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Abstract. Although North American grasslands are diverse and biotically rich, their conservation has never received high priority. As a result, the prairie landscape has all but disappeared. However, one prairie region has retained its essential pre-Columbian features. This is the Nebraska Sand Hills Prairie, a 4.8 million ha stabilized dune region of Holocene origin. Because the Sand Hills lie at the heart of the North American grasslands, their biota is influenced by the adjacent short- and tallgrass prairies and by northern (cool-season) and southern (warm-season) grasslands. In addition, the Sand Hills have their own distinctive sand-dependent biota. Equally important, however, is the heritage conveyed by their uninterrupted landscape and rich cultural history. Although the Sand Hills could be threatened by turning of their erodible soils for agronomic purposes that are not sustainable in the long term, implementation of the Conservation Reserve Program has reinforced historic patterns of sound land management. As a result, privately managed land in the Sand Hills serves a conservation function of global significance. In this region the optimal long-term public and private land use appears to be native prairie.

Key Words. Sandhills, prairie, Nebraska, preservation.

INTRODUCTION

> "The ranchman understood and loved the land the way he found it — grass side up. He knew, even as the Indian knew, that much of it could not be profitably farmed, that to break its thin, root-bound skin would deface and ruin it for years to come"
>
> Nellie Snyder Yost

This paper has its foundations in a series of studies (Whitcomb *et al.* 1986, 1987, and 1988, Whitcomb and Hicks 1988) that were conducted on the ecology and evolution of leafhoppers of North American grasslands. These studies pointed out both the significance of the Sand Hills and the need to make their importance known to others.

At the time of European settlement of the New World, the North American continent was rich in both mesic and semiarid grasslands. Today, the mesic grasslands that constituted the true prairie have been largely turned over to intensive agriculture. The Nebraska Sand Hills Prairie (Pool 1914, Keech and Bentall 1978, Wolfe 1984, Bleed and Flowerday 1989) is a 4.8 million ha region which has not declined in condition since European settlement. If landscape as well as grass is considered, the Nebraska Sand Hills is the last prairie. To relate the significance of the Sand Hills to others, this paper has been organized first to describe the ecosystem and then to address the issue of conservation.

DISCUSSION

Nebraska Sand Hills: The Heart of the North American Grasslands

The grassland types of the United States were mapped by Küchler (1964 and 1985). This work defined a "potential vegetation" in which vegetation was classified in terms of the natural communities that dominated the landscape before European settlement and that would reassert dominance in the absence of human disturbance. In addition to grasslands, of which 44 were described, several other formations were described, such as juniper-pinyon and ponderosa pine forests, which are in fact preponderantly grassland. The Nebraska Sand Hills lie at the heart of these North American grasslands (Figure 1).

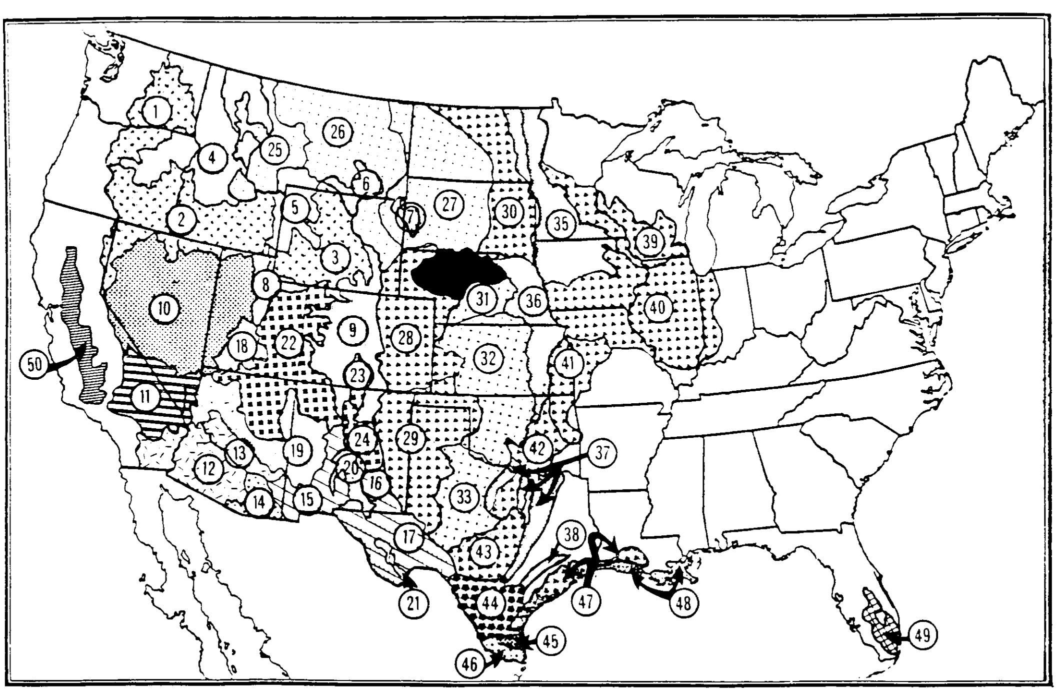

FIG. 1. Grassland regions of the United States; modified from Küchler (1964 and 1985). The Nebraska Sand Hills Prairie (solid black) lies at the heart of the North American grasslands (modified from Whitcomb *et al.* 1987); see this publication for descriptions of the illustrated regions.

East of the Sand Hills, wherever terrain permitted, the prairie has been almost quantitatively converted into cropland. Regions that were originally true prairie, or mosaics of prairie and woodland, generally receive 500 or more mm of annual precipitation, a reasonable proportion of which falls during the growing season. These prairies were dominated by tall grasses, including many warm-season (C_4) species. Principal dominant grasses of this region include big bluestem (*Andropogon gerardii* Vitman), little bluestem (*Andropogon scoparius* Michx.), indiangrass [*Sorghastrum nutans* (L.) Nash], and switchgrass (*Panicum virgatum* L.). The regions in which these grasses were dominant include tallgrass prairie, oak savanna, deciduous forest-prairie mosaic, and the Fayette and Blackland Prairies of Texas.

South of the Sand Hills, the mixed prairie is a transitional grassland composed largely of short and tall warm-season grasses; this prairie formation receives 380-500 mm of annual precipitation. In this region, buffalograss [*Buchloe dactyloides* (Nutt.) Engelm.] and blue grama [*Bouteloua gracilis* (Willd. *ex* H. B. K.) Lag. *ex* Griffiths] assume considerable importance. North of the Sand Hills, the transitional region between mesic and dry grassland is dominated by cool-season grasses such as western wheatgrass (*Agropyron smithii* Rydb.) and prairie junegrass [*Koeleria pyramidata* (Lam.) Beauv.]. Northwest of the Sand Hills, the semiarid prairie, although containing a minor component of short, warm-season grasses (blue grama and buffalograss) is largely a wheatgrass (*Agropyron*) prairie. To the west and southwest of the Sand Hills, the semiarid short-grass prairie, which receives 250-380 mm of annual precipitation, is dominated by blue grama and buffalograss.

With these different influences, it is small wonder that the Sand Hills have a biotic diversity that would not be predicted from their apparently monotonous physiognomy. This would be so, even if they were not composed of a seemingly infinite variety of combinations of sand and soil and water distributed along latitudinal and elevational gradients.

Climate

The Sand Hills region is large enough to exhibit considerable climatic variation. Annual precipitation in the Sand Hills ranges from about 580 mm in the east to less than 430 mm in the west (Wilhite and Hubbard 1989). As much as half of the precipitation is received during the prime growing season from May through July. Mean precipitation values for the Sand Hills can be deceiving, since precipitation varies greatly from year to year. For example, long-term records for Ewing, Nebraska show annual precipitation from as high as 960 mm to as low as 320 mm, the latter occurring in the 1936 drought. The Sand Hills were affected by the "great drought" of the 1930s, but they suffered less than many other Great Plains regions largely because the native flora is well adapted to withstand such variations in precipitation. Also, droughts, although severe, were of short enough duration that they did not severely affect the groundwater reserves. Snowfall, which ranges from 560 mm in the south to 1,440 mm in the north, is an important factor in groundwater recharge.

Mean temperatures in the Sand Hills range from 20-25 C. The freeze-free season varies from 150 days in the east to 120 in the west, primarily a reflection of elevational differences (approximately 1,220 m in the west to about 610 m in the east). Prevailing winds usually have a westerly component but frequently also are northerly or southerly; east winds are uncommon (Wilhite and Hubbard 1989).

Geology and Soils

About 98 million years before present (YBP), the present-day area of the Sand Hills was covered by Cretaceous seas (Swinehart and Diffendal 1989). Sediments of these seas were deposited for about 33 million years, until sea level fell worldwide. The Cenozoic strata found today between the recently deposited eolian (wind-deposited) sand and the underlying Jurassic and Cretaceous strata consist of either fine-grained volcanic sediments or alluvial sediments (Figure 2). Whereas the volcanic sediments originated from distant source areas, alluvial sands originated in regions immediately to the west of the Sand Hills. For example, material of the White River Group probably are derived in large part from what is now Colorado. Even in the early Tertiary, alluvial sands had begun to accumulate in the present-day Sand Hills region. A paleovalley of the White River Group with as much as 15 m of Chadron Formation sand occurs under most of Garden County (Swinehart and Diffendal 1989). The Arikaree group, formed 28-19 million YBP, covers the western third of the Sand Hills. One Arikaree paleovalley, as wide as 40 km in some places, is filled with more than 61 m of fine to medium sand.

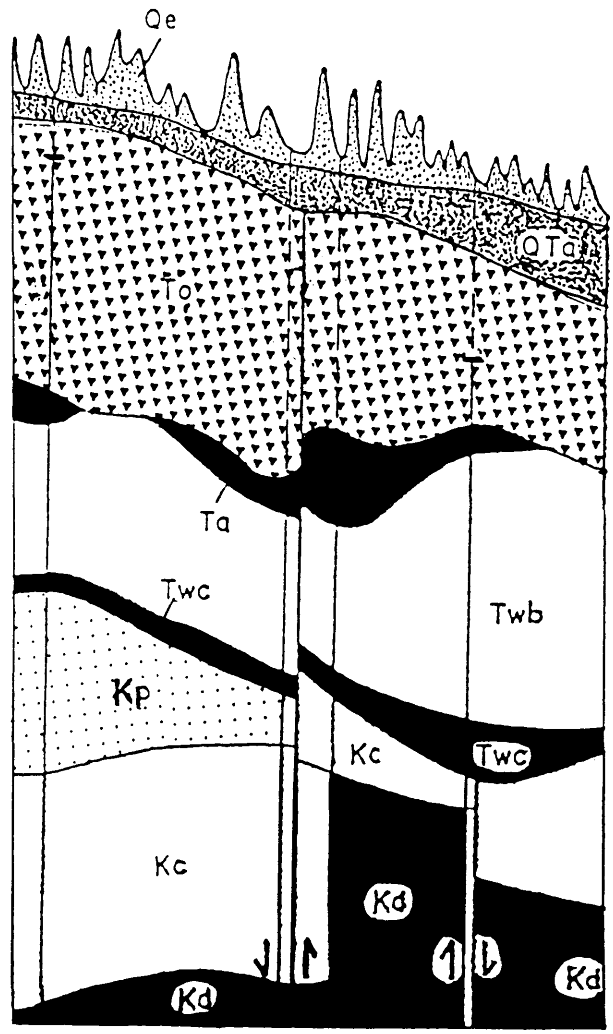

FIG. 2. Geologic section, west to east, of Grant County in the west central Sand Hills. Vertical exaggeration of diagram causes slopes to appear steeper than they actually are. Designations: Qe = Eolian sand of Holocene origin; QTa = Alluvial sand and silt of Quaternary and/or Pliocene origin; To = Ogallala Group (Miocene); Ta = Arikaree Group (Miocene and Oligocene); Twb and Twc = Brule formation and Chadron formation (respectively) of the White River Group (Oligocene); Kp and Kc = Pierre Shale and Colorado Group (respectively) of the Upper Cretaceous; and Kd = Dakota Group of the Lower Cretaceous. Two oil and gas tests are diagrammed: the end of the cased zone is indicated by a short horizontal line. Two faults are also diagrammed: arrows show direction of relative movement. Modified from a geologic section of the entire Sand Hills region of Swinehart and Diffendal (1989).

Beginning about 19 million YBP, in the Miocene, Ogallala group sediments began to accumulate in a major sedimentary basin (Figure 2). The drainage systems of this basin were diffuse. Ogallala sediments may have been deposited as alluvial fans or as sediments of braided rivers in wide shallow valleys. Thus, this group may represent an alluvial plain with a complex history (Swinehart and Diffendal 1989). Source areas of these sediments include present-day Wyoming and Colorado. These areas continued to be sources of alluvial sand in the Pliocene. Evidence for this is the presence in the sands of coarse sediments of that age consisting of uncommon materials such as anorthosite, an uncommon igneous rock of Wyoming's Laramie Mountains, or quartz pebble conglomerate from Wyoming's Snowy Range.

A scarcity of sediments between 2 million and 40,000 YBP makes assessment of the early Quaternary speculative. It is possible that significant erosion of the Ogallala and overlying younger strata occurred during the Pleistocene.

Modern drainage systems such as the Loup, as well as the Calamus and Niobrara (Figure 3), began to form about 20,000 YBP at the time of the last major pulse of continental glaciation. At that time, the area of today's Sand Hills may have been a broad alluvial plain with sandy streams flowing in valleys of low relief. Voorhies and Cormer (1985), for example, estimate that the central Niobrara valley during this period was 2-3 times wider but only half as deep as the modern Niobrara River.

Dramatic changes in the Great Plains region occurred 12,000 YBP as the last continental ice sheets retreated. By 9,000 YBP, spruce forests with prairie inclusions and aspen-pine parklands had given way to prairie (Fredlund and Jaumann 1987). But even during the Holocene, Sand Hills drainage patterns experienced dynamic changes. May and Holen (1985), for example, documented five distinct Holocene alluvial fills in the South Loup Valley. Also, Swinehart and Diffendal (1989) believe that the modern Dismal River valley is less than 1,500 years old.

But the current major geologic feature of the Sand Hills region is its stabilized eolian sand (Figure 2). In the south central and west central Sand Hills it is common to find 9-18 m of eolian sand; in other areas the thickness is 1-9 m. The sands contain between 1 and 4% silt and clay, giving the soils a cohesive property not possessed by pure sand. In many areas, vertical walled trenches can be dug in the dunes.

Although the Sand Hills are the largest eolian sand body in the western hemisphere, they are smaller than the large unstabilized sand areas of North Africa, Arabia, Asia, and Australia (Wilson, 1973). They are, however, one of the largest stabilized sand regions in the world.

Presumably, eolian activity is at least roughly correlated with dry climatic conditions. Large dunes tend to form in sandy regions when vegetation cover is less than 20% (Swinehart 1989). Under current precipitation regimes, cover in the Sand Hills greatly exceeds this percentage. Although some modern sand seas have less than 100 mm of annual precipitation, the Sand Hills may have developed with annual precipitation of nearly 250 mm per year (Swinehart 1989).

Although not obvious at the ground level, there are strong patterns in the arrays of large and small dunes. For example, satellite images of the west-central Sand Hills show strong alignments of straight to slightly curved ridges, with long axes trending west to east (Swinehart *et al.* 1989).

Further, the dunes of the Sand Hills have many forms (Smith 1965, Swinehart 1989). Parabolic dunes develop a "U" or "V" shape because their arms are anchored by vegetation. These dunes, essentially confined to the southwestern Sand Hills, have a consistent southeastern orientation. Dune-forming winds must, there-

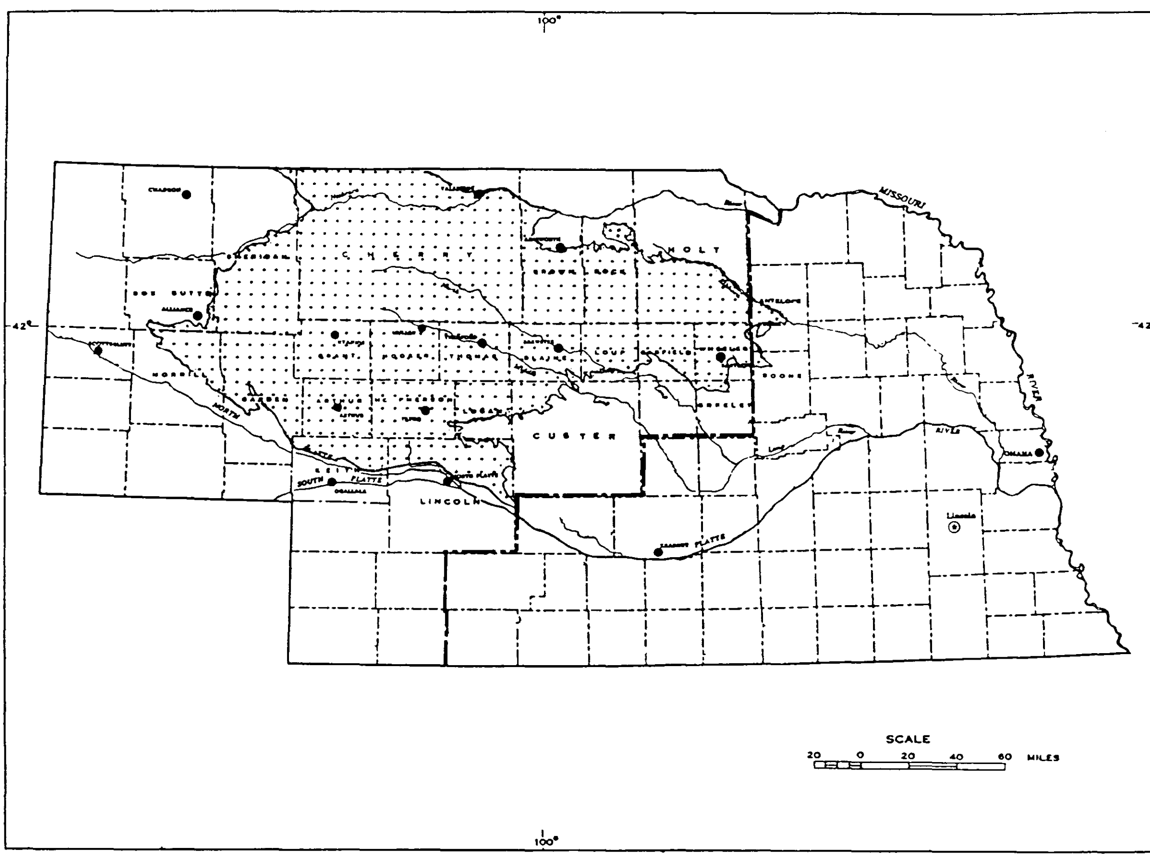

FIG. 3. The Sand Hills region of Nebraska (shaded). Kinkaid Counties (see text: European Colonization) lie to the west of the broad dashed line. A small portion of the Sand Hills extends into southern South Dakota.

fore, have blown from the northwest. In northeastern Colorado (Ramaley 1939) and southwestern Nebraska, the presence of dunes similar in age to the Sand Hills indicate that winds there must also have blown predominantly from the northwest (Muhs 1985) (Figure 4).

Most of the dunes have blowouts which, on a landscape level, impart a dimpled or pockmarked texture to large areas of the dune system. Pool (1914) described the cycle by which these depressions are generated and, eventually, revegetated. Blowouts originate on exposed upper slopes where the cover is broken or depleted from disturbances such as fire or overgrazing. During early stages, the blowout is simply a patch of bare sand a few meters wide and a few centimeters deep. Roots of deeper-rooted plants are exposed by the wind and, in time, the entire plant is blown away. When the young blowout is no more than 4-5 cm in depth the sand begins to slide into the depression, from which it is then blown away. After a number of years, the blowout may be hundreds of meters across. The inner slope that faces the wind is long and extensive. The opposite side is much steeper, in some cases nearly perpendicular. The steepness of this slope is often maintained by growth of sand-colonizing plants that are sheltered from the wind by the lee side of the blowout. Eventually the blowout reaches a size from which sand is no longer blown. Instead, the sand slides to the bottom of the blowout and remains there. At the bottom of such blowouts, numerous seeds, carried like the sand to the bottom, are able to germinate. The revegetation process initiated in this way eventually reclaims the blowout. The plant assemblages of blowouts are the most distinctive of the Sand Hills (Tolstead 1942) and include blowout grass [*Redfieldia flexuosa* (Thurb.) Vasey] and the endemic blowout penstemon (*Penstemon haydenii* S. Wats.).

At one time, it was believed that the Sand Hills dated to the Pleistocene (Lugn 1935, Swinehart 1989). However, Ahlbrandt *et al.* (1983) studied 7 sites at which radiocarbon-dated material less than 10,000 years old was overlain by eolian sand. The best documented interval of activity occurred 3,500 to 1,500 YBP. The linear dunes and most of the sand sheets, totalling about 2.1 million ha, probably formed at this time. Ahlbrandt *et al.* (1983) hypothesized that larger dunes occurred 8,000 to 5,000 YBP during the middle Holocene warm and dry period (altithermal) (Barry 1983). Corroborative evidence for Holocene origin of the Sand Hills has now come from many other sources (Bleed and Flowerday 1989). For example, Muhs (1985) found only immature soil profiles on Sand Hills dunes with thin A horizons that contain little organic matter (Lewis 1989). Even in soils of subirrigated meadows with thick A horizons, subsoils are unstructured and show no signs of clay accumulation. Thus, it appears that Sand Hills soils are in early stages of development. Many may be no more than 1,500 years old.

All available evidence, therefore, favors creation of the Sand Hills during multiple episodes of eolian activity during the last 10,000 years. Because these episodes were asynchronous, the dune fields have a complex history (Bradbury 1980). Present day eolian activity in the Great Sand Dunes area of south-central Colorado, in contrast to the pattern of stabilization in the Sand Hills, is a current example of such complexity and demonstrates that eolian activity is not necessarily correlated with contemporary climate. Nevertheless, it is reasonable to infer that appearance of the large dunes was related to the altithermal. Following about 2,000 yrs of stabilization, the climate again became dry, permitting further eolian activity. Extensive modification of crescentic dunes to domelike and domal-ridge dunes may have taken place in the central and eastern portion of the dune field at this time (Swinehart, 1989). After this eolian activity ceased, about 1,500 YBP, minor periods of drought have occurred, during which blowout processes have modified local dune structures (Swinehart 1989).

The source of the Sand Hills sand is indicated clearly by the geologic nature of its underlying sediments. As much as 60 m of Pliocene and Quaternary alluvial sand underlies the southeastern Sand Hills, and Quaternary sands are widespread in the northwest. The sand worked by Holocene eolian activity was derived, therefore, simply from unconsolidated alluvial sands that covered most of the present area of the Sand Hills during the early Holocene (Swinehart 1989).

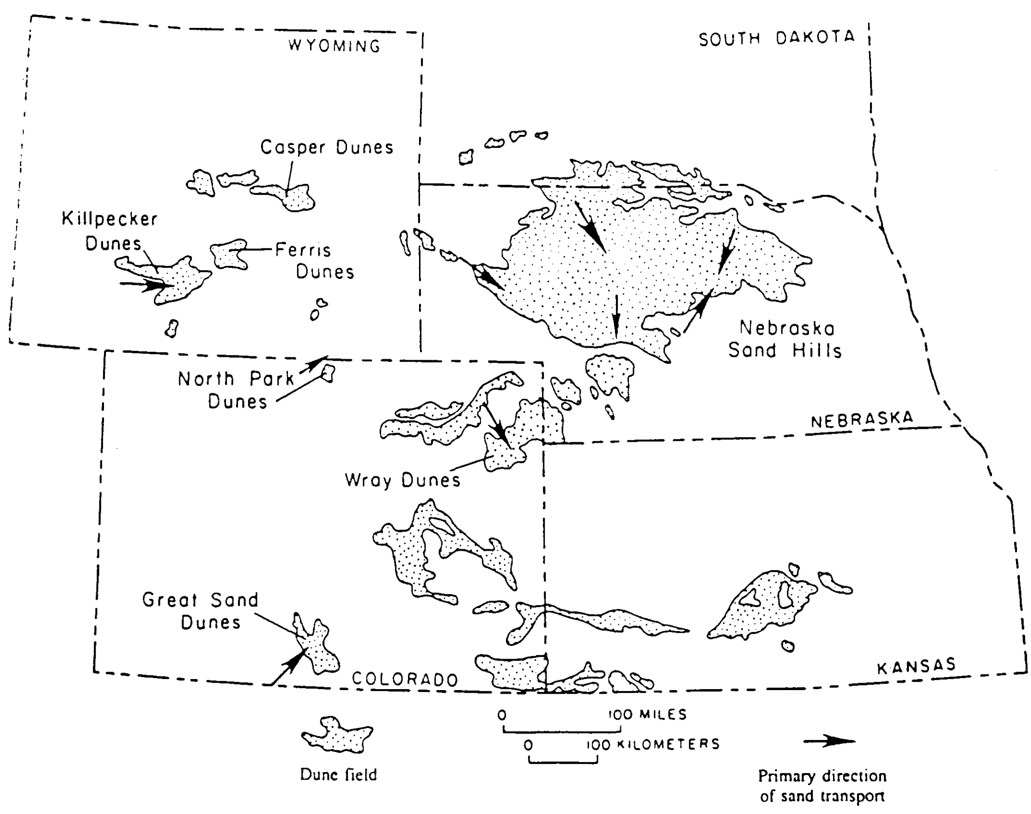

FIG. 4. Archipelago of sand regions in the west central Great Plains and central Rocky Mountain states. Figure from Ahlbrant *et al.* (1983) as modified by Swinehart (1989)

Water Resources

The Sand Hills are underlain by the High Plains Aquifer (Bleed 1989). Although the thickness of this aquifer (from 60-270 m) varies greatly, the portion underlying the Sand Hills is generally thicker than in other plains regions. The principal groundwater reservoir of the Sand Hills generally coincides with the base of the Ogallala Group. The aquifer generally slopes downward to the east, an orientation that coincides with the overall direction of the regional groundwater flow pattern. In some parts of the Sand Hills, the water table is at or near the surface, forming lakes, marshes, and subirrigated meadows.

A unique set of conditions is responsible for the rich groundwater resources of the Sand Hills. Although precipitation is only moderate and evapotranspiration rates are high, the combination of thick deposits of consolidated and gravelly sands, together with highly permeable surface sands, produces ideal conditions for aquifer recharge. Groundwater sequestered under such circumstances is mostly very low in dissolved solids.

The groundwater reserves of the Sand Hills are of national significance (Bleed 1989). Overflow from the aquifer feeds the Niobrara River and other streams and rivers. And, because the water is an important component of the Platte system, it is an important resource for downstream regions. Although large, this water resource is also fragile. Therefore, in areas where groundwater is close to the surface, extensive pumping could lower local water tables, severely impacting wetland ecosystems. High soil permeability, which facilitates recharge, would also facilitate groundwater contamination if pesticides or fertilizers were used on a large scale. Control of infiltration of such contaminants into the groundwater would be very difficult. For such reasons, the water resources of the Sand Hills require careful management (Bleed 1989).

Much of the western third of the region lacks streams and is referred to as the "Closed Basins Area" (Figure 3). The Niobrara river, whose headwaters are in eastern Wyoming, is the only Sand Hills river that originates outside the region. Other drainage systems originate in the hills themselves. Since these streams are largely derived from relatively steady groundwater seepage, they have a nearly constant discharge rate (Bentall 1989).

In general, Sand Hills lakes (Bleed and Ginsberg 1989) tend to be at least slightly alkaline. One of the lakes is among the most alkaline natural inland bodies of water known. Some lakes are also hypersaline.

Flora

The plant species composition of the Sand Hills suggests that their flora has been recruited largely from the surrounding prairie. Blowout or Hayden's penstemon is an exception to a rule of relatively low plant endemism. It is likely, given the Holocene origin of the Sand Hills and repeated subsequent pulses of eolian activity in the region (Ahlbrandt and Fryberger 1980, Ahlbrandt *et al.* 1983, Swinehart 1989), that changes in the Sand Hills biota have been extensive and dynamic. In addition, an archipelago of smaller sand regions (Fig. 4) in the plains and Rocky Mountain regions (Ahlbrandt *et al.* 1983, Swinehart 1989) has supplied an extensive, although fragmented, sand substrate. Hence, the present sand flora, and its associated fauna, may have been widely distributed during the Holocene.

Of about 700 plant species recorded from the Sand Hills, only about 50 are introduced. This number of exotic species is remarkably low for an area so large. In contrast, Kaul and Rolfsmaier (1987), while cataloging 300 native species on a tallgrass prairie of about 100 ha near Lincoln, also cataloged 60 introduced species. Further, most of the introduced Sand Hills plant species occur in disturbed areas such as roadsides, cultivated fields, and heavily grazed rangeland, which constitute a small fraction of the total Sand Hills area.

The Sand Hills Prairie, especially on xeric and mesic sites, is dominated by grasses (Sutherland 1984). There have been numerous efforts to group these grasses, and associated forbs, into communities (Pound and Clements 1900, Pool 1914, Weaver 1965, Harrison 1980, Kaul 1989). Kaul (1989) recognized 10 general types of vegetational community: bunchgrass, sand muhly, blowouts and draws, needle-and-thread, three-awn grass, short-grass, meadow, wet meadow, marsh, and aquatic. Sand Hills grasses can also be classified, more or less, on the basis of their adaptedness for soil sandiness, soil moisture, and/or alkalinity (Table 1). Particularly in a region such as the Sand Hills, where plant densities on many sites are relatively low (Pool, 1914), such a classification may be more appropriate than one based on community membership.

Table 1. Diagrammatic representation of the grasses of the Sand Hills ordinated by their position on the moisture gradient (vertical axis), soil sandiness (horizontal axis, upper portion of table) and water alkalinity (horizontal axis, lower portion).

More sandy — *Less sandy*

Redfieldia flexuosa
Muhlenbergia pungens
Triplasis purpurea
Calamovilfa longifolia — *Bouteloua hirsuta*
Buchloe dactyloides
Koeleria pyrimidata
Bouteloua gracilis
Bouteloua curtipendula
Stipa comata
Stipa viridula
Andropogon scoparius
Muhlenbergia cuspidata
Sporobolus cryptandrus
Agropyron smithii
Aristida purpurea
Paspalum setaceum
Dichanthelium oligosanthes
Dichanthelium acuminata
Dichanthelium wilcoxianum
Eragrostis spectabilis
Andropogon hallii
Eragrostis trichodes
Poa pratensis
Elymus canadensis
Elymus virginicus
Sorghastrum nutans
Andropogon gerardii

Mesic

Sporobolus airoides
Hordeum jubatum
Agrostis stolonifera
Puccinellia nutalliana
Distichlis spicata
Muhlenbergia asperifolia
Sphenopholis obtusata
Spartina gracilis
Spartina pectinata
Leersia oryzoides
Polypogon monspeliensis
Alopecurus aequalis
Phalaris arundinacea
Phragmites australis
Glyceria striata
Glyceria grandis
Catabrosa aquatica
Beckmannia syzigachne

Hydric

More alkaline — **Less alkaline**

Kaul (1989) has listed some of the important Sand Hills forbs and the communities in which they occur. Common forbs in xeric communities include Arkansas rose (*Rosa arkansana* Porter), Bush morning glory (*Ipomoea leptophylla* Torr.), leadplant (*Amorpha canescens* Pursh), lemon scurfpea (*Psoralea lanceolata* Pursh), New Jersey tea [*Ceanothus herbaceus* Raf. var. *pubescens* (T. & G.) Shinners], penstemon species (including the endemic blowout penstemon), pincushion cactus [*Coryphanta vivipara* (Nutt.) Britt. & Rose], poison ivy (*Toxicodendron rydbergii* (Small) Greene], and sand cherry [*Prunus pumila* var. *besseyi* (Bailey) Gl.]. In addition, various composites, such as asters (*Aster* spp. and sunflowers (*Helianthus* spp.) occur in these communities.

In marshes, wet meadows, and aquatic habitats, a variety of sedges, rushes, bulrushes, and reed species are found, as well as such forbs as arrowheads (*Sagittaria* spp.), clammy-weed [*Polanisia dodecandra* (L.) DC subsp. *trachysperma* (T. & G.) Iltis], cowlily [*Nuphar luteum* (L.) Sibth. & Small], duckweeds (*Lemna* spp.), floating azolla (*Azolla mexicana* Presl.), giant duckweed [*Spirodela polyrhiza* (L.) Schleid.], horned pondweed (*Zannichellia palustris* L.), water milfoil (*Myriophyllum* spp.) naiad (*Najas* spp.), pondweed (*Potamogeton* spp.), smartweed (*Polygonum* spp.), swamp milkweed (*Asclepias incarnata* L.), watercress (*Nasturtium officinale* R. Br.), waterlily (*Nymphaea* spp.), watermeal (*Wolffia* spp.), waterweed (*Elodea* spp.), water hemlock (*Cicuta* spp.), water plantain (*Alisma* spp.)., winged pigweed [*Cycloloma atriplicifolium* (Spreng.) Coult.], and widgeon grass (*Ruppia maritima* L. var. *occidentalis* (S. Wats.) Graebn.] (Great Plains Flora Association 1986).

If the vast majority of dry Sand Hills, wet meadows, and zoned aquatic niches seem to be monotonous, the flora of the Sand Hills river systems does not. This flora is recruited not only from surrounding prairie vegetation but from eastern, northern, and western floristic systems as well. For example, the vegetation of the Niobrara Valley reflects boreal, arid montane, and eastern deciduous forest elements (Kaul *et al.* 1988, Kaul 1989). Some of these elements are apparently relict populations that have persisted through the Holocene.

In general, the Sand Hills region, like much of the arid Great Plains, is now drier than it was during pluvial periods of the Pleistocene. Throughout the prairies and Great Plains there has been a tendency for complete retreat of spruce forests. In more recent time, there appears to have been a colonization by ponderosa pine (*Pinus ponderosa* Laws.) and cedars (*Juniperus* spp.) (Wells 1983), largely on scarps that are at least somewhat protected from fire. In the Sand Hills today, in the absence of periodic fire (now human controlled), there is a tendency for ponderosa pine to expand its local range, particularly in the vicinity of scarps (Steinauer and Bragg 1987).

Plant communities in the Sand Hills, like other communities, are determined in part by proximate and in part by historical determinants. Because the Sand Hills are recent in origin, there has been little time for development of soil diversity or for stochastic accumulation of species. The present-day climax communities are therefore relatively simple in terms of species numbers.

Among proximate factors, plant species occurrence is related strongly to topography. Although blowout communities have relatively few species, dune communities exceed those of the valleys and wet swales in species richness (Kaul 1989). The availability of subsurface water may be the most important factor determining plant species occurrence. The species richness of the dunes is explained by soil texture. Dune soils are coarse textured and have little organic matter. Because of the high infiltration rates, subsurface moisture is readily replenished. In contrast, in drier interdunal valleys the soils are more finely textured, and less water percolates into the soil. These soils hold more water in the spring than sandier soils but are depleted by midsummer. Thus, in dry summers these soils have less available moisture than those of the dunes (Barnes and Harrison 1982). Plants of the dune tops are deep-rooted warm-season (C_4) grasses (Barnes and Harrison 1982, Barnes and Heinisch 1984). The interdunal valleys are often dominated by cool-season (C_3) grasses such as western wheatgrass (*Agropyron smithii* Rydb.) or needlegrasses (*Stipa* spp.). The seasonal growth flush of these grasses occurs in the spring, when the subsurface moisture content of the interdunal soils is high.

Communities on north-facing slopes are often substantially different from those on south-facing slopes (Bragg 1978). Barnes (1980) felt that the temporal and spatial distribution of available water along local elevational gradients in the Sand Hills controlled such species differences through interactions with rooting morphology, photosynthetic physiology, and transpirational water loss. Competitive interactions also may play a role in the local distribution of Sand Hills grasses. For example, Heinisch (1981) demonstrated the role of root morphology in the niche partitioning of blue grama and hairy grama (*Bouteloua hirsuta* Lag.) in the western Sand Hills.

Sand Hills communities react dynamically to grazing pressures and fire disturbance and variations in precipitation. Responses to grazing pressure are rarely neutral. Plant species tend to either increase or decrease when grazed (Frolik and Shepherd 1940, Brinegar and Keim 1942, Sylvester 1957, Burzlaff 1962, Wolfe 1973, Bragg 1978, Stubbendieck 1989).

In earlier times, prairie fires were common (Pool 1914, Wolfe 1973, Richards 1980). Although there have been a few sporadic attempts to use prescribed burning on the Sand Hills range, fires have been generally feared by landowners, who believe that they are destabilizing. Indeed, rich growth flushes of the prairie after fire may be short lived if the new grass is exposed to desiccating late summer winds before the new growth has had an opportunity to regenerate a protective moisture-retaining thatch (Pool 1914). In general, the resulting changes in grassland quality after accidental fires have not suggested to land managers that burning would be a useful tool in the Sand Hills. In some reserves, however, fire has been used as a tool for increasing the content of fire-tolerant warm-season grasses at the expense of exotic cool-season grasses such as Kentucky bluegrass (*Poa pratensis* L.).

The landowners are among the best ecologists in the Sand Hills. These range managers, reinforced by specialists of the Soil Conservation Service and the University of Nebraska, are among the best in North America (Stubbendieck 1989). For this reason, and because of the close relationship between ecology and range management, advances in basic ecology will no doubt find their way rapidly into management practices in the Sand Hills.

Fauna

The Sand Hills fauna is very rich, reflecting eastern and western, northern, and southern influences.

Fish.

More than 75 species of fish have been recorded from the Sand Hills during historic times (Hrabik 1989). Only one species is presumed lost from the pre-European colonization inventory. In the Sand Hills, as elsewhere, fish diversity increases with increasing downstream position in the drainage basin. The Niobrara drainage system, in accord with its general biotic richness, has the second-highest number of fish species in the entire Missouri River basin (Bliss and Schainost 1973). In contrast to streams, Sand Hill lakes are less diverse with some playa like and others highly alkaline. Fewer species of resident fish are adapted to these limiting conditions.

Amphibians and reptiles.

Twenty seven species of amphibians and reptiles occur in the Sand Hills (Freeman 1989a).

Mammals.

In the late Pleistocene, mammoth, mastodon, horse, and camel were found in the present-day Sand Hills region. By 11,000 YBP, however, perhaps as a result of climatic change, perhaps because of activities of hunter-gatherers, or perhaps for both reasons, all became extinct. More recently, elk (*Cervus elaphus*), bison (*Bison bison*), and bighorn sheep (*Ovis canadensis*) have also been extirpated. But many species of mammals remain.

Of about 81 species of Nebraska mammals, 58 occur in the Sand

Hills (Freeman 1989b). This list includes three species that occur only in the Niobrara Valley. Moreover, two-thirds of Nebraska mammal species reach a regional, distributional limit in the state (Jones 1964) with some of these limits occurring in the Sand Hills. The Sand Hills, thus, act as a barrier that divides the range of some species. For example, a population of the eastern woodrat (*Neotoma floridana*) that occurs along the Niobrara River is disjunct from the main population to the south.

The occurrence of common species may be divided into two Sand Hills habitat zones, wet and dry. In wet areas are found opossum (*Didelphis virginiana*), masked shrew (*Sorex cinereus*), short-tailed shrew (*Blarina brevicauda*), least shrew (*Cryptotis parva*), eastern mole (*Scalopus aquaticus*), eastern cottontail rabbit (*Sylvilagus floridanus*), fox squirrel (*Sciurus niger*), gray fox (*Urocyon cinereoargenteus*), and least weasel (*Mustela nivalis*). In drier habitats, desert cottontail (*Sylvilagus audubonii*), black-tailed jackrabbit (*Lepus californicus*), spotted ground squirrel (*Spermophilus spilosoma*), Ord's kangaroo rat (*Dipodomys ordii*), silky pocket mouse (*Perognathus flavus*), western harvest mouse (*Reithrodontomys megalotis*), and northern grasshopper mouse (*Onychomys leucogaster*) occur. In addition, beaver (*Castor canadensis*) and coyotes (*Canis latrans*) are common in the Sand Hills. Raccoons (*Procyon lotor*) are common even in the absence of trees, since they can den in such habitats as burrows or clumps of cattails. Bobcats (*Lynx rufus*) are uncommon. Pronghorn antelope (*Antilocapra americana*) have been extirpated from the eastern Sand Hills, but they occur in some western parts. Mule deer (*Odocoileus hemionus*) and white-tailed deer (*Odocoileus virginiana*) are common (Freeman 1989b).

Birds.

The avifauna of the Sand Hills is spectacular by any standard spectacular (Table 2). Seven special features of the region contribute to this richness. First, the numerous Sand Hills lakes (Bleed and Ginsberg 1989) serve as refugia for migratory waterfowl. Second, and even more importantly, these lakes serve as breeding areas for waterfowl, shorebirds, and other water birds. A large assemblage of breeding bird species are restricted to the vicinity of the lakes including the eared grebe (*Podiceps nigricollis*), western grebe (*Aechmophorus occidentalis*), 13 duck species, black tern (*Chlidonias niger*), American avocet (*Recurvirostra americana*), willet (*Catoptrophorus semipalmatus*), and Wilson's phalarope (*Phalaropus tricolor*). Third, an additional assemblage of seven bird species breed in fresh water marshes including the yellow-headed blackbird (*Xanthocephalus xanthocephalus*) and five rail and bittern species. Fourth, a distinctive assemblage of avifauna is made up of twenty-five species that breed in dry or mesic prairie. Of this group, those of special interest are the long-billed curlew (*Numenius americanus*), upland sandpiper (*Bartramia longicauda*), sharp-tailed grouse (*Tympanuchus phasianellus*), greater prairie chicken (*Tympanuchus cupido*), Swainson's hawk (*Buteo swainsoni*), golden eagle (*Aquila chrysaetos*), short-eared owl (*Asio flammeus*), burrowing owl (*Athene cunicularia*), and chestnut-collared longspur (*Calcarius ornatus*). Fifth, an additional feature of the Sand Hills is the Niobrara River Valley, whose riparian vegetation provides habitats for many eastern bird species. Sixth, the introduction of pine forests into the Sand Hills, now administered as two National Forest units, provides coniferous forest habitat. Seventh and last, but certainly not least, a crucial feature of the Sand Hills for faunal conservation is the large size of the region. It is now generally recognized that long-term species conservation requires large habitat units that can accommodate large populations (Soule 1986). Large population sizes serve to assure genetic diversity and to buffer against oscillations associated with climatic fluctuations, predator/parasite-prey cycles, or other periodic perturbations. The concurrent presence of all these conservation features in a single grassland region makes the Sand Hills of special interest in North American avifaunal conservation.

Table 2. Breeding bird species of the Nebraska Sand Hills; an expansion of lists by Molhoff (1985) and Labedz (1989). Alphabetic codes following common name are for (a) occurrence within the Sand Hills (codes before colon) and (b) habitat (codes after colon). Occurrence code: T = throughout; N,S,E,W = north, south, east, and west; L = local; A = accidental. Habitat: F = forest; H = habitations; L = lakes; M = marsh; P = prairie; R = riparian. * = Status uncertain. Scientific names may be obtained from American Ornithologists' Union (1983).

Pied-billed grebe, T:L; Eared grebe, T:L; Western grebe, W:L; Double-crested cormorant, W:L; American bittern, T,M; Least bittern, E,M; Great blue heron, T:L,R; Cattle egret, N:L; Green-backed heron, EN:L,R; Black-crowned night heron, T:L,R; White-faced ibis, LA:L; Trumpeter swan, W:L; Canada goose, T:L; Wood duck, T:L; Greenwinged teal, N:L; Mallard, T:L; Northern pintail, T:L; Blue-winged teal, T:L; Cinnamon teal, W:L; Northern shoveler, T:L; Gadwall, T:L; American wigeon, W:L; Canvasback, W:L; Redhead, T:L; Lesser scaup L:L; Ruddy duck, T:L; Turkey vulture, N:P,R; Northern harrier, T:P; Sharp-shinned hawk, N:R; Cooper's hawk*, L:R; Swainson's hawk, T:P; Red-tailed hawk, T:R; Ferruginous hawk, W:P; Golden eagle, L:P; American kestrel, T:R,H; Gray partridge, L:P; Greater prairie chicken, T:P; Sharp-tailed grouse, T:P; Wild turkey, N,R; Northern bobwhite, E:P,R; Ring-necked pheasant, T:P,R; Virginia rail, T,M; Sora, T:M; American coot, T:L,M; Piping plover, L:L; Killdeer, T:L,R,H; Black-necked stilt, L,L; American avocet, W:L; Willet, N:L; Spotted sandpiper, L:L,R; Upland sandpiper, T,P; Long-billed curlew, W:P; Common snipe, N:P; American woodcock*, E:R; Wilson's phalarope, T:L; Forster's tern, W:L; Least tern, L:L; Black tern, T:L; Rock dove, T:H; Mourning dove, T:L,P,R,H; Black-billed cuckoo, T:R; Yellow-billed cuckoo, T:R; Barn owl, T:H; Common screech owl, T:L,P,R,H; Great horned owl, T:P,R,H; Burrowing owl, T:P; Long-eared owl, L:R; Short-eared owl, T:P; Northern saw-whet owl, L:F; Common nighthawk, T:P; Common poorwill, W:P; Whip-poor-will, N:R; Chimney swift, T:H; Belted kingfisher, T:L,R; Red-headed woodpecker, T:R,H; Red-bellied woodpecker*, E:R,; Downy woodpecker, T:R,H; Hairy woodpecker, T:R; Northern flicker, T:R,H; Western wood pewee, W:P,R; Eastern wood pewee, E:R; Willow flycatcher*, L:P,R; Eastern phoebe, E:H; Say's phoebe, W:H; Great crested flycatcher, EN:R; Cassin's kingbird*, LW:P; Western kingbird, T:P,R; Eastern kingbird, T:P,R; Horned lark, T:P; Purple martin*, L:H; Tree swallow, E:L,R; Rough-winged swallow, T:R; Bank swallow*, L:R; Cliff swallow, T:H; Barn swallow, T:H; Blue jay, T:P,R,H; Black-billed magpie*, L:P; American crow, T:P,R; Black-capped chickadee, T:P,R; White-breasted nuthatch, E:R,H; House wren, T:H,R; Sedge wren*, L,P; Marsh wren, T:M; Eastern bluebird, T:H,R; Mountain bluebird, WL:P; Wood thrush, N:R; American robin, T:H,R; Gray catbird, T:P,R; Northern mockingbird, A:H; Brown thrasher, T:P,R; Cedar waxwing*, L:R; Loggerhead shrike, T:P; European starling, T:H; Bell's vireo, T:P,R; Warbling vireo, T:P,R; Red-eyed vireo, T:P,R; Yellow warbler, T:P,R; Black-and-white warbler, EN:R; American redstart, N:R; Ovenbird, EN:R; Common yellowthroat, T:P,R,M; Yellow-breasted chat, T:P,R; Scarlet tanager*, EN:R; Northern cardinal, E:H,R; Rose-breasted grosbeak, E:R; Black-headed grosbeak, W:R; Blue grosbeak, T:P; Lazuli bunting*, W,R; Indigo bunting, E:R; Dickcissel, T:P; Rufous-sided towhee, E:R; Chipping sparrow, N:H,R; Field sparrow, T:P,R; Vesper sparrow, N:P; Lark bunting, T:P; Savannah sparrow, N:P; Lark sparrow, T:P; Grasshopper sparrow, T:P; Song sparrow, E:L; Swamp sparrow, E:M; Chestnut-collared longspur, N:P; Red-winged blackbird, T:M,P,R,; Eastern meadowlark, TL:P, Western meadowlark, T:P; Yellow-headed blackbird, T:M,P,R; Brown-headed cowbird, T:H,M,P,R; Common grackle, T:H,R; Orchard oriole, T:P,R; No. (Baltimore) oriole, T:P,R; House finch*, SL,H; Pine siskin, N:F; American goldfinch, T:R; House sparrow, T:H

Invertebrate Fauna.

Although the invertebrates of the Sand Hills have not been intensively investigated, some groups have received attention (Hagen 1970, Whitcomb et al. 1988). The strong influence of the sandy substrate on the plant communities assures that the associated insect assemblages will be of special interest. This perspective can be illustrated with some insights from our own research.

In a comparison of the cicadellid fauna of five major grassland regions, we found the Nebraska Sand Hills assemblage to be especially diverse (Whitcomb *et al.* 1988). Because cicadellids are highly host specific, the underlying factors governing this diversity are easily surmised. Grassland leafhopper species can be classified as either generalists or specialists. Many generalists are actually broadly oligophagous species that confine their feeding to either grasses or forbs (Whitcomb *et al.* 1986 and 1987). Leafhopper diversity, therefore, directly reflects the diversity of dominant, perennial, native grasses and forbs (Whitcomb *et al.* 1986). Because the Sand Hills have recruited vegetational elements from surrounding prairie formations (east and west, north and south), and have, in addition, an assortment of plant communities dependent on a sandy substrate, they are vegetationally rich. The cicadellid species richness that we noted is therefore a direct reflection of plant species richness.

Several Sand Hills leafhoppers proved to be of special interest. These include especially species of the genus *Flexamia*. Members of this genus are closely associated with dominant, perennial, native chloridoid grasses (Whitcomb and Hicks 1988). We hypothesized that grasses fitting this description but that were only locally dominant, and therefore regionally uncommon or rare, could be hosts for undescribed *Flexamia* species. Two Sand Hills grasses appeared to fit this profile, both dominants of the blowout association; sand muhly [*Muhlenbergia pungens* Thurb.) and blowout grass, [*Redfieldia flexuosa* (Thurb.) Vasey]. It turned out that each was colonized by an undescribed *Flexamia* species. *Flexamia celata* was associated with blowout grass, and *F. arenicola* with sand muhly. These species were recently described by Lowry and Blocker (1987). The type locality for each is a research natural area of Crescent Lake National Wildlife Refuge in the western Sand Hills.

At first we thought that these new species would turn out to be endemics of the Nebraska Sand Hills. Further search, however, turned up other populations of these species (Whitcomb and Hicks 1988). In each case, however, the male genitalia of the extralimital populations show evidence of divergence from the Sand Hills populations. The case of *F. arenicola* is especially interesting, in that the recently discovered population (Anasazi form) in the Four Corners area (Arizona-New Mexico-Utah-Colorado) is clearly disjunct from the Nebraska population. The host, sand mulhy, is itself essentially disjunct, blocked on the northwest face of the Colorado Rockies by a combination of the Uinta Mountains and the dry *Agropyron* steppe of Wyoming and northern Colorado, and on the east by nonsand areas of Colorado and New Mexico (Whitcomb and Hicks 1988). Male genitalia of the Four Corners population are invariably broken, an event that presumably occurs during copulation. Therefore, it appears that the process of genetic divergence between the two populations has begun. From a conservation point of view, the important feature of the Nebraska Sand Hills population is that it is in little danger of extinction since its host reservoir is very large, and the regional population is divided into a large number of subpopulations, permitting "hedging" in the event of regional catastrophe. Populations of the Anasazi form may be stressed by increasing aridity in the Four Corners region.

For all of its sand biota, the Sand Hills provide an extent of habitat that is large enough to support viable populations. Especially because episodes of eolian activity appear to be more frequent than once supposed (Ahlbrandt *et al.* 1983, Swinehart 1989), extinction rates in small sand regions may prove to be high. Clearly, from all considerations of classical island biogeography (MacArthur and Wilson 1967), the largest sand reserve is surely the best. And for many invertebrate species, there will prove to be no extralimital populations, and the Sand Hills forms will prove to be indisputable endemics. Thus, when more complete invertebrate inventories are available, an increasingly large list of endemic invertebrates can be expected.

Finally, the very large size of the Sand Hills contributes to the diversity of its biota by permitting it to encompass geographic gradients. For example in many insect groups, such as mosquitoes (Lunt 1987), eastern or western, or northern and southern, range limits are encountered. This situation is not limited to invertebrates; many plant and animal species reach one or another range limit within the region (Jones 1964, Great Plains Flora Association 1986).

Sand Hills History

Just as an understanding of the geologic history of the Sand Hills region is vital to an understanding of its present-day physiognomy and biota, an understanding of human colonization of the Sand Hills is important to considerations of its future.

Native American colonization.

There is considerable evidence for colonization of the Great Plains at least 11,500 YBP. Indeed, many workers believe that the plains may have been colonized as early as 20,000 YBP. Thus, early native Americans were certainly on the scene at the time of formation of the Sand Hills in the Holocene. It is by no means certain that the Sand Hills were avoided by hunter-gatherers during periods of eolian activity, inasmuch as bison tracks occur in dune sand dated 7,260 YBP. These tracks suggest the presence of semipermanent water, even during dune-building episodes (Holen, 1989).

In the Paleo-Indian Period, at the close of Wisconsinan glaciation, Native Americans hunted mammoth and mastodon. After extirpation of these prehistoric mammals, bison probably served as the main prey for the hunters. Other species that were hunted included elk, deer, antelope, and smaller mammals. Waterfowl and fish were also probably hunted. Mass bison kills have been dated between 8,000 and 10,000 YBP. Steep-sided gullies were used as traps into which the bison were driven. Also, prehistoric agriculture may have been practiced on stream terraces and around some of the Sand Hills lakes.

There is abundant evident of agriculture in the Archaic period, 7,000-2,000 YBP. For example, many grinding stones for processing seeds have been recovered. Many artifacts from this period document extensive use of the Sand Hills for hunting.

In the Woodland period (2,000-1,000 YBP), ceramic vessels were used indicating a more sedentary lifestyle than that of the earlier hunter-gatherers. Pottery from this period is common along Sand Hills lakes and streams. Squash and beans were among the crops that were cultivated. Some maize was also grown late in the period.

After the Woodland period, 500-1000 YBP, Central Plains Tradition and Initial Coalescent peoples (thought to be ancestral to the Pawnee and Arikara) inhabited the plains, practicing a mixed economy of corn, beans, and squash, in addition to hunting.

In all, there is only limited evidence for permanent occupation of the Sand Hills during the Holocene. It is clear, however, that a number of the tribes that resided around the periphery of the Sand Hills used the region for seasonal hunting (Holen 1989). For example, the Plains Apache, although essentially southwestern, are well documented archaeologically in the Sand Hills, where they must have competed with the Pawnee for bison-hunting range. The Comanche appear to have been short-term occupants in the 1700s.

In historic times, a wide array of tribes utilized the Sand Hills. From 1540 to 1740, a mixed economy based on horticulture and hunting was practiced in the eastern plains. Farther west, other groups were predominantly hunter-gatherers, following a seasonal cycle in which bison were the main food supply. Both types of economy, however, led to use of the Sand Hills for hunting.

A 1718 map shows 12 villages of the Skidi-band Pawnee on the Loup River and another group of 12 villages that represented the Grand band of Pawnees (Tucker 1942). Skidi hunting territory appears to have been from the Platte River north into the Sand Hills to the Dismal River. Some of the eastern Sand Hills were hunted by the Omaha (Holen 1989).

On the northern edge, the Ponca hunted west along the Niobrara River and ventured south into the hills. But if they went too far they encountered Brule, Oglala, or Cheyenne. Some areas of the central Sand Hills (e.g., Shell Creek north to the Niobrara), may have been disputed by the Omaha and Cheyenne, as well as by the Pawnee and Ponca. Certain Sioux tribes also utilized the hills; by the 1830s the Brule Sioux were contesting the hunting grounds of the Pawnee and Omaha.

European colonization.

European colonists were slow to discover the Sand Hills. The region was known to early settlers as the "Sand Hills Desert" and was studiously avoided by early travellers. It was, in the words of B. Richards

> "avoided as no other part of the cattle country. The awe of this desert was widespread and real. Men had been known to venture into the region, lose their way and never be seen again. The hills were covered with a rather long grass [presumably prairie sandreed [*Calamovilfa longifolia* (Hook) Scribn.]; all hills looked alike; there were few landmarks; and water was uncertain, often alkaline."
>
> B. Richards Jr., 1980

The value of the region was apparently first discovered by cowboys of the N Bar Ranch, which was located 80 km east of Chadron on the Niobrara River (Figure 3). During the winter, the N Bar deployed line riders along the northern edge of the Sand Hills to prevent cattle wandering into them. In March 1879, however, an intense blizzard forced the line riders to seek shelter for survival, and some 6,000 N bar cattle drifted into the hills. An expedition was organized to rescue the lost cattle, and the N bar wagon headed into the hills on April 15.

As told by Jim Dahlman, who later became mayor of Omaha, as they entered the hills, the members of the expedition began to find native cattle:

> "as fat as any ever brought out of a feed lot; mavericks [unbranded] from one to four years old. We could hardly believe our eyes . . . Remember these cattle had no feed except native grass, and this was the month of April, after a terrific winter."
>
> Jim Dahlman, 1927

The expedition was a long one, and provisions ran low. Camping near a lake one day, the party had a dinner consisting solely of bean soup. In honor of that dinner, the lake was named Bean Soup Lake. In all, the expedition, which lasted five weeks, netted 8,000 bar N cattle and 1,000 head of "natives" that had been there for years (Dahlman 1927). It was this expedition that established the Sand Hills as exceptional cattle range.

At the time of their "discovery," the Sand Hills were almost totally in the public domain. From the time of the American Revolution, disposition of western lands had been an important issue. For many years after the Revolution, proceeds from land sales were used to reduce the national debt. Speculation in western lands became a common business enterprise. Land was cheap. For example, under the Preemption Act of 1841, 65 ha (160 A) could be purchased for \$3.09/ha (\$1.25/A). At such prices, most arable land east of the Mississippi River passed readily into private ownership. To encourage westward migration, President Lincoln in 1862 signed the Homestead Act, under which settlers were given title to tracts of 65 ha of surveyed public domain if they cultivated the land and lived on it for five years. However, while arable land east of the Sand Hills could often be homesteaded successfully, the Sand Hills, even more than the semiarid lands to the west, were not amenable to settlement of a mere 65 ha.

Encouraged by the construction of railroads, floods of settlers arrived in the plains in the 1880s to take up either farming or, to be lured by the open range in the public domain, cattle ranching. And, with vast acreages of public land available, the cattle business could be immensely profitable. For example, the cattle enterprise in 1895 in the northern Sand Hills was estimated to have yielded \$2,000,000 (Richards 1980).

By the turn of the century, Sand Hills ranching had become a large-scale operation. For example, on a large ranch two or three windmills were established at each water station, each fitted with a 7.5-10.0 cm pump operated by a 3.7 m wooden windmill. Water from these mills flowed into reservoirs 6-9 m in diameter. The stations cost as much as \$1,000 each; costs such as these were, of course, beyond the means of small operators. An indication of the size of a large operation can be obtained by measuring some of the tasks; in July, the Spade, one ranch operation, cut 15,000 tonnes of hay and plowed 644 km of fireguards. By the early 1900s, the Spade was the largest cattle company in Nebraska, running between 20,000 and 40,000 head.

Fire was a real threat, especially in the fall and winter, when the grasses became tinder dry. Fires, if not extinguished, burned over large areas, destroying range and winter feed. For this reason, large ranches like the Spade (Richards 1980) employed crews that plowed parallel fireguards that completely encircled their range. The grass between the guards was burned between August and October.

Fire, however, was not the only natural threat to ranching in the Sand Hills. Severe losses due to climatic variations, such as those experienced in the droughts and severe winters of 1885-87 made it clear that planning for winter range, good water, and hay for feed during winter snows were essential for a cattle operation. It was impossible to manage in this way without fencing. For example, it was necessary to protect lower hay meadows from untimely grazing. Under an open range system, the cattle grazed hay meadows preferentially in the summer. These hay meadows and winter pastures needed to be fenced and protected from grazing and fire during the summer months. In the winter, the cattle were given access to the protected pastures and supplied with hay during winter snows.

But throughout the semiarid grasslands, and especially in the Sand Hills, it was virtually impossible for stockmen, within the law, to obtain outright ownership of enough lands for their needs. "It took much scheming, scrambling, and perjury to assemble the acreage necessary for a sound ranching operation" (Larson 1965).

As a result of the fencing controversy, legislators from Great Plains states introduced legislation in 1901 under which federal lands adjacent to ranch holdings could be leased. But President Theodore Roosevelt, although generally sympathetic to conservation interests and no stranger to the plains, was unsympathetic to the fences. In his administration, the fencing act of 1885 was to be enforced: "Gentleman, the fences must come down." And in 1904, Congress passed the Kinkaid Act, which,. in 37 counties of western Nebraska (Figure 3), increased the size of homestead tracts from 65 to 260 ha. Unfortunately, this act combined 15 counties that were predominantly Sand Hills with 22 others of greater farming potential. Whereas some semiarid lands could be farmed in units of 260 ha, few Sand Hill tracts of that size were "proved up." Efforts to liberalize the law to permit land to pass more readily into private ownership were made. One was an amendment to the Kinkaid Act by which 194 ha (480 acre) isolated or disconnected tracts could be sold. In 1912, sale was authorized of 65 ha tracts "the greater part of which is mountainous or too rough for cultivation." In the same year, the time required to gain title under the Kinkaid Act was reduced from five to three years. By all these devices, the public domain of the Sand Hills eventually devolved into private ownership.

But the process was made no easier by the failure of Congress to devise legislation that was appropriate for the Sand Hills. As stated by Richards (1980): "The argument by Sand Hill ranchers, tirelessly reiterated, that their area was unique and should be handled as a grasslands unit . . . convinced few people in Washington."

Today's ranches, the product of numerous consolidations, are, for the most part, large enough to engage in the management practices devised by the earlier stockmen. In the east, some ranches of about 500 ha are proving to be sustainable, whereas in the west, average sizes are 1,600-2,400 ha (Miller 1989). But now, as always, the secret to effective stewardship of Sand Hills land is respect for the ecological forces that created the grassland and that are responsible for maintaining it.

Grassland conservation.

In general, interest in grassland conservation in the United States is geographically uneven (Whitcomb 1986). Predictably, greatest concern for losses of prairie come from states in which present-day destruction is nearly complete. These are, essentially, states such as Minnesota, Wisconsin, Iowa, Illinois, and Missouri that originally had extensive savannas or forest-prairie mosaics. Conservation groups in these states are very active and in some cases (e.g., Missouri) have managed to salvage small but significant preserve areas. However, in many instances, prairie destruction has gone too far, and restoration, rather than conservation, is being attempted. Unfortunately, even the botanical elements of prairie cannot be wholly reconstructed, and faunal restoration is totally hopeless.

It would certainly be helpful if states with an existing prairie inventory were to give grassland conservation the priority status it deserves. The fate of tall-grass prairie rests today on a few remnants that are managed as rangeland or hay meadows. Unfortunately, because these tracts are almost exclusively in private ownership, they will eventually be subjected to some or many of the same pressures that have already destroyed most prairie. In such regions, it is surely desirable to sequester prairie reserves. I wish to stress, however, that landowner participation should be a vital part of this process. In many instances, the public owes landowners a deep debt of gratitude, since retention of their lands as grassland has involved personal decisions that fully recognized the intrinsic value of the land as natural grassland.

In semiarid grasslands west of the Sand Hills, disappearance of native communities is less imminent, but many problems exist nonetheless. For example, there are many controversial issues regarding optimal land use. In much of the semiarid west and southwest, grasslands are under public ownership, in many cases by the USDA Forest Service or Bureau of Land Management. Although personnel of these agencies are almost unanimously concerned about proper management, they are constrained by the definition of their missions. The missions of these agencies, particularly concerning the balance between conservation and exploitation, is a proper subject for public debate. The western third of the nation is a confetti-like assortment of tiny vegetation units defined by climatic and elevational barriers and the topographies of mountain ranges, valleys, and river systems (Küchler 1985). Research on many plant or insect taxa indicates an exceptionally high species richness in this part of the United States, particularly in the southwest, where extinctions attributable to glacial cycles have been minimized by altitudinal migrations of communities. Preserve design in the face of such complexity is at present difficult or impossible (Whitcomb 1986). Rather, it is reasonable to hope that the bulk of the semiarid lands will be forever held in public ownership and managed for the common good, balancing resource needs with responsible management of biological and historical resources.

Biotic heritage.

A compelling case for conservation of Sand Hills grasslands can be made of the basis of biotic conservation. Because the Sand Hills are the largest sand dune area in the Western hemisphere and are one of the largest stabilized dune areas in the world (Bleed and Flowerday 1989), they are globally significant as a refugium for all of the plant and invertebrate species — whether or not their biologies are currently known — that evolved with the sand prairies of the Pleistocene and Holocene. Also, because the Sand Hills are the last prairie, they are of significance for many prairie animal or plant species that have vanished from, or are threatened or endangered in, prairie formations elsewhere.

The conservation significance of the Sand Hills has not gone completely unnoticed. Three national wildlife refuges have been established in the region; Valentine (28,942 ha), Crescent Lake (18,616 ha), and Fort Niobrara (7,739 ha). Also, the Nature Conservancy has acquired two preserves; the Niobrara Valley Preserve (21,853 ha) (Harrison 1980) and Arapaho Prairie (780 ha). However, given the relatively low carrying capacity of Sand Hills soils, the large acreages in these preserves are deceptive. The carrying capacity of dry Sand Hills prairie, with its thin topsoil and easily erodible soils, may be no more than a tenth of that of richer soils of, for example, eastern deciduous forest.

The small size of the Sand Hills prairie preserves seems anomalous when contrasted with its planted forests (Hunt 1965, Schmidt 1986). These units, established as experiments in type conversion of prairie to forest, occupy more than 81,000 ha. By this measure, more effort has been made to establish "reserves" that destroy prairie by replacing it with an artificial fire- and drought-sensitive formation than to preserve the native vegetational communities.

Important though they may be, the existing prairie reserves are not large enough to be self-sufficient; they are dependent on good management of surrounding range. As a result, their value would be fatally compromised if the Sand Hills around them were to be diverted to nongrassland uses. But today these grasslands stand intact. Guarantors, in a sense, of the preserves. Together, public and private lands function as a complete prairie ecosystem, not a mere remnant of one. The long-billed curlews, avocets, and phalaropes that we see in the refuges are in fact members of regional populations whose long-term existence requires not only the refuges but the privately owned grasslands that surround them.

Landscape heritage.

> "The Sand Hills are beautiful today, soft and green and dotted with flowers. . . . You feel that you are not trespassing when you stroll over the hills or lie at length on the sand, watching the shadows of the clouds drift over the dimpled hills."
>
> Joe Wing, Breeders Gazette, July, 1904

There are various fundamental criteria by which a society deserves to be judged. One of these is the degree of respect that it accords to its natural heritage. As rich and deserving as is the case for conservation of the Sand Hills on biotic grounds, unquestionably the greatest case lies in their landscape itself.

In the early years of park and forest planning in the United States, there was a clear appreciation of the value of bigness. In his tenure as President, Theodore Roosevelt ensured the sequestering of 61 million ha of public domain into the National Forest System. As exploitative as the free enterprise system was of the environment, means were found to create parks of the size of Yellowstone (about 900,000 ha), Yosemite (about 300,000 ha), and Grand Canyon (about 500,000 ha). There can be no question, in contemplating the diverse natural features of these parks, that they are the work of an ambitious nation that placed great value in its finest and unique natural features. But scenic wonders notwithstanding, the very size of these parks may be their most important characteristic.

The success of such parks could never have been achieved had they been niggardly in inception. Had the park process preserved the equivalent of Yellowstone Park in pieces (a geyser here, a hot spring there, a montane lake here, and a waterfall there) the cumulative impact of the separate pieces would not add up to a scintilla of the Yellowstone experience enjoyed by today's park visitors. Or imagine preservation of a "representative section" of the Grand Canyon.

In what we choose to conserve, we make an important statement about space. From the time of European settlement of the New World, possibility has been an open-ended process, and it has been symbolized in an important way in the relationship of Americans with unoccupied land. In a great nation, there is a national need for vastness.

Unfortunately, we have been grossly negligent in our planning for prairie space. Of the millions of km^2 of Pre-Columbian tallgrass and transitional prairie (approximately 550,000 km^2 exclusive of the Nebraska Sand Hills) and Oak savanna/deciduous forest-prairie mosaic (about 460,000 km^2), none has been saved in National Park or National Grassland, and essentially none in National Forest. The neglect of prairie grassland in our national aspiration for space represents a glaring and unacceptable omission. The national need for prairie space is supplied today by the private, not the public sector, in the Nebraska Sand Hills.

CONCLUSIONS

So the Nebraska Sand Hills Prairie today, in the vast majority (90%) of grassland that remains unplowed (Miller 1989), retains its character as native grassland. Preservation of the region has been achieved not through the park process, but as a result of natural economic forces. As reforestation of the Sand Hills was once a dream (Hunt 1965), so the concept of intensive agriculture has more recently proved again to be unsustainable, even in the short term. The Conservation Reserve Program is the most recent vehicle by which incentives for grassland maintenance are being reinforced. In the Sand Hills region, maintenance of native grassland has proven to be the best economic alternative.

I argue that Sand Hills landowners have contributed to the nation a more-or-less unrecognized public good. These landowners are good stewards of the land not only because it is in their economic interest but also because they know the land and its limitations (Stubbendieck 1989). They care for the land as no casual visitor or short-term manager could (Madson 1978). In so doing, they have regularly performed many of the vital functions of the park process; they have maintained, and are continuing to maintain, an entire vegetational region in an essentially pre-Columbian condition. It is not clear that this function has been recognized even in verbal terms, let alone in the structuring of economic incentives.

In the Sand Hills, history strongly suggests that optimal long-term public and private land use may be one and the same. Is it not possible that means can be found, by adjustments in public or private policy, to encourage this historic silent partnership between wise land managers and a nation made richer by the treasure that they have preserved? It is my hope that the future may see a new direction in conservation, one that seeks specific means to stabilize desirable land use patterns by encouraging wise private stewardship. Such an approach would pay rich dividends in the Nebraska Sand Hills.

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LITERATURE CITED

Ahlbrandt, T.S. 1973. Sand dunes, geomorphology and geology, Killpecker Creek Area, Northern Sweetwater County, Wyoming. Doctor of Philosophy Thesis, University of Wyoming, Laramie.

Ahlbrandt, T.S., and S.G. Fryberger. 1980. Eolian deposits in the Nebraska Sand Hills. United States Geological Survey Professional Paper 1120A:1-24.

Ahlbrandt, T.S, J.B. Swinehart, and D.G. Maroney. 1983. The dynamic Holocene dune fields of the Great Plains and Rocky Mountain basins, USA. Pages 379-406. *In* M.E. Brookfield and T.S. Ahlbrandt (eds.). Eolian sediments and processes, developments in sedimentology, Volume 38. Elsevier Science Publishers, Amsterdam, The Netherlands.

American Ornithologists' Union. 1983. Checklist of North American birds. 6th Edition.

Barnes, P.W. 1980. Water relations and distributions of several dominant grasses in a Nebraska Sand Hills Prairie. Master of Science Thesis. University of Nebraska, Lincoln.

Barnes, P.W., and A.T. Harrison. 1982. Species distribution and community organization in a Nebraska Sand Hills prairie as influenced by plant/soil water relationships. Oecologia 52:192-201.

Barnes, P.W., and S.P. Heinisch. 1984. Vegetation patterns in relation to topography and edaphic variation in Nebraska Sand Hills prairie. Prairie Naturalist 16:145-158.

Barry, R.G. 1983. Climatic environment of the Great Plains, past and present. Transactions of the Nebraska Academy of Sciences 11:45-55.

Bentall, R. 1989. Streams. Pages 93-114. *In* A. Bleed and C. Flowerday (eds.). An atlas of the Sand Hills. University of Nebraska Conservation and Survey Division Resource Atlas Number 5.

Bleed, A. 1989. Groundwater. Pages 67-92. *In* A.Bleed and C. Flowerday (eds.). An atlas of the Sand Hills. University of Nebraska Conservation and Survey Division Resource Atlas Number 5.

Bleed, A., and C. Flowerday (eds.). 1989. An atlas of the Sand Hills. University of Nebraska Conservation and Survey Division Resource Atlas Number 5.

Bleed, A., and M. Ginsberg. 1989. Lakes and wetlands. Pages 115-122. *In* A. Bleed and C. Flowerday (eds.). An atlas of the Sand Hills. University of Nebraska Conservation and Survey Division Resource Atlas Number 5.

Bliss, Q.P. and S. Schainost. 1973. Niobrara River stream inventory report. Nebraska Game and Parks Commission, Lincoln.

Bragg, T.B. 1978. Effects of burning, cattle grazing and topography on vegetation of the choppy sands range site in the Nebraska Sand Hills Prairie. Pages 248-253. *In* D.N. Hyder (ed.). Proceedings of the First International Rangeland Congress, Denver.

Bradbury, J.P. 1980. Late Quaternary vegetation history of the Central Great Plains and its relationship to eolian processes in the Nebraska Sand Hills. United States Geological Survey Professional Paper 1120C:25-36.

Brinegar, R.E., and F.D. Keim. 1942. The relations of vegetative composition and cattle grazing on Nebraska range land. University of Nebraska Agricultural Experiment Station Research Bulletin 123.

Burzlaff, D.F. 1962. A soil and vegetation inventory and analysis of three Nebraska Sand Hills range sites. University of Nebraska Agricultural Experiment Station Research Bulletin 206.

Dahlman, J. 1927. Recollections of cowboy life in western Nebraska. Nebraska History Magazine 10:335-339.

Fredlund, G.G., and P.J. Jaumann. 1987. Late Quaternary paleological and paleobotanical records from the central Great Plains. Pages 167-178. *In* W.C. Johnson (ed.). Quaternary environments of Kansas. Kansas Geological Survey Guidebook Series 5.

Freeman, P. 1989a. Amphibians and reptiles. Pages 157-160. *In* A. Bleed and C. Flowerday (eds.). An atlas of the Sand Hills. University of Nebraska Conservation and Survey Division Resource Atlas Number 5.

Freeman, P. 1989b. Mammals. Pages 181-188. *In* A. Bleed and C. Flowerday (eds.). An atlas of the Sand Hills. University of Nebraska Conservation and Survey Division Resource Atlas Number 5.

Frolik, A.L., and W.O. Shepherd. 1940. Vegetative composition and grazing capacity of a typical area of Nebraska Sand Hill rangeland. University of Nebraska Agricultural Experiment Station Research Bulletin 117.

Great Plains Flora Association. 1986. Flora of the Great Plains. University Press of Kansas, Lawrence.

Hagen, A.F. 1970. An annotated list of grasshoppers (Orthoptera, Acrididae) from the eleven Panhandle counties of Nebraska. Nebraska Agricultural Experiment Station Research Bulletin 238.

Harrison, A.T. 1980. The Niobrara Valley Preserve: Its biogeographical importance and description of its biotic communities. Report to the Nature Conservancy. Minneapolis.

Heinisch, S.P. 1981. Water allocation and rooting morphology of two *Bouteloua* species in relation to their distribution patterns in the Nebraska Sand Hills. Master of Science Thesis. University of Nebraska, Lincoln.

Holen, S.R. 1989. Anthropology: The native american occupation of the Sand Hills. Pages 189-205. *In* A. Bleed and C. Flowerday (eds.). An atlas of the Sand Hills. University of Nebraska Conservation and Survey Division Resource Atlas Number 5.

Hrabik, R.A. 1989. Fishes. Pages 143-156. *In* A. Bleed and C. Flowerday (eds.). An atlas of the Sand Hills. University of Nebraska Conservation and Survey Division Resource Atlas Number 5.

Hunt, J.C. 1965. The forest than men made. Parts I and II. American Forests.

Jones, J.K., Jr. 1964. Distribution and taxonomy of the mammals of Nebraska. University of Kansas Publications of the Museum of Natural History 16:1-356.

Kaul, R. 1989. Plants. Pages 127-142. *In* A. Bleed and C. Flowerday (eds.). An atlas of the Sand Hills. University of Nebraska Conservation and Survey Division Resource Atlas Number 5.

Kaul, R.B., and S.B. Rolfsmaier. 1987. The characteristics and phytogeography of the flora of Nine-Mile Prairie, a western tallgrass prairie in Nebraska. Transactions of the Nebraska Academy of Sciences. XV:23-35.

Kaul, R.B., G.E. Kantak, and S.P. Churchill. 1988. The Niobrara River Valley, a postglacial migration corridor and refugium of forest plants and animals in the grasslands of central North America. Botanical Review 54:44-81.

Keech, C.F., and R. Bentall. 1978. Dunes on the plains, the Sand Hills region of Nebraska. University of Nebraska Conservation and Survey Division Resource Report Number 4.

Küchler, A.W. 1964. Potential natural vegetation of the conterminous United States. Special Publications, American Geographical Society, Washington, D.C.

Küchler, A.W. 1985. Potential natural vegetation. National Atlas of the United States of America. Department of the Interior, U.S. Geological Survey, Reston, Virginia.

Labedz, T.E. 1989. Birds. Pages 161-180. *In* A. Bleed and C. Flowerday (eds.). An atlas of the Sand Hills. University of Nebraska Conservation and Survey Division Resource Atlas Number 5.

Larson, T.A. 1965. History of Wyoming. University of Nebraska Press, Lincoln.

Lewis, D.T. 1989. Origin of Sand Hills soils. Page 57. *In* A. Bleed and C. Flowerday (eds.). An atlas of the Sand Hills. University of Nebraska Conservation and Survey Division Resource Atlas Number 5.

Lowry, J.E., and H.D. Blocker. 1987. Two new species of *Flexamia* from the Nebraska Sand Hills (Homoptera: Cicadellidae:Deltocephalinae). Proceed-ings of the Entomological Society of Washington 89:57-60.

Lugn, A.L. 1935. The Pleistocene geology of Nebraska. University of Nebraska Conservation and Survey Division Bulletin Number 10, Second Series.

Lunt, S.R. 1987. North American mosquito species with geographical distribution limits in Nebraska. Nebraska Academy of Sciences Annual Meeting 97:18-19.

MacArthur, R., and E.O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey.

Madson, J. 1978. Land of long sunsets. National Geographic 154:493-517.

May, D.W., and S.R. Holen. 1985. A chronology of Holocene erosion and sedimentation in the South Loup Valley, Nebraska. Geological Perspectives 56:8-12.

Miller, S.M. 1989. Land development and use. Pages 207-226. *In* A. Bleed and C. Flowerday (eds.). An atlas of the Sand Hills. University of Nebraska Conservation and Survey Division Resource Atlas Number 5.

Molhoff, W.J. 1985. The Nebraska breeding bird atlas project. Nebraska Academy of Sciences Annual Meeting 94:23.

Muhs, D. 1985. Age and paleoclimatic significance of Holocene sand dunes in northeastern Colorado. Annals of the Association of American Geographers 75:566-582.

Pool, R.J. 1914. A study of the vegetation of the Sand Hills of Nebraska. Minnesota Botanical Studies 4:189-312.

Pound, R., and F.E. Clements. 1900. The phytogeography of Nebraska. General survey. University of Nebraska Botanical Survey, Lincoln.

Ramaley, F. 1939. Sand Hill vegetation of northeastern Colorado. Ecological Monographs 9:1-51.

Raup, H.Y., and G.W. Argus. 1982. The Lake Athabasca sand dunes of northern Saskatchewan and Alberta, Canada. 1. The land and vegetation. Canadian Museum of Natural Sciences Publications in Botany 12:1-96.

Richards, B., Jr. 1980. Bartlett Richards: Nebraska Sand Hills cattleman. Nebraska State Historical Society, Lincoln.

Schmidt, T.L. 1986. Forestland resources of the Nebraska Sand Hills. *In* T.D. Wardle (ed.). University of Nebraska and Nebraska Forest Service, Lincoln.

Smith, H.T.U. 1965. Dune morphology and chronology in central and western Nebraska. Journal of Geology 73:557-578.

Soule, M. (ed.). 1986. Conservation biology. Sinauer Associates Incorporated, Sunderland, Massachusetts.

Steinauer, E.A., and T.B. Bragg. 1987. Ponderosa pine (*Pinus ponderosa*) invasion of the Nebraska Sand Hills Prairie. American Midland Naturalist 118:358-365.

Stubbendieck, J. 1989. Range management. Pages 222-233. *In* A. Bleed and C. Flowerday (eds.). An atlas of the Sand Hills. University of Nebraska Conservation and Survey Division Resource Atlas Number 5.

Sutherland, D.M. 1984. Vegetative key to grasses of the sand hills region of Nebraska. Transactions of the Nebraska Academy of Sciences 12:23-60.

Sylvester, D.D. 1957. Response of Sand Hill vegetation to deferred grazing. Journal of Range Management 10:255-292.

Swinehart, J.B. 1989. Wind-blown deposits. Pages 43-56. *In* A. Bleed and C. Flowerday (eds.). An atlas of the Sand Hills. University of Nebraska Conservation and Survey Division Resource Atlas Number 5.

Swinehart, J.B., and R.F. Diffendal, Jr. 1989. Geology of predune strata. Pages 29-42. *In* A. Bleed and C. Flowerday (eds.). An atlas of the Sand Hills. University of Nebraska Conservation and Survey Division Resource Atlas Number 5.

Tolstead, W.L. 1942. Vegetation of the northern part of Cherry County, Nebraska. Ecological Monographs 12:255-292.

Tucker, S.J. 1942. Indian villages of the Illinois Country. Scientific Papers, Atlas, Volume 2, Part 1. Illinois State Museum, Springfield.

Voorhies, M.R., and R.G. Cormer. 1985. Small mammals with boreal affinities in Late Pleistocene (Rancholabrean) deposits of Eastern and Central Nebraska. Pages 125-141. *In* W. Dort, Jr. (ed.). TER-QUA Symposium Series: Institute for Tertiary-Quaternary Studies. Nebraska Academy of Sciences.

Weaver, J.E. 1965. Native vegetation of Nebraska. University of Nebraska Press, Lincoln.

Wells, P.V. 1983. Late Quaternary vegetation of the Great Plains. Transactions of the Nebraska Academy of Sciences XI:83-89.

Whitcomb, R.F. 1986. North American forests and grasslands: Biotic conservation. Pages 163-176. *In* D.A. Saunders, G.W. Arnold, A.A. Burbridge, and A.J.M. Hopkins (eds.). Nature conservation: The role of remnants of native vegetation. Surrey Beatty and Sons, Sydney.

Whitcomb, R.F., and A.L. Hicks. 1988. Genus *Flexamia:* New species, phylogeny, and ecology. Great Basin Naturalist Memoirs 12:224-323.

Whitcomb, R.F., A.L. Hicks, D.E. Lynn, K. Allred, and H.D. Blocker. 1987. Geographic variation in host relationships of leafhoppers (Homoptera:Cicadellidae) in North American grasslands. Pages 293-325. *In* M.R. Wilson and L.R. Nault (eds.). Proceedings of the 2nd International Workshop on Leafhoppers and Planthoppers of Economic Importance. Commonwealth Institute of Entomology, London.

Whitcomb, R.F., J. Kramer, M.E. Coan, and A.L. Hicks. 1986. Ecology and evolution of leafhopper-grass relationships in North American prairies, savanna, and ecotonal biomes. Current Topics in Vector Research 4:125-182.

Whitcomb, R.F., A.L. Hicks, H.D. Blocker, and J.P. Kramer. 1988. Host specificity: a major mechanism enhancing insect diversity in grasslands. Paper 11.06 *In* A. Davis and G. Stanford (eds.). Proceedings of the Tenth North American Prairie Conference, Denton, Texas.

Wilhite, D.A., and K.G. Hubbard. 1989. Climate. Pages 17-28. *In* A. Bleed and C. Flowerday (eds.). An atlas of the Sand Hills. University of Nebraska Conservation and Survey Division Resource Atlas Number

Wilson, I.G. 1973. Ergs. Sedimentary Geology 10:77-106.

Wolfe, C.W. 1973. Effects of fire on a Sand Hills grassland environment. Proceedings of the Tall Timbers Fire Ecology Conference 12:241-255.

Wolfe, C.W. 1984. Physical characteristics of the Sand Hills: Wetlands, fisheries and wildlife. Pages 54-61. *In* The Sand Hills of Nebraska - Yesterday, Today, and Tomorrow. Proceedings of the University of Nebraska Water Resources Seminar Series.