1

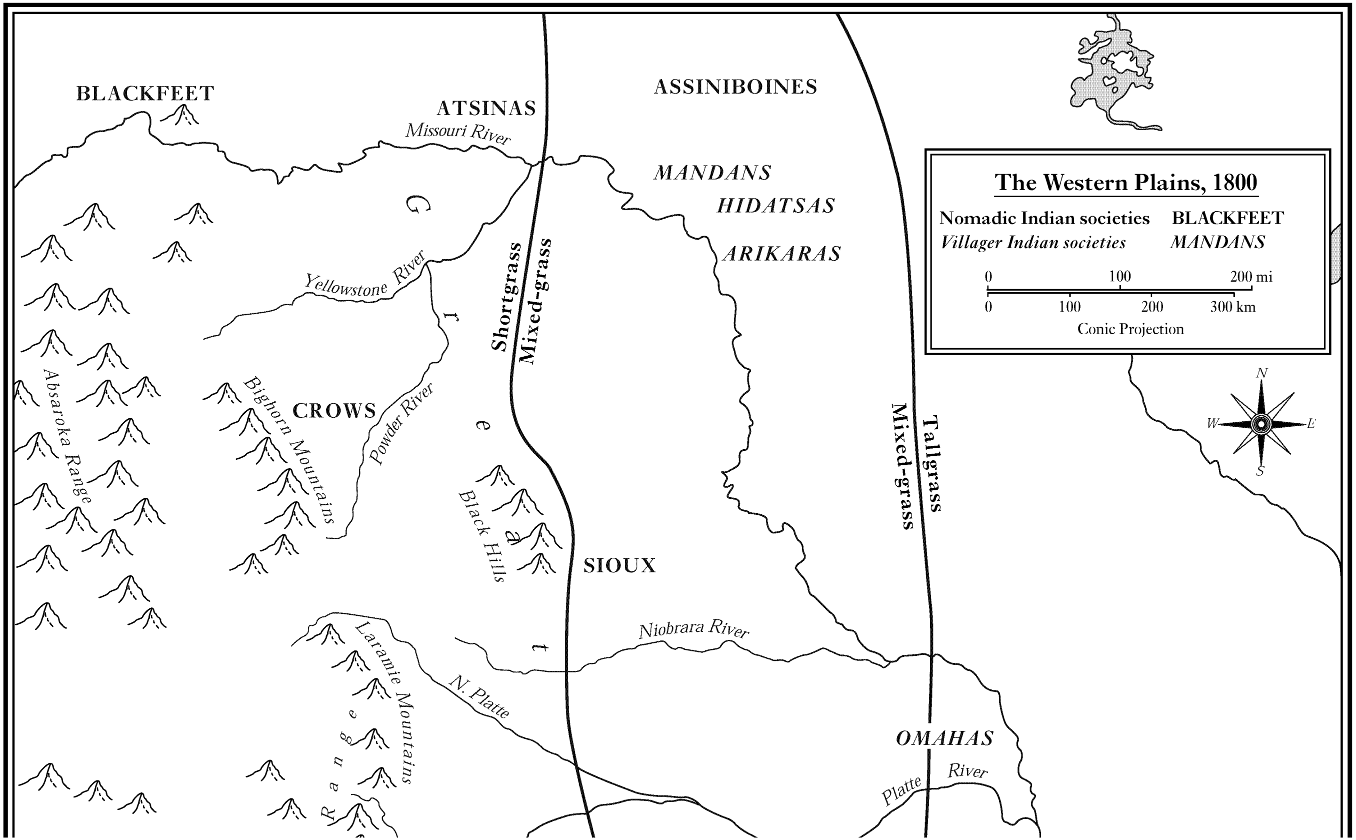
The Grassland Environment

The Great Plains, extending from the Missouri River valley in the east to the base of the Rocky Mountains in the west, and from Canada south to Mexico, is the largest biome in North America.[1] Although flatness is popularly believed to be the distinguishing characteristic of the plains, its topography is quite varied. Between 50 and 70 million years ago, surging molten rock from beneath the earth's surface created the Black Hills of western South Dakota and several ranges in Montana, among them the Highwood, Bearpaw, Judith, and Crazy Mountains. During the last five to ten million years, geological forces have carved a multitude of hills and bluffs in the region, from the Badlands of South Dakota to the Flint Hills of Kansas. Generally, the area between the Rocky Mountains and the Missouri River slopes from 5,000 feet above sea level at the base of the mountains to 2,000 feet above sea level at the Missouri.[2] An ubiquitous flatness exists only to the east of the Missouri and in the Llano Estacado, or Staked Plains of west Texas. In general, the region consists of many landscapes: primarily shortgrass and mixed-grass rolling plains but also wooded river valleys and high, forested hills.(See Map 1.1.)

The Mandan Indians, whose villages on the banks of the Missouri date from at least the thirteenth century, attributed the variety of the western Great Plains landscape to their chief god. According to Mandan myth, this god divided the work of shaping the landscape between himself and the first man. The god diversified the west bank of the Missouri with hills, valleys, and stands of trees, but the first man left the east bank flat and featureless. When they met after finishing their labors, the god expressed his disappointment in the man's work, saying, "all is level, so that it will be impossible to surprise buffaloes or deer, and approach

[1] A biome is a terrestrial region "characterized throughout its extent by similar plants, animals, and soil type." Donald D. Chiras, *Environmental Science: Action for a Sustainable Future*, 4th ed. (Redwood City, Cal.: Benjamin/Cummings, 1994), 576.

[2] Donald E. Trimble, *The Geologic Story of the Great Plains* (Medora, N.D.: Theodore Roosevelt Nature and History Association, 1990; reprint of U.S. Geological Survey Bulletin 1493), 1–2, 10–22, 32. See also Edwin Thompson Denig, *Five Indian Tribes of the Upper Missouri: Sioux, Arikaras, Assiniboines, Crees, Crows*, ed. John C. Ewers (Norman: University of Oklahoma Press, 1961), 4, 10; Preston Holder, *The Hoe and the Horse on the Plains: A Study of Cultural Development among North American Indians* (Lincoln: University of Nebraska Press, 1970), 2–3.


The Western Plains, 1800
Nomadic Indian societies BLACKFEET
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BLACKFEET
ATSINAS
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HIDATSAS
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CROWS
SIOUX
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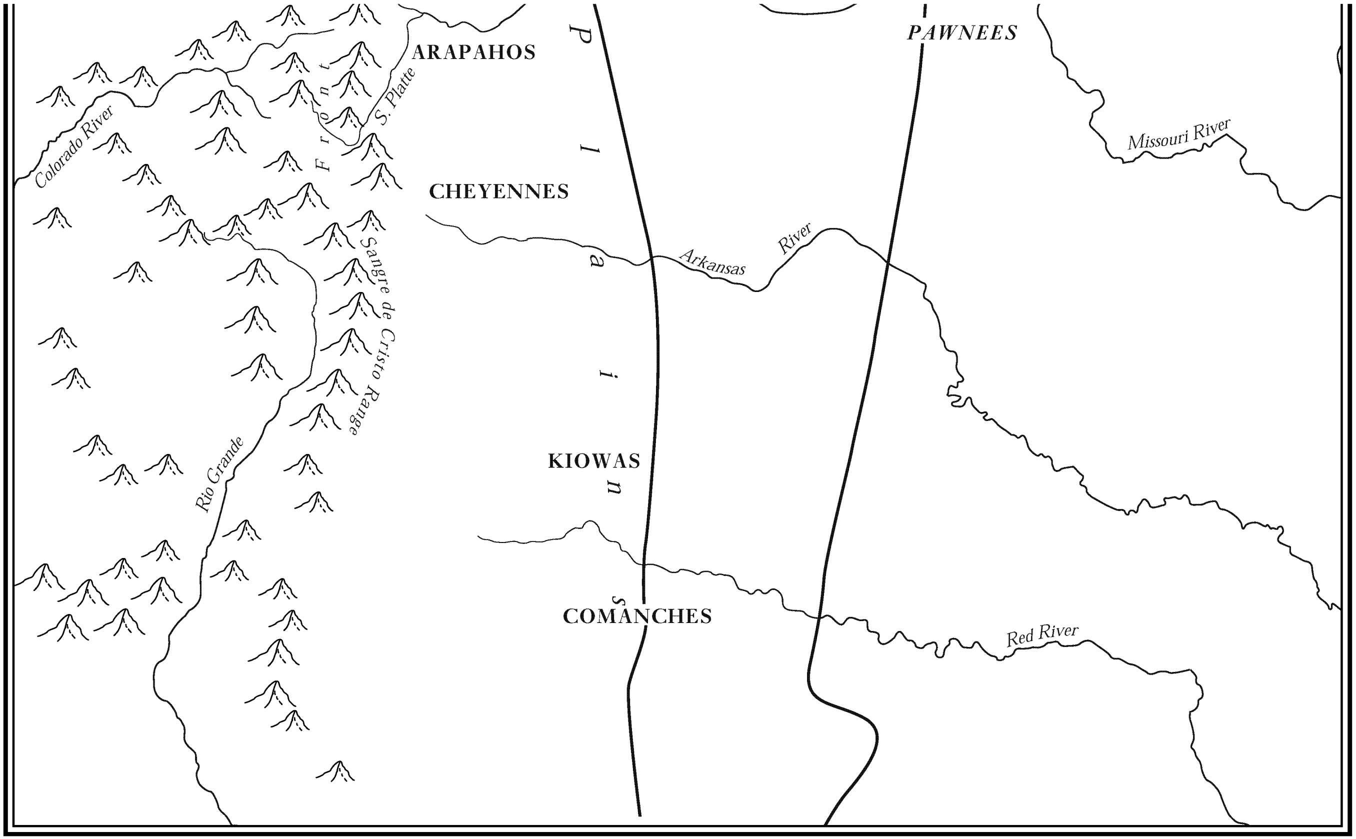
Missouri River
Yellowstone River
Powder River
Niobrara River
N. Platte
Platte River
Absaroka Range
Bighorn Mountains
Black Hills
Laramie Mountains
Range
G r e a t
Shortgrass
Mixed-grass
Mixed-grass
Tallgrass


ARAPAHOS
PAWNEES
CHEYENNES
KIOWAS
COMANCHES
Plains
Front
S. Platte
Colorado River
Missouri River
Arkansas River
Sangre de Cristo Range
Rio Grande
Red River

them unperceived. Men will not be able to live there. See here, I have made springs and streams in sufficient abundance, and hills and valleys, and added all kinds of animals and fine wood. Here men will be able to live by the chase, and feed on the flesh of those animals."[3] Bison did indeed thrive on the diversity of the Great Plains environment. Although they subsisted primarily on the shortgrasses of the high plains they also sought the shelter of river valleys in the winter. Hunters, who subsisted in the western plains for approximately 12,000 years, from the end of the last Ice Age to the nineteenth century, also relied on the diversity of the landscape. Like the bison, they took to the valleys in the winter. They drove bison and other animals to their deaths over the escarpments of the western Great Plains.[4]

The definitive characteristic of the Great Plains is not flatness but aridity. Between the Rocky Mountains and the ninety-eighth meridian, which divides North Dakota, South Dakota, Nebraska, Kansas, Oklahoma, and Texas, the average annual rainfall is less than 24 inches. Most of the region receives less than 16 inches of rainfall each year.[5] Except in river valleys, the sparse precipitation is insufficient to support trees or the tall grasses of the Iowa and Illinois prairies. John Bradbury, a naturalist who accompanied a fur trading expedition up the Missouri in 1811, described the striking difference between the river valley and the surrounding plains. After ascending a bluff along the river, Bradbury "found that the face of the country, soil, &c. were entirely changed. As far as the eye could reach, not a single tree or shrub was visible. The whole of the stratum immediately below the vegetable mould is a vast bed of exceedingly hard yellow clay."[6] Thomas Farnham, who crossed this "Great American Desert" in 1839, lamented that as he ascended into the high plains, both trees and the "green, tall prairie grass" gave place to "a dry, wiry species, two inches in height."[7]

Outside of the river valleys, which constitute approximately seven percent of the region, the semi-arid climate dictated that Farnham would find primarily shortgrasses. Annual precipitation minus evaporation – the effective precipitation – determines a region's vegetation. The forests of eastern North America and the coastal Pacific Northwest grow where rainfall exceeds the drying capacity of the air. In desert climates, by contrast, effective precipitation is

[3] Maximilian, Prinz zu Wied-Neuwied, *Travels in the Interior of North America* (London: Ackermann, 1843), in *Early Western Travels, 1748–1846*, vol. 23, ed. Reuben Gold Thwaites (Cleveland: Clark, 1904), 306–307. Maximilian's *Reise in das innere Nord-Amerika in den Jahren 1832 bis 1834* was originally published in Koblenz in two volumes in 1839–1841.

[4] Waldo R. Wedel, "The Prehistoric Plains," in Jesse D. Jennings, ed., *Ancient Native Americans* (San Francisco: W. H. Freeman, 1978), 188–192.

[5] Trimble, *Geologic Story of the Great Plains*, 2; Walter Prescott Webb, *The Great Plains* (Boston: Ginn, 1931), 17.

[6] John Bradbury, *Travels in the Interior of America in the Years 1809, 1810, and 1811* (London: Sherwood, Neely, and Jones, 1817), in *Early Western Travels*, vol. 5, 70–71.

[7] Thomas Farnham, *Travels in the Great Western Prairies* (London: Bentley, 1843), in *Early Western Travels*, vol. 28, 93.

minimal. Rain often evaporates before it reaches the ground. The low available moisture in desert climates means sparse vegetation. In steppe regions such as the Great Plains, effective precipitation is higher than in the desert but considerable moisture is nonetheless lost to evaporation. In such regions, grasses and shrubs predominate.[8]

Geographical peculiarities that interrupt the flow of moisture-bearing air currents produce aridity. In central North America, the Rocky Mountains cast a "rain shadow" over the plains to create semi-arid conditions. Moisture-bearing air currents moving across the continent from the Pacific Ocean are trapped on the western slopes of the Rockies. In the tall-grass prairie of the upper Mississippi River watershed, the influence of the rain shadow wanes and precipitation and evaporation are evenly balanced. The mean annual precipitation in the tall-grass prairie is 100 centimeters or 40 inches, approximately the same amount of moisture that is lost to evaporation. Closer to the mountains, in the shortgrass plains, evaporation exceeds the amount of annual precipitation. Between the eastern tall-grass prairie and the western shortgrass plains, tall-grass and shortgrass species compete for dominance in the so-called mixed-grass zone. South of the Great Plains in the arid Sonoran desert, latitude and remoteness from moisture-bearing winds conspire to create a region too harsh even for the durable grasses of the American steppes.[9]

Located in the center of the North American continent, in the shadow of the Rocky Mountains, the western plains climate is characterized by droughts of several years' duration interspersed with years of above-average rainfall.[10] Climatologists chart rainfall over the centuries by studying tree rings; narrow rings indicate past dry years. Scientists conducted a number of such dendrochronological studies in the plains in the wake of the prolonged drought of the 1930s. By studying the width of tree rings in river valleys, scientists plotted the precipitation history in the surrounding plains. A study of tree-ring growth in the vicinity of Havre, Montana, showed that between 1784 and 1949 precipitation varied from one-fourth of the average to two times the average. A similar tree-ring study published in 1946 found that between 1406 and 1940 the area near Bismarck, North Dakota, had 11 periods of low precipitation lasting ten

[8] Robert E. Gabler, Robert J. Sager, Sheila M. Brazier, and Daniel L. Wise., *Essentials of Physical Geography*, 3d ed. (Philadelphia: Saunders, 1987), 205.

[9] Paul Sears, *Lands Beyond the Forest* (Englewood Cliffs, N.J.: Prentice-Hall, 1969), 31, 58; Carl Friedrich Kraenzel, *The Great Plains in Transition* (Norman: University of Oklahoma Press, 1955), 12–13; Douglas B. Bamforth, *Ecology and Human Organization on the Great Plains* (New York: Plenum, 1988), 53; Tom McHugh, *The Time of the Buffalo* (Lincoln: University of Nebraska Press, 1972), 19.

[10] Drought may be defined as a year in which precipitation is 65 percent or less of average, although not all the studies cited adhere to this definition. Average temperature, evaporation, and wind speed are also higher during drought. See Robert T. Coupeland, "The Effects of Fluctuations in Weather upon the Grasslands of the Great Plains," *Botanical Review*, 24 (May 1958), 284–286.

years or longer, and nine wet periods lasting ten years or more. Another tree-ring study surveying western Nebraska discovered six droughts lasting five years or more between 1539 and 1939. These droughts lasted an average of 13 years. The average period between droughts was just over 20 years. A study that measured rainfall in eastern Montana between 1878 and 1946 found that precipitation was low in 32 of those 69 years. The average annual rainfall over the entire period surveyed was 8.2 inches. The study characterized three years between 1881 and 1904 and seven years between 1917 and 1939 as "killer years," during which drought was so severe it killed grass on the range.[11]

However prone to drought these studies showed the northern and central plains to be, the southern plains were still more subject to deficient rainfall. As one moves from north to south in the Great Plains, the climate becomes increasingly hotter and drier. The change in climate is the result of both latitude and prevailing southwesterly winds from arid Mexico and New Mexico. Greater average wind velocity also contributes to the drier climate of the southern plains.[12] In addition, precipitation in the northern plains tends to be more evenly distributed throughout the year. The region south of the Arkansas River suffers longer periods of less precipitation.[13] Overall, drought in the southern plains tends to be both more frequent and more prolonged than in the north. When drought struck the southern plains in the 1930s after farmers had plowed under large swaths of native grasses to plant wheat, it created the infamous "dust bowl." When the wheat withered, strong winds picked up the topsoil and carried it as far as the Atlantic Ocean.[14]

Although the native vegetation of the western plains also suffered during the 1930s, it is better adapted to drought than exotic species such as wheat. The shortgrasses consist primarily of two species: *Bouteloua grácilis*, or blue grama, and *Bouteloua dactyloides*, or buffalo grass. Blue grama is the dominant species of the shortgrass plains. It is a densely tufted perennial plant; its blades are one to two millimeters wide and three to ten centimeters long. Its dense root structure is confined to the twenty centimeters of soil closest to the surface. *Bouteloua dactyloides* is the second most common species in the shortgrass plains. Its curly blades are one to two millimeters wide and ten to twelve centimeters long. Like blue grama, buffalo grass has a dense root structure close to the surface of the soil. Other common species in the historic shortgrass plains were hairy grama (*Bouteloua hirsuta*), black grama (*Bouteloua eriopoda*), and James' galleta (*Hilaria jamesii*) in the southern plains and plains muhly (*Muhlenbergia cuspidata*) in the northern grasslands.[15]

[11] Kraenzel, *Great Plains in Transition*, 17–23.
[12] For wind velocity in the plains, see Webb, *Great Plains*, 23.
[13] Bamforth, *Ecology and Human Organization*, 53–54.
[14] Donald Worster, *Dust Bowl: The Southern Plains in the 1930s* (New York: Oxford University Press, 1979), 13.
[15] A. S. Hitchcock, *Manual of the Grasses of the United States* (Washington, D.C.: Government Printing Office, 1935), 519–527. J. E. Weaver, *North American Prairie* (Lincoln: University of Nebraska

These species share with blue grama and buffalo grass dense root structures and short blades.[16] In the nineteenth century, Euroamerican settlers relied on the dense root structures of these grasses to build their sod houses.

Grama and buffalo grasses are admirably adapted to the unpredictable, semi-arid climate of the plains. They can endure drought and take advantage of brief bursts of summer rain. Blue grama allocates up to 76 percent of its annual carbon budget to the construction and maintenance of below-ground structures. By increasing its extensive fibrous root system rather than its leafage, blue grama keeps its leaf area low and its transpirational water loss to a minimum. In years of above-average rainfall, shortgrasses translocate a greater amount of available carbon to above-ground shoots. In hot and dry years, shortgrasses allocate more carbon to below-ground biomass. During drought years, blue grama rolls its leaves and assumes a dormant state.[17]

Not adapted to the extreme heat, light, and dryness of the western plains, tall grasses such as big bluestem (*Andropogon gerardi*) and needlegrass (*Hesperostipa spartea*) grow as high as seven feet in the eastern prairies but die out in most of the western plains. They survive only in creekbeds, depressions, and on the leeward sides of hills, where they catch runoff and are protected from extreme light and wind, or river valleys, where their deep roots tap the moist soil.

Blue grama concentrates 85 percent of its roots in the 20 centimeters closest to the surface because in the high plains little soil water is found below this point. The extensive root system close to the surface can take advantage of sudden rainfall before the water is lost to runoff. This ability is crucial to survival, because rainfall events in the plains are brief. The north–south axis of the Rocky Mountains facilitates the movement of cold and dry Arctic air south from Canada and tropical maritime air currents north from the Gulf of Mexico. The warm and moist air from the Gulf typically travels up the Mississippi River valley and then turns eastward, avoiding the Great Plains entirely. Occasionally the moist Gulf air veers into the plains and meets the cold air from the north to produce violent rainstorms. These sudden showers generally occur between April and September and provide most of the region's annual precipitation.[18] As much as one-third of average annual precipitation can fall in one hour. Apart from these brief storms, parts of the western plains may endure as long as four months without

Press, 1954), 66, 92; Victor E. Shelford, *The Ecology of North America* (Urbana: University of Illinois Press, 1963), 344; Bamforth, *Ecology and Human Organization*, 32.

[16] Lauren Brown, *Grasslands* (New York: Knopf, 1985), 54–61.

[17] James K. Detling, "Processes Controlling Blue Grama Production in the Shortgrass Prairie," in *Perspectives in Grassland Ecology*, ed. Norman R. French (New York: Springer-Verlag, 1979), 25–39; Shelford, *Ecology of North America*, 340; Philip L. Sims, J. S. Singh, and W. K. Lauenroth, "The Structure and Function of Ten Western North American Grasslands I: Abiotic and Vegetational Characteristics," *Journal of Ecology*, 66 (March 1978), 270; Sims and Singh, "The Structure and Function of Ten Western North American Grasslands II: Intra-Seasonal Dynamics in Primary Producer Compartments," *Journal of Ecology*, 66 (July 1978), 565.

[18] Kraenzel, *Great Plains in Transition*, 12–13.

rain.[19] Blue grama can utilize as little as five millimeters of rainfall. In the plains, rainfall events of ten millimeters or less account for 41 percent of the rainfall during the growing season and 83 percent of all precipitation, and events of five millimeters or less contribute 25 percent of the growing season rainfall and 70 percent of all precipitation. By concentrating their roots at the top of the soil, and keeping their leafage minimal, shortgrass species conserve their moisture and take advantage of scarce rainfall.[20]

The ability to utilize scarce water enables shortgrasses to recover rapidly from drought. Biologists made note of shortgrasses' durability during the droughts of the 1930s and early 1950s. In an ungrazed shortgrass community near Hays, Kansas, the basal cover decreased from 89 percent in 1934 to 22 percent in 1939. Buffalo grass in particular, however, recovers from drought quickly, spreading new stolons after slight rainfalls, and by 1943, the Hays shortgrass community had regained its original density, with buffalo grass comprising five-sixths of the community. Blue grama, which is initially more resistant to drought but spreads more slowly, reached parity with buffalo grass in 1951. Almost immediately thereafter, drought struck the western plains again. By 1954, the basal cover had declined to 28 percent. At a moderately grazed grassland near Quinter, Kansas, buffalo grass and blue grama increased from a combined 8 percent of the basal cover in 1940 to 95 percent in 1943. Most of the recovery was made by the fast-growing buffalo grass.[21]

Though drought kills shortgrasses in the western plains, it opens niches for buffalo grass and blue grama in the mixed-grass zone. Adapted to moisture-deficient conditions, blue grama and other shortgrasses grow taller in the subhumid mixed-grass plains, but in wet years the taller species that are better adapted to the moist conditions eventually choke them out. The dominant species of the mixed-grass plains is little bluestem (*Schizachyrium scoparium*), a smaller version of the tall-grass bluestem. Also common is needle-and-thread (*Hesperostipa comata*), a smaller relative of needlegrass. Little bluestem and needle-and-thread reach heights of between one and two feet. To label any species dominant in the changeable mixed-grass plains is something of a misnomer, however; the constituency of the mixed-grass plains changes annually, epitomizing the volatility of the grasslands. In wetter years, tall-grass species dominate; in drought years, the shortgrass species replace the tall grasses.[22] Between 1932 and 1937, for instance, drought reduced a little bluestem community in the mixed-grass plains from five-sixths of the total grass cover to a mere 4 percent. Shortgrasses, an insignificant presence in the area in 1932, comprised 90 percent of the

[19] Coupeland, "Effects of Fluctuations," 283.

[20] O. E. Sala and W. K. Lauenroth, "Small Rainfall Events: An Ecological Role in Semiarid Regions," *Oecologia*, 53 (June 1982), 301–304.

[21] Coupeland, "Effects of Changes in Weather Conditions upon Grasslands in the Northern Plains," in Howard B. Sprague, ed., *Grasslands* (Washington, D.C.: American Association for the Advancement of Science, 1959), 292–293; Coupeland, "Effects of Fluctuations," 288–307.

[22] Shelford, *Ecology of North America*, 335, 340.

community in 1937.[23] Changes in the constitution of the mixed-grass zone likely occurred in the nineteenth century, as shortgrasses invaded the area during drought years. In his geological survey for 1867–69, a dry period in the plains, Ferdinand Hayden listed only buffalo and grama grasses as the important grasses west of the one-hundredth meridian. The one-hundredth meridian now cuts through the middle of the mixed-grass zone.[24] "Herein lies the major problem of steppe regions," wrote one geographer. They "seem like better-watered deserts at one time and like slightly subhumid versions of their humid climate neighbors at another."[25]

Early Euroamerican explorers of the Great Plains found the desiccated grassland mysterious and exotic. To Henry Brackenridge, an American fur trader who ascended the Missouri River in 1811, the plains seemed especially foreign. He compared the grassland to "the Steppes of Tartary or the Saharas of Africa."[26] To other early observers, the landscape seemed cheerless. Farnham called the plains an "arid waste" and "a scene of desolation scarcely equalled."[27] The impressions of Brackenridge and Farnham were typical of nineteenth-century characterizations of the plains; Euroamericans generally saw the region as a desolate wilderness.[28] Yet in one seemingly incongruous sense the shortgrass plains were abundant: the region teemed with animal life. Stephen Long, a New Hampshire native and Dartmouth College graduate who explored the southern plains in 1819 and 1820 at the head of an Army expedition, remarked that although the plains were "wholly unfit for cultivation, and of course uninhabitable by a people depending upon agriculture for their subsistence," they were nonetheless "peculiarly adapted as a range for buffaloes, wild goats, and other wild game."[29] Josiah Gregg, who traveled through the southern plains in the 1830s, agreed that the plains were "all too dry to be cultivated. These great steppes seem only fitted for the haunts of the mustang, the buffalo, the antelope, and their migratory lord, the prairie Indian."[30]

[23] Coupeland, "Effects of Changes in Weather upon Grasslands," 293.

[24] F. V. Hayden, *U.S. Geological Survey of the Territories for 1867, 1868, 1869*, cited in Floyd Larson, "The Role of the Bison in Maintaining the Short Grass Plains," *Ecology*, 21 (April 1940), 113–121.

[25] Gabler, et al., *Essentials of Physical Geography*, 210.

[26] Henry M. Brackenridge, *Journal of a Voyage up the River Missouri Performed in 1811* (Baltimore: Coale and Maxwell, 1816), in *Early Western Travels*, vol. 6, 153.

[27] Farnham, in *Early Western Travels*, vol. 28, 108–109.

[28] Roderick Nash, *Wilderness and the American Mind*, 3d ed. (New Haven: Yale University Press, 1982), 23–43. For an analysis of views of the Great Plains, see Brian W. Blouet and Merlin P. Lawson, eds., *Images of the Plains: The Role of Human Nature in Settlement* (Lincoln: University of Nebraska Press, 1975).

[29] Stephen H. Long, "A General Description of the Country Traversed by the Exploring Expedition," in Edwin James, *Account of an Expedition from Pittsburgh to the Rocky Mountains, Performed in the Years 1819, 1820* (London: Longman, Hurst, Rees, Orme and Brown, 1823), in *Early Western Travels*, vol. 17, 147–148.

[30] Josiah Gregg, *Commerce of the Prairies* (New York: Langley, 1845), in *Early Western Travels*, vol. 20, 248.

Indeed, the shortgrass plains supported tens of millions of bison, the largest land animal in North America.[31] Subsisting largely on the stunted shortgrasses, an average full-grown bull nonetheless stands from five to six feet at his shoulder, is nine to ten feet long, and weighs sixteen hundred pounds. The average cow is five feet tall, seven feet long, and weighs from seven hundred to twelve hundred pounds. Given their size, bison are surprisingly swift; in quarter-mile stretches, they can reach speeds over 40 miles per hour, nearly as fast as racehorses.[32]

To survive, the shortgrasses and the bison adapted not only to the semi-arid climate but to each other. Bison concentrated in the western shortgrass and mixed-grass plains rather than in the tall-grass prairies not because the shortgrasses were more nutritious. Indeed, by virtue of their greater size, tall grasses contain considerably more carbohydrates than shortgrasses, but a considerably smaller proportion of protein per unit of volume. The bison concentrated in the western plains and in the mixed-grass zone when and where shortgrasses could be found because their digestive system requires one part protein for every six parts carbohydrates. Shortgrasses offer a sufficiently high ratio of protein to carbohydrates. Even when they mature and dry out in the fall, shortgrasses contain 15 to 20 percent protein and 75 to 80 percent carbohydrates.[33]

The bison thrived on the forage of the historic western plains; shortgrasses, in turn, were well adapted to the bison. Although shortgrasses dominate the western plains primarily by virtue of their suitability to the semi-arid climate, the bison's presence helped select shortgrasses for dominance. Bison droppings returned fertilizers to the soil.[34] Buffalo grass responds to heavy grazing by increasing its uptake of nitrogen from the soil.[35] Grazing induces new growth to

[31] The American bison, or buffalo, like the European wisent belongs to the genus *Bison*. Scientists refer to the species as the bison rather than the buffalo to distinguish it from the African Cape buffalo, the wild Indian buffalo, the domesticated water buffalo, and other ruminants that belong to the *Bos* genus. The American bison once belonged to the *Bos* genus before being reclassified, the wisent (*bison bonasus*) was once classed not as a subspecies but as a different species altogether, and the *Bos* and *Bison* genera share similar chromosomal structures and blood types. To complicate nomenclature further, nineteenth-century naturalists classified two subspecies of the bison in North America: the plains bison (*bison bison*) and the less numerous wood bison (*bison athabascae*) in northern Canada. See McHugh, *Time of the Buffalo*, 27–38. A recent study suggests that the wood bison is an ecotype rather than a phenotype. See Valerius Geist, "Phantom Subspecies: The Wood Bison *Bison bison* "*athabascae*" Rhoads 1897 is Not a Valid Taxon, but an Ecotype," *Arctic*, 44 (December 1991), 283–300. Nineteenth-century observers consistently used the term "buffalo" to refer to both American subspecies (or ecotypes). For the purposes of this study, the terms bison and buffalo both refer to the plains bison unless otherwise noted.

[32] Martin S. Garretson, *The American Bison: The Story of Its Extermination as a Wild Species and Its Restoration Under Federal Protection* (New York: New York Zoological Society, 1938), 26; Francis Haines, *The Buffalo* (New York: Crowell, 1975), 29–30; McHugh, *Time of the Buffalo*, 171.

[33] Charles W. Johnson, "Protein As a Factor in the Distribution of the American Bison," *Geographical Review*, 41 (April 1951), 330–331.

[34] Shelford, *Ecology of North America*, 334.

[35] Detling, "Grasslands and Savannas: Regulation of Energy Flow and Nutrient Cycling by Herbivores," in Lawrence R. Pomeroy and James J. Alberts, eds., *Concepts of Ecosystem Analysis: A Comparative View* (New York: Springer-Verlag, 1988), 146–147.

restore the lost parts of the plant, producing a thick "grazing lawn."[36] Overgrazing, especially in combination with drought, could eventually degrade a range, but shortgrasses endure heavy grazing better than tall grasses.[37] Just as drought opens niches for shortgrasses in the eastern plains, when large herbivores graze in the mixed-grass plains, shortgrasses gradually replace tall grasses.[38]

The bison was so well adapted to the shortgrass plains that until the end of the nineteenth century, the species was ubiquitous in the region. While traveling on the Santa Fe Trail in 1839, Thomas Farnham reported seeing bison cover the whole country for three days. He calculated that the herd covered 1,350 square miles. Another traveler on the Santa Fe Trail in 1825 saw a herd that "could not have been less than 100,000." On the Arkansas River in 1871, Colonel Richard Irving Dodge wrote that "the whole country appeared one mass of buffalo." At the juncture of the Platte and Missouri rivers in the central plains, a member of Stephen H. Long's expedition reported "immense herds of bisons, grazing in undisturbed possession and obscuring with the density of their numbers the verdant plain; to the right and left as far as the eye was permitted to rove, the crowd seemed hardly to diminish, and it would be no exaggeration to say that at least ten thousand here burst on our sight in the instant." At the mouth of the White River in 1806, the American explorers Meriwether Lewis and William Clark saw a herd they estimated to be 20,000 strong. At the juncture of the Heart and Missouri rivers in the northern plains, John Bradbury ascended a bluff and counted 17 herds numbering more than 10,000 animals.[39] Sightings such as these prompted exaggerated estimates of the aggregate bison population. In the 1860s, the bison hunter Robert M. Wright and General Philip Sheridan calculated that 100 million bison roamed the Great Plains. Wright and Sheridan thought the number to be a conservative guess.[40]

Such estimates failed to consider that enormous herds congregated only during the summer months for the rutting season. During the summer, the shortgrasses were at their thickest and most nutritious and could support large aggregations of bison. During the winter, the huge herds dispersed into small groups to search for forage and shelter from the elements.[41] Every one of the

[36] Bamforth, *Ecology and Human Organization*, 37–38.

[37] For a recent analysis of the problems of overgrazing, see Elliott West, *The Way to the West: Essays on the Central Plains* (Albuquerque: University of New Mexico Press, 1995), 34–35.

[38] Sims, et al., "The Structure and Function of Ten Western North American Grasslands I," 256; Shelford, *Ecology of North America*, 335, 340.

[39] Farnham, in *Early Western Travels*, vol. 28, 96; Doctor Willard, "Inland Trade with New Mexico," *Western Monthly Review*, 2 (April-May 1829), in *Early Western Travels*, vol. 18, 334; Richard J. Dodge, *The Plains of North America and Their Inhabitants* (Newark: University of Delaware Press, 1989), 140; James, in *Early Western Travels*, vol. 15, 239; Meriwether Lewis and William Clark, *The History of the Lewis and Clark Expedition*, ed. Elliott Coues (New York: Harper, 1893), vol. 3, 1196–1197; Bradbury, in *Early Western Travels*, vol. 5, 148–149.

[40] Robert M. Wright, *Dodge City: The Cowboy Capital* (Wichita, 1913), 75.

[41] Symmes C. Oliver, *Ecology and Cultural Continuity as Contributing Factors in the Social Organization*

foregoing sightings – and they are but a small sampling of such reports – occurred during the summer months. Reckoners such as Wright and Sheridan assumed large summer herds were spread throughout the plains throughout the year. Yet "the American buffalo is a migratory animal," the naturalist George Perkins Marsh wrote in 1864. Therefore, "at the season of his annual journeys, the whole stock of a vast extent of pasture ground is collected into a single army."[42] Marsh concluded that although reports of huge summer herds may have been accurate, they actually reveal little about the total number of bison that inhabited the plains.

A better way to approximate the number of bison in the historic plains is to establish the carrying capacity of the grassland. As estimates of range carrying capacity become more precise, and as historians and ecologists suggest more factors possibly limiting the bison population, estimates of the historic bison population have fallen considerably. In 1929, the naturalist Ernest Thompson Seton estimated that before 1800 there were 75 million bison in North America. Seton based his estimate on the Agricultural Census of 1900, which counted 24 million horses and cattle and six million sheep in the rangelands of North Dakota, South Dakota, Montana, Wyoming, Nebraska, Kansas, Colorado, Texas, and Oklahoma. Considering that in 1900 the richest bottomlands were fenced in, and that bison are more effective grazers than domestic livestock, Seton estimated that if the western grasslands supported 30 million domestic livestock in 1900 it must have sustained 40 million bison a century earlier. The tall-grass prairie, according to Seton, was only one-third as large but four times as fertile as the shortgrass plains, so he set the bison population there at 30 million. The pre-Columbian forests, Seton figured, supported a further 5 million bison.[43]

Not only did Seton not account for the bison's preference for shortgrasses, or competition from other grazers, or thinning of the herd by fire, drought, severe winters, bovine diseases, and wolves, but he assumed that bison were found everywhere throughout North America even more densely than early twentieth-century ranchers stocked their ranges. The density of favored organisms in an artificial monoculture such as ranching is normally greater than the density of any single species in an unmanaged environment. Yet later writers have accepted Seton's calculations uncritically. As late as 1974, David Dary accepted Seton's calculation in his history of the bison. Frank Gilbert Roe, in a study published in 1951, implied that Seton's total was too low because, among other things, it underestimated the bison's prolific rate of natural increase.[44]

of the Plains Indians. University of California Publications in American Archaeology and Ethnology, vol. 48, no. 1 (Berkeley: University of California Press, 1962), 17.

[42] George Perkins Marsh, *Man and Nature: Or, Physical Geography as Modified by Human Action*, ed. David Lowenthal (Cambridge, Mass.: Belknap Press, 1965), 73–74.

[43] Ernest Thompson Seton, *Lives of Game Animals* (New York: Doubleday, 1929), vol. 3, pt. 2, 654–656.

[44] David A. Dary, *The Buffalo Book: The Full Saga of the American Animal* (Chicago: Swallow, 1974),

Recent studies that have taken more seriously the environmental limitations on the bison indicate that the semi-arid grassland could have supported no more than 30 million bison. According to the zoologist Tom McHugh, who observed bison in Yellowstone Park for several years, one bison could live for one year on 25 acres of grassland – provided that during that year those 25 acres received sufficient rainfall. That figure translates to 26 bison per square mile, or 32 million in the plains. Allowing for competition from other grazers, McHugh calculated that the nineteenth-century grasslands supported no more than 30 million bison.[45] The historian Dan Flores has arrived at a comparable figure by employing a similar methodology. According to the Census of 1910 – a year of median rainfall – the southern plains supported seven million cattle, horses, and mules. Bison are 18 percent more efficient grazers than these domestic animals; thus in a year of median precipitation the pre-horse southern plains could have supported just over eight million bison. The entire plains, according to this calculation, could have supported between 28 and 30 million bison.[46]

Evidence from a twentieth-century bison preserve indicates that the bison population at its highest may have been smaller still. In the mid-1920s, the 29-square-mile National Bison Range in Montana supported 550 bison and an equal number of elk (*Cervus canadensis*).[47] If the conditions at the Montana preserve were representative of the plains before its transformation by Euroamerican settlement, then the carrying capacity of the grassland was less than 24 million. The Montana preserve, however, did not exactly recreate the conditions of the western plains before the coming of Euroamericans; the number of elk did not equal the bison population in the historic plains.[48] A bison requires three times as much forage as an elk, so if the Montana range had stocked only bison, it might have supported 733. Based on this figure, the plains might have supported 27 million bison.

29; Frank Gilbert Roe, *The North American Buffalo: A Critical Study of the Species in Its Wild State* (Toronto: University of Toronto Press, 1951), 489–520.

[45] McHugh, *Time of the Buffalo*, 16–17.

[46] Dan Flores, "Bison Ecology and Bison Diplomacy: The Southern Plains from 1800 to 1850," *Journal of American History*, 78 (September 1991), 470–471. See also James H. Shaw, "How Many Bison Originally Populated Western Rangelands?" *Rangelands*, 17 (October 1995), 148–150.

[47] W. C. Henderson, Acting Chief of the Bureau of Biological Survey, Washington, D.C., to William T. Hornaday, New York Zoological Park, 20 November 1923; E. W. Nelson, Chief of the Bureau of Biological Survey, Washington, D.C., to Martin Garretson, Secretary, American Bison Society, Clifton, New Jersey, American Bison Society Papers, Box 272, File 27, Conservation Collection, Western History Department, Denver Public Library.

[48] James M. Peek, "Elk," in Joseph A. Chapman and George A. Feldhammer, eds., *Wild Mammals of North America: Biology, Management, and Economics* (Baltimore: The Johns Hopkins University Press, 1982), 851–852; Olaus J. Murie, *The Elk of North America* (Harrisburg, Penn.: Stackpole, 1951), 293–294. The North American elk (*Cervus elaphus canadensis*) is a large deer. (The European relative, *Cervus elaphus elaphus*, is known as the red deer.) The North American elk is perhaps more accurately called a wapiti, to distinguish it from the European elk (*Alces alces*), a smaller relative of the North American moose (*Alces americanus*).

The nineteenth-century bison population was not static but constantly in flux. Changing ecological factors exerted downward pressure on the bison's numbers. In the desiccated plains, lightning periodically ignited grass fires. Some fires gathered enough force and size to become fire storms that consumed every living thing over a broad area.[49] During the winter, many bison died attempting to cross rivers that had frozen over. At weak points in the ice, some bison broke through and drowned. In 1805, the fur trader Charles McKenzie observed that, as a consequence, "in the Spring both sides of the [Missouri] River are in several places covered with rotten carcasses."[50]

In the early nineteenth century, perhaps 1.5 million plains wolves (*Canis lupus nubilis*) attended the bison. The wolves, wrote one fur trader, "follow in the wake of the buffalo in bands of several hundreds."[51] Wolves largely preyed on the aged, diseased, and very young; they may have killed as many as one-third of bison calves.[52] Even after their first year, juvenile bison are more liable to die than adults. During the course of a study of bison in Yellowstone Park, only one-half of the bison that survived their first year lived to 2.5 years of age.[53] At modern preserves in the Dakotas and Oklahoma, fire, drowning, falls, or inclement weather kill between 3 and 9 percent of the bison annually.

In the historic plains, horses, which have an 80 percent dietary overlap with bison, competed with the herds for forage. Equestrian Indian hunters watered their horses at the very places frequented by the bison. In the early nineteenth century, the estimated 60,000 Indians who inhabited the western plains maintained horse herds that ranged in size from six to fifteen horses per person. Thus, between 360,000 and 900,000 domesticated horses grazed in the early nineteenth-century plains. Furthermore, an additional two million wild horses grazed in the southern plains alone.[54] These horses consumed forage that might have supported between 1.9 and 2.3 million bison.

[49] Richard J. Vogl, "Effects of Fire on Grasslands," in *Fire and Ecosystems*, ed. T. T. Kozlowski and C. E. Ahlgren (New York: Academic Press, 1974), 145–146.

[50] "Charles McKenzie's Narratives," in W. Raymond Wood and Thomas D. Thiessen, eds., *Early Fur Traders on the Northern Plains: Canadian Traders Among the Mandan and Hidatsa Indians, 1738–1818* (Norman: University of Oklahoma Press), 239. For the drowning of bison during the winter, see Roe, *North American Buffalo*, 160–179.

[51] Denig, *Five Indian Tribes*, 119–120. The estimate of the wolf population in the plains is from John K. Townsend, *Narrative of a Journey Across the Rocky Mountains to the Columbia River* (Boston: Perkins and Marvin, 1839), in *Early Western Travels*, vol. 21, 170; and George Catlin, *North American Indians: Being Letters and Notes on Their Manners, Customs, and Conditions, Written During Eight Years' Travel Among the Wildest Tribes of Indians in North America, 1832–1839*, vol. 1 (Philadelphia: Leary, Stuart, 1913), 59.

[52] Flores, "Bison Ecology," 481–482.

[53] Margaret Mary Meagher, *The Bison of Yellowstone National Park*. National Park Service Scientific Monograph Series, 1 (Washington, D.C.: Government Printing Office, 1973), vi.

[54] Flores, "Bison Ecology," 481–482; James Sherow, "Workings of the Geodialectic: High Plains Indians and Their Horses in the Region of the Arkansas River Valley, 1800–1870," *Environmental History Review*, 16 (Summer 1992), 68.

The most destructive influence of the plains environment on the bison was the periodic visitation of drought. The central plains suffered droughts from 1761 to 1773, from 1798 to 1803, and from 1822 to 1832.[55] In the northern plains, there were nine dry years between 1752 and 1786; seven dry years between 1802 and 1830; and a 15-year drought between 1836 and 1851.[56] During extended dry periods, between 70 and 90 percent of plains vegetation dies, causing a significant decline in range carrying capacity.[57] In southeastern Montana, for instance, rainfall in 1934 was a mere 38 percent of the average. The drought reduced the carrying capacity of the range to 36 percent of its 1933 capacity.[58]

It is impossible to know precisely how many bison died during such dry periods in the eighteenth and nineteenth centuries. During the droughts of the 1880s, an estimated 15 percent of the cattle in the plains perished – although blizzards, fences, and overstocking of the range also contributed to the decline.[59] In past centuries, the loss of forage no doubt caused the numbers of bison to decline precipitously. This fluctuation of the population has probably persisted since the bison emerged as the dominant species in the plains at the end of the last Ice Age. Indeed, at sites in the southern plains where pedestrian hunters drove bison to their deaths there are two long periods – from 6000 to 2500 B.C.E. and from 500 to 1300 C.E. – when bison were absent from the kill sites. The absence of bison remains indicates a dramatic decline in the density of the herds.[60]

The bison's rate of increase was as volatile as its rate of mortality. On modern game preserves, the bison reproduces at an annual rate of 20 percent or higher. On preserves, approximately 35 percent of the bison are females between three and thirteen years old – the bison's prime breeding age. At one preserve near the Badlands of South Dakota, between 58 and 75 percent of cows between three and thirteen years old produced a calf every year.[61] If these figures are applicable to the historic grasslands, a population of 27 to 30 million bison included between 9.5 and 10.5 million cows of breeding age who produced between 5.5 and 7.9 million calves every year. These figures may be too high, however. At the Wichita Mountains Wildlife Refuge in Oklahoma, during a seven-year study between 1960 and 1966, calf production by cows older than one year varied between

[55] Harry E. Weakly, "A Tree-Ring Record of Precipitation in Western Nebraska," *Journal of Forestry*, 41 (November 1943), 819; Merlin P. Lawson, *The Climate of the Great American Desert: Reconstruction of the Climate of the Western Interior United States, 1800–1850*. University of Nebraska Studies, New Series no. 46 (Lincoln: University of Nebraska Press, 1974).

[56] Kraenzel, *Great Plains in Transition*, 19.

[57] Charles Rehr, "Buffalo Population and Other Deterministic Factors in a Model of Adaptive Processes on the Shortgrass Plains," *Plains Anthropologist*, 23 (November 1978), 23–39.

[58] Coupeland, "Effects of Fluctuations," 288, 292.

[59] Richard White, "Animals and Enterprise," in *The Oxford History of the American West*, ed. Clyde A. Milner II, et al. (New York: Oxford University Press, 1994), 266.

[60] Tom D. Dillehay, "Late Quaternary Bison Population Changes in the Southern Plains," *Plains Anthropologist*, 19 (August 1974), 180–196.

[61] Joel Berger and Carol Cunningham, *Bison: Mating and Conservation in Small Populations* (New York: Columbia University Press, 1994), 99–101, 132–135, 145–148; Flores, "Bison Ecology," 476.

47 and 60 percent. The average during the period was 52 percent.[62] That figure accords with a study, conducted between 1963 and 1969, of the Yellowstone Park bison, where the pregnancy rate for all cows 2.5 years and older was also 52 percent.[63] Delayed puberty – most females did not reach sexual maturity until four years old – and lower fecundity at Yellowstone are likely a response to the environment's severe winters and sub-optimal forage. Generously assuming that the historic bison's rate of increase was the higher rate of 58 to 75 percent of adult cows observed in South Dakota, between 5.5 and 7.9 million calves would have been born each year. Wolf predation likely reduced the number of surviving calves by one-third, to between 3.7 and 5.3 million. The annual increase of the bison herd was, as a result, probably between 13.6 and 17.6 percent. Each year, natural mortality and competition from other grazers might have eliminated between 2.6 and 4.5 million bison, a decrease of between 10 and 15 percent. The combination of wolf predation, competition from other grazers, and accidents raised the natural mortality of the bison to the point that in some years it may have exceeded its natural increase.

When drought struck the grassland, it probably exceeded in severity all other causes of bison mortality, causing an acute decline in the population. A drought's effect on the bison was not limited to the number who died as a result of reduced forage. Bison assembled as large breeding groups in the summer, when relatively heavy rainfall produced thick, nutritious shortgrasses that could support large aggregations. Mammals and birds that rely on such communal breeding systems require a sufficiently large breeding group to insure reproductive success. When drought prevented the congregation of summer breeding groups, it threatened population stability. An extended drought could cause a long-term population decline.[64]

Paradoxically, the absence of drought, severe winters, competition from other grazers, and wolf predation could have similarly destabilized the bison population. Without these limitations on the bison's numbers, the herds were liable to increase beyond the capacity of the shortgrass plains to sustain them. Such irruptions of ungulate populations are almost always followed by sharp declines, as increased numbers are unable to find forage. Because they are so prolific in the absence of predators, ungulate populations seem to be particularly liable to such irruptions and crashes. One ecologist has argued that at any given time, it is likely that the biomass of an ungulate population and the biomass of forage are at disequilibrium with each other. Such fluctuations can be relatively minor: There

[62] Arthur F. Halloran, "Bison (Bovidae) Productivity on the Wichita Mountains Wildlife Refuge, Oklahoma," *Southwestern Naturalist*, 13 (May 1968), 23–26.

[63] Meagher, *Bison of Yellowstone*, v.

[64] See H. Ronald Pulliam and Thomas Caraco, "Living in Groups: Is There an Optimal Group Size?" in J. R. Krebs and N. B. Davies, eds., *Behavioral Ecology: An Evolutionary Approach*, 2d ed. (Sunderland, Mass.: Sinauer, 1984).

were over 100 subirruptions of deer populations in the United States between 1900 and 1945. They can also be catastrophic. A population of 29 reindeer (*Rangifer tarandus*) introduced in 1944 to St. Matthew Island in the Bering Sea had increased to 6,000 by the summer of 1963 before crashing to fewer than 60 the following winter.[65] Similarly, the generally favorable conditions for bison from the mid-eighteenth to the mid-nineteenth centuries may have raised the population to an unsustainably high level, increasing the severity of the late-nineteenth-century decline.

In general, the greater the number of variables affecting a population – predation, competition from other grazers, and availability of forage being the most important – the more likely it is that the population will be prone to unpredictable upward and downward fluctuations.[66] In the western plains, the variables affecting the bison were numerous. Thus, whereas the maximum possible sustainable bison population was probably between 27 and 30 million, the population was not static. Irruptions could have briefly increased the population to well above the sustainable maximum. Severe drought in combination with other factors could have depressed the population to far lower levels. The bison's dominance of the plains was as subject to change as the plains environment itself.

The volatility of the bison population is the key to understanding its near-extinction in the nineteenth century. Ecologists once generally agreed that ecosystems were characterized by equilibrium. The extinction of a species – especially one so dominant in its biome as was the bison in the Great Plains – was unlikely to result from drought or other environmental shocks. Disruptions occurred, but they were temporary aberrations; the stability of an ecological community was threatened less by natural disaster than by humanity's destructiveness. There is a certain validity to this perspective. Until the nineteenth century, although environmental changes periodically decimated the plant and animal species in the Great Plains, the durable shortgrasses and resilient bison always recovered and reestablished their dominance in the region.[67] In recent

[65] See Graeme Caughley, "Wildlife Management and the Dynamics of Ungulate Populations," in T. H. Coaker, ed., *Applied Biology*, vol. 1 (London: Academic Press, 1976), 189, 240. And Caughley, "Plant-Herbivore Systems," in Robert M. May, ed., *Theoretical Ecology: Principles and Applications* (Philadelphia: W. B. Saunders, 1976). For suberuptions in deer populations, see A. Leopold, L. K. Sowls, and D. K. Spencer, "A Survey of Over-Populated Deer Ranges in the United States," *Journal of Wildlife Management*, 11 (1947), 162–177; for the reindeer, see David R. Klein, "The Introduction, Increase, and Crash of Reindeer on St. Matthew Island," Ibid., 32 (April 1968), 350–367.

[66] To survive random environmental change, a population must be very large. The historic bison population, although quite large, was thus liable to acute decline in the stochastic environment of the plains. See Michael E. Soulé, ed., *Viable Populations for Conservation Biology* (Cambridge: Cambridge University Press, 1987).

[67] Such views were advanced in the early twentieth century by plant ecologists such as Frederic Clements and John Weaver. See Ronald C. Tobey, *Saving the Prairies: The Life Cycle of the Founding School of American Plant Ecology, 1895–1955* (Berkeley: University of California Press, 1981), 76–109, and Donald Worster, "The Ecology of Order and Chaos," in *The Wealth of Nature:*

years, however, many ecologists have come to believe that nature does not tend toward equilibrium. Although not diminishing the role of human beings in altering the environment, the new ecology of dynamism argues that rather than tending toward self-regulating equilibrium, nonhuman nature is characterized by change.[68] Some parts of the environment are more volatile than others. Studies of environmental dynamism focus particularly on climate and wildlife population, which in the Great Plains are characteristically volatile.

The complex and constant changes inherent in the Great Plains environment played fundamental roles in the decline of the bison in the nineteenth century. The near-extinction of the species cannot be understood simply as the result of hunting. It was surely also the consequence of less direct human alteration of the bison's habitat: displacement of bison from river valleys by Indians' horses and the livestock of Euroamerican emigrants; and the introduction of cattle to the bison's range. More important, however, the volatile plains environment itself contributed to the near-extinction of the herds. The pressures of drought, fires, blizzards, and other animals chronically depressed the bison's numbers. Favorable conditions – rain, abundant forage, and mild winters – could also ultimately be disastrous, as an irruption of the population could lead to overgrazing and a population crash. Human hunters pressured the bison in combination with these unpredictable environmental forces. Thus, the destruction of the bison was not merely the result of human agency, but the consequence of the interactions of human societies with a dynamic environment.

Environmental History and the Ecological Imagination (New York: Oxford University Press, 1993), 156–170.

68 For a summary of these new perspectives, see James Gleick, *Chaos: Making a New Science* (New York: Penguin, 1987). See also Daniel B. Botkin, *Discordant Harmonies: A New Ecology for the Twenty-first Century* (New York: Oxford University Press, 1990).