References and Notes

1. L. Kilham and G. Margolis, *Science* **143**, 1047 (1964).
2. L. Kilham and L. J. Olivier, *Virology* **7**, 428 (1959).
3. W. P. Herringham and F. W. Andrewes, *St. Barth.'s Hosp. Rept.* **24**, 112 (1888).
4. L. Kilham, *Proc. Soc. Exptl. Biol. Med.* **106**, 825 (1961).
5. L. Kilham and J. B. Moloney, *J. Natl. Cancer Inst.* **32**, 523 (1964).
6. Kindly supplied by H. Toolan.
7. H. W. Toolan, *Bull. N.Y. Acad. Med.* **37**, 305 (1961).

8. Aided by grants CA-06010 from the National Cancer Institute and NB-5160 from the National Institute of Neurological Diseases and Blindness.

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Scarp Woodlands, Transported Grassland Soils, and Concept of Grassland Climate in the Great Plains Region

Abstract. *Nonriparian woodlands occur on escarpments and other topographic breaks throughout the grassland province of central North America. Grassland vegetation is mainly correlated with gently sloping or flat terrain mantled by deep, transported soils of Pleistocene or younger age. Paleobotanical evidence suggests that extensive treeless grasslands may be a relatively recent development on the plains. Interaction of topography, wind, and fire may partly account for the observed distribution of vegetation.*

The extensive grasslands of central North America have long been regarded as corresponding to a grassland or steppe climate (*1*). The treeless condition of the flat or gently rolling plains was supposed to be determined primarily by a range of seasonal precipitation too scanty and irregular to support tree growth. The general restriction of trees to riparian habitats is a well-known feature of the Great Plains, and long stringers of gallery forest are shown extending westward along the streams on most vegetation maps. However, one of the more striking vegetational features of the plains region is the widespread but local occurrence of woodlands along escarpments or abrupt breaks in topography, remote from fluvial irrigation (Figs. 1 and 2). A number of nonriparian woodlands of the grassland province, such as the extensive stands of *Pinus ponderosa* along the Pine Ridge escarpment in Nebraska, have received incidental notice in the literature (*2*), but numerous other examples of scarp woodlands in the plains region have apparently escaped much attention. The significance of the prevalence of scarp woodlands throughout the grassland province has therefore not been understood.

The presence of grassland on deep soils with mature profiles contributes to an appearance of great antiquity. There has been a notion that the black or dark-colored grassland soils (chernozems, for example) of the plains region are residual on a variety of underlying bedrocks, which are continually weathering downward under the influence of grassland climate and vegetation to produce a mantle of soil in equilibrium with the denuding agencies of erosion (*3*). However, most of the grassland soils are derived from transported parent materials, chiefly silt and sand, because most of the plains region is mantled by unconsolidated sediments of eolian, alluvial, lacustrine, or glacial origin (*4*). Since the surficial deposits are late Pleistocene or more recent in age, the grassland soils derived from them cannot be of greater antiquity. Eolian silt (loess) or sand (*5*) has spread out in great sheets from alluvial sources, such as periodically dry floodplains of rivers carrying heavy loads of sediment through the plains from glaciated headwaters (*6*). The presence of a constructional mantle of silt or sand has often subdued irregularities on the old erosion surfaces of underlying deposits. The vast sheets of loess have been particularly effective in augmenting the flatness of an already essentially horizontal topography.

There is, then, in the plains region a pattern of very large areas of grassland on deep, transported soils, corresponding to gently sloping or flat topography, and relatively small but widely distributed areas of woodland on escarpments or breaks in topography, characterized by steep slopes and thin, residual soils with bedrock at or near the surface. The type of bedrock on which the scarps are cut is not usually a limiting factor for the occurrence of woodland. Sandstone, shale, limestone, basalt, and other rock types exhibit wooded scarps in various parts of the plains (*7*). Nor is the orientation of the scarp with reference to the sun consistently limiting; woodland often occurs on slopes facing southward as well as northward. The principal features common to the wooded scarps of the plains are their great abruptness, height, and length. Low or gently sloping scarps, or abrupt scarps of small extent, usually lack woodland. The dominant woodland trees are not only reproducing on the thin, rocky soils of the scarps, but in many instances certain species are spreading to the deeper soils of the adjacent grasslands (*8*). Nevertheless, the rule of restriction of nonriparian woodlands to the vicinity of scarps and other rough or broken topography has wide application throughout the vast region of grassy plains; and this is true despite the great diversity in floristic composition of both woodland and grassland, corresponding to the great diversity of climatic conditions (Fig. 1). It may be noted that, on the average, the 50-cm isohyet traverses sectors of the central plains where nonriparian woodlands are few, but it happens that these sectors are particularly lacking in bold escarpments. On the other hand, the average position of the 40-cm isohyet intersects numerous scarp woodlands on the more dissected plains to the west. This suggests that physiography outweighs climate as a factor in the distribution of extensive treeless grasslands.

It is, therefore, misleading to describe the range of climate in the Great Plains as a grassland or steppe climate, with the implication that precipitation, or a combination of precipitation and potential evapotranspiration, is limiting for tree growth. A number of woodland species, notably the junipers, *Juniperus monosperma* and *J. pinchotii*, are remarkably drought resistant. Their present range extends into the Chihuahuan Desert region as extensive woodlands, which intergrade with desert scrub. The junipers often grow in association with one of the most xerophytic shrubs of the American deserts, the creosote bush (*Larrea divaricata* Cav.), under a mean annual precipitation of less than 35 cm, which is highly erratic and interspersed with extremely prolonged and severe droughts. On the other hand, the ranges of the same ecospecies, and other species of *Juniperus*, are continuous with less xerophytic woodlands of ponderosa pine or various oaks, growing in areas with a mean annual precipitation of more than 50 cm; and these woodlands are often continuous with the main bodies of eastern deciduous forest and Rocky Mountain coniferous forest (*9*).

Apparently, there is no range of climate in the vast grassland province of the central plains of North America which can be described as too arid for all species of trees native to the region. The western sector of the plains is evidently too dry for an upland growth of most broad-leaf deciduous trees which form scarp woodlands along the eastern border of the plains, but this is not true of the more xerophytic conifers which do frequent the scarps of the High Plains. There is evidence from shelter belts, and other artificial plantings in upland situations from North Dakota south to Texas, that a number of native and introduced tree species are adapted to grow under a wide range of ecological conditions in the Great Plains region (*10*). Where grasslands have been planted with upland tree species native to scarp woodlands, such as *Pinus ponderosa* in the bluestem prairies of the Nebraska National Forest (which was created for this experiment), rather extensive areas (about 100 km^2) of forest became established. The largest stands of pines were planted on coarse, sandy soil in the Nebraska Sandhills. However, successful plantings were also made on fine-textured, hardland soil in the same area. A grove of ponderosa pine set out as seedlings on the grassland soil of a hardland site attained an average height of 7 m and a diameter of 17 cm when 30 years old. Growth of native red cedar (*Juniperus virginiana*) from planted seedlings has also been successful. The bulk of these plantations, which furthermore include exotic species from more humid regions, have survived in a "grassland" climate for more than 50 years, including the longest and most severe drought periods on record. It is noteworthy that the original plantings of conifers in the tall grass prairies of central Nebraska suffered more from fire than from drought. In 1910, a prairie fire, which

A. Mont., E. Wyo. and W. Dakota. Woodland: *Pinus ponderosa* Laws., *Juniperus scopulorum* Sarg. Grassland: *Bouteloua gracilis* HBK, *Agropyron smithii* Rydb., *Stipa comata* Trin. and Rupr.
B. Pembina escarpment and Turtle Hills, N.D.; Erskine and Big Stone Moraines, Minn. Woodland: *Populus tremuloides* Michx., *Quercus macrocarpa* Michx. Grassland: *Andropogon scoparius* Michx., *A. gerardi* Vitman, *Agropyron trachycaulum* (Link) Malte.
C. Pine Ridge escarpment, S.D., Neb., Wyo. Vegetation similar to *A*.
D. Niobrara escarpments, Neb. Woodland: *P. ponderosa*, *J. scopulorum*, *J. virginiana* L., *Q. macrocarpa*. Grassland: *B. gracilis*, *S. comata*, *A. scoparius*.
E. Sandhills area, Neb. Woodland: isolated stands of *P. ponderosa*, *J. virginiana*, *Celtis occidentalis* L. Grassland: *Andropogon hallii* Hack., *A. scoparius*, *Calamovilfa longifolia* (Hook.) Scribn.
F. Western Kan. Woodland: isolated stands of *J. virginiana*. Grassland: *A. scoparius*, *B. gracilis*, *Buchloe dactyloides* (Nutt.) Engelm.
G. Wildcat Hills, Neb. Vegetation similar to *A*.
H. Cedar Point, Colo. Woodland: *P. ponderosa*, *J. scopulorum*. Grassland: *B. gracilis*, *Buchloe dactyloides*.
J. Black Mesa-Mesa de Maya area, Okla., N.M., Colo. Woodland: *Pinus edulis* Engelm., *P. ponderosa*, *Juniperus monosperma* (Engelm.) Sarg., *J. scopulorum*, *Quercus undulata* Torr. Grassland: *B. gracilis*, *Buchloe dactyloides*.
K. Canadian escarpment, N.M., Vegetation similar to *J*.
L. Llano Estacado, N.M., Tex. Woodland: on northwest, *P. edulis*, *J. monosperma*, *Q. undulata*; on east (Break of the Plains), *Juniperus pinchotii* Sudw., *Quercus mohriana* Buckl. Grassland: *B. gracilis*, *Buchloe dactyloides*.
M. Callahan Divide, Tex. Woodland: *Quercus virginiana* Mill., *Q. shumardii* Buckl., *Q. mohriana*, *Juniperus ashei* Buchholz, *J. pinchotii*. Grassland: *B. gracilis*, *Buchloe dactyloides*.
N. Edwards Plateau, Tex. Woodland: Similar to *M*. Grassland: *A. scoparius*, *Bouteloua curtipendula* (Michx.) Torr.
O. Okla., E. Kan. Woodland: *Quercus stellata* Wang., *Q. marilandica* Muenchh., *Q. muehlenbergii* Engelm., *Q. shumardii*, *J. virginiana*. Grassland: *A. gerardi*, *A. scoparius*, *Sorghastrum nutans* (L.) Nash, *Panicum virgatum* L.

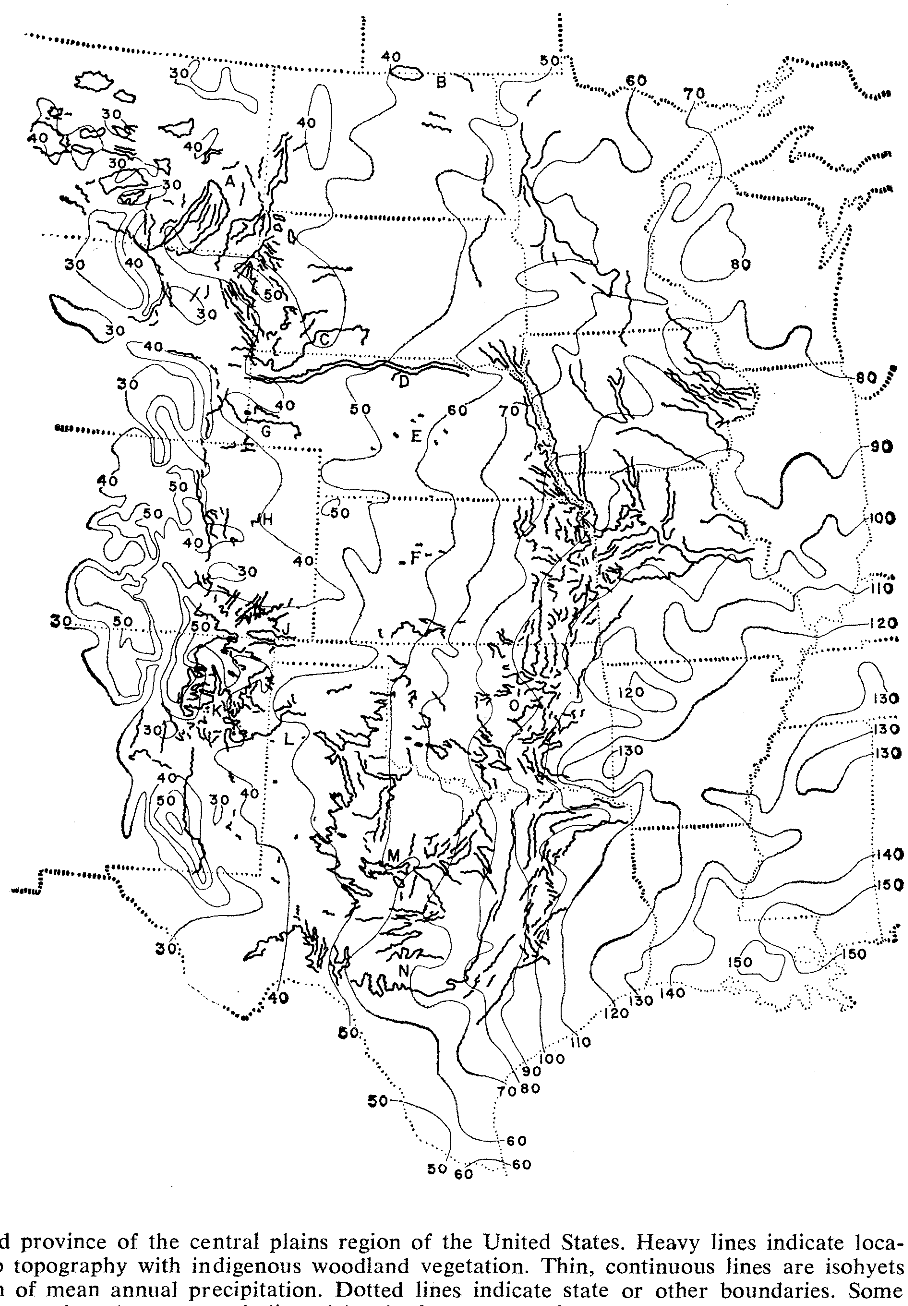

Fig. 1. Nonriparian woodlands in the grassland province of the central plains region of the United States. Heavy lines indicate location of scarps or other rough, broken, or steep topography with indigenous woodland vegetation. Thin, continuous lines are isohyets at 10-cm intervals, ranging from 30 to 150 cm of mean annual precipitation. Dotted lines indicate state or other boundaries. Some dominant species of nonriparian vegetation from selected areas are indicated by the letters *A* to *O*.

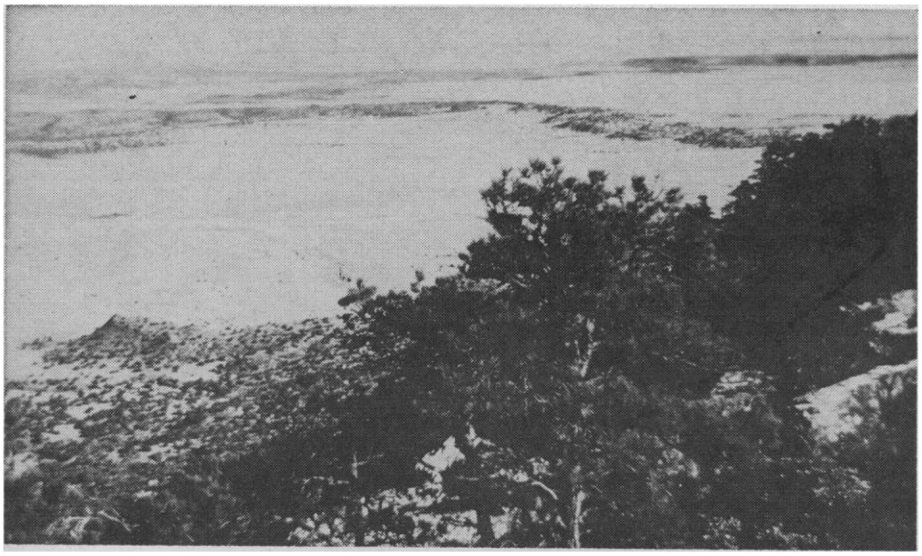

Fig. 2. Scarp woodland of ponderosa pine (fore) on the high plains of eastern New Mexico; rim of Canadian Escarpment, east of Las Vegas. Extending to the horizon across the short-grass plains 300 m below are long lines of scarps darkened by xerophilous woodland of pinyon pine (*P. edulis*) and juniper (*J. monosperma*). The dominant grass (light tone), on both the lower plains shown and the high plain back from the rim (top of Las Vegas Plateau, elevation 2000 m, not shown), is blue grama (*Bouteloua gracilis*).

covered a linear distance of 200 km in a single day, swept through the Bessey Division, destroying most of the original plantation; the area was successfully replanted (*11*).

A recent analysis of pollen from Hackberry Lake in the Nebraska Sandhills suggests that sediment at a depth of 5 m, with a radiocarbon age of about 5000 years, contains more than twice the percentage of arboreal pollen (chiefly pine) and less than one-fifth the percentage of grass pollen found in sediment at the top of the profile (*12*). The same pollen profile also suggests a twofold higher percentage of arboreal pollen from sediment at a depth of less than 1 m, which is considerably younger than a radiocarbon date of about 1100 years, obtained just above the 2-m level. Indeed, at the present time, native woodlands of ponderosa pine persist in parts of the Nebraska Sandhills region, chiefly in the vicinity of scarps (Fig. 1, *D* and *E*).

A study of a 10-m core of sediments from Muscotah Marsh in northeastern Kansas yielded leaves and wood of spruce (*Picea*) with a radiocarbon age of about 15,000 years, at a depth of 10 m. A pollen profile of the core showed a long sequence of high percentages (up to 95 percent) of arboreal pollen (including *Abies, Picea, Populus, Larix, Tsuga, Pinus,* and *Quercus*) in the lower 4 m, which shifted abruptly to a sequence containing almost exclusively nonarboreal pollen in the upper 6 m (*13*).

Numerous pollen studies on the Llano Estacado, or High Plains of eastern New Mexico and the Texas panhandle, have also established the presence of very high percentages of arboreal pollen in late Pleistocene sediments (*14*). Profiles with pine pollen exceeding 90 percent of pollen counted were obtained from sediments in Crane, Tahoka, and Rich lakes; one horizon of the latter profile had a radiocarbon age of about 17,000 years. At present, the pollen rain on the grasslands of the Llano Estacado shows very low percentages of conifer pollen, despite the fact that coniferous woodlands are still widely distributed on scarps which bound this vast, flat-topped plateau of some 50,000 km^2 (Fig. 1*L*). These data suggest that, during Wisconsin time, pine forest or woodland grew extensively on the southern part of the Llano Estacado, which borders on the Chihuahuan Desert province and is at present the most arid sector of the entire Great Plains region. If this area was not arid enough to harbor extensive treeless grassland during a pluvial of the Pleistocene, it is unlikely that any other area of the plains region was. Hence, the prevalent notion that extensive treeless grasslands have had a continuous existence on the Great Plains since mid-Tertiary time is open to question.

The widely cited evidence of fossil fruits of grasses and borages from Miocene and Pliocene sediments of the High Plains (Ogallala formation) was supposed to imply the existence there of treeless grasslands in the Tertiary (*15*). Fruits of *Stipidium* and other fossil genera of grasses are associated in the same sediments with large numbers of fossilized hackberry (*Celtis*) fruits. The consistent presence of abundant fossils of the hackberry tree throughout the Ogallala formation (*16*) might have raised some doubt about the treeless condition of the postulated Tertiary grasslands. MacGinitie, in his recent analysis of an upper Miocene flora from the Ogallala formation in the Sandhills of north-central Nebraska, has identified abundant leaves, fruits, and pollen of a varied assemblage of tree species (*17*). The fossils are in lacustrine shales, interbedded with typical, coarse, Ogallala stream deposits containing the usual fossilized remains of indurated, erosion-resistant fruits of hackberry and certain grasses. The fossil flora implies an open, grassy woodland of evergreen oak and pine on the uplands, and a forest of broad-leaf deciduous trees along the streams. Apparently, there is no definite paleobotanical evidence indicating the existence of widespread *treeless* grassland or steppe in the Tertiary (*17*). Together with the recent findings from pollen studies of Pleistocene and later sediments, there is a suggestion that the bleak landscape of extensive treeless grassland in the plains region may be a relatively recent development.

The scarp woodlands of the plains are evidently relicts of formerly more extensive woodlands. The question arises as to why woodland vegetation should persist on exposed, wind-swept escarpments, widely scattered over a vast extent of grassy plains, with a correspondingly wide range of precipitation, temperature, and evapotranspiration. It is futile, as well as unnecessary, to explain these distributions solely in terms of climate, since topographic and soil differences are clearly involved. The thin, rocky, residual soils usually associated with scarps are less favorable for a dense growth of grasses than the deeper, transported soils of the plains, where grasses often form a continuous cover (*18*). However, the reverse is not always true of trees, for there is evidence that trees grow well on both the lithosols of the scarps and the deeper grassland soils of the adjacent plains (*8*). The key to these puzzling distributions may lie in the correlation of woodland with degree of abruptness, height, and length of escarpments. Even though thin, coarse, or rocky soil may be present, there is a general lack of woodland on gentle scarps of small height and extent, which interrupt the flat monotony of the more featureless central sectors of the plains, such as in western Kansas. Nonriparian woodlands are restricted to the boldest escarpments and the steeper or more dissected topography in the central plains region. But the observed distributions are not adequately explained by existing conditions of terrain and climate alone (*8, 10, 11*). It is quite possible that the distribution of woodland vegetation in the plains region may be accounted for by the simple fact that abrupt scarps or topographic breaks have acted as natural fire breaks (*19*). Given the seasonal droughts of the regional climate, and the presence of dry grass as a fire-conducting matrix, topography and wind may have conspired repeatedly to sweep fires across the smooth surface of the flat, well-grassed plains for great distances, until the advancing front of the blaze was stopped by the obstacle of an abrupt and often sparsely grassed break in topography. Grassland vegetation may burn and regenerate annually, whereas woody vegetation usually requires many years for complete recovery following destruction by fire. Hence, the combination of a fire-conducting ground cover of seasonally dry grasses with extreme flatness and continuity of topography has been a hazardous environment for woody plants in a region of droughty climate and strong winds, where the incidence of fire had undoubtedly been increased for at least the last 11,000 years by the presence of man (*20*). Therefore, scarps or abrupt topographic breaks may have served primarily as refugia from grass fires for the nonriparian woodlands of the plains region.

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References and Notes

1. B. E. Livingstone and F. Shreve, *Carnegie Inst. Wash. Publ. 284* (1921); C. W. Thornthwaite, *Geogr. Rev.* **21**, 633 (1931); J. R. Borchert, *Ann. Assoc. Amer. Geogr.* **40**, 1 (1950).
2. C. E. Bessey, *Amer. Natur.* **11**, 928 (1887); R. S. Kellogg, *U.S. Dep. Agr. Forest Serv. Bull.* **66**, 1 (1905); I. Bowman, *Forest Physiography* (Wiley, New York, 1911), p. 426–430; R. J. Pool, *Minn. Bot. Stud.* **4**, 189 (1914); J. H. Foster, *J. Forestry* **15**, 442 (1917); N. M. Fenneman, *Physiography of Western United States* (McGraw-Hill, New York, 1931), pp. 17, 32; F. W. Emerson, *Ecology* **13**, 347 (1932); F. W. Albertson, *Trans. Kansas Acad. Sci.* **43**, 85 (1940); W. L. Tolstead, *Ecol. Monogr.* **12**, 255 (1942); ——, *Ecology* **28**, 180 (194 A. L. McComb and W. E. Loomis, *Bull. Torrey Bot. Club* **71**, 46 (1944); T. E. Williams and H. E. Holch, *Ecology* **27**, 139 (1946); M. E. Hale, *Trans. Kansas Acad. Sci.* **58**, 45 (1955); M. F. Buell and V. Facey, *Bull. Torrey Bot. Club* **87**, 46 (1960); L. D. Potter and D. R. Moir, *Ecology* **42**, 468 (1961); L. D. Potter and D. L. Green, *ibid.* **45**, 10 (1964); P. Buck, *ibid.* **45**, 336 (1964); P. V. Wells and G. E. Morley, *Trans. Kansas Acad. Sci.* **67**, 65 (1964); A. W. Küchler, "Potential Natural Vegetation of the Conterminous United States" *Amer. Geogr. Soc. Spec. Publ.* **36**, (1964). Data from these and other sources, including my own field observations and collections made in the area from Montana south to Texas, isohyetal data from *Climate and Man* (U.S. Department of Agriculture Yearbook, Washington, D.C., 1941), and physiographic data from E. Raisz, *Landforms of the United States* (Cambridge, Massachusetts, 1954), were used in the preparation of Fig. 1.
3. K. D. Glinka, *The Great Soil Groups of the World and Their Development*, C. F. Marbut, trans. (Edwards, Ann Arbor, Michigan, 1927), p. 5, 75.
4. J. Thorp and H. T. U. Smith, chairmen, *Map of Pleistocene Eolian Deposits of the United States, Alaska and Parts of Canada* (Geological Society of America, New York, 1952); J. C. Frye and A. B. Leonard, *Univ. Kansas Publ. State Geol. Surv. Kansas Bull.* **99**, 1 (1952); J. G. Livingstone, S. Ramarathnam, D. Richards, *Quart. Colo. School Mines* **57**, 1 (1962); R. F. Flint, chairman, *Glacial Map of North America* (Geological Society of America, New York, 1945).
5. The practical implications of eolian origin for problems of soil conservation in the Dust Bowl region of the Great Plains are evident. The recurrent dust storms of drought years are reworking silt and sand deposits often previously transported by wind, but more or less stabilized by grasses or other vegetation prior to the profound disturbances of modern agriculture. For a penetrating ecological and historical analysis see J. C. Malin, *The Grassland of North America: Prolegomena to Its History* (Edwards, Ann Arbor, Michigan, 1947), p. 120.
6. R. F. Flint, *Glacial and Pleistocene Geology* (Wiley, New York, 1957), p. 187.
7. Some examples of wooded scarps of diverse lithology: Dakota sandstone and Morrison shale (Fig. 1*K*; Fig. 2); Ft. Union shales (Fig. 1*A*); Ogallala caliche and Edwards limestone (Fig. 1, *L, M*, and *N*); basalt (Fig. 1*J*).
8. C. E. Bessey, *Science* **10**, 768 (1899); R. S. Kellogg, *U.S. Dep. Agr. Forest Serv. Bull.* **66**, 1 (1905); H. L. Shantz, *Bot. Gaz.* **42**, 179 (1906); W. L. Bray, *Bull. Univ. Tex.* **82**, Sci. Ser. 10 (1906); J. H. Foster, *J. Forestry* **15**, 442 (1917); J. M. Aikman, *Proc. Iowa Acad. Sci.* **35**, 99 (1928); F. W. Emerson, *Ecology* **13**, 347 (1932); W. E. Loomis and A. L. McComb, *Proc. Iowa Acad. Sci.* **51**, 217 (1944); M. F. Buell and J. E. Cantlon, *Ecology* **32**, 294 (1951); L. D. Potter and D. L. Green, *Ecology* **45**, 10 (1964). I have observed local reproduction of tree species of scarp woodlands on deeper soils occupied by grasslands in the following areas of the plains region: Canadian Escarpment, N.M.; Llano Estacado, N.M., Tex.; Callahan Divide and Edwards Plateau, Tex.; Black Mesa, Okla.; Mesa de Maya and Purgatoire Canyon area, Colo.; at numerous localities east of the Flint Hills, Kan.; Wildcat Hills and Niobrara River areas, Neb.; Pine Ridge Escarpment, Neb., Wyo., S.D.,; Tongue River area, Mont.
9. For example, woodlands of *Juniperus pinchotii*, which intergrade with desert scrub dominated by *Larrea* on the Stockton Plateau, Tex., extend eastward on the Edwards Plateau and intergrade with woodlands of live oak (*Quercus virginiana*) and *Juniperus ashei*. The latter, in turn, contact woodlands of post oak (*Quercus stellata*) on the northeast, which extend to the main body of eastern deciduous forest in eastern Oklahoma and Texas. Also, woodlands of *Juniperus monosperma*, which intergrade with desert scrub dominated by mesquite (*Prosopis*) and *Larrea* in the Pecos Valley, N.M., extend northward to the Canadian Escarpment, N.M., where they intergrade with woodlands of *Pinus ponderosa*. The latter are continuous along scarps with the main body of Rocky Mountain coniferous forest. In the northern plains, extensive woodlands of *Pinus ponderosa* and western red cedar (*Juniperus scopulorum*) in western Nebraska extend eastward along scarps of the Niobrara Valley more than half way across the state, where they are replaced by eastern red cedar (*Juniperus virginiana*), bur oak (*Quercus macrocarpa*) and other deciduous trees, which, in turn, extend eastward, chiefly along scarps and valleys, to the main body of eastern deciduous forest.
10. E. N. Munns and J. H. Stoeckler, *J. Forestry* **44**, 237 (1946).
11. C. G. Bates and R. G. Pierce, *U.S. Dep. Agr. Forest Serv. Bull.* **121**, 1 (1913); W. L. Tolstead, *Ecol. Monogr.* **12**, 290 (1942); Nebraska National Forest, Rocky Mountain Region, *Self Guided Tour: Bessey Nursery and Plantation* (Government Printing Office, Washington, D.C., 1963).
12. P. B. Sears, *Science* **134**, 2038 (1961).
13. W. H. Horr, *Univ. Kans. Sci. Bull.* **37**, 143 (1955).
14. U. Hafsten, in *Paleoecology of the Llano Estacado*, F. Wendorf, Ed. (Museum of New Mexico Press, Santa Fe, 1961), p. 59.
15. M. K. Elias, *Geol. Soc. Amer. Spec. Papers 41* (1942).
16. R. W. Chaney and M. K. Elias, *Carnegie Inst. Wash. Publ. 476* (1938), p. 1; J. C. Frye, A. B. Leonard, A. Swineford, *Univ. Kansas Publ. State Geol. Surv. Kansas Bull.* **118**, 44 (1956).
17. H. D. MacGinitie, *Univ. Calif. Berkeley Publ. Geol. Sci.* **35**, 67 (1962).
18. The excessively well-drained, stony soil or creviced bedrock of escarpments may be a more favorable substratum for the xeromorphic, woody, thick-barked roots of trees than for the diffuse, fibrous, and relatively unsuberized roots of grasses. It is probable that deep infiltration of rainfall, and in some instances, melt-water from wind-drifted snow and runoff from rock surfaces, is favored by the coarse, rudaceous soils and the fractures, crevices, or bedding planes in the rocks of scarps. Less of the deeply infiltrated water could be exploited by grasses than by the better adapted root systems of woody plants. On the other hand, the relatively shallow average penetration of moisture in the finer-textured soils occurring on the plains could potentially permit exploitation by both grasses and trees. Surface drainageways are poorly developed on the flat plains, and much of the rainfall is quickly absorbed by the soil. If infiltration is shallow, there may be a greater loss through evaporation at the surface. It is also probably true that more of the water absorbed by the finer-textured soils would be unavailable to plants, because of the greater amount of colloidally bound water held at high tensions (greater than 15 atm); but then there would also be a greater amount of water retained in the available range from field capacity to wilting point. Nevertheless, the extensive root systems of individual xerophilous trees are capable of drawing on the water resources of large volumes of soil, so that soil moisture deficiencies could have been reflected merely in a decreased number of individuals per unit area, as in open, grassy woodland or savanna, rather than *treeless* grassland. For a discussion of the role of edaphic factors in the segregation of woody vegetation and grassland in California, see P. V. Wells, *Ecol. Monogr.* **32**, 79 (1962).
19. C. O. Sauer, *Kentucky Geol. Surv.* **25**, 128 (1927); *Geogr. Rev.* **34**, 551 (1944); *J. Range Manage.* **3**, 16 (1950).
20. For time element, see C. V. Haynes, *Science* **145**, 1408 (1964); W. R. Wedel, *Prehistoric Man on the Great Plains* (Univ. of Oklahoma Press, Norman, 1961), p. 280.
21. Supported in part by NSF grant GB-1821.

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