GRASSLANDS AND SAVANNAS

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Summary

Grasslands are typically defined as lands on which the existing plant cover is dominated by grasses. Savannas are broadly defined as grasslands with scattered trees. Grasslands and savannas together cover approximately 5% of Earth's surface. Grasslands evolved during the Cenozoic era, in the course of a period of cooling and drying of the global climate. Evolution of savanna ecosystems and their constituent organisms may have already been in progress in the Eocene and Oligocene epochs. By definition, grasslands and savannas can be either anthropogenic or natural. Anthropogenic grasslands and

savannas require some form of disturbance, such as cultivation, heavy grazing, burning, or mowing to persist. Natural grasslands occur across a wide range of climatic and geological conditions, with soil and climate being the major limiting factors to their distribution. Natural savannas, conventionally considered tropical savannas, occur in the seasonal wet–dry zones sandwiched between the humid equatorial zones and the arid zones in the mid latitudes, between lat 10° and lat 30° north and south of the equator. Since for thousands of years both savannas and grasslands around the world have been manipulated by humans for their benefit, it can be difficult in some areas at times to separate the influence of humans from that of nature in the formation or maintenance of these ecosystems. Today we have the potential to use knowledge and technology to sustain these ecosystems indefinitely and without environmental deterioration. However, management tools and decisions must be tailored to the specific type of ecosystem and the management objective.

1. Introduction

Grasslands and savannas together cover approximately 5% of Earth's surface, and make up an estimated 23% of Earth's terrestrial biomes (see Figure 1). Grasslands are typically defined as lands on which the existing plant cover is dominated by grasses. Savannas are broadly defined as grasslands with scattered trees. The two biomes are distinct, though they commonly grade into each other. In addition, they have both unique and shared ecological processes, structures, and biotic assemblages. Distributions of both grasslands and savannas are regulated by climate and soils, and modified by disturbance (natural and/or anthropogenic). Grasslands are categorized on a broad scale as either temperate or tropical. Savannas are conventionally considered an exclusively tropical biome, and the terms tropical grasslands and savannas are often used interchangeably.

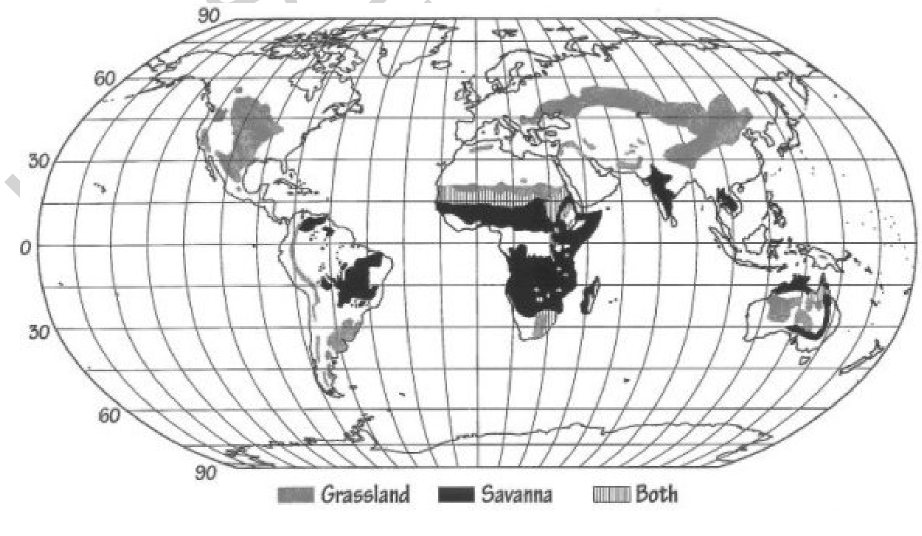

Figure 1. Natural grasslands and savannas of the world

2. Evolution

Grasslands evolved during the Cenozoic Era (66.4 million years ago to the present), in the course of a period of cooling and drying of the global climate. During this era, the continents assumed their modern configuration and geographic positions, and Earth's flora and fauna evolved toward those of the present. The grass family (Poaceae or Graminae) evolved early in the Cenozoic era, an era commonly referred to as the Age of Mammals due to the rapid spread and diversification of mammals during that time. The date of the earliest appearance of grasslands varies from region to region. In several regions, a succession of vegetation types can be recognized in the Cenozoic fossil record as the climate progressively dried out. For example, in central Australia during the past 50 million years tropical rainforests gave way successively to savanna, grassland, and finally, desert. In some places expansions of grasslands to something approaching their modern extent occurred only during the past two million years in the extremely cold, dry intervals, called Ice Ages. See *Tertiary, Quaternary*.

Evolution of savanna ecosystems and their constituent organisms may have already been in progress in the Eocene (38–54 million years BP) and Oligocene (26–38 million years BP) epochs. If savannas are considered exclusively tropical, and are defined as possessing a more-or-less continuous grass cover, it is thought they cannot have come into being before the Eocene, because the first records of pollen grains of grasses from the tropics date from the Middle Eocene. However, low open vegetation types constituted by herbs other than grasses may have existed before that time. Savanna evolution continued during Miocene (5.1–23 million years BP) and Pliocene (1.8–5.0 million years BP) times, with extreme changes during the Quaternary period (2 million years BP), when climates in the tropics seemed to have alternated between rainy periods and drier spells. During these time periods, there was possibly large-scale and repeated expansion of savanna vegetation during dry climatic intervals. It is also possible that present areas of savanna were considerably smaller during periods of general increases of precipitation in ecotones between savanna and rain forest, due to the invasion of savannas by rain forest.

3. Distribution

By definition, grasslands and savannas can be either manmade or natural. Anthropogenic grasslands of cereal crops, pastures, playing fields, or other types require some form of disturbance, such as cultivation, heavy grazing, burning, or mowing to persist. Human-made grasslands exist the world over, and are central to human welfare, as they provide a major source of food when managed as cropland or rangeland. Anthropogenic savannas, historically maintained by fire, also provide humans with food, pasture for grazing animals, and recreational areas, in addition to being a source of wood products. Since for thousands of years both savannas and grasslands around the world have been manipulated by humans for their benefit, it can be difficult in some areas at times to separate the influence if humans from that of nature in the formation or maintenance of these ecosystems.

Natural grasslands occur across a wide range of climatic and geological conditions, with soil and climate being the major limiting factors to their distribution. Natural savannas, conventionally considered tropical savannas, occur in the seasonal wet–dry zones sandwiched between the humid equatorial zones and the arid zones in the mid latitudes: between lat 10^{o} and 30^{o} north and south of the equator. In general, natural grasslands and savannas can be considered intermediates in an environmental gradient, with forests at one end and deserts at the other. Forests primarily occupy environments where the nature of soil and amount of moisture are conducive to growth and survival of tall, dense vegetation dominated by trees. Savannas are found where moisture, soil texture, nutrients, herbivory, and fire allow codominance of grasses and trees. Deserts are found where moisture is so lacking that a continuous permanent vegetation cover cannot be maintained. A dynamic balance commonly exists between grasslands and related vegetation types (i.e., desert, forest, savanna). Changes in the severity or frequency of disturbance events (i.e., grazing, fire, drought, flooding) can cause a change from one vegetation type to another.

Distribution of grasslands and savannas could also conceivably be influenced by global climate change. Many models of the atmosphere and global climate suggest that substantial warming of the atmosphere (1.5–5.5 °C) will accompany increasing concentrations of greenhouse gases: carbon dioxide (CO_2), nitrous oxide (N_2O), methane (CH_4), and chlorofluorocarbons. Carbon dioxide, the major greenhouse gas, is a principal by-product of the combustion of anything containing carbon, particularly coal and petroleum. Methane is produced by grazing livestock and rice paddies, and is a by-product of the combustion of wood, natural gas, coal, and oil. Nitrous oxide comes from chemical fertilizers and automobile emissions, and chlorofluorocarbons are synthetic chemicals that until recently were used for a variety of uses including refrigeration and air conditioning. All of these gases have been released at an accelerating rate in recent years. The warming results from the absorption of infrared (heat) radiation emitted from the surface of Earth (greenhouse effect). Most models predict that higher concentrations of CO_2 and other trace gases in the atmosphere will make Earth a warmer and more humid planet in the future, and that temperature and precipitation patterns will change. Some scenarios predict that heat and drought would become more prevalent in much of the midlatitudes, and milder temperatures would prevail in higher latitudes. Some arid lands might receive more rainfall, ice caps could melt, and global sea levels would rise. If this occurs, it will most likely influence the distributions of many terrestrial plants and animals. *See Greenhouse Gasses*.

4. Ecology

4.1. Climate

The ecological components of grasslands and savannas vary according to climate, soil, and biotic factors. Climate provides a source of energy and water for ecosystems. The sun is the main source of energy for Earth's biota-energy flows into the biological world from the sun, which supplies heat and light by solar radiation. Solar energy warms the earth's surface making it habitable, in addition to being captured by green plants and converted into chemical forms of energy that power the growth, maintenance, and reproduction of most living things (see Figure 2).

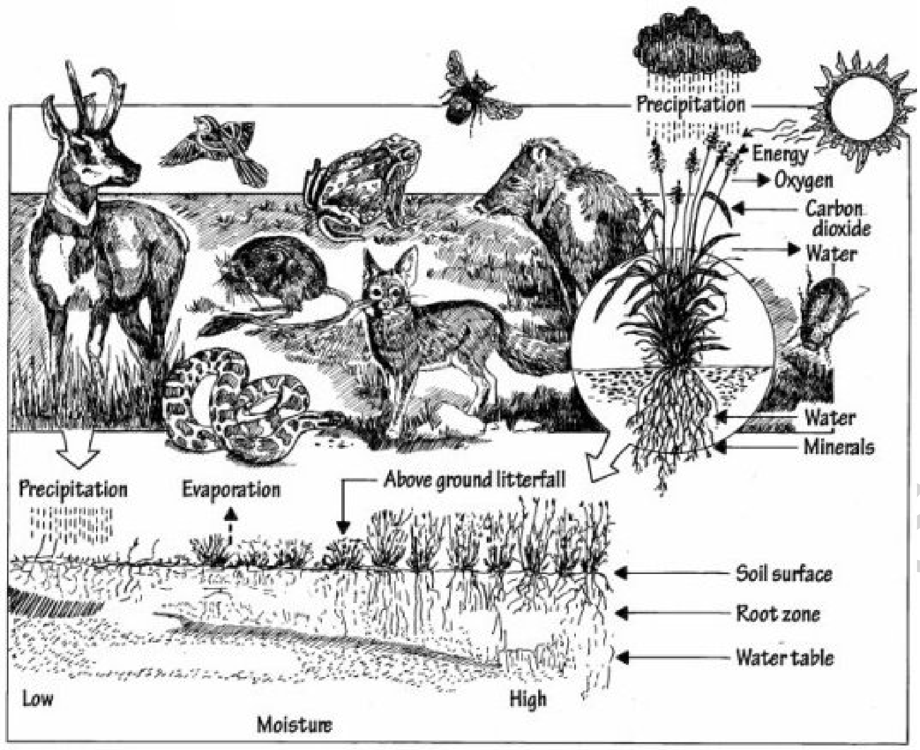

Figure 2. Ecology of grasslands and savannas

The way Earth revolves about the sun and rotates on its axis influences the distribution of solar radiation at its surface, and the quantity of heat absorbed. As a result of Earth's curvature, the low latitudes or tropics receive more solar radiation than do middle and higher latitudes. The polar regions receive only about 40% of the solar energy received at the equator. To balance this unequal distribution of energy, there is a large-scale transfer of heat poleward, through atmospheric and oceanic circulation. These circulations moderate the buildup of heat in equatorial regions and the lack of heat in polar regions, thereby making both those latitudinal zones more habitable than they would be otherwise. The frictional effects of the rotating Earth's surface on airflow cause these circulations to be relatively complex. Nevertheless, the solar energy and atmospheric and oceanic circulations are distributed over the planet in an organized fashion. These factors, in turn, produce recognizable world patterns of temperature and precipitation, the two most important climatic elements. See *Atmosphere and Climate*.

4.1.1. Temperature

Temperature is a measure of the amount of heat energy within a substance (internationally measured in °C). The temperature of air and soil is important to biotic distribution patterns. Fewer species of both plants and animals can survive in cold regions than in areas of more moderate temperatures. Plants, in particular, have a limited tolerance for low temperatures because they experience tissue damage and other physical disruption when their cellular water freezes. Many animals have evolved protection against low temperatures, and are able to avoid cold by moving around to seek warmth or shelter. Variations in temperature on and within the surface of Earth have a variety of causes, including the effects of latitude and altitude; continental, seasonal, and diurnal effects; microclimatic effects; and, in soil and water, the effects of depth.

The angle at which Earth is tilted relative to the sun changes over an annual cycle, and this drives some of the main temperature differentials on Earth's surface (recall the angle of incoming radiant energy relative to the planet's surface affects the quantity of heat absorbed). This differential heating produces the seasons. The seasons are also characterized by different lengths of day and night. In general, heating is most intense when the sun is directly overhead, so that incoming solar radiation strikes perpendicular to Earth's surface. Therefore, the higher latitudes are cooler than the tropics because the same quantity of solar radiation is dispersed over a greater surface area and passes through a thicker layer of filtering atmosphere. Seasonality of climate increases with increasing latitude due to variations in sun angles and length of day. For example, tropical latitudes are always warm/hot because they always have high sun angles and consistent day lengths that are close to 12 h long. Conversely, the polar regions are consistently cold because they always have low sun angles in spite of 24-h days in summer. Only the areas poleward of 66.5° have 24-h days and nights. *See Insolation.*

4.1.2. Precipitation

Precipitation is defined as all forms of condensation of atmospheric water, including rainfall, snowfall, and icefall. The most important geographic aspect of atmospheric moisture is the spatial distribution of precipitation. The broad-scale pattern is based on latitude, but many other factors are involved and the overall pattern is complex. The amount of precipitation on any part of Earth's surface is determined by the nature of the air masses involved and the degree to which the air is uplifted. The humidity, temperature, and stability of the air masses are mostly dependent on where the air originates (over land or water, in high or low latitudes) and on the trajectory it has followed. The amount of uplifting is determined largely by zonal pressure patterns, topographic barriers, and storms and other atmospheric disturbances.

The most conspicuous feature of the worldwide annual precipitation pattern is that tropical latitudes contain most of the wettest areas. Dry lands are most prominent on the western sides of continents in subtropical latitudes (centered at lat 25° or 30°). Dry zones are most extensive in North Africa and Australia, primarily because the blocking effects of landmasses or highlands to the east prevent moisture from coming in from that direction. Dry regions in the midlatitudes are most extensive in central and southwestern Asia, but they also occur in western North America and southeastern South America. In each case, the dryness is due to lack of access to moist air masses. In the high latitudes, there is not much precipitation anywhere. Areas of open water are scarce and cold, so little opportunity exists for moisture to evaporate into the air. As a result, polar air masses have low absolute humidity and precipitation is slight. These regions are referred to as cold deserts. In addition, because continental coastal regions are closer to moisture sources than interior regions, they usually receive more precipitation.

Precipitation levels vary seasonally. Over most of the globe, the amount of precipitation received in summer is considerably different from the amount received in winter. This variation is most pronounced over continental interiors, where most of the year's precipitation occurs during summer months. Coastal areas often have a more balanced seasonal precipitation regime, due to their nearness to moisture sources. In general, summer is the time of maximum precipitation over most of the world. Northern hemisphere regions experience heaviest rainfall in July, and southern hemisphere locations receive most precipitation in January. The only important exceptions to this generalization occur in narrow zones along western coasts between lat 35° and 60° in the United States, South America, New Zealand, and southernmost Australia. The most conspicuous variation in seasonal precipitation is found in monsoon regions (principally southern and eastern Asia, northern Australia, and West Africa), where summer tends to be very wet and winter is generally dry. *See Precipitation*.

4.2. Soil

Soil, the outer, highly weathered layer of the earth's crust, is the substrate in which nearly all plants grow. Soil's main constituents are (a) mineral matter, which makes up the bulk of most soils; (b) organic matter, in the form of living or dead organisms; and (c) pore spaces, filled with a mixture of water and air, which make up about half the total volume of most soils. Millions of years of weathering of rocks by physical and biological processes have produced the particles from which soils are formed. Physical processes include freezing and thawing, and water and wind erosion. Biological processes include microorganism effects on the weathering of rock (e.g., lichens); addition of organic material through decomposition of plants, animals, and microbes; and plant root and microbe alteration of the chemical composition of soil. Plant roots also aerate, mix, and drain the soil (as do burrowing animals), in addition to providing nutrients from the soil to the growing plant (see Figure 2).

Temperature and moisture are the climatic variables of greatest significance to soil formation. In general, both the chemical and biological processes in soil are usually accelerated by high temperatures and abundant moisture, and are slowed by low temperatures and lack of moisture. The effectiveness of soil as a growth medium is based largely on the availability of nutrients. In general, tropical soils are prone to nutrition depletion because, where annual precipitation exceeds annual evapotranspiration, water movement is predominantly downward in the soil, and leaching is a pronounced process. In addition, temperatures in the tropics are relatively high throughout the year. High temperatures coupled with dense rainfall cause organic matter in the tropics to decompose rapidly, allowing only low levels of humus (organic matter) to accumulate. Soils rich in humus are generally more productive than those poor in humus. However, plant nutrients are not completely removed by leaching, as natural vegetation can also quickly absorb many nutrients in solution. In addition, if vegetation is relatively undisturbed, nutrients will cycle rapidly, and the soil will not be totally impoverished by the speed of mineral decomposition and leaching. In temperate regions, where annual precipitation is generally less than potential evapotranspiration, principal soil moisture movement is upward, and leaching is limited. Materials that would be carried downward in other moisture regimes, instead become concentrated in the soil. Therefore, temperate soils generally have high productivity due to high levels of humus. *See Soil.*

Humus contributes to the fertility or productivity of soil through its positive effects on the chemical, physical, and biological properties of the soil. It has a nutritional function in that it serves as a reservoir of nitrogen, phosphorous, and sulfur for plant growth; a physical function in that it promotes a good soil structure as it increases the ability of soil to resist erosion and enables the soil to hold more water (when humus is lost, soils tend to become hard and compact); and a biological function in that it serves as a source of carbon and energy for soil organisms. Black or dark brown soils usually indicate a considerable humus content; the blacker the soil, the more humus it contains. Tropical and subtropical soils are commonly reddish and yellowish in color owing to low organic content from leaching. *See Macronutients and Micronutrients*.

4.3. Productivity

Plants, algae, and some bacteria have the ability to harvest sunlight's energy, along with water and carbon dioxide, to make organic compounds and release oxygen, a process called photosynthesis (see Figure 2). It has been estimated that ~1–5% of the solar energy that falls on a plant is converted to organic material. Primary productivity is a measure of the amount of sunlight converted to plant growth, and is considered a basic indicator of ecosystem functioning. Primary productivity includes photosynthesis and chemosynthesis, the chemical oxidation of simple inorganic compounds like ammonium, nitrite, and sulfide. Secondary productivity refers to the rate that consumers store energy.

Productivity is not evenly spread across the earth, because solar energy can be efficiently captured only when water and nutrients are available, and when temperatures are in the range suitable for plant growth. There is a general trend (with much variation) of increasing productivity with decreasing latitude. However, this trend does not hold in areas of land that receive abundant solar radiation, but lack adequate water (e.g., the continental interior of Australia). The amount of rainfall in a region is closely correlated with its productivity. For example, in North America the amount of annual rainfall influences the height of grassland vegetation, with taller grasses generally occurring in wetter regions (i.e., tallgrass prairie) and shortgrass occurring in drier regions (i.e., shortgrass steppe; see Figure 2). In addition, small differences in topography, and microclimatic conditions can result in large differences in productivity.

Primary productivity is a term used to describe the amount of organic matter produced from solar energy in a given area during a given period of time. While sunlight, carbon dioxide, water, and soil nutrients are the resources required for primary production, temperature has a strong influence on the rate of photosynthesis. Therefore, the length of the growing season is a function of both precipitation and temperature variation. Growing seasons in hot climates vary between 120 and 190 days each year. In more temperate climates, the growing season commences when the average temperature reaches about 5 °C to 10 °C and extends from 100 d to more than 165 d. During the course of a year, the productivity of a community may be limited by many factors, including drought, low rates of nutrient cycling (i.e., carbon and nitrogen cycles), or by grazing animals reducing leaf area available for capturing sunlight for photosynthesis. *See Productivity*.

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Biographical Sketch

Paulette Ford is a Research Ecologist with the USDA Forest Service Rocky Mountain Research Station in Albuquerque, NM. She holds a B.S. (1989) in Biology and Psychology and an M.S. (1992) in Biology from the University of New Mexico, in addition to a Ph.D. (2000) in Renewable Natural Resources from the University of Arizona. She has worked extensively in Latin America and the American Southwest on research ranging from the systematics of parasites and amphibians, to small mammal and amphibian community structure in deserts, grasslands, and tropical deciduous forests. Her current research interests include the role of disturbance in structuring grassland and desert communities, and scale and ecosystem resilience. Results of her research have been published in numerous scientific journals and both national and international symposium proceedings. Paulette's ongoing research in northeastern New Mexico uses a long-term (18-y) experimental framework to analyze the effects of season and frequency of fire on shortgrass steppe.