TEMPERATE GRASSLAND AND SHRUBLAND ECOSYSTEMS

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GLOSSARY

convention on biological diversity The convention was first enacted in June 1992, and it has been signed by many countries. Its objectives are the conservation of biological diversity, the sustainable use of its components, and the fair and equitable sharing of the benefits arising from the utilization of genetic resources, including by appropriate access to genetic resources and by appropriate transfer of relevant technologies, taking into account all rights over those resources and technologies, and by appropriate funding.

functional type A group of species that share morphological and physiological characteristics that result in a common ecological role.

global biodiversity assessment The Global Biodiversity Assessment is an independent peer-reviewed analysis of the biological and social aspects of biodiversity commissioned by the United Nations Environment Programme.

international geosphere biosphere programme A scientific program that is part of International Council of Science and provides an international and interdisciplinary framework for the conduct of global change science.

niche complementarity Refers to how the ecological niches of species may not fully overlap and complement each other. Consequently, an increase in the number of species that complement each other may result in a larger volume of total resources utilized and in a higher rate of ecosystem processes.

sampling effect Refers to the phenomenon in which increases in the number of species increase the probability of including in the community a species with a strong ecosystem effect. This phenomenon yields an increase in ecosystem processes with increases in diversity without invoking niche complementarity.

scientific committee on problems of the environment An international organization that is part of the International Council for Science and is charged with synthesizing current scientific understanding associated with environmental issues.

GRASSLANDS are water-limited ecosystems, and water availability defines the distribution of grasslands. Grassland ecosystems occur in areas of the world that have an annual precipitation between 150 and 1200 mm and mean annual temperature between 0 and 25°C. Temperature controls the distribution of grasslands mainly indirectly by modulating water demand and consequently water availability. Increases in temperature result in increases in soil evaporation and plant transpiration; consequently, for a similar precipitation regime, the water balance becomes more negative as temperature increases. In contrast with most biological phenomena, primary production of North American grasslands decreases with increasing temperature, highlighting the indirect mechanism of the temperature control on the distribution of grasslands.

I. GRASSLAND DISTRIBUTION

How does the distribution in temperature and precipitation space translate into the distribution of grasslands in geographical space? Along precipitation gradients grasslands are located between forests and deserts. Several of the International Geosphere Biosphere Programme terrestrial transects (Koch *et al.*, 1995) are located along precipitation gradients and they intersect forests, grassland–forest ecotones, grasslands, and deserts. This pattern is repeated in the North Eastern China transect, in the Great Plains transect in North America, and in the Patagonian transect in South America (Fig. 1).

Although temperature and precipitation are the major determinants of the distribution of grasslands, fire also may play an important role. Fire becomes particularly important in the grass–forest ecotones where the dominance of grasses or woody plants in many cases is determined by the frequency and intensity of fires. For example, in North American tallgrass prairie, the area covered with woody plants has increased dramatically in the past 100 years and the human intervention in reducing fire frequency is largely responsible for the change (Briggs *et al.*, 1998). Similarly, data from pollen profiles, tree ring analysis, and photographic sources documented a shift in the grassland–forest ecotone in northern Patagonia with woody vegetation invading the grassland (Veblen and Markgraf, 1988). Again, changes in the human-induced fire regime were responsible for the forest expansion.

This article focuses exclusively on climatically determined grasslands, in contrast with grasslands resulting from human intervention. Anthropogenically determined grasslands are located in areas where potential natural vegetation is forest. Humans, in an attempt to produce forage for domestic animals, have logged forests and have maintained these plots as grasslands by mowing them periodically.

Worldwide, temperate grasslands are represented in all continents and potentially cover a vast area of 49 × 10^6 km^2 that represents 36% of the earth's surface

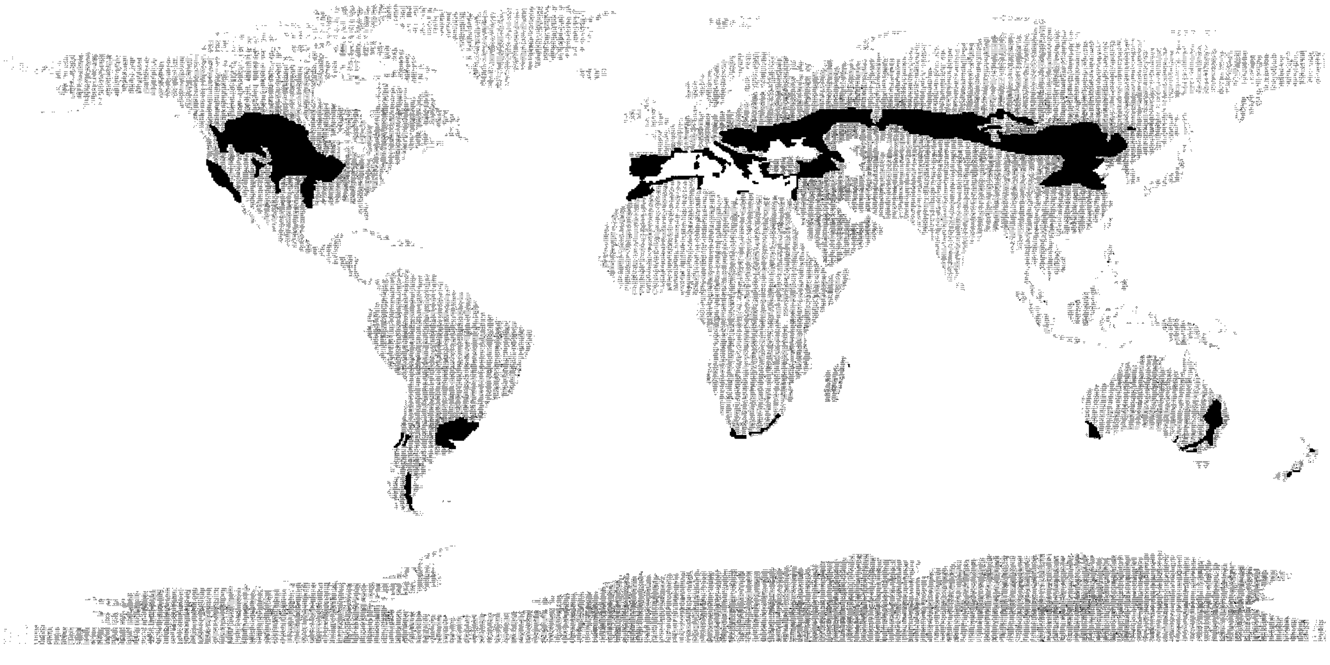

FIGURE 1 Map of the global distribution of temperate grasslands (adapted from Bailey, 1998).

(Shantz, 1954). Our definition of temperate grasslands excludes tropical and subtropical savannas but includes grass and shrub deserts. In North America, grassland is the potential natural vegetation of most of the Great Plains and it reaches from the Chihuahuan desert in the south to the deciduous forests of Canada in the north and from the Rocky Mountains in the west to the deciduous forest of the eastern United States (Fig. 1). In South America, grassland is the potential vegetation of the vast pampas and most of the Patagonian steppe. Finally, in Asia, grassland ecosystems cover a huge area from the Ukraine to China.

II. EXTENT OF BIODIVERSITY IN TEMPERATE GRASSLANDS

Biodiversity can be examined in many different ways, and multiple definitions exist for what constitutes "biodiversity." Nevertheless, the authors of the Global Biodiversity Assessment, using definitions originally proposed by the Convention on Biological Diversity, defined biological diversity as "variability among living organisms from all sources" (Heywood and Baste, 1995). Here, we focus on biodiversity in terms of taxonomically defined species, and the vast majority of studies quantifying ecosystem variation have used this measure. However, genetic biodiversity (genetic variation among a single species) and ecological diversity (including landscape diversity and functional group diversity) are also important components of biological diversity. The definition of biodiversity, therefore, will depend to a certain extent on one's objective and scale of interest, ranging from the gene to the ecosystem.

A. Diversity of Plants

Floristic diversity in grasslands varies broadly, with many natural grasslands having a very high level of plant diversity, at times approaching that seen in mainland tropical forests (Groombridge, 1992). For example, the Pampa region in Argentina represents some of the highest diversity grassland, with more than 400 species of grasses (Cabrera, 1970). In North America, more than 250 native species are found in tallgrass prairie (Freeman, 1998), the vast majority of which are perennial grasses.

Plant species of grasslands can be categorized into four functional types: grasses, shrubs, succulents, and herbs (Sala *et al.*, 1997). The classification of plant species into functional types only has epistemological value and serves the purpose of facilitating the study of grasslands. This classification can be divided into many new subcategories or aggregated into fewer units depending on the needs of the analysis. The relative contribution of the four functional types depends on the seasonality of precipitation and the soil texture, which are the factors controlling the distribution of water availability in the soil profile. Water penetrates deeper into the soil profile in coarse-textured soils than in fine-textured soils. Similarly, water penetrates deeper into the soil in regions in which most of the precipitation occurs during the cold time of the year when evaporative demand is low. In general, grasses and shrubs have contrasting rooting patterns, with grasses having predominantly shallow roots and shrubs having deep roots (Jackson *et al.*, 1996). Consequently, grasses dominate in regions in which the wet and warm seasons are in synchrony and in areas with predominantly fine-textured soils (Sala *et al.*, 1997; Fig. 2).

Grassland plant species can also be classified according to their photosynthetic pathway into C_3 and C_4 species. The two groups of species have differences in the physiology of photosynthesis and in the morphology of leaves that result in different ecological characteristics that separate them in time and space. Regional analyses of the distribution of these two types of grass species showed that C_3 species decrease southward in North America and northward in South America and C_4 species show the opposite pattern (Paruelo *et al.*,

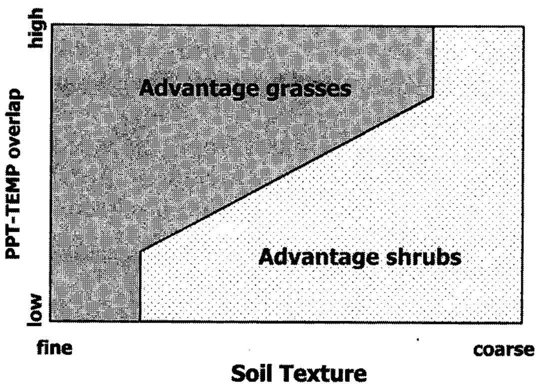

FIGURE 2 Conceptual model explaining the distribution of the functional groups grasses and shrubs with changes in seasonality of temperature and precipitation (congruence of warm and wet seasons) and soil texture. The gray shaded area represents conditions that are likely to favor the persistence of grasses, whereas the speckled area represents conditions that favor the shrub functional group. The intersection of the two areas represents points at which biotic influences are likely to be most pronounced (adapted from Sala *et al.*, 1997).

1998). Similarly, the abundance of C_3 species increases whereas that of C_4 decreases along an altitudinal gradient (Cavagnaro, 1988). These biogeographical analyses correlate with ecophysiological studies showing that C_4 species have photosynthesis optima at higher temperature, have higher water use efficiency, and are better adapted to low water availability conditions (Kemp and Williams, 1980).

B. Aboveground Diversity of Animals

All major taxonomic groups are represented in grasslands, but despite their large areal extent (36% of the area of terrestrial ecosystems), overall faunal diversity is lower than in many other biomes. The number of bird and mammalian species that are found primarily in grasslands are estimated to be 477 and 245, respectively, representing only 5% of the world's species for each taxonomic group (Groombridge, 1992). Local diversity can be high in specific areas (e.g., there are an estimated 208 avian species for tallgrass prairie; Kauffman *et al.*, 1998), but general patterns show lower diversity for most taxonomic groups compared with other ecosystems.

One of the striking features of grasslands in terms of animal diversity is the presence of large herbivores as a prominent component of secondary production. These large grazing mammals have an important impact on the functioning of grasslands, altering patterns of nutrient cycling, primary production, and plant species composition (McNaughton, 1993), although their presence and diversity varies across different continents. For example, in the Great Plains of North America, nearly all the large grazing mammals went extinct during the glaciation of the Pleistocene, but the proliferation of a very few species, particularly *Bison bison* (plains bison), dominated the plant–herbivore interactions until the introduction of domestic cattle at the beginning of the twentieth century (Lauenroth and Milchunas, 1992). In contrast, African grasslands contain a very high level of mammalian diversity of grazers, with up to 20 species coexisting in a single reserve (Cumming, 1982). Finally, many South American grasslands evolved without the presence of large grazers, and their primary herbivory prior to the introduction of sheep and cattle was due to insect species (Bucher, 1982). Thus, although there is variation in the diversity of the large herbivores, their presence and importance is a distinctive characteristic of grassland ecosystems.

Small mammals, birds, reptiles, amphibians, and insects also play an important role in the functioning of grasslands. Species richness of small mammals is actually higher than that for large mammals (168 vs 77 species overall), and they are mostly granivores or omnivores (Groombridge, 1992). In contrast, in Australian deserts small mammals are mostly insectivorous. Fluctuations in seed supply caused by unpredictable environmental conditions and the infertile soils could be an explanation for these differences (Morton, 1993).

Avian diversity in grasslands represents 5% of the total species of the world species diversity, and again the fluctuating climate has an important control on this distribution. In this case, birds can migrate to remote areas outside of the grassland biome to seek alternative resources in periods of unfavorable conditions. In North American grasslands, which demonstrate a strong seasonality, there are large annual variations of passerines in response to climatic conditions. Additionally, within the grassland ecosystems, there exists a gradient of avian biomass that decreases with precipitation and primary production from the tallgrass prairie to the mixed prairie and shortgrass steppe (Lauenroth and Milchunas, 1992).

Reptiles in grasslands are less diverse than mammals and birds, and amphibians are less diverse than reptiles in the tallgrass prairie of North America (Kauffman *et al.*, 1998). Latitude has an effect on the biodiversity of reptiles and amphibians because they are ectotermic organisms, with an increase in the number of species from north to south of the tallgrass prairie (Kucera, 1992).

Insects are a diverse element of the terrestrial macrofauna of tallgrass prairie (Kauffman *et al.*, 1998), reflecting general patterns of diversity for terrestrial ecosystems in which insects represent more than 50% of the species (Strong *et al.*, 1984). They have a very important role as herbivores, pollinators, predators, parasitoids, and decomposers. Herbivorous insects are probably the most conspicuous functional group in tallgrass prairie (Kauffman *et al.*, 1998) and may replace large grazing mammals as the primary consumer in some South American grasslands (McNaughton *et al.*, 1993).

C. Diversity of Soil Organisms

The diversity of belowground organisms (bacteria, fungi, and micro-, meso-, and macrofauna) is known in much less detail than that of plants and animals aboveground, but it may constitute a very important component of the biota, often equaling or exceeding the aboveground biomass in grasslands (Paul *et al.*, 1979). The large biomass of roots and other underground organs in grasslands and the high concentration of organic matter provide substrate for a large variety of bacteria, fungal, and nematode groups, and all are represented in grassland systems. Additionally, the arthropods, constituting the largest proportion of invertebrates in the shortgrass steppe and primarily herbivores, take advantage of the large amount of belowground primary production (Lauenroth and Milchunas, 1992). The studies that have been done show a very diverse group of organisms in grasslands soils in a variety of functional roles. For the shortgrass steppe, the relative importance in terms of biomass of the different functional groups is bacteria > fungi > nematodes > protozoa > macroarthropods > microarthropods (Lauenroth and Milchunas, 1992). In terms of species numbers, a soil invertebrate study in tallgrass prairie showed more than 200 species of nematodes, with fungivores constituting 40% of the nematode species (Ransom *et al.*, 1998) and the nematode biomass was exceeded only by that of bacterial and fungal groups. Another study in the shortgrass steppe found soils to contain more than 100 species of fungi during the summer season (Christensen and Scarborough, 1969).

III. BIODIVERSITY AND ECOSYSTEM FUNCTIONING IN GRASSLANDS

The relationship between biological diversity and the functioning of ecosystems has been central in the development of ecological ideas, and grassland ecosystems have been crucial in testing these ideas. McNaughton (1993) traced the idea of the relationship between biodiversity and ecosystem functioning to statements by Charles Darwin about how increasing species diversity in a plot might result in higher productivity as a result of niche complementarity. Most species in Darwin's plot supposedly exploited different resources, and consequently the larger the number of species, the larger the volume of resources exploited. For example, plots containing only shallow-rooted or deep-rooted species should have lower productivity than plots containing both groups of species that jointly have access to water and nutrients stored in both upper and lower layers of the soil.

Species not only differ in their ability to exploit resources but also in their response to the environment. Species show a variety of responses to abiotic factors such as temperature or water availability as well as biotic factors such as predation or competition. These relationships led to the diversity–stability hypothesis or portfolio hypothesis that stated that higher species diversity results in greater ecosystem stability (McNaughton, 1993). Consequently, ecosystem processes will vary more in space or time in less diverse than in more diverse communities.

The basic theory of the relationship between biodiversity and ecosystem functioning has been established for decades, but its empirical support has been scarce and fragmentary. Pimm's (1984) review of experimental results and later the Scientific Committee on Problems of the Environment (SCOPE) project led by Hal Mooney (Schulze and Mooney, 1993) reinvigorated the field and highlighted the gaps in our understanding. The value of possessing a quantitative understanding of the relationship between biodiversity and ecosystem functioning is underscored by the fact that we are in the midst of the sixth major extinction event in the history of life (Chapin *et al.*, 1998). The major difference between this and previous extinction episodes is that the current wave of extinction is the result of human activity. Society is urged to identify the consequences of the human-driven changes in biodiversity for the functioning of ecosystems that provide so many goods and services, including grasslands, that are at the basis of human well-being (Sala and Paruelo, 1997).

A large SCOPE project had the responsibility of assessing and evaluating the vast number of observations and experiments that addressed in different ways the role of biological diversity on the functioning of ecosystems. An initial meeting and corresponding volume synthesized the theory and formulated a plan of action (Schulze and Mooney, 1993). The second step was to address the same questions on a biome by biome basis. Finally, a large synthesis assessed the differences and commonalties among biomes in the relationship between biodiversity and ecosystem functioning (Mooney *et al.*, 1995a, b, 1996). Results for the grassland biome emphasized the effects of changes in biodiversity on primary productivity, decomposition, water balance, atmospheric properties, landscape structure, and species interactions (Sala *et al.*, 1995, 1996). This effort synthesized our knowledge and it also highlighted the gaps in our understanding and the need for further experimentation.

Grassland ecosystems played a key role in the experimentation regarding the functional roles of biodiversity mostly because of the small size and short life span of grasses, which made manipulative experiments feasible with few resources and in short periods of time. The most widely accepted hypothesis indicates that the rate of ecosystem processes, such as primary productivity or nutrient cycling, might increase linearly as species richness increases and that this relationship eventually saturates as ecological niche overlap increases (Fig. 3) (Vitousek and Hooper, 1993).

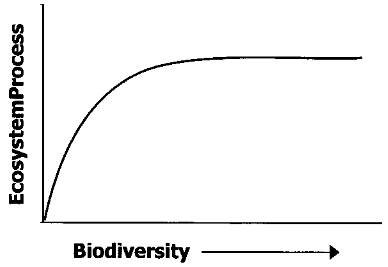

FIGURE 3 Theoretical relationship between biodiversity and ecosystem functioning. Species richness (number of species) is the most common indicator of biodiversity, although this axis term could also include genetic diversity (diversity within species) to landscape diversity. Ecosystem process could signify processes occurring at the ecosystem level, including primary production and decomposition, and components of nutrient cycling (adapted from Vitousek and Hooper, 1993).

The first experiment specifically designed to test this hypothesis was carried out under controlled conditions at the Imperial College Ecotron facility (Naeem *et al.*, 1994). The experiment used synthetic communities with three trophic levels and three levels of species diversity, from the simplest with 1 species of a secondary consumer, 3 primary consumers, 2 producers, and 3 decomposers to the most diverse that had 31 species. The results of this experiment supported the hypothesis described in Fig. 3 in that carbon fixation (an indirect measure of primary productivity) increased with diversity. The first large-scale field experiment specifically designed to test this hypothesis was located in the North American tallgrass prairie (Tilman *et al.*, 1996). The experiment consisted of sowed plots with seven levels of plant diversity and 20 replicates per level. Each replicate was a random draw from a pool of 24 native species. Consequently, replicates had the same diversity level but could have a different or equivalent species composition. Results follow a pattern similar to that of Fig. 3, with total plant cover (a nondestructive way of estimating light interception and production) and nutrient uptake increasing with species richness up to a level of approximately 10 species. Beyond 10 species, the different estimates of ecosystem functioning did not change. Recently, a large consortium of scientists organized a large-scale field experiment across Europe with the purpose of testing the same hypothesis (Hector *et al.*, 1999). The same experimental design was repeated in eight locations in Europe from Sweden to Greece and it consisted of five diversity treatments with richness ranging from 1 to 32 species. Species identity varied among the sites since species for each treatment were always drawn from a pool of species adapted to local conditions. A single model represented the loglinear increase of aboveground biomass with increasing species richness for all sites.

The different experiments designed to test the effect of diversity on ecosystem functioning yielded results that are similar to those predicted from the hypothesis described in Fig. 3. These results can be interpreted as evidence of niche complementarity; that is, the higher the number of species with niches that do not overlap, the larger the total volume of resources exploited (Tilman *et al.*, 1997). Alternatively, the same results can be interpreted as resulting from the sampling effect (Huston, 1997; Tilman *et al.*, 1997). It indicates that as the number of species increases, the probability of including in the mix a species with strong ecosystem effects increases. This species may be a nitrogen fixer, a deep-rooted species, or simply a species with a combination of characters that maximizes production in these circumstances.

IV. THE FUTURE OF BIODIVERSITY IN GRASSLANDS

Biodiversity in grassland ecosystems is seriously threatened by human activity. Grassland ecosystems, in two of three possible scenarios of biodiversity change for the Year 2100, appear to be the most threatened biome; in the third scenario, grasslands appear behind only tropical forests, arctic ecosystems, and southern temperate forests (Sala *et al.*, 2000).

What makes biodiversity in grassland ecosystems so vulnerable to human impact? Are grassland ecosystems particularly sensitive? Are they located in areas that will be affected the most? A recent study identified the most important drivers of biodiversity change in grasslands as changes in land use, climate, nitrogen deposition, biotic exchange (accidental or deliberate introduction of plant or animal species to an ecosystem), and atmospheric CO_2 and studied their expected change and the sensitivity of each biome (Sala *et al.*, 2000). The study concludes that grasslands are both quite sensitive ecosystems and are located in parts of the world where ecosystems are going to be affected most by human activity (Fig. 4).

The expected change of each of the drivers was assessed using other scenarios, such as climate change or land use change, that were developed independently (Alcamo, 1994; Haxeltine and Prentice, 1996). The dif-

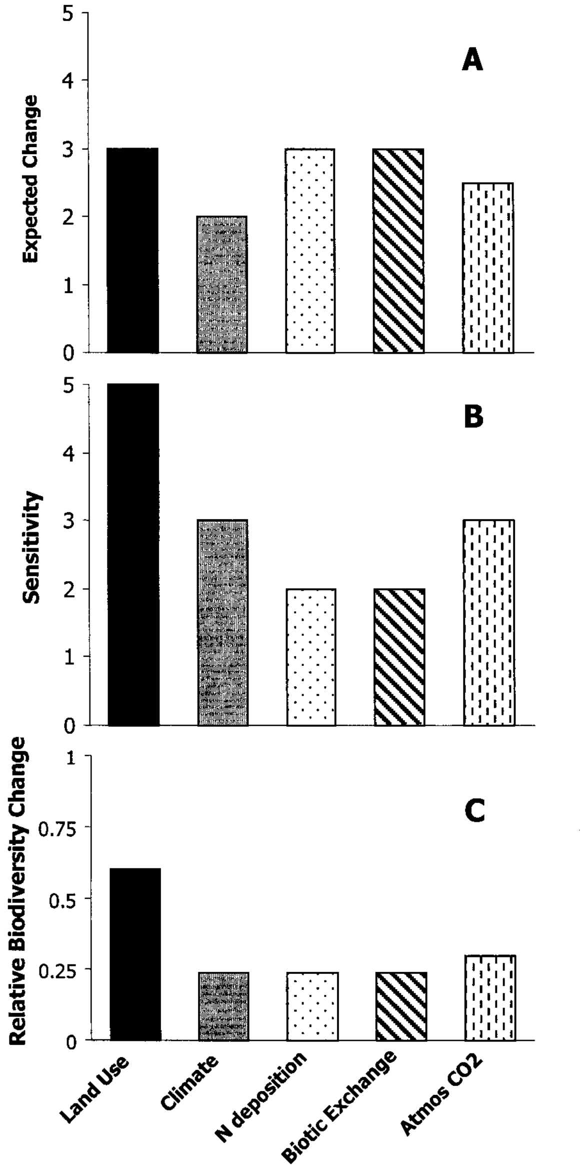

FIGURE 4 Scenarios of biodiversity change in grasslands for the Year 2100. (A) Expected change of the major drivers of biodiversity change in a relative scale from 1 to 5. (B) Sensitivity of grasslands to unit changes in each driver using the same relative scale. (C) Grassland biodiversity change resulting from changes in each driver and calculated as the product of the expected change of each driver multiplied by the sensitivity of grasslands to each driver (adapted from Sala *et al.*, 2000).

ferent drivers of biodiversity change were originally expressed in different units from parts per million to hectares and degrees Celsius. In order to compare the rate of change among drivers, they were all converted into a 1 to 5 arbitrary scale. Land use, nitrogen deposition, and biotic exchange are expected to be the drivers that are going to change the most in grassland ecosystems (Sala *et al.*, 2000) (Fig. 4A). The most dramatic changes in land use in grasslands are those that result in changes in land cover, such as the conversion into croplands. Grasslands are among the biomes that are going to experience the largest conversion in land use because of their mild climate and favorable soil conditions that made them quite suitable for agriculture. The conversion into agricultural land is not expected to be even across the world but driven by the patterns of food demand and population growth that indeed are quite idiosyncratic. For example, the IMAGE2 model (Alcamo, 1994) predicts for the Year 2100 a large increase in agricultural area in Africa and a reduction in North America resulting from an increase in demand and an increase in intensification, respectively. Biodiversity losses resulting from conversion to agriculture in one part of the world are not offset by a similar area that will be abandoned and reverts to grassland but that is located in a different part of the world. Therefore, total change in grassland area grossly underestimates the impact of land use change on biodiversity. Finally, the expected change of nitrogen deposition and biotic exchange in grasslands are among the highest of all biomes. Densely human-populated regions are predominantly located in temperate regions where the potential native vegetation is that of grasslands. Nitrogen deposition is associated with industrialization, whereas biotic exchange is associated with trade patterns and ultimately with human density.

Sensitivity to changes in each driver is the magnitude of change in biodiversity due to a change in a unit of driver. Sensitivity varies among biomes, and grasslands are quite sensitive to changes in land use, climate, and CO_2 concentration in the atmosphere (Fig. 4B). Grasslands are most sensitive to land use change, which means the conversion into croplands that implies plowing of native grasslands and sowing of a monospecific crop. This activity clearly results in the local extinction of all the native plant species that, in turn, determine the major characteristics of the habitat of animals and microorganisms. Consequently, land use change drives all plant species to local extinction and drastically affects the diversity of other organisms (Anderson, 1995). Biodiversity may be quite sensitive to changes in CO_2 concentration in ecosystems that are limited by water availability such as grasslands. There are well-known differences in the species response in water use efficiency due to changes in CO_2 (Jackson *et al.*, 1994). Consequently, changes in CO_2 will first affect the competitive balance and then the relative abundance, and they may result in the local extinction of species.

The biodiversity change resulting from each driver (Fig. 4C) can be calculated as the product of the expected change (Fig. 4A) multiplied by the biome sensitivity to that driver (Fig. 4B). The largest biodiversity change for the Year 2100 in grasslands is expected to occur due to changes in land use. The second largest effect will result from the expected increase in CO_2 because although the atmospheric concentration of this trace gas will increase uniformly throughout the world (Fung *et al.*, 1987), grassland biodiversity may be particularly sensitive to it.

Finally, the total biodiversity change in grasslands expected for the Year 2100 can be calculated as the sum of the individual effects of each driver (Fig. 4C). This calculation assumes no interaction among drivers. Comparison of the total biodiversity change in grasslands against that of all the other terrestrial biomes of the world indicates that grasslands and Mediterranean ecosystems appear to be the biomes that will experience the largest change and will be affected the most (Sala *et al.*, 2000).

Other scenarios consider the assumption that there are synergistic interactions among the drivers of biodiversity change. We can envision several examples of the synergistic interactions among drivers. For example, the effect of biotic exchange will be amplified if combined with a land use change that results in fragmentation. Similarly, the effects of elevated CO_2 on biodiversity when occurring in conjunction with increased nitrogen deposition will be much larger than the sum of the individual effects. The scenario developed using the assumption of a synergistic interaction among drivers also indicated that grasslands and Mediterranean ecosystems are the most vulnerable (Sala *et al.*, 2000). The only scenario in which grasslands are not the most vulnerable ecosystem is when an antagonistic interaction was assumed and the total biodiversity change was equated with the change resulting from the driver with the maximum value. This scenario is plausible only under extreme conditions, such as those of slash-and-burn that destroy most of the plant and animal species, and further change due to the other drivers is not possible. Even in the antagonistic scenario, grasslands are among the most vulnerable biomes, following tropical, arctic, and southern temperate ecosystems.

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See Also the Following Articles

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Bibliography

Alcamo, J. (1994). *Image 2: Integrated Modeling of Global Climate Change*. Kluwer, Dordrecht.

Anderson, J. M. (1995). The soil system. In *Global Biodiversity Assessment: Section 6* (H. A. Mooney, J. Lubchenco, R. Dirzo, and O. E. Sala, Eds.), pp. 406–412. Cambridge Univ. Press, Cambridge, UK.

Bailey, R. G. (1998). *Ecoregions: The Ecosystems Geography of the Oceans and Continents*. Springer, New York.

Briggs, J. M., Nellis, M. D., Turner, C. L., Henebry, G. M., and Su, H. (1998). A landscape perspective of patterns of processes in tallgrass prairie. In *Grassland Dynamics: Long-Term Ecological Research in Tallgrass Prairie* (A. K. Knapp, J. M. Briggs, D. C. Hartnett, and S. L. Collins, Eds.), pp. 265–279. Oxford Univ. Press, New York.

Bucher, E. H. (1982). Chaco and Caatinga—South American arid savannas, woodlands and thickets. In *Ecology of Tropical Savannas* (B. J. Huntley and B. H. Walker, Eds.), pp. 48–79. Springer-Verlag, New York.

Cabrera, A. (1970). *Flora de la Provincia de Buenos Aires: Gramineas*. Insituto Nacional de Tecnología Agropecuara, Buenos Aires.

Chapin, F. S., Sala, O. E., Burke, I. C., Grime, J. P., Hooper, D. U., Lauenroth, W. K., Lombard, A., Mooney, H. A., Mosier, A. R., Naeem, S., Pacala, S. W., Roy, J., Steffen, W., and Tilman, D. (1998). Ecosystems consequences of changing biodiversity. *BioScience* 48, 45–52.

Christensen, M., and Scarborough, A. M. (1969). Soil microfaunal investigations, Pawnee site, Colorado State University Report No. 23, U.S. IBP Grassland Biome, Colorado State University, Fort Collins.

Cumming, D. H. M. (1982). The influence of large herbivores on savanna structure in Africa. In *Ecology of Tropical Savannas* (B. J. Huntley and B. H. Walker, Eds.), pp. 217–245. Springer-Verlag, New York.

Epstein, H., Laurenroth, W., Burke, I., and Coffin, D. (1996). Ecological responses of dominant grasses along two climatic gradients in the Great Plains of the United States. *J. Vegetation Sci.* 7, 777–788.

Freeman, C. C. (1998). The flora of Konza prairie. A historical review and contemporary patterns. In *Grassland Dynamics: Long-Term Ecological Research in Tallgrass Prairie* (A. Knapp, J. Briggs, D. Hartnett, and S. Collins, Eds.), pp. 69–80. Oxford Univ. Press, New York.

Fung, I. Y., Tucker, C. J., and Prentice, K. C. (1987). Application of advanced very high resolution radiometer vegetation index to study atmosphere–biosphere exchange of of CO_2. *J. Geophys. Res.* **92D**, 2999–3015.

Groombridge, B. (1992). *Global Biodiversity: Status of the Earth's Living Resources*. Chapman & Hall, London.

Haxeltine, A., and Prentice, I. C. (1996). BIOME3: An equilibrium terrestrial biosphere model based on ecophysiological constraints, resource availability, and competition among plant functional types. *Global Biogeochem. Cycles* **10**, 693–709.

Hector, A., Schmid, B., Beierkuhnlein, C., Caldeira, M. C., Diemer, M., Dimitrakopoulos, P. G., Finn, J. A., Freitas, H., Giller, P. S., Good, J., Harris, R., Högberg, P., Huss-Danell, K., Joshi, J., Jumpponen, A., Körner, C., Leadley, P. W., Loreau, M., Minns, A., Mulder, C. P. H., O'Donovan, G., Otway, S. J., Pereira, J. S., Prinz, A., Read, D. J., Scherer-Lorenzen, M., Schulze, E. D., Siamantziouras, A. S. D., Spehn, E. M., Terry, A. C., Troumbis, A. Y., Woodward, F. I., Yachi, S., and Lawton, J. H. (1999). Plant diversity and productivity experiments in European grasslands. *Science* **286**, 1123–1127.

Heywood, V. H., and Baste, I. (1995). Introduction. In *Global Biodiversity Assessment*, pp. 5–19. Cambridge Univ. Press, Cambridge, UK.

Huston, M. A. (1997). Hidden treatments in ecological experiments: Re-evaluating the ecosystem function of biodiversity. *Oecologia* **110**, 449–460.

Jackson, R. B., Sala, O. E., Field, C. B., and Mooney, H. A. (1994). CO_2 alters water use, carbon gain, and yield for the dominant species in a natural grassland. *Oecologia* **98**, 257–262.

Jackson, R. B., Candell, J., Ehleringer, J. R., Mooney, H. A., Sala, O. E., and Schulze, E. D. (1996). A global analysis of root distributions of terrestrial biomes. *Oecologia* **108**, 389–411.

Kauffman, D. W., Fay, P. A., Kaufman, G., and Zimmerman, J. L. (1998). Diversity of terrestrial macrofauna. In *Grassland Dynamics: Long-Term Ecological Research in Tallgrass Prairie* (A. Knapp, J. Briggs, D. Hartnett, and S. Collins, Eds.), pp. 101–112. Oxford Univ. Press, New York.

Kemp, P. R., and Williams, G. J. (1980). A physiological basis for niche separation between *Agropyron smithii* (C3) and *Bouteloua gracilia* (C4). *Ecology* **61**, 846–858.

Koch, G. W., Scholes, R. J., Steffen, W. L., Vitousek, P. M., and Walker, B. H. (1995). The IGBP Terrestrial Transects: Science Plan, Report No. 36. International Geosphere–Biosphere Programme, Stockholm.

Kucera, C. L. (1992). Tallgrass prairie. In *Natural Grasslands: Introduction and Western Hemisphere* (R. T. Coupland, Ed.), pp. 227–268. Elsevier, Amsterdam.

Lauenroth, W. K., and Milchunas, D. G. (1992). Short-grass steppe. In *Natural Grasslands: Introduction and Western Hemisphere* (R. T. Coupland, Ed.), pp. 183–226. Elsevier, Amsterdam.

Lieth, H., and Whittaker, R. (1975). *Primary Productivity of the Biosphere*. Springer-Verlag, New York.

McNaughton, S. J. (1993). *Biodiversity and function of grazing ecosystems*. In *Biodiversity and Ecosystem Function* (E. D. Schulze and H. A. Mooney, Eds.), pp. 361–383. Springer-Verlag, Berlin.

McNaughton, S. J., Sala, O. E., and Oesterheld, M. (1993). Comparative ecology of African and South American arid to subhumid ecosystems. In *Biological Relationships between Africa and South America* (P. Goldblatt, Ed.), pp. 548–567. Yale Univ. Press, New Haven, CT.

Mooney, H. A., Lubchenco, J., Dirzo, R., and Sala, O. E. (1995a). *Biodiversity and Ecosystem Functioning: Basic Principles*. Cambridge Univ. Press, Cambridge, UK.

Mooney, H. A., Lubchenco, J., Dirzo, R., and Sala, O. E. (1995b). *Biodiversity and Ecosystem Functioning: Ecosystem Analyses*. Cambridge Univ. Press, Cambridge, UK.

Mooney, H. A., Cushman, J. H., Medina, E., Sala, O. E., and Schulze, E. D. (1996). *Functional Roles of Biodiversity: A Global Perspective*. Wiley, Chichester, UK.

Morton, S. R. (1993). Determinants of diversity in animal communities. In *Species Diversity in Ecological Communities* (R. E. Ricklefs, Ed.), pp. 159–169. Univ. of Chicago Press, Chicago.

Paruelo, J., Jobbágy, E., Sala, O., Lauenroth, W., and Burke, I. (1998). Functional and structural convergence of temperate grassland and shrubland ecosystems. *Ecol. Appl.* **8**, 194–206.

Paul, E. A., Clark, F. E., and Biederbeck, V. O. (1979). Microorganisms. In *Grassland Ecosystems of the World: Analysis of Grasslands and Their Uses* (R. T. Coupland, Ed.), pp. 87–96. Cambridge Univ. Press, Cambridge, UK.

Pimm, S. L. (1984). The complexity and stability of ecosystems. *Nature* **307**, 321–326.

Ransom, M. D., Rice, C. W., Todd, T. C., and Wehmueller, W. A. (1998). Soils and soil biota. In *Grassland Dynamics: Long-Term Ecological Research in Tallgrass Prairie* (A. Knapp, J. Briggs, D. Hartnett, and S. Collins, Eds.), pp. 48–66. Oxford Univ. Press, New York.

Sala, O. E., and Paruelo, J. M. (1997). Ecosystem services in grasslands. In *Nature's Services: Societal Dependence on Natural Ecosystems* (G. C. Daily, Ed.), pp. 237–252. Island Press, Washington, DC.

Sala, O. E., Lauenroth, W. K., McNaughton, S. J., Rusch, G., and Zhang, X. (1995). Temperate grasslands. In *Global Biodiversity Assessment*, pp. 361–366. Cambridge Univ. Press, Cambridge, UK.

Sala, O. E., Lauenroth, W. K., McNaughton, S. J., Rusch, G., and Zhang, X. (1996). Biodiversity and ecosystem function in grasslands. In *Functional Role of Biodiversity: A Global Perspective* (H. A. Mooney, J. H. Cushman, E. Medina, O. E. Sala, and E. D. Schulze, Eds.), pp. 129–149. Wiley, New York.

Sala, O. E., Lauenroth, W. K., and Golluscio, R. A. (1997). Plant functional types in temperate semi-arid regions. In *Plant Functional Types* (T. M. Smith, H. H. Shugart, and F. I. Woodward, Eds.), pp. 217–233. Cambridge Univ. Press, Cambridge, UK.

Sala, O. E., Chapin, F. S., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L. F., Jackson, R. B., Kinzig, A., Leemans, R., Lodge, D. M., Mooney, H. A., Oesterheld, M., Poff, N. L., Sykes M. T., Walker, B. H., Walker, M., and Wall, D. H. (2000). Global biodiversity scenarios for the Year 2100. *Science* **287**, 1770–1774.

Schulze, E. D., and Mooney, H. A. (1993). *Biodiversity and Ecosystem Function*. Springer-Verlag, Berlin.

Shantz, H. (1954). The place of grasslands in the earth's of vegetation. *Ecology* **35**, 142–145.

Smith, T., Shugart, H. H., and Woodward, F. I. (1996). *Plant Functional Types*. Cambridge Univ. Press, Cambridge, UK.

Strong, D. R., Lawton, J. H., and Southwood, R. R. S. (1984). *Insects on Plants: Community Patterns and Mechansims*. Harvard Univ. Press, Cambridge, MA.

Tilman, D., Wedin, D., and Knops, J. (1996). Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature* **379**, 718–720.

Tilman, D., Lehman, C., and Thomson, K. (1997). Plant diversity and ecosystem productivity: Theoretical considerations. *Proc. Natl. Acad. Science USA* **94**, 1857–1861.

Veblen, T. T., and Markgraf, V. (1988). Steppe expansion in Patagonia? *Quaternary Res.* **30**, 331–338.

Vitousek, P. M., and Hooper, D. U. (1993). Biological diversity and terrestrial ecosystem biogeochemistry. In *Biodiversity and Ecosystem Function* (E. D. Schulze and H. A. Mooney, Eds.), pp. 3–14. Springer-Verlag, Berlin.