have been observed worldwide with well-known examples from Australia, Africa, and South America. In North America, this phenomenon has been documented in mesic tallgrass prairies of the eastern Great Plains, subtropical grasslands and savannas of Texas, desert grasslands of the Southwest, and the upper Great Basin. Purported drivers of the increase in woody plant abundance are numerous and include changes in climate, atmospheric CO_2 concentration, nitrogen deposition, grazing pressure, and changes in disturbance regimes such as the frequency and intensity of fire. Although the drivers vary, the consequences for grassland ecosystems are strikingly consistent. In many areas, the expansion of woody species increases net primary production and carbon storage, but reduces biodiversity. The full impact of shrub encroachment on grassland environments remains to be seen.

Another threat to native grasslands is the increase of non-native grass species. For example, in California, it is estimated that an area of approximately 7 000 000 ha (about 25% of the area of California) has been converted to grassland dominated by non-native annuals primarily of Mediterranean origin. Conversion to non-native annual vegetation was so fast, so extensive, and so complete that the original extent and species composition of native perennial grasslands is unknown. In addition, across the western US, 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 populations of exotics, usually with very mixed results.

Conservation and Restoration

Because grasslands have tremendous economic value as grazing lands and also serve as critical habitat for many plant and animal species, efforts to conserve the remaining grasslands and restore grasslands on agricultural land are underway in many states and around the world. The most obvious conservation practice is the protection and management of existing grasslands. This includes both private and public lands. Probably the largest private holder of grasslands in the world is The Nature Conservancy. The Nature Conservancy is a global organization that works in all 50 states in the United States of America, and in 27 countries, including Canada, Mexico, Australia, and countries throughout the Asia-Pacific region, the Caribbean, and the Latin America.

However, as mentioned numerous times, the factors that led to the establishment of grasslands and, in particular, the organic-rich soils derived from the dominant biota have facilitated the agricultural exploitation of grasslands. Consequently, many grasslands that were historically persistent have been converted to cropland. Thus, restoration of grasslands is also a very important conservation practice. Grassland restoration is the process of recreating grassland (including plant and animal communities, and ecosystem processes) where one existed but now is gone. Grassland restoration can include planting a new grassland where one had been broken and farmed, or it can include improving a degraded grassland (e.g., one that was never plowed but lost many plant and animal species due to prior land management practices). Restoration practices of existing grasslands may include reintroducing fires into grasslands following extended periods of fire suppression. On areas that have been moderately to heavily grazed (but not completely overgrazed), reducing the intensity of grazing may be required. In addition, mowing is also a cost-effective method of restoring grasslands. Mowing can be effective on sites that have been invaded by brush and forest, but the grasses are still present.

In areas where the grasses are completely absent (agriculture fields) or in a very degraded state, reseeding of grasses is usually necessary. There are proven techniques, complete with specialized equipment (seed drills) for restoration of grasslands, and, for the most part, it is fairly easy to get the dominant grasses established in an area. Indeed, some of the earliest examples of restoration ecology come from efforts to restore native tallgrass prairie in North America. As a result, the market for restoration of grasslands (at least in North America) has developed to the point that obtaining enough grass seed (sometimes even local native seed) is not a problem. A bigger challenge, however, in restored grasslands is increasing establishment of the nongrass species which are so critical for biodiversity. Seeds may be more difficult to obtain (especially for rarer plants), and then getting the forbs to survive and reproduce in many grassland restoration projects has been challenging. Further research is needed regarding what management techniques are important to their establishment and growth in these restored areas.

In addition to the prairie flora that is at risk, grassland animals (particularly birds and butterflies) suffer when grassland quality declines. In North America, grassland birds were historically found in vast numbers across the prairies of the western Great Plains. Today, the birds of these and other grasslands around the world have shown steeper, more consistent, and more geographically widespread declines than any other group. These losses are a direct result of the declining quantity and quality of habitat due to human activities like conversion of native prairie to agriculture, urban development, and suppression of naturally occurring fire.

See also: Agriculture Systems; Fire; Savanna; Tropical Seasonal Forest.

Further Reading

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Stream Management

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Introduction

Ecological stream management is the process of altering a stream ecosystem to either preserve current conditions, or change one or more components of the stream ecosystem to obtain a desired outcome. The management of larger streams and rivers differs from that of smaller streams due to the physical and ecological properties associated with an increase in scale (**Table 1**). Humans have been altering streams since at least 6000 BC when Mesopotamians began agricultural irrigation. Since then, actions such as waste disposal, channel modification, flow alterations, removal of riparian vegetation, and species introductions have degraded many stream ecosystems worldwide to a point that has significantly affected stream ecosystem integrity. Structural and functional modifications include the alteration of energy flow and nutrient cycling efficiency (ecosystem function), the reduction of native species abundances and increased species introductions (ecosystem structure), and the degradation of water quality and quantity. Many streams are presently in need of intervention to maintain or restore their ecological integrity. Several