7. Temperate Grasslands

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The temperate-grassland biome occupies a large portion of the planet. Temperate grasslands represent the potential natural vegetation of an area of 49 × 10^6 km^2, which is equivalent to 36% of the earth's surface (Shantz 1954). This estimate of the area occupied by grasslands excludes savannas, but it does include grass and shrub deserts. The area covered exclusively by grasslands is 15 × 10^6 km^2, which accounts for 11% of the earth's surface. The grassland biome occurs in almost all continents (Singh et al. 1983) from the Americas to Asia and from Europe to Australia (Fig. 7.1). In North America, most of the Great Plains is dominated by grasslands from the boundary with subtropical biomes in the south of the United States to the boundary with the Canadian temperate forest in the north. In South America, the pampas and large expanses of Patagonia are covered by grasslands. In Asia, vast areas are occupied by grasslands from Ukraine to China.

Grasslands are water-limited ecosystems, and their existence is associated with droughts occurring at least once during the year. Grasslands occur in areas with annual precipitation ranging between 150 and 1200 mm/year and mean annual temperatures ranging between 0 and 25°C (Lieth and Whittaker 1975). Along a precipitation gradient, temperate grasslands occur between deserts and forests, with forests taking over sites with more than 1200 mm/year of precipitation and deserts dominating regions with less than 150 mm of precipitation. A clear example of these vegetation shifts along a precipitation gradient occurs in western Patagonia, where precipitation declines

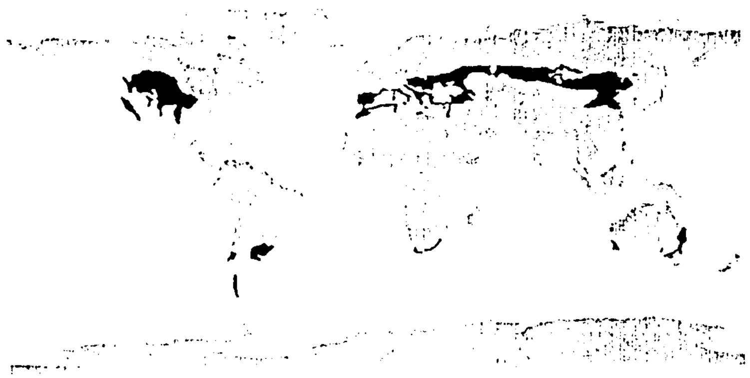

Figure 7.1. Global distribution of the grassland biome. Adapted from Bailey (1998). This figure includes Mediterranean grasslands, which will be addressed in Chapter 9.

drastically and vegetation shifts from closed forest to grassland, steppe, and desert in less than 200 km (Schulze et al. 1996).

Temperature interacts with precipitation to determine the distribution of grasslands. As temperature increases, the forest–grassland and desert–grassland boundaries occur at higher values of precipitation as a result of the increasing evaporative demand and the negative effect on the availability of water. For example, in North American Great Plains where isohyets run in a north–south direction and temperature isopleths in an east–west direction, the grassland–forest boundary has a clear SE–NW direction (Bailey 1998).

The concept of biodiversity is quite broad and encompasses different levels, from diversity within species or genetic diversity and species diversity, to ecological diversity that includes landscape diversity and diversity of functional groups (Mooney et al. 1995). In this chapter, I will focus on species and functional group diversity because most information about biodiversity has been collected at these levels.

This chapter will describe succinctly the natural patterns of biodiversity in grasslands and develop scenarios of changes in biodiversity that might occur in this biome for the year 2100. In order to construct the scenarios, I will follow the approach used throughout this book. I will independently assess the patterns of the drivers of changes in biodiversity and the sensitivity of grasslands to changes in each driver. Finally, I will combine the expected changes in drivers with the sensitivity patterns to assess total expected changes in biodiversity for the biome.

Patterns of Biodiversity in Grasslands

Biodiversity within the grassland biome varies enormously, with many native grasslands having levels of diversity as high as those characteristic of tropical forests (Sala et al. 2001). Grasslands of the Pampa, in southern South America, are an example of a high-diversity system with more than 400 species of grasses alone (Cabrera 1970). The tallgrass prairie in North America similarly has more than 250 species of plant species, most of them perennial grasses (Freeman 1998). In contrast, some grasslands of Patagonia, for example, have approximately 30 species of plants (Golluscio and Sala 1993). Diversity of vascular plants may be only a poor indicator of diversity within other taxa, however, as has been shown clearly for tropical forests (Lawton et al. 1998).

The high diversity of grassland-plant species has been simplified by grouping species into functional types. Species within a functional type share morphological and physiological characteristics that result in a common ecological role (Chapin et al. 1995). There is not a unique grouping of plant species into functional types, but groupings vary according to the purpose of the study and the availability of data. One classification divides grassland-plant species into grasses, shrubs, succulents, and herbs (Sala et al. 1997). In addition to the obvious morphological differences among these groups, species within each group share many other characteristics with important ecological meaning. For example, shrub species tend to have deeper roots than do grasses (Jackson et al. 1996); consequently, they dominate in sites with coarse-textured soils, whereas grasses dominate in finer-textured soils (Sala et al. 1997). Similarly, shrubs are more abundant in regions where precipitation occurs during the cold season because this seasonal pattern favors penetration of water into deep layers of the soil. Another classification of grassland species is based on photosynthetic pathways and divides plant species into C_3 and C_4 species. These two groups of species have differences in the anatomy of leaves and in the biochemistry of photosynthesis that result in differences in the distribution of species along latitudinal and elevation gradients. C_4 species tend to be distributed at low elevation and low latitudes, whereas C_3 have the opposite patterns (Cavagnaro 1988, Paruelo et al. 1998).

Faunal diversity is lower than it is in other biomes when we take into account the large area that grasslands occupy. Grasslands have a total of 477 species of birds and 245 species of mammals, that is only 5% of the total number of species for each group (Groombridge 1992). Specific grasslands and taxonomic groups represent important exceptions. For example, birds are quite diverse in North American tallgrass-prairie with 208 species representing 16 orders (Kauffman et al. 1998). The abundance and diversity of large mammals characterize the grassland biome. The patterns of diversity of large mammals are quite different among climatically similar grasslands. For example, the total number of species of large mammals in Africa and South

America is approximately 200 in both regions; however, the contribution of different orders is strikingly different. In Africa, the order *Artiodactyla* (bovidae) has 80 species, whereas in South America has less than 20 (Vrba 1993). In contrast, in South America, *Marsupiala* has 80 species and *Edentata* 30 species, but those orders are not present in Africa.

Diversity of below-ground organisms is known in much less detail than is diversity of above-ground organisms. There is a strong indication, however, that below-ground organisms represent a very important component of the grassland biota. Grasslands, in general terms, have more biomass and higher production below ground than they do above ground (Sims and Singh 1978). The concentration of organic matter below ground provides the substrate for diverse bacteria, fungal, and nematode groups. For example, all groups are present in the shortgrass steppe, although bacteria are the most abundant (in terms of biomass), followed by fungi, nematodes, protozoa, macroarthropods, and microarthropods (Lauenroth and Milchunas 1992). In terms of species numbers, more than 100 species of fungi and more than 200 species of nematodes have been reported for the shortgrass steppe and tallgrass prairie, respectively (Christensen and Scarborough 1969; Ransom et al. 1998).

Scenarios of Changes in Biodiversity

The Effects of Land-Use Change on Biodiversity

Changes in land use are expected to be large in grasslands (Table 7.1). They result from a broad range of human activities that culminate either in changes in land cover or simply in changes in land use. One of the most drastic

Table 7.1. Biodiversity changes in grasslands and its determinants for the year 2100

	Land use	Climate	N deposition	Biotic exchange	Atoms CO_2
Expected change in drivers	3	2	3	3	2.5
Sensitivity	5	3	2	2	3
Predicted biodiversity change	0.6	0.24	0.24	0.24	0.3

The first row presents the expected changes in the five major drivers of biodiversity change, for the grassland biome, in an arbitrary scale from 1 to 5. We used a business-as-usual scenario to estimate climate change (Haxeltine and Prentice 1996), scenario A1 of the IMAGE 2 model (Alcamo 1994) to estimate changes in land use, and the MOGUNTIA model of nitrogen deposition (Holland et al. 1999). Row 2 describes the sensitivity of grasslands to a unit change of each one of the drivers in an arbitrary scale of 1 to 5. Row 3 is the expected relative change in diversity as a result of each driver in a scale from 0 to 1. It was calculated by multiplying rows 1 and 2 and dividing by 25.

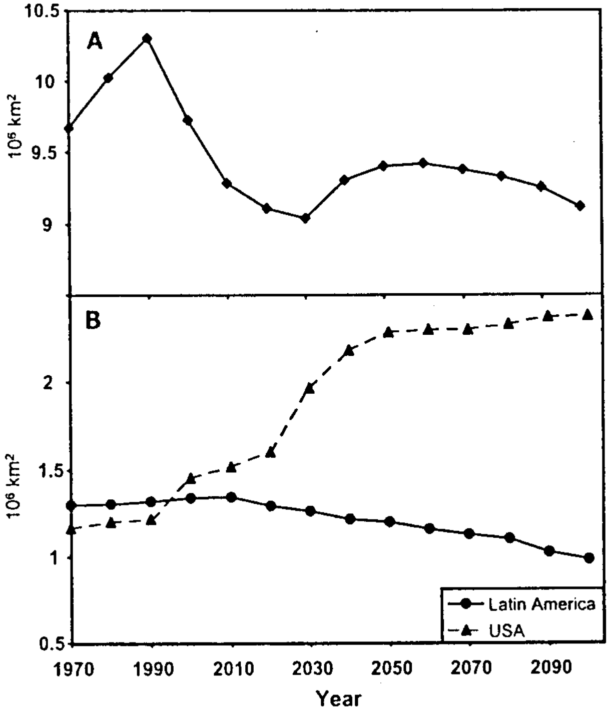

Figure 7.2. (A) Trajectory of the total area covered by grasslands in the world from 1970 until 2100 as predicted by the IMAGE 2 model (Alcamo 1994). (B) Trajectories of the area covered by grasslands in the United States and Latin America that are two contrasting regions of the 13 regions in which IMAGE 2 divides the world.

changes that grasslands may experience is the conversion into agricultural land. Temperate grasslands have optimal conditions for agriculture, with mild temperatures and moderate precipitation (Lieth and Whittaker 1975); consequently, a large fraction of native grasslands has already been converted into cropland. For example, the original tallgrass prairie in North America supports most of the current corn-belt of the United States. The vast grasslands of the Pampa are similarly now the basis for the large-scale grain exports from Argentina.

The IMAGE 2 model (Alcamo 1994), used in this exercise to estimate changes in land use, indicates that the total area covered by grasslands will remain approximately constant in the next century (Fig. 7.2A). This single datum, however, can be misleading. The total area of grasslands has losses and gains. The losses represent native grasslands that are plowed and converted into urban or agricultural land. The gains come from two sources: (1)

agricultural land that is being abandoned and returns to its potential natural vegetation; and (2) forests that are being cut down and replaced by grasslands with the purpose of feeding domestic animals. The United States and Latin America are regions that are expected to undergo opposite trajectories during the next century as a result of different social and economic forces (Fig. 7.2B). The IMAGE 2 model (Alcamo 1994) indicates that agricultural land will be reduced in the United States as a result of intensification, and that the abandoned land will revert to grassland, which was the potential natural vegetation of the region. In contrast, the grassland area in Latin America will be reduced as a result of agricultural expansion. The boreal forest is expected to undergo a similar phenomenon, although one driven by climate change instead of land-use change (see Chap. 6). The total area will remain constant, although the boreal forest will shift north with the consequent loss of boreal forest to temperate forest and grassland in the southern boundary that will be compensated by gains from areas that are currently tundra.

Habitat loss resulting from the transformation of grasslands into agricultural land is the major driver of biodiversity change in grasslands. The conversion of grasslands into agricultural land includes plowing and seeding with an exotic species that drives plant species into local extinction. If the phenomenon extends in time and space, local extinctions may turn into global extinctions. Losses of biodiversity in one part of the world, due to conversion of grasslands into agriculture, are not compensated by abandoned fields in another part of the world because of differences in the biota being gained or lost. The agricultural land that reverts to grassland in the United States has a different biota than the area of grassland that is plowed in Latin America (Fig. 7.2). Although both grasslands have similar climates, their flora and fauna are partially unrelated: North America belongs to the Holarctic realm; South America to the Neotropical realm (Udvardy 1975), and species lost in South America are lost forever. Changes in plant-species diversity drastically alter the habitat for microorganisms and above-ground animals, resulting in changes in animal species diversity. Even in a single region the weedy species that colonize an early successional grassland are quite distinct from those that occupy late successional grasslands that might be lost to agriculture or urbanization.

Another more subtle but pervasive change in land use with consequences for grassland biodiversity is overgrazing. Grazing with domestic animals is the major way of utilizing grasslands, and a large fraction of grasslands in the world is being overgrazed. Species diversity has the hump-shaped curve in response to grazing intensity, with maximum diversity occurring at intermediate intensities of grazing (Fig. 7.3) (Milchunas et al. 1988; Milchunas and Lauenroth 1993). The effect of grazing on diversity is modulated by water availability and the evolutionary grazing history of the area. The conceptual model, which was developed by Milchunas and colleagues, was corroborated by a thorough literature review that included 97 articles representing 276 data sets (Milchunas et al. 1988; Milchunas and Lauenroth

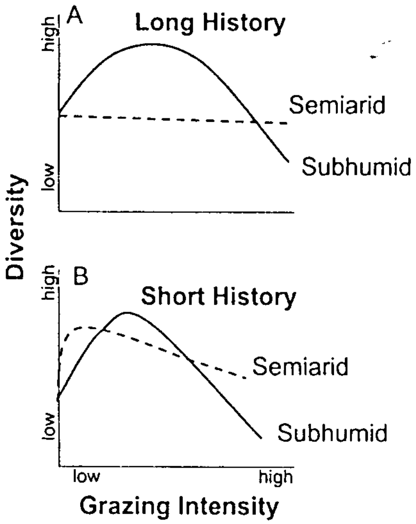

Figure 7.3. A conceptual model of the effect of grazing intensity on plant species diversity as modulated by moisture availability and evolutionary grazing history. As grazing intensity increases grasslands are invaded by species that have adaptations to herbivory increasing total diversity, further increases in grazing, decreases diversity because species that are less tolerant to grazing are driven to local extinction. Adaptations that provide resistance to drought also provide resistance to herbivory; consequently, grasslands from semiarid regions are less vulnerable to invasions and show a smaller response to grazing. Evolutionary grazing history either long (A) or short (B) further modulates the effect of grazing on diversity. Redrawn from Milchunas et al. 1988 and Milchunas and Lauenroth 1993.

1993). Grazing results in a partial or total loss of plant organs, and particular plant characteristics confer adaptive advantages under those circumstances. For example, low stature, high root–shoot ratios, location of basal meristems close to the ground and protected by basal sheaths are plant adaptations to grazing. At low levels of grazing, increases in grazing intensity favor the introduction of plant species that possess adaptations to grazing resulting in a moderate increase in species diversity. At very high levels of grazing, only the most resistant species remain in the community with the less-tolerant or intolerant species being locally driven to extinction.

Water availability modulates the effect of grazing on diversity because of the convergent selection for drought and grazing resistance. Both drought and herbivory result in the loss of plant organs, and both provide similar selection pressures. Characteristics that provide adaptations to drought resistance (e.g., high root–shoot ratio) also confer resistance to herbivory (Coughenour 1985). Grassland plant communities from semiarid regions, although subjected to low-grazing intensity, consequently, possess some adaptations (exaptations) to herbivory. As a result, the effect of grazing in semiarid regions is moderate because selection pressure does not change significantly along a grazing intensity gradient (Fig. 7.3A). In contrast, in a subhumid grassland, selection pressures shift along a gradient in grazing intensity. Low-grazing sites are dominated by plants with characteristics that allow effective competition for light (e.g., high stature and low root–shoot ratio), whereas at high-grazing intensity the opposite characteristics become most adaptive because they represent adaptations to grazing. The shift in the direction of selection pressures results in drastic changes in community composition and diversity.

The grazing history in evolutionary time further modulates the effects of grazing and moisture on diversity. Grasslands that did not have large-hooved and congregating animals during the Holocene tend to lack species with adaptations to herbivory. For example, the Inter-Mountain West in North America lacked the large herds of bison (Mack and Thompson 1982) that shaped the adjacent shortgrass steppe (Milchunas et al. 1988). Grasslands with short evolutionary-grazing history are consequently more vulnerable to invasions by species with adaptations to herbivory and shift their diversity at lower levels of grazing intensity (Fig. 7.3B).

The Effects of Climate Change on Biodiversity

The expected climate change in the grassland biome will be moderate in comparison with other biomes (Table 7.1 and Chap. 15). Global circulation models agree in predicting larger increases in temperature at higher latitudes (Kattenberg et al. 1996). Temperate grasslands are located at midlatitudes (Fig. 7.1) and will consequently experience a moderate-to-low increase in temperature as a result of the increase in greenhouse gases in the atmosphere. Changes in precipitation are more idiosyncratic and do not have clear latitudinal patterns (e.g., those described for temperature). Although generalizations about changes in precipitation for the entire biome are difficult to assemble, observations of GCM outputs indicate that most of the grassland biome will be located in areas with either no change or with a small increment depending on the season under consideration (Kattenberg et al. 1996). Soil moisture is the variable that is most closely related to the functioning of grassland ecosystems, and its status results from the combined effects of changes in precipitation and temperature. In general terms, grasslands will experience a decrease in soil moisture at the time of doubling CO_2, indicating that the warming effect will overshadow the neutral-to-slightly positive changes in precipitation (Kattenberg et al. 1996).

The functioning of grasslands is most sensitive to changes in water availability. Annual precipitation accounts for most of the year-to-year variability in primary production, whereas other environmental variables (e.g., temperature) are not related to the interannual production pattern (Lauenroth and

Sala 1992; Knapp et al. 1998). Species or groups of species respond quite differently to changes in total water availability and its seasonal distribution. Years when precipitation patterns yield high grass production consequently do not result in high forb production in North American tallgrass prairie (Knapp et al. 1998). In the Patagonian steppe, conditions leading to high production of shrubs also do not coincide with those yielding high production of grasses (Jobbágy and Sala 2000).

Directional changes in water availability (i.e., those predicted under climate change scenarios) will affect certain grassland species in detriment of others; consequently, they will have major detrimental effects on grassland biodiversity (Table 7.1). The overall effect of climate change on grassland biodiversity will be high, more as a result of the high sensitivity of grasslands than of the expected changes in climate. Prolonged changes in water availability will certainly alter the competitive balance among species that, in turn, will lead to local extinctions. If changes are sustained through time and encompass a large area, local extinctions may result in global extinctions. Water availability may decrease as a result of a direct decrease in precipitation or as a consequence of an increase in temperature that increases evaporative demand and negatively affects the ecosystem–water balance. The more drought-resistant plant species of a community will have a competitive advantage over the more mesic species in regions where water availability is expected to decrease. On the contrary, in regions where water availability will increase, plant species with high relative growth rate and high shoot–root ratio will outcompete and ultimately drive to local extinction other species with characteristics that made them more drought resistant and less capable of using higher water availability. Plant characteristics associated with drought resistance and its components of tolerance and avoidance include morphological and physiological features (e.g., rooting depth, capacity for osmotic regulation, stomatal control of transpiration water losses, or duration of life cycles) (Kramer 1969). Enormous variability has been reported among plant species in the characteristics associated with drought resistance, highlighting that directional changes in water availability will inevitably result in large changes in biodiversity.

Soil microorganisms show differential responses to soil water content in a way that is similar to the differential responses reported for plant species (Freckman et al. 1987). Soil–water thresholds at which microorganisms turn into drought-induced quiescence vary among species. As a result, it appears that changes in the frequency of wet-soil conditions may result in changes in the composition of the community of microorganisms and ultimately in their biodiversity.

The Effects of Changes in Nitrogen Deposition on Biodiversity

Nitrogen deposition has increased over background levels as a direct result of human activity (see Chap. 3). Nitrogen deposition occurs mostly downwind of regional pollution sources and not far from them (Holland et al. 1999). Areas of industrial concentration and urbanization are located mostly in regions where the potential natural vegetation is temperate forests (Headrick 1990). Eastern North America, northern Europe, and Japan currently concentrate most of the industrial activity and show the highest levels of NO_x and NH_4 deposition (Holland et al. 1999). In the twenty-first century, industrialization and the associated pollution will expand into other regions (e.g., China and countries of Southeast Asia). Temperate grasslands are and will be adjacent to these high-industrial concentration areas and, in most cases, are downwind from them. The vicinity of temperate grasslands to sources of pollution and specifically to regions where fossil fuel combustion is concentrated indicates that they will be subjected to heavy nitrogen deposition (Table 7.1).

Increases in nitrogen availability have a negative effect on plant biodiversity in grasslands (Berendse and Elberse 1990; Huenneke et al. 1990; Tilman 1993). For example, Tilman (1993) performed a long-term experiment where he added nitrogen fertilizer from 0 to 27 g/m²/year. After 11 years of treatment, the species richness had declined significantly such that plots that received the most nitrogen had less than 50% of the original plant biodiversity (Fig. 7.4). The loss did not occur uniformly across different functional groups, with forbs losing many more species than perennial grasses. The loss of species within the forb group, which included the nitrogen-fixing legumes, suggest that there might be associated losses in the nitrogen-fixing bacteria. This is an example about how changes in plant-species composition driven

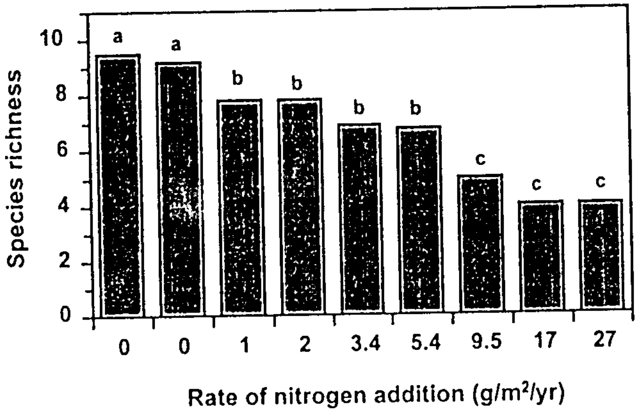

Figure 7.4. The effect of increasing N availability on plant species richness in the North American tallgrass prairie. Nitrogen fertilizer was added annually during an 11-year period, and results show species richness at the end of the experiment. Redrawn from Tilman 1993.

by increased nitrogen availability may affect microbial composition. Studies with forest soils indicate losses of ectomycorrhizal fungi diversity as a result of nitrogen deposition (Arnolds 1991).

The Effects of Biotic Exchange on Biodiversity

Introductions of exotic species into grassland ecosystems first increase local diversity, but, later, exotic species may outcompete native species, driving them to local extinction and reducing diversity. The magnitude of the successful invasions and their consequences for biodiversity depend on the amounts of exotic propagules (seeds and individuals) that reach a given grassland site and its sensitivity. Prediction of "invasibility" of grasslands is difficult, however, because some systems that become seriously invaded contrast with other apparently similar grasslands that do not become invaded even when receiving similar loads of invading species (Mack 1989).

Seeds of exotic plant species or exotic animals arrive in grassland ecosystems largely as a result of human activities. In some cases, humans have introduced plant species because of their superior forage quality that consequently escaped from cultivated paddocks and invaded an entire grassland region (Mack 1989). In other cases, introductions occur accidentally when agriculture tools or animals are exchanged among regions, bringing plant seeds and animals. The amount of propagules received by ecosystems depends directly on the level of human activity. Grasslands are expected to receive high levels of propagules (Table 7.1) because they are among the biomes with the highest human impact. Temperate grasslands have been and will continue being prime locations for agriculture. A large fraction of grasslands has consequently been transformed into croplands, which is an activity that brought along many alien plant species and their associated animals. The alien-plant group ranges from cultivated varieties to weedy species and the associated pests and parasites.

Grassland types vary dramatically in their invasibility. North America provides two of the most striking examples of grasslands that have been invaded to a degree that has drastically transformed their functioning (Mack 1989). The Inter-Mountain West has been invaded by *Bromus tectorum* after the introduction of cattle by European settlers. This annual grass species outcompeted the native perennial grasses, resulting in severe changes in the fire regime, in the biogeochemistry of the region, and, finally, in the animal-carrying capacity. California's Central Valley was similarly originally dominated by perennial grass species of the genera *Stipa*, *Aristida*, or *Festuca*. After the arrival of European settlers and their cattle, the annual grass species *Avena barbata* replaced perennial grasses so completely that few remnant fragments are currently left in their pristine condition. Almost adjacent to some of the most vulnerable grasslands are other grasslands that have received many alien plants but were not invaded. For example, the North American shortgrass steppe, which is adjacent to the Inter-Mountain West although separated by the massive Rocky Mountains, has proven to be quite resistant to invasions. Mack (1989) suggests that the major characteristics that distinguish between the two types of grasslands and which determine their invasibility is the presence of large-hooved, congregating mammals in the Holocene and dominance by cespitose grasses.

It appears that grasslands have moderate vulnerability to invasions, or sensitivity to invasions, in comparison to other biomes (Table 7.1). The factors that make one ecosystem more vulnerable to invasions than another is a question of active debate and research. Environmental severity is one factor that has been proposed to control invasibility. More mesic environments may be more vulnerable to invasions than are xeric ecosystems (Rejmánek 1989). Vulnerability to invasions could also increase with the frequency and intensity of disturbances (Rejmánek 1989). Finally, original biodiversity levels could be associated with vulnerability to invasions, with the more diverse ecosystems being less vulnerable (Rejmánek 1996). Experimental studies confirm the effect of biodiversity on determining vulnerability to invasions, but they highlight the role of other factors that often overshadow the biodiversity effect (Levine 2000).

In synthesis, grasslands, as a biome, receive abundant propagules of exotic species because they are located in regions that have been severely transformed by agriculture, and they are close to major heavily industrialized zones. Grasslands as a whole are moderately vulnerable to invasions, although there is large variability in invasibility within the grassland biome.

The Effects of Increased CO_2 Concentration on Biodiversity

The change in the concentration of CO_2 experienced by grasslands will be similar to that experienced by all other biomes because atmospheric CO_2 mixes globally in short periods of time (Fung et al. 1987). Nonetheless, grasslands are expected to be among the most responsive ecosystems to increased CO_2 concentrations. A synthesis of all the elevated CO_2 experiments up to 1995 showed that grasslands were the ecosystems in which productivity responded most strongly to a doubling CO_2 (Koch and Mooney 1995). The Californian annual grassland showed a 40–60% of increase in productivity relative to productivity under ambient CO_2; this was surpassed only by Kansas tallgrass prairie. Grasslands were already hypothesized to be among the most responsive ecosystems before scientists started whole-ecosystem elevated CO_2 experiments (Mooney et al. 1991). Perhaps the most consistent response to elevated CO_2 observed in different kinds of experiments has been a reduction in stomatal conductance and transpiration that result in an increase in water-use efficiency. For example, in a Californian annual grassland, doubling CO_2 resulted in a 50% reduction in stomatal conductance and transpiration, and a doubling of water-use efficiency (Jackson et al. 1994). An alteration of the water-use efficiency will have the largest impact on ecosystems that are frequently limited by water availability. Grasslands, which are shaped by water limitation, are consequently among the ecosystems with greatest potential response to elevated CO_2.

A CO_2-induced change in water-use efficiency can affect the entire ecosystem–water balance, modifying the seasonal pattern of water availability as well as the total amount of water available for plants (Jackson et al. 1998). Changes in water availability and the distribution pattern in the soil profile and throughout the growing season will alter the competitive balance of the plant species in the community. For example, plants that grow faster and have higher transpiration rate will outcompete the slower growing and more drought-resistant species. Field et al. (1995) found that increasing CO_2 in an annual grassland resulted in a large increase in soil water content predominantly at the end of the growing season. This increase will benefit a small group of species that are vegetative during late season, but it will not benefit the dominant species *Avena barbata* that is senescent at that time. This is an example of how changes in stomatal conductance may result in changes in species composition. It is expected that alterations of the competitive balance may result in local extinctions. If the phenomenon is extended in space and time, local extinctions may result in global extinctions.

Changes in CO_2 may affect animals by altering the physical and chemical environments. Elevated CO_2 increased the carbon–nitrogen ratio of leaf tissue in several grassland ecosystems (Field et al. 1995; Owensby et al. 1996). Increases in the carbon–nitrogen ratio negatively affect the quality of the diet of animals feeding on those plants. In an experiment using large open-top chambers in tallgrass prairie, Owensby et al. (1996) found that forage quality, estimated by the proportion of acid detergent fiber and in vitro dry-matter digestibility, sharply decreased under elevated CO_2 conditions relative to ambient conditions. Moreover, sheep grazing inside the chambers showed a lower intake than did control sheep. Owensby et al. (1996) speculated that the CO_2 impact will be greater for wild ruminants than it is for domestic ones. Results with ruminants in grasslands seem to be different than results obtained with insects and trees. Insects fed with leaves of trees grown under elevated CO_2 showed increased consumption rate, although the insect growth rate was decreased (Lindroth 1996).

Conclusions

Our exercise suggests that biodiversity in temperate grassland ecosystems will be severely affected by the year 2100. The five drivers of biodiversity change (i.e, land use, climate, nitrogen deposition, biotic exchange, and atmospheric CO_2) will have moderate-to-high effects on grassland biodiversity (Table 7.1). The mesic climatic conditions, which are characteristic of grasslands, make them ideal for agriculture; consequently, a large fraction of the grassland area will be transformed into cropland. The geographical location of grasslands, adjacent to urban and highly industrialized areas, results in grasslands receiving high human impact including high nitrogen deposition and large amounts of propagules of exotic plant and animal species. The changes of drivers will be large in grasslands, and their sensitivity to those changes will be very high (Table 7.1). Grasslands host species with a wide variety of morphological and physiological characteristics. For example, within the plants, grassland diversity ranges from shrubs to grasses, from plants with C_3 to C_4 photosynthetic pathways, and from deep- to shallow-rooted species. Changes in environmental conditions will alter the competitive balance of grassland species rapidly. Changes in the competitive balance will yield changes in abundance that will result in local extinctions in the short-to-medium term. When changes in drivers persist in time or affect large expanses of grasslands, local extinctions will turn into global extinctions.

The scenario for changes in biodiversity in grasslands contrasts with the scenarios for other biomes that show equally large impacts (e.g., tropical forests or southern temperate forests) (see Chaps. 11 and 12). Those two forest biomes will undergo large changes in biodiversity mostly as a result of very large changes in a single driver (land use). In contrast, grasslands will show moderate-to-high effects that result from all five drivers. From this point of view, the grassland scenario is similar to the scenario for Mediterranean ecosystems (see Chap. 9).

One of the limitations of this exercise has been the scale at which I was able to work. Scenarios at the scale of the entire biome mask specific differences among grassland types that will be large for some drivers. For example, even though some grassland types will continue to be plowed and transformed into agricultural land, others will experience the opposite pattern with cropland being abandoned and reverting slowly to the grassland condition. The scale limitation affects both the magnitude of the error associated with this exercise and constrains its applicability because most management decisions occur at more-detailed scales than the one used here.

Another limitation of this exercise is that it has not considered the interactions among drivers of biodiversity change. It is likely that there will be important synergistic interactions among drivers. The combined effects on biodiversity of nitrogen and CO_2 enrichment will probably be much larger than the sum of the independent effects of those two drivers. The effect of habitat fragmentation on biodiversity could similarly be enlarged by the presence of abundant propagules of exotic species. Exotic species may not succeed in invading a particular grassland type if the environment had not been modified by climate change or elevated CO_2. I can also envision an antagonistic interaction among drivers. For example, when alteration of the environment is very large (e.g., in the case of plowing that destroys all native vegetation) other drivers may not cause further losses of diversity. Our understanding of interactions is so limited that I have chosen not to include them in this chapter.

Mitigation of the expected changes in grassland biodiversity will result from reduction in the rate of change of drivers at the global scale and development of detailed management plans tailored for the particular ecological, social, and economic conditions of each grassland type. The development of management plans will require a better understanding of interactions among drivers as well as trade-offs among the goods and services that grasslands yield.

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