The Niobrara River Valley, a Postglacial Migration Corridor and Refugium of Forest Plants and Animals in the Grasslands of Central North America

Author(s): Robert B. Kaul, Gail E. Kantak, Steven P. Churchill

Reviewed work(s):
Source: *Botanical Review*, Vol. 54, No. 1 (Jan. - Mar., 1988), pp. 44-81
Published by: Springer on behalf of New York Botanical Garden Press
Stable URL: http://www.jstor.org/stable/4354105
Accessed: 17/04/2012 14:28

THE BOTANICAL REVIEW

VOL. 54 JANUARY–MARCH, 1988 NO. 1

The Niobrara River Valley, a Postglacial Migration Corridor and Refugium of Forest Plants and Animals in the Grasslands of Central North America

ROBERT B. KAUL
School of Biological Sciences
University of Nebraska
Lincoln, Nebraska 68588-0118, U.S.A.

GAIL E. KANTAK
Department of Biology
Saginaw Valley State University
University Center, Michigan 48710-0001, U.S.A.

STEVEN P. CHURCHILL
The New York Botanical Garden
Bronx, New York 10458-5126, U.S.A.

Copies of this issue [54(1)] may be purchased from the Scientific Publications Department, The New York Botanical Garden, Bronx, NY 10458-5126 USA. Please inquire as to prices.

I. Abstract

The Niobrara River Valley of northern Nebraska contains numerous bryophyte, vascular plant, and animal species more typical of forests far to the east, north, and west than to other forests in the grasslands that surround the Valley. Some species are probably relicts of cooler glacial and early postglacial times, when much of what is now grassland was covered by boreal and cool-temperate forests. Others entered the Valley from the east in postglacial times, and some entered from the west as the climate became semi-arid. There is a steep decline in total number of vascular plant species from the mouth of the Missouri River up through the Niobrara Valley, suggesting an environmental gradient and differential migration and extirpation of species at various times since the Pleistocene.

Abstraktum

Das Niobrara Flusstal nördliches Nebraska enthält viele Laubmoose, Gefässpflanzen, und Tiere Arten, die mehr typisch für ostliche, nördliche, und westliche Wälder sind, als andere Wälder auf der umgebenden Wiesen. Manche Arten sind vielleicht Hinterbliebene von kühleren verglet-scherten und frühe nach vergletscheten Zeiten. Andere eintraten ins Tal von Osten während nachvergletscherten Zeiten, und manche eintraten von Westen, während das Klima halb dürr wurde. Es gibt eine steile Neige in die Summe Gefässpflanzenarten von der Mündung des Missouri Fluss bis dem Niobrara Tal, die eine Umgebungsteigung und Unterscheidungswanderung und Ausrottung Arten um verschiedene Zeiten seitdem Pleistozän vorschlagen.

Resumen

El Valle del Rio Niobrara, en el norte de Nebraska, contiene un gran número de especies de briofitas, plantas vasculares, y animales que son tipicos de los bosques del este, norte, y oeste de Estado Unidos que de las praderas que rodean al Valle. Alqunas de estas son probablemente vestigios de peridos frios de glaciación y tempranos eventos pos-glaciales, cuando gran parte de lo que es hoy pradera estaba cubierto por bosques boreales y templados. Otras especies entraron al Valle del este en el periodo pos-glacial, y otras entraron del oeste segun el clima se torno semiárido. Hay un alto declive en el número total de plantas vasculares desde

le boca del Rio Missouri atravesando el Valle Niobrara, sugiriendo un gradiente ambiental, migración diferencial y extirpación de especies en varias épocas desde el Pleistoceno.

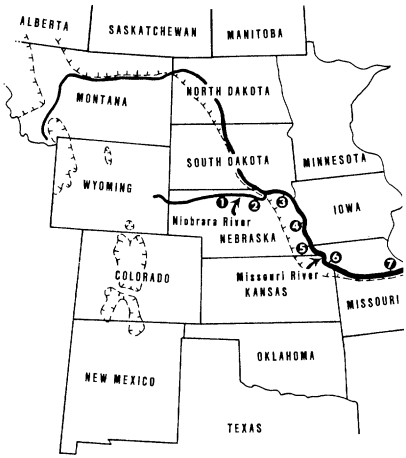
II. Introduction

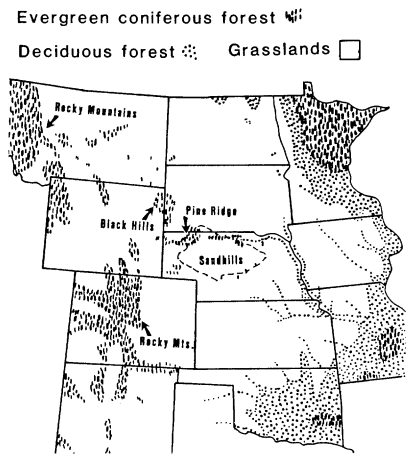
The grasslands of central North America formed during and after the retreat of the Pleistocene continental and alpine glaciers (Fig. 1), and therefore are young. They extend from Alberta to Mexico, east of the Rocky Mountains, and reach eastward to the borders of continuous deciduous forest near and beyond the Mississippi River (Fig. 2).

As the Pleistocene drew to a close about 12,000–10,000 years B.P., the ice retreated to the northeast, and the periglacial boreal forest and tundra yielded to a pine-spruce/steppe mosaic in what is now the central plains, and to deciduous forest in the eastern plains (Bradbury, 1980; Delcourt & Delcourt, 1980; Ritchie, 1976; Wright, 1976, 1981). These were then replaced by the modern prairie. The prairie-forest ecotone moved eastward from the lower Niobrara Valley and Sandhills areas of Nebraska (Figs. 1, 2, 3) 11,000–9000 years B.P. (Bernabo & Webb, 1977). In the west, the retreat of the massive alpine glaciers was probably paralleled by a retreat of the displaced coniferous mountain forest from what are now the western parts of the mixed-grass and short-grass prairies. When these forests retreated, individuals of some species remained in suitable habitats within what became grasslands, and forests became established in newly deglaciated places such as the Missouri River Valley (Fig. 2).

The Quaternary vegetation history of the forests of eastern North America is becoming better-known because of extensive palynological research, but there is less such information about the grasslands. It is now possible to map the prehistoric movements of many species, especially trees (e.g., Bernabo & Webb, 1977; Davis, 1983) and grasses (Brown & Gersmehl, 1985), and of entire vegetation zones (e.g., Delcourt & Delcourt, 1980). The evidence for the details of movements of forests and prairies in what is now the mid-continental grassland has been reviewed over a 65 year period by Axelrod (1985), Axelrod and Raven (1985), Davis (1983), Gleason (1922), Grimm (1983), Grüger (1973), McAndrews (1966), Ritchie (1976), Schaffner (1926), Sears (1935), Transeau (1935), Watts and Wright (1966), Wells (1968, 1970, 1983), Wright (1968, 1971, 1981), and Wright, Almendinger, and Grüger (1985), among others.

The movements of vegetation types were probably caused, accompanied, or followed by distributional changes in animal species, especially those with narrow ecological tolerances. The geographic displacement within and reinvasion of the Great Plains by mammals with respect to climate and movement of deciduous and boreal forest ecotones were





1 MAXIMUM GLACIATION 2 MODERN VEGETATION

Figs. 1, 2. Glaciation-political and vegetation maps of central North America. **1.** Glaciation and political map showing states, the Niobrara and Missouri rivers with floristic sampling stations numbered, and combined Pleistocene glacial maxima. **2.** Modern vegetation, with significant physiographic features identified.

reviewed by Hibbard (1970) and Hoffman and Jones (1970). Fish distributional changes in relation to a climatic warming trend since the Pleistocene were discussed by Cross (1970), while Mengel (1970) discussed avian isolation and hybridization in the Great Plains with respect to those Pleistocene and early Holocene events.

In the past decade the modern distributions of the plants and animals of these grasslands and their included forests have become well-known because of extensive field and museum research. Thus, it is now possible to discern modern biogeographic patterns that might be useful in interpreting past biotic relationships. However, it is evident that not all species and communities retreated and advanced at the same rate in glacial and post-glacial times, and so modern associations of species are not necessarily like those of the past (Davis, 1983). The species in deglaciated areas are obviously immigrants, probably from more than one Pleistocene refugium. The recolonization of glaciated and periglacial areas was followed by successional and climatically-induced changes, and the modern associations therefore are products of biotic and abiotic events. Some species, however, are extremely disjunct and could be relicts *in situ* of glacial and early postglacial times, particularly species of low dispersability or of very restricted environments.

Here we consider the modern distributions of plant species that are possibly relicts of cool, mesic, postglacial forests in the Niobrara River

Valley of Nebraska. Also included are some that invaded the Valley from the east following deglaciation, and from the west when the Holocene climate became more arid. Most are species of non-riparian forests, but we include some grassland, aquatic, and riparian forest species if they are currently restricted to the Valley as well. Animal distributions that parallel those of plants are also presented. All are native species whose modern ranges in the central grasslands are essentially restricted to the Niobrara and Missouri River valleys, but some occur in the Pine Ridge and Black Hills, and some range westward into the grasslands for a short distance up other rivers of the Mississippi drainage. Their presence in the Niobrara Valley is well-documented in museum collections; many of the specimens are vouchers from our extensive field work. We have listed only those species for which we have evidence as specimens or, for breeding animals, reliable reports. Undoubtedly others will be added to the lists as further information becomes available. We have mapped the distributions of representative species, subspecies, varieties, and hybrids to illustrate the various modern distributional patterns that we discuss.

Most of the plant species were first collected in the Valley and adjacent areas in the late nineteenth century, and all are known to be there yet. Many others, especially bryophytes, have been discovered in recent years, and the flora of the Valley is now well known.

The distributions of all vascular plant species in the central grasslands were mapped in 1977 (Great Plains Flora Association, 1977); numerous additions and corrections have been made since then and are incorporated here. Detailed range information for the Valley, the Great Plains, and nearby areas is provided by Beal and Monson (1954), Brooks and Hauser (1978), Cooperrider (1958), Dorn and Dorn (1972), Freeman and Churchill (1983), Great Plains Flora Association (1977, 1986), Kaul, Challaiah, and Keeler (1983), Lakela (1965), Larson (1979), Little (1971, 1976, 1977), Melhus (1936), Morley (1969), Moss (1983), Petrik-Ott (1979), Rolfsmeier, Kaul, and Sutherland (1987), Steyermark (1963), Sutherland and Kaul (1986), Tryon (1980), Van Bruggen (1985), and by recent intensive field work. Nomenclature for vascular plants follows the "Flora of the Great Plains" (Gt. Pl. Flora Assoc., 1986) and Wagner and Wagner (1986). Distributional information about mosses is based on Churchill (1982, 1985a, 1985b, and unpubl.), Gier (1955), and van der Linden et al. (1985), and nomenclature follows Churchill (1982, 1985a, 1985b).

Faunal distributional information has been extracted from these sources: *butterflies*—Ferris and Brown (1981), Johnson (1972), Johnson and Balogh (1977), Miller and Brown (1981), Opler and Krizek (1984), Perkins and Perkins (1967), Rosche (1986), Scott (1986); *fish*—Bliss and Schainost (1973), Hesse et al. (1982), Lee et al. (1980), Madsen (1985), Morris, Morris, and Witt (1972); *reptiles*—Catalogue of American Amphibians

and Reptiles (1962 et seq.), Lynch (1985), Stebbins (1985); *birds*—American Ornithologists' Union (1983), Brogie and Mossman (1983), Johnsgard (1978, 1979a, 1979b), Mossman and Brogie (1983), Sibley and Short (1959, 1964), Short (1961, 1965); *mammals*—Hall (1981), Jones (1964), Jones et al. (1983), Wiley (1980); *Niobrara vertebrates*—Kantak (1983).

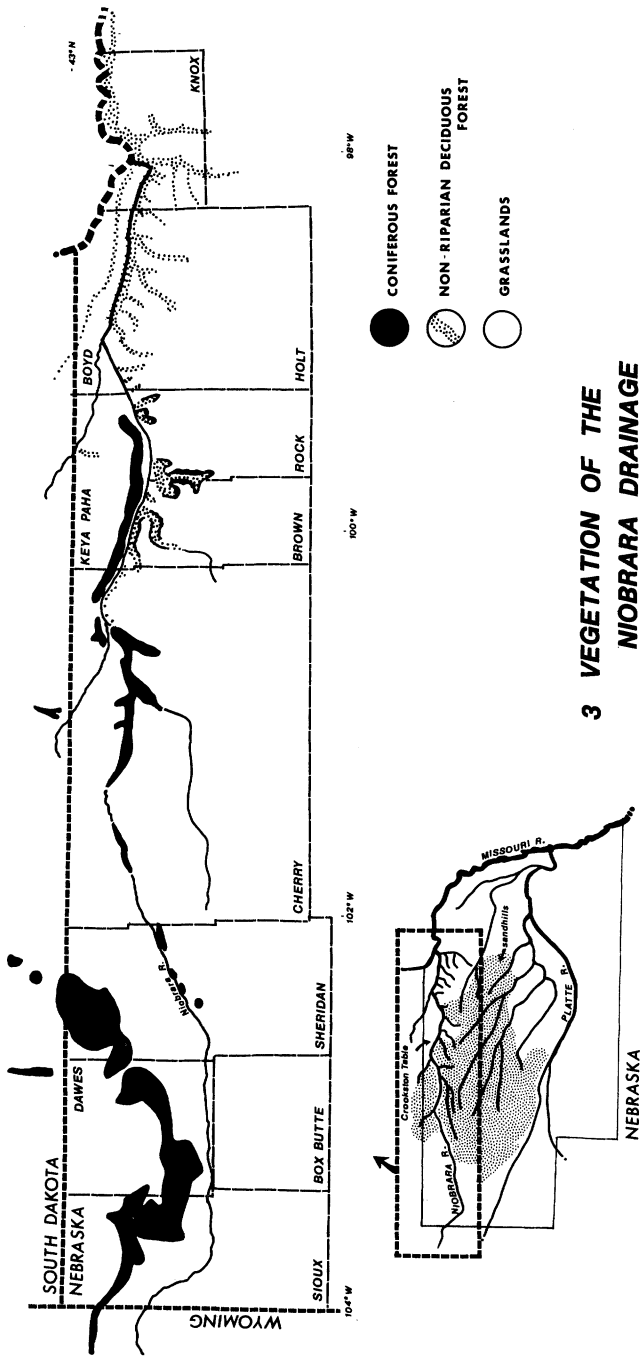
III. The Niobrara Valley

For our purposes, we define the Valley as the floor and walls of the deep, often narrow canyons cut by the Niobrara River and all its tributaries. We exclude the extensive grasslands between those canyons, even though they are within the Niobrara drainage basin, but we have included a few species that are restricted, in this part of their range, to the transition between the Valley and its adjacent grasslands. Furthermore, there are areas of prairie on north- and south-facing steep slopes of the Valley walls.

The Valley has long been known for the presence of many forest plants, animals, and communities not typical of other forests that penetrate the grasslands. Bessey (1887) first described Long Pine Canyon, a short tributary of the Niobrara River Valley on the border of Brown and Rock counties (Fig. 3), as "a meeting place for two floras," referring to the mixture of eastern and western plants there. The Niobrara Valley and the Pine Ridge are the only places across the modern grasslands where non-riparian elements of the Rocky Mountain, boreal, and eastern deciduous forests meet (Figs. 2, 3) (Bessey, 1887; Kaul, 1975; Nixon, 1967; Pound & Clements, 1900; Tolstead, 1942a, 1942b, 1947). Some species of eastern plants found in the Valley also extend to the Pine Ridge and Black Hills, both north of the upper reaches of the Valley (Fig. 2), and a few appear on the east slope of the Rocky Mountains (Figs. 6, 7). The co-occurrence in the Pine Ridge of boreal, Rocky Mountain, southeastern, and southwestern plant species has been reviewed by Nixon (1967).

The Niobrara River originates at about 1500 m elevation in Niobrara County, eastern Wyoming, and flows eastward through unglaciated terrain for about 480 km to its junction with the Missouri River in Knox County, Nebraska, at about 425 m elevation (Fig. 3). The river is bounded by approximately 99–105°W long., and 42°30′–43°N lat. Its basin extends 480 km along its east-west axis, and 97 km along its longest north-south axis, encompassing about 30,768 km^2, more than 15% of the area of Nebraska (Nebraska Natural Resources Commission, 1976). The Valley is about 140 m deep at its deepest, and most of that depth was cut by the close of Pleistocene glaciation.

The tableland along the upper reaches of the Niobrara River (in Niobrara County, Wyoming, and Sioux, Dawes, Box Butte, and Sheridan counties, Nebraska) is bordered on the north by the forested Pine Ridge



3 VEGETATION OF THE NIOBRARA DRAINAGE

and on the southeast by the vast, grassy Sandhills (Figs. 2, 3). Shallow drains, swales, and small isolated buttes are characteristic of the tableland. Here the tributaries are small, intermittent streams, in contrast to those in the central and eastern part of the basin, where they are larger and perennial. Unique geologic and hydrologic conditions exist in the central counties (Cherry, Brown, Rock), where the Sandhills to the south absorb vast quantities of rainwater that accumulate in the dune sands above a buried, impervious stratum. This groundwater emerges on the south wall of the Valley, where the river has cut a deep canyon that exposes the contact of the surface sands with the impervious stratum beneath them. These conditions produce permanently flowing tributaries, often in "springbranch" canyons, as well as numerous springs, seepages, and subirrigated meadows on the south wall of the central Niobrara Valley. That wall is thus not only well-watered, but also shaded and protected from the prevailing southerly winds of the growing season because it faces north (see Tolstead, 1942a, for a cross-sectional diagram of the Valley). It is here that many of the plants typical of mesic northern and eastern woodlands grow. In contrast, the Crookston Table on the north side of the Valley (Fig. 3) has fine, sandy, loamy soils that do not absorb sufficient rainwater to form a water table high enough to maintain numerous springs. Instead, runoff has eroded many deep canyons into the Table. Thus the north wall has no abundant water source, and also is exposed to southerly winds and to the sun, so it is much drier. The modern flora is accordingly very different there, consisting of dry prairie and ponderosa pine (*Pinus ponderosa*) forest, often with juniper (*Juniperus virginiana*), chokecherry (*Prunus virginiana*), and associated understory herbs. Such forests are best developed in Cherry and Keya Paha counties (Fig. 3), but they also occur on the dry crest of the south wall, and barely extend into the adjacent Sandhills, especially in Brown and Rock counties (Fig. 3). East of the central part of the basin the stratigraphy lacks absorbent dune sands and

←

Fig. 3. Vegetation of the Niobrara drainage (after Kaul, 1975), with states and counties named. The extensive coniferous (ponderosa pine) forest of the Pine Ridge is shown in Sioux, Dawes, and Sheridan counties. Its eastward extension on escarpments above the Niobrara River and tributaries is shown for Sheridan, Cherry, Brown, Rock, and Keya Paha counties. In Brown and Rock counties the pine forest occupies the rim of the valleys, but in Keya Paha County it occurs on the south-facing slope. The eastern deciduous, non-riparian forest is shown in the Niobrara Valley and its tributaries from Cherry County eastward into the Missouri River Valley in Knox County. It is mostly confined to protected, spring-fed north-facing slopes and cool, deep, narrow canyons of tributary streams. Riparian forests of cottonwood, willow, elm, and silver maple are extensive on the floodplains of the Missouri and lower Niobrara rivers, but are not shown on this map. The inset shows the relationship of the Niobrara drainage to the Platte River drainage, the sandhills, and the Crookston Table.

an exposed, impermeable stratum, and hence the springbranch canyons and seepages diminish in number from Rock County eastward, although numerous surface streams exist in Holt and Knox counties (Fig. 3).

Like the Niobrara, most of the other rivers in these grasslands flow eastward, eventually to join the Mississippi River (except the Red River of the North, which flows northward to Hudson Bay). Their valleys, however, lack the combination of topographic, edaphic, and hydrologic features that support the distinctive vegetation of the Niobrara Valley. The non-riparian forests along them show a pronounced upstream impoverishment and, in fact, many have only riparian forests (or no forests) in their middle and upper reaches. The non-riparian forests of the escarpments have species mostly not shared by the riparian forests of the nearby floodplains, but in the latter a few western species extend eastward, and some eastern species extend westward. The Sandhills are mostly drained by tributaries of the Platte River, but a small part of them is drained by the Niobrara system (Fig. 3). The Platte and its tributaries occupy broad, shallow, sandy valleys that are unsuitable for many species of the Niobrara Valley.

IV. Past and Present Climates

The interior continental location of the Niobrara Valley produces a highly seasonal climate with cold winters and hot summers (climatic data from Lawson et al., 1977). The mean annual number of days with freezing temperatures ranges from more than 170 in the west to about 160 in the east, at the confluence of the Niobrara and Missouri rivers in Knox County, Nebraska (Fig. 3). Occasional winter maxima of 26°C and minima of −41°C have been recorded. The mean dates of last spring and first fall frosts range, respectively, from 5 May and 5 October in the east, to 20 May and 20 September in the west. Summer temperatures are ordinarily high, with an average of 32–46 days reaching 32°C, and maxima of 40°C or more are common and often accompanied by strong southerly winds. July is the hottest month, but temperatures can reach 40°C from late May through mid-September.

Average annual precipitation ranges from about 45 cm in the upper reaches of the Valley to about 60 cm at the river's mouth. December and January are the driest months, with 0.5 cm or less throughout the Valley; some winters yield heavy snow, but others have little or none. May and June are the wettest months, with 3.5 to 4.5 cm in the upper and lower reaches, respectively. Intense thunderstorms yielding heavy rain are often frequent in summer, as are late-afternoon showers, but summer droughts are not rare.

The glacial Pleistocene and many Holocene summers in central North America were certainly cooler than modern ones, and climatic fluctuations

in the Holocene (beginning about 12,000 B.P.) had major effects on the postglacial vegetation. The mid-Holocene Hypsithermal Interval (8000–4000 B.P.), with its increasing aridity, caused the prairie-forest boundary to move eastward and the coniferous and mixed coniferous-hardwood forests to move northward. The general cooling that followed the Hypsithermal Interval caused some southward movement of the forests and westward movement of the prairie-forest border, but neither reached the Niobrara Valley again. These events are detailed by Axelrod (1985), Bernabo and Webb (1977), Delcourt and Delcourt (1980), and Wright (1968, 1977).

The modern rigorous climate, with its periodic droughts, has made the adjacent grasslands prone to fires, and is thus one factor restricting the forests to protected escarpments (Gleason, 1913; Wells, 1968, 1970). It is easily shown that forests will survive and spread into at least the eastern part of the central grasslands when fire is suppressed, as they are now doing in Kansas (Bragg & Hulbert, 1976) and the Nebraska Sandhills (Steinauer & Bragg, in press). Furthermore, numerous recently-introduced plant species are well-adapted to the area and reproduce vigorously, but others are seldom or never able to establish seedlings and are not permanent members of the flora.

V. Geographic Affinities of the Biota

For descriptive and analytical purposes, we recognize three groups of species based upon their modern continental ranges relative to the Niobrara Valley: A) species of western affinity with ranges mainly west, southwest, or northwest of the Valley, including Rocky Mountain, Great Basin, and Pacific coastal areas in various combinations (Table I); B) species with main ranges both east and west of the grasslands but which, in the central grasslands, are essentially restricted to the Niobrara Valley (Table II), sometimes occurring also in the Pine Ridge, Black Hills, and grasslands and Canadian forests far to the north of the Valley; C) species with affinity to the east, north, northeast, and southeast, with main ranges mostly in the coniferous evergreen and deciduous forests of eastern North America (Table III). Many other species occur in the Valley and adjacent areas. For example, in one site of 22,000 hectares in the Valley and nearby Sandhills, 521 native species in 104 families are known (Churchill et al., in prep.).

Numerous animal species not listed or discussed here reach distributional limits in Nebraska (see references in Introduction). Those included in this paper are significant in that their range limits are generally in the Niobrara Valley, providing evidence for unique historical or ecological conditions there; all breed in the Valley or, in a few instances, at the edge of the Valley, where it borders the grassland.

A. SPECIES OF WESTERN AFFINITY

1. Plants

Seven species of mosses of western affinity are considered here (Table I); nearly all are associated with xeric habitats, and most can be considered calciphiles. Both *Brachythecium collinum* (Fig. 4)[1] and *Encalypta vulgaris* occur on pine–juniper slopes. On exposed grassland or in open pine–juniper woodland on calcareous escarpments are found *Barbula acuta* var. *bescherellei, Hypnum vaucheri, Jaffueliobryum raui,* and *J. wrightii.* Interestingly, the latter two are also disjunct in the Driftless Area of Iowa and Wisconsin, which suggests an earlier xeric period, possibly prior to the Holocene Hypsithermal. Only *Bryum gemmiparum* is semi-aquatic, occurring on wet calcareous rocks along streams.

Fourteen vascular plant species with main ranges to the west, southwest, or northwest of the Niobrara Valley are shown in Table I and Figures 5 and 6. There is but one tree in this group, *Pinus ponderosa* (Fig. 5); it forms the rather open forests on the south-facing Valley walls and at the tops of the north walls, and is the dominant tree of the Pine Ridge. There is a single shrub, *Ribes setosum,* and one vine, *Clematis ligusticifolia* (Fig. 6). The Rocky Mountain juniper, *Juniperus scopulorum,* occurs in the Pine Ridge, but the common juniper in the Valley is taxonomically closer to *J. virginiana.*

2. Animals

Twenty-eight animal species of western or southwestern affinity are presented in Table I and Figures 9 and 11: 17 butterflies, one fish, four reptiles, five birds, and one mammal.

The butterflies range eastward from their western distributional centers, utilizing primarily the pine-covered escarpments of the Valley, although several also venture into more open habitats. Most species are limited in Nebraska to the western portion of the Niobrara Valley, and some also reach regional distributional limits there. *Erynnis lucilius afranius, Limenitis weidemeyerii oberfoelli, Lycaena rubidus longi,* and *Pontia sisymbrii nordini* are eastern allopatric subspecies of western species (e.g., Fig. 9) (Ferris & Brown, 1981; Johnson & Balogh, 1977; Perkins & Perkins, 1967).

The mountain suckerfish (*Catastomus platyrhynchus*) is a Rocky Mountain species collected from the Niobrara River in 1896 and apparently now extirpated in Nebraska (Madsen, 1985). However, it is presently

[1] Figures 4–12 are grouped at the end of the review for ready comparison of the plant and animal ranges.

found in streams in South Dakota that probably were once part of the Niobrara drainage, but were captured by the White River system of South Dakota (Mayden, 1987).

The reptiles are primarily plains or grassland species and are postglacial immigrants, whereas the birds use a range of habitats (Table I). The western tanager (*Piranga ludoviciana*) nests eastward at least to the Pine Ridge, where a possible hybrid with the eastern scarlet tanager (*Piranga olivaceus*), has been reported (Ford, 1959). The scarlet tanager nests west at least to Cherry County. Similarly, the western and eastern wood pewees, with breeding ranges like those of the tanagers, are suspected to hybridize in the Valley (Short, 1961). The prairie falcon (*Falco mexicanus*) is a western species that has been sighted in the Valley (Mossman & Brogie, 1983), and may be expected to breed there because suitable habitat is present; we have not listed it in Table I because we have no evidence of breeding.

The ranges of many other western species of plants and animals reach into the grasslands on the Pine Ridge escarpments of Nebraska and South Dakota. Only those that occur also in the Niobrara Valley are considered here.

B. SPECIES WITH MAIN RANGES EAST AND WEST OF THE GRASSLANDS, AND USUALLY ALSO TO THE NORTH

1. Plants

Among the nineteen moss species in this category are those of broadly northern, and in part circumboreal, distribution. These are found in mesic and xeric forests. In the drier pine–juniper (sometimes with oak) forests are *Desmatodon heimii, Orthotrichum obtusifolium, Saelania glaucescens* (Fig. 4), and *Tortula mucronifolia.* In the cool, moist, springbranch canyons are *Dicranum muhlenbeckii, Encalypta ciliata, Orthodicranum flagellare, Plagiomnium ellipticum,* and *Thuidium delicatulum.*

Forty vascular plant species, subspecies, or varieties have ranges abutting the grasslands on the east and west, and sometimes also north (Table II; Figs. 6, 8). This group includes two tree species and one hybrid, and four shrubs. At least eight species are circumboreally distributed, with outliers in the grasslands: *Arenaria lateriflora, Botrychium simplex, Campanula rotundifolia, Carex buxbaumii, Equisetum fluviatile, Menyanthes trifoliata, Myosotis laxa,* and *Stellaria longifolia.* The very closely related western *Clematis ligusticifolia* and eastern *C. virginiana* meet in the Valley (Fig. 6).

Some woodland species of eastern-western distribution are shared by the Niobrara Valley and Black Hills, but are otherwise of restricted distribution or absent in the central grasslands: *Adiantum pedatum, Betula*

Table I

Species, subspecies, and varieties of western affinity, reaching eastern limits in the Niobrara Valley

Taxon	Habitat
Mosses	
Barbula acuta	dry grassland
Brachythecium collinum (Fig. 4)	dry woodland
Bryum gemmiparum	moist grassland
Encalypta vulgaris	dry woodland
Hypnum vaucheri	dry grass- and woodland
Jaffueliobryum raui	dry grassland
J. wrightii	dry grassland
Vascular plants	
Astragalus spatulatus, draba milk-vetch	dry grassland
Clematis ligusticifolia, western clematis (Fig. 6)	dry woodland edges
Dalea cylindriceps, massive-spike prairie clover	dry grassland
Draba nemorosa, yellow whitlowort	dry grassland
Oenothera latifolia, pale evening primrose	dry grassland
Phlox andicola, plains phlox	dry grassland
Physostegia parviflora, obedient plant	moist meadows
Pinus ponderosa, ponderosa pine (Fig. 5)	dry woodland
Poa juncifolia	dry grassland
Psoralea hypogaea, little bread-root scurf pea	dry grassland
Ribes setosum, bristly gooseberry	woodland edges
Scolochloa festucacea, sprangletop	watersides
Selaginella densa, spikemoss	dry grassland
Silene menziesii, catchfly (Fig. 5)	moist woodland
Butterflies	
Amblyscirtes oslari, Oslar's roadside skipper	moist grassland edges
Coenonympha ochracea, ochre ringlet	pine woodland by water
Erynnis lucilius afranius, dusky wing	open woodland, prairie
Hesperia pahaska pahaska, Pahaska skipper	mesic bottomland
Incisalia eryphon, an elfin	pine woodland
Limenitis weidemeyerii oberfoellii	pine woodland by willows
Lycaena rubidus longi, a copper	pine woodland, grassland
Mitoura siva, a hairstreak	juniper woodland
Oarisma garita, Garita skipper	pine woodland edges
Papilio multicaudata, a swallowtail	escarpments, brush
Plebejus icarioides	pine slopes

Table I
Continued

Taxon	Habitat
Poanes taxiles, a skipper	riparian groves
Pontia sisymbrii nordini, a white (Fig. 9)	pine woodland
Speyeria coronis, a fritillary	pine woodland ravines
S. edwardsii, a fritillary	pine woodland
Vanessa annabella, a painted lady	open areas
Yvretta rhesus	grassland
Fishes	
Catastomus platyrhynchus, mountain sucker	clear streams
Reptiles	
Eumeces multivirgatus multivirgatus, many-lined skink	prairie, brush
Kinosternon flavescens, yellow mud turtle	streams
Phrynosoma douglassi, short-horned horned toad	pine woods, prairie
Thamnophis elegans, wandering gartersnake	near water
Birds	
Contopus sordidulus, western wood pewee[a]	pine woodland
Passerina amoena, lazuli bunting	deciduous woods, brush
Pica pica, black-billed magpie	bottomland woods, brush
Pheucticus melanocephalus, black-headed grosbeak	open deciduous woodland
Piranga ludoviciana, western tanager[a]	pine woodland
Mammals	
Perognathus fasciatus fasciatus, olive-backed pocket mouse	open areas

[a] Breeding presence suspected.

papyrifera, Botrychium virginianum, Campanula rotundifolia, Populus tremuloides, Pterospora andromedea, Pyrola elliptica, and *P. virens,* for examples. Conversely, the Black Hills are home to numerous species that are unknown in the Niobrara Valley, even though suitable habitats apparently exist there: *Adiantum capillis-veneris, Anemone multifida, Asplenium trichomanes, Calypso bulbosa, Circaea alpina, Corallorhiza trifida, C. wisteriana, Cornus canadensis, Dryopteris filix-mas, Geranium bicknellii, Goodyera oblongifolia, G. repens, Gymnocarpium dryopteris, Habenaria dilatata, H. orbiculata, Matteucia struthiopteris, Oryzopsis asperifolia, Pellaea atropurpurea, P. glabella, Pteridium aquilinum, Pyrola asarifolia, P. secunda,* and *Streptopus amplexifolius,* for examples.

Table II

Species, subspecies, and varieties with main ranges both east and west of the grasslands, and usually also to the north

Taxon	Habitat
Mosses	
Aulacomnium palustre	dry grassland
Brachythecium rivulare	moist woodland
Bryoerythrophyllum recurvirostre	dry woodland
Bryum algovicum	moist woodland
Desmatodon heimii	dry grassland
D. plinthobius	dry grass- and woodland
Dicranum muehlenbeckii	moist or dry woodland
Encalypta ciliata	moist woodland
Mnium ambiguum	moist woodland
Orthodicranum flagellare	moist woodland
O. montanum	moist woodland
Orthotrichum diaphanum	dry woodland
O. obtusifolium	moist or dry woodland
Plagiomnium ellipticum	moist woodland
Pleurozium schreberi	moist or dry woodland
Pohlia nutans	moist or dry woodland
Saelenia glaucescens (Fig. 4)	moist or dry woodland
Thuidium delicatulum	moist woodland
Tortula mucronifolia	ledges, banks
Vascular plants	
Actaea rubra, baneberry	moist woodland
Adiantum pedatum, maidenhair fern	moist woodland
Amelanchier alnifolia, Saskatoon service-berry	moist woodland
Aralia nudicaulis, wild sarsaparilla (Fig. 6)	moist and dry woodland
Arenaria lateriflora, grove sandwort	moist grass- and woodland
Aster laevis, smooth blue aster	dry grass- and woodland
Betula papyrifera, paper birch (Fig. 6)	moist woodland
Botrychium virginianum, rattlesnake fern	moist woodland
B. simplex	moist woodland
Campanula rotundifolia, harebell (Fig. 6)	dry woodland
Carex buxbaumii, sedge	wet meadows, seeps
C. diandra, sedge	wet meadows, seeps
C. saximontana, sedge	moist and dry woodlands
Equisetum fluviatile, water horsetail	wet meadows, seeps
Glyceria borealis, northern mannagrass	wet meadows, seeps
Gratiola neglecta, hedge hyssop	wet meadows
Habenaria hyperborea, northern green orchis	wet meadows, seeps

Table II
Continued

Taxon	Habitat
Helianthemum bicknellii, frostweed	dry grass- and woodland
Heracleum spondylium subsp. *montanum,* cow parsnip	moist grass- and woodland
Heuchera richardsonii, alum-root	dry grass- and woodland
Juniperus horizontalis, creeping juniper	dry woodland
Lilium philadelphicum var. *andinum,* wild lily	moist and dry woodland
Menyanthes trifoliata, bog-bean	aquatic
Myosotis laxa	watersides
Ophioglossum vulgatum var. *pseudopodum,* adder's tongue fern	moist grassland
Osmorhiza longistylis, anise root (Fig. 6)	moist woodland
Populus tremuloides, quaking aspen	moist and dry woodland
P. tremuloides × *P. grandidentata,* hybrid of quaking and bigtooth aspens (Fig. 8)	moist woodland
Pterospora andromedea, pinedrops	dry woodland
Pyrola elliptica, wintergreen	moist woodland
P. virens, wintergreen	moist woodland
Ribes oxyacanthoides, a gooseberry	moist woodland
Schizachne purpurascens, false melic	dry woodland
Scrophularia lanceolata, figwort (Fig. 6)	moist woodland
Spiranthes romanzoffiana, hooded lady's tresses	wet meadows
Stellaria longifolia, long-leaved stitchwort	moist grass- and woodland
Symphoricarpos albus, white coralberry	dry grass- and woodland
Triglochin palustris, arrowgrass	moist meadows
Viola canadensis var. *rugulosa,* tall white violet	moist woodland
Viola nephrophylla, northern bog violet	moist grassland
Butterflies	
Boloria selene sabulicollis, silver-bordered fritillary (Fig. 9)	moist meadows
Nymphalis milberti, Milbert's tortoise shell	forest edges
Phyciodes batesii, tawny crescent	deciduous riparian woodland
Satyrodes eurydice, northern eyed brown	marshy meadows
Fishes	
Catostomus catostomus, longnose sucker (Fig. 10)	clear, cold waters
Couesius plumbeus, lake chub (Fig. 10)	various waters
Culaea inconstans, brook stickleback	cool, clear streams with submersed vegetation
Etheostoma exile, Iowa darter	clear, sluggish streams with submersed vegetation

Table II
Continued

Taxon	Habitat
Phoxinus eos, northern redbelly dace	cool, sluggish streams
P. neogaeus, finescale dace	cool, sluggish streams
Semotilus margarita, pearl dace	cool, clear unvegetated streams
Reptiles	
Opheodrys vernalis, smooth green snake	grassy borders of streams
Birds	
Certhia americana, brown creeper (Fig. 11)	woodland
Gallinago gallinago, common snipe	streamsides
Sitta canadensis, red-breasted nuthatch (Fig. 11)	coniferous woodland
S. carolinensis, white-breasted nuthatch	woodland
Spizella pallida, clay-colored sparrow	woody ecotones
Tachycineta bicolor, tree swallow	woodland near water

2. *Animals*

Eighteen species and subspecies of animals whose main ranges are in the north, with southern extensions to the east and west of the central grasslands, occur in the Valley (Table II; Figs. 9–11).

There are four northern butterflies, two characteristic of bogs or marshy meadows (*Boloria selene sabulicollis* [Fig. 9]; *Satyrodes eurydice* sensu Opler and Krizek, 1984), and two in moist woods (*Nymphalis milberti* and *Phyciodes batesii*). *Boloria selene sabulicollis* is a western Great Plains subspecies (Kohler, 1977). *Phyciodes batesii* occurs in the Great Plains in only a few disjunct locales far removed from the main range in Canada and the northeastern United States. Similarly, the main range of the smooth green snake (*Opheodrys vernalis*) is to the northeast, but there are a number of outlier populations in the Great Plains, including the Niobrara Valley, where it is found in grassy areas.

The lake chub fish (*Couesius plumbeus* [Fig. 10]) was described as a glacial relict in Nebraska (Madsen, 1985), and was recently collected from a tributary of the Niobrara River (Stasiak, 1986). Several northern species of fishes (*Culaea inconstans, Etheostoma exile, Phoxinus eos, P. neogaeus,* and *Semotilus margarita* [Fig. 10]) are glacial relicts in Nebraska (Stasiak, 1986 and pers. comm.), and are found in cool, spring-fed streams in the northern part of the state, including the Niobrara River. They provide evidence for the refugial nature of the Valley and also of nearby sandhills streams.

The clay-colored sparrow (*Spizella pallida*) breeds in brushy borders, and deciduous or mixed woodlands are favored by the brown creeper (*Certhia americana* [Fig. 10]), red-breasted nuthatch (*Sitta canadensis* [Fig. 10]), and white-breasted nuthatch (*S. carolinensis,* which also breeds in riparian forests of some other grasslands rivers). The tree swallow (*Tachycineta bicolor*) is found in open, deciduous woodlands near water, and the common snipe (*Gallinago gallinago*) breeds in the marshy edges of streams. The Valley is the southern breeding limit for other bird species, such as the least flycatcher (*Empidonax minimus*) and savannah sparrow (*Passerculus sandwichensis*), but they are not limited, in the grasslands, to the Niobrara Valley and are therefore not listed here.

C. SPECIES OF EASTERN, NORTHEASTERN, AND SOUTHEASTERN AFFINITY

1. Plants

Fifteen moss species in the Valley are of eastern affinity (Table III). The majority in this group occur in the deciduous forests of the Valley walls and in birch forests of the cool springbranch canyons. Several (*Desmatodon plinthobius, Dicranum condensatum* [Fig. 4], *Funaria americana, Orthotrichum disphanum,* and *Tortella humilis*) are primarily distributed to the south or southeast of the central grasslands. More typical eastern species that extend across the grasslands via the Valley are *Anomodon minor, Atrichum altecristatum, Brachythecium acuminatum,* and *Lindbergia brachyptera* (Fig. 4). Of this group, the only Black Hills outlier of eastern affinity is *Timmia megapolitana* subsp. *megapolitana.*

The largest group of vascular plants of concern here (62 species, subspecies, varieties, and hybrids) has ranges mainly east of the central grasslands, but many reach far to the southeast, northeast, or north, and some extend northwestward from Minnesota to Alberta and beyond, abutting or overlapping the northern parts of the ranges of some entities of western affinity. Included here are eight tree species that, collectively, dominate the deciduous, non-riparian forests. There are seven shrub and two woody vine species; the others are mostly perennial herbs. Many are confined to the cooler, moister, north-facing valley walls and springbranch canyons, but some survive in drier, more open places. A disjunct hybrid, *Populus balsamifera* × *P. deltoides,* is known in the Valley (Fig. 8); *P. balsamifera* does not occur there today, but *P. deltoides* does.

Three eastern species also occur as disjunct outliers on the eastern slope of the Rocky Mountains: *Apios americana, Gentiana andrewsii,* and *Physocarpus opulifolius* (Fig. 7). Eleven appear as outliers in the Black Hills too: *Amphicarpaea bracteata, Apios americana, Aquilegia canadensis, Carex peckii, Circaea lutetiana* subsp. *canadensis, Lonicera dioica, Ostrya*

Table III

Species of eastern, northeastern, and southeastern affinity, mostly reaching western limits in the Niobrara Valley

Taxon	Habitat
Mosses	
Anomodon minor	moist woodland
Atrichum altecristatum	moist woodland
Brachythecium acuminatum	moist woodland
B. rutabulum	moist woodland
Bryum uliginosum	moist woodland
Dicranum condensatum (Fig. 4)	dry woodland
Didymodon rigidulus	dry grassland
Entodon cladorrhizans	moist woodland
E. seductrix	moist woodland
Funaria americana	moist and dry woodland
Leskea gracilescens	moist woodland
Lindbergia brachyptra (Fig. 4)	moist and dry woodland
Platygyrium repens	moist woodland
Pylaisiella selwynii	moist woodland
Timmia megapolitana subsp. *megapolitana*	moist woodland
Vascular plants	
Acer saccharinum, silver maple	moist woodland
Agalinis purpurea, gerardia	moist woodland
Allium perdulce, wild onion	dry grassland
Amphicarpaea bracteata, hog peanut	moist and dry woodland
Anemone virginiana, tall anemone	dry woodland
Apios americana, groundnut	moist woodland edges
Aquilegia canadensis, columbine	moist and dry woodland
Aralia racemosa, spikenard	moist woodland
Arisaema triphyllum jack-in-the-pulpit (Fig. 7)	moist woodland
Athyrium filix-femina, lady-fern	moist woodland
Boehmeria cylindrica, false nettle	wet meadows, watersides
Botrychium campestre, field grapefern	moist woodland
Campanula americana, American bellflower	moist woodland edges
Carex peckii, sedge	moist woodland
C. tribuloides, sedge	moist grass- and woodland
Cinna arundinacea, woodreed	moist woodland
Circaea lutetiana subsp. *canadensis,* enchanter's night-shade	moist woodland
Clematis virginiana, virgin's bower (Fig. 6)	moist woodland edges
Corylus americana, hazelnut	moist and dry woodland
Cuscuta gronovii, dodder	moist grass- and woodland

Table III
Continued

Taxon	Habitat
Cyperus engelmannii	moist grassland
Dryopteris spinulosa, spinulose woodfern	moist woodland
Euonymus atropurpureus, wahoo	moist woodland
Eupatorium rugosum, white snakeroot	moist and dry woodland
Euthamia graminifolia var. *major*	moist grassland
Festuca obtusa, nodding fescue	moist woodland
Gentiana andrewsii, bottle gentian	moist grass- and woodland
Geranium maculatum, wild cranes-bill	moist woodland
Hemicarpha micrantha	watersides
Impatiens pallida, pale jewel-weed	moist grass- and woodland
Juglans nigra, black walnut (Fig. 7)	moist and dry woodland
Juncus scirpoides	moist grassland
Laportea canadensis, wood nettle	moist woodland
Lonicera dioica, wild honeysuckle	moist woodland
Lycopus virginicus, bugle-weed	moist grassland
Mimulus ringens, Alleghany monkey-flower	wet meadows, watersides
Morus rubra, red mulberry	moist and dry woodland
Muhlenbergia glomerata, muhly grass	moist grassland
Osmorhiza claytonii, sweet cicely	moist woodland
Ostrya virginiana, hop hornbeam (Fig. 7)	moist and dry woodland
Parthenocissus quinquefolia, woodbine	moist woodland
Physocarpus opulifolius, ninebark (Fig. 7)	moist woodland
Poa sylvestris, woodland bluegrass	moist woodland
Populus balsamifera × *P. deltoides,* hybrid of balsam poplar and cottonwood (Fig. 8)	moist woodland
Prunus mexicana, big-tree plum	moist grass- and woodland
Pyrus ioensis, Iowa crabapple	moist woodland
Quercus macrocarpa, bur oak	moist and dry woodland
Rhamnus lanceolata var. *glabratus,* lance-leaved buck-thorn	moist woodland
Sagittaria graminea	watersides
S. rigida	watersides
Salix petiolaris, meadow willow	moist grassland
Sambucus canadensis, elder-berry	moist grass- and woodland
Scrophularia marilandica, figwort	moist woodland
Scutellaria parvula var. *leonardii,* small skullcap	dry grass- and woodland
Selaginella rupestris, spikemoss	dry grassland
Silene stellata, starry campion	dry woodland
Solidago speciosa var. *rigidiuscula,* showy-wand golden-rod	dry grass- and woodland

Table III
Continued

Taxon	Habitat
Tilia americana, basswood (Fig. 7)	moist woodland
Ulmus rubra, red elm	moist woodland
Viola pubescens, downy yellow violet (Fig. 7)	moist woodland
V. sororia, downy blue violet	moist woodland
Zanthoxylum americanum, prickly ash	moist woodland
Butterflies	
Euphydryas phaeton, Baltimore (Fig. 9)	deciduous woods by water
Wallengrenia egeremet, northern broken dash (Fig. 9)	moist deciduous woods
Fishes	
Esox americanus, grass pickerel	streams with vegetation
Notropis heterolepis, blacknose shiner (Fig. 10)	cool, clear ponds
Rhinichthys atratulus, blacknose dace	cool, gravelly streams
Reptiles	
Diadophis punctatus, ringneck snake	woods
Elaphe vulpina, fox snake	woods, grasslands
Emydoidea blandingii, Blanding's turtle	shallow waters
Heterodon platyrhinos, eastern hognose snake	by sandy woodland streams
Birds	
Aix sponsa, wood duck	riparian woodland
Caprimulgus vociferus, whip-poor-will (Fig. 11)	woodland edges
Colinus virginianus, bobwhite	brush, open woodland
Contopus virens, eastern wood pewee	riparian woodland
Hylocichla mustelina, wood thrush	deciduous woodland
Melanerpes carolinus, red-bellied woodpecker	open woodland
Mniotilta varia, black-&-white warbler (Fig. 11)	riparian forest edges
Otus asio, eastern screech owl	woodland
Passerina cyanea, indigo bunting	edges of woodland
Piranga olivacea, scarlet tanager	oak woodland
Sayornis phoebe, eastern phoebe	wooded cliffs by water
Seiurus aurocapillus, ovenbird	deciduous woodland
Setophaga ruticilla, American redstart	riparian woodland
Sialis sialis, eastern bluebird	edges of woodland
Vireo flavifrons, yellow-throated vireo (Fig. 11)	riparian woodland
V. olivaceus, red-eyed vireo	riparian woodland
Mammals	
Neotoma floridana baileyi, eastern wood rat (Fig. 12)	woodland

virginiana (Fig. 7), *Physocarpus opulifolius* (Fig. 7), *Selaginella rupestris, Ulmus rubra,* and *Viola pubescens* (Fig. 7).

Some eastern forest species are known in the Niobrara Valley but not the Black Hills, although suitable habitats apparently exist there: *Acer saccharinum, Aralia racemosa, Arisaema triphyllum* (Fig. 7), *Campanula americana, Festuca obtusa, Geranium maculatum, Juglans nigra* (Fig. 7), *Morus rubra, Pyrus ioensis, Scrophularia marilandica, Tilia americana* (Fig. 7), *Viola sororia,* and *Zanthoxylum americanum.* Conversely, others appear in the Black Hills but not the Niobrara Valley, where again suitable habitats are likely: *Bromus kalmii, Carex convoluta, Corallorhiza odontorhiza, Isopyrum biternatum, Maianthemum canadense, Picea glauca, Sambucus racemosa* subsp. *pubens, Sanguinaria canadensis, Thalictrum dioicum, Viburnum lentago,* and *V. opulus* var. *americanus.*

2. *Animals*

Twenty-six animal species show strong eastern affinities: 2 butterflies, 3 fishes, 4 reptiles, 16 birds, and one mammal (Figs. 9–12).

The butterfly *Euphydryas phaeton* has been recorded from one Valley county (Fig. 9), but most of its range is east of the Mississippi River; *Wallengrenia egeremet* likewise has a disjunct population in the western Niobrara Valley (Fig. 9).

Two of the fishes inhabit cool, clear streams such as those of the springbranch canyons of the central Valley, but *Esox americanus* is more common in sluggish streams with aquatic vegetation.

All but four of the bird species are characteristic of eastern deciduous or mixed forest, but they venture westward in forests near rivers. The exceptions are bobwhite (*Colinus virginianus*), whip-poor-will (*Caprimulgus vociferus* [Fig. 11]), eastern bluebird (*Sialis sialis*), and indigo bunting (*Passerina cyanea*), all favoring brushland or woody ecotones.

The eastern woodrat, *Neotoma floridana baileyi,* is represented by an endemic subspecies 190 km from the contiguous ranges of other subspecies (Fig. 12).

VI. Modern Trends in Species Richness in the Niobrara and Missouri River Valleys

The Missouri River valley between the mouth of the Niobrara and the union of the Missouri with the Mississippi River was covered by glaciers in the Pleistocene, and therefore its modern forest appeared since deglaciation. The colonizers were mostly from the south and east, but not all of them migrated equally far upstream. Only a relative few reached the Niobrara Valley, and some of those probably disappeared from there with increasing aridity in the Holocene. Table IV shows the general modern

Table IV

Gradients of species richness: number of species (cf. Fig. 1) and Kendall's rank correlation coefficient τ, with significance level P

Site:	*1* (West)	*2*	*3*	*4*	*5*	*6*	*7* (East)	τ	P
Trees	23	24	25	40	50	61	75	1.0	0.001
Shrubs	33	31	34	33	36	46	55	0.81	0.02
Woody and semi-woody vines	7	8	10	13	14	14	20	0.90	0.001
Ferns	6	9	6	13	16	21	33	0.81	0.01
Mosses	55	32	30	47	51	92	117	0.76	NS

westward decline in plant species numbers in the Niobrara-Missouri drainage for five groups with distributions known in detail: trees, shrubs, woody and semi-woody vines, ferns, and mosses. These numbers include all native species in all forest and forest-border habitats in the counties adjacent to the sites numbered 1–7 on Figure 1. Data are taken from Churchill (1982, 1985a, 1985b, and unpublished), Gier (1955), Great Plains Flora Association (1977, 1986), Little (1971, 1976), Steyermark (1963), and van der Linden et al. (1985), and from our recent field work. We tested the correlation between species richness and eastward extension along the Valley using Kendall's rank correlation in a test for trend (in Conover, 1971) (Table IV). The most drastic upstream percentage decline among numbers of vascular plant species—from 33 to 6 species—occurs among the ferns. Tree and vine species decrease by about two-thirds, and shrub species are reduced least of those tested. A similar trend is noted for the mosses except for the westernmost site (7), where the number of species actually increases, probably because of the mixture of plant communities there. None of the western plant species occurs farther east than the mouth of the Niobrara River, but many eastern species extend into the upper Niobrara Valley. (However, some western species not considered here because they are not confined to the Valley do extend farther east in the Missouri Valley. *Mentzelia decapetala* and *Yucca glauca,* for example, reach southeastward to southwestern Iowa and northwestern Missouri, respectively, in the loess hills on the east side of the Missouri River Valley (Gt. Pl. Flora Assoc., 1977)).

Most of the decline in numbers of plant species occurs from the mouth of the Missouri River (site 7 in Fig. 1) upstream to the mouth of the Niobrara River (between sites 2 and 3). Above that point, at sites 1 and 2, the numbers in each category change little (except for the mosses), but that is due largely to substitution of western and northern species for eastern and southern species.

Sorenson's community similarity coefficients in Table V likewise display upstream decline, even where actual numbers of species are little altered. In general, the more remote the sites are from each other, the less is their floristic similarity. (The higher the coefficient, the more alike are the sites in terms of species richness. A coefficient of 100 would indicate identical floras, and one of zero would indicate no shared species.)

VII. Discussion

Local topographic and hydrologic features, unique to the Niobrara Valley in the central grasslands, have provided refuge for many plant species that were probably widespread during cooler, wetter Pleistocene and early Holocene times. Other species have colonized the Valley since the retreat of the glaciers, but some undoubtedly vanished from there when the climate warmed and dried in the Holocene Hypsithermal Interval. The extremely limited palynological evidence now available does not allow us to distinguish the relictual from the immigrant species on our lists, but those with low mobility and with disjunct, as opposed to continuous (peninsular), ranges are more likely to be relictual.

The rates of colonization are unknown, but for plants with small, anemochorous seeds and fruits it could have been rather rapid. Large-fruited species, such as oaks, might also have invaded rapidly through the activities of squirrels, jays, and woodpeckers.

The steep decline in numbers of plant species from east to west suggests that postglacial colonization by eastern species has been at different rates, or perhaps at similar rates but followed by differential retreat, with western limits set for each species by local climatic and topographic factors. Some eastern species no doubt retreated from the Valley with the onset of the modern, semi-arid climate, but the constant groundwater outflow on the south wall of the Valley protects some species from the hazards of increasing climatic aridity. Far fewer western than eastern species occur in the Valley, and most are plants of drier environments than those required by the eastern species. It is likely, therefore, that they are recent invaders from the west that found suitable habitats along the drier Valley walls, when the climate approached its present semi-arid state. These western species are perhaps confined to the Valley by fires; some observations show that a few, including *Pinus ponderosa,* are expanding from the Valley into the sandhills now that fires have been controlled for more than half a century (Steinauer & Bragg, in press). Elsewhere, as in the Pine Ridge escarpments to the north of the upper reaches of the Valley, some occupy less restricted sites.

The information from a century of collecting and observation in the Niobrara Valley gives no evidence of modern expansions of ranges of

Table V

Sorenson's community similarity coefficients[a] on the Upper Niobrara–Lower Missouri gradient (cf. Fig. 1)

	Site: (West)	*1*	*2*	*3*	*4*	*5*	*6* (East)	*7*
Trees	*1*							
	2	89						
	3	52	51					
	4	47	49	61				
	5	47	49	61	89			
	6	38	40	51	77	88		
	7	29	34	42	66	74	88	
Shrubs	*1*							
	2	90						
	3	83	86					
	4	70	75	84				
	5	58	63	71	87			
	6	48	52	58	65	80		
	7	41	42	47	56	68	85	
Woody and semi-woody vines	*1*							
	2	80						
	3	71	89					
	4	60	76	78				
	5	57	73	83	96			
	6	57	73	83	96	100		
	7	44	57	67	79	82	82	
Ferns	*1*							
	2	80						
	3	66	53					
	4	63	72	53				
	5	36	56	55	83			
	6	30	46	44	71	86		
	7	26	38	31	48	61	74	
Mosses	*1*							
	2	48						
	3	49	68					
	4	37	56	70				
	5	43	51	64	76			
	6	38	40	48	59	69		
	7	38	36	38	51	56	72	

[a] Community similarity coefficient: $200\ S_{ab}/(S_a + S_b)$. S_{ab}: number of species in common, sites a, b. S_a, S_b: numbers of species, sites a, b, respectively.

native plant species. On the contrary, the markedly disjunct, possibly relictual ones are very localized, and their populations are apparently static. Our field observations are similar to those of early collectors, as shown on the labels of their herbarium specimens; many species are very restricted but locally abundant, some are rare and occur as scattered individuals, but others are common in many areas of the Valley.

There is some genetic evidence for Pleistocene sympatry of what are now allopatric eastern and western plant species bordering the grasslands. Such temporary sympatry could have occurred in cooler, moister Pleistocene times between the drier Pliocene and Holocene times. Eckenwalder (1984) found isolated populations of *Populus* ×*jackii* (*P. deltoides* × *P. balsamifera*) (Fig. 8) in the Niobrara Valley and in southwestern North Dakota, neither of which is a modern area of sympatry of the parental species. The populations of *P. balsamifera* closest to the Niobrara Valley today are so far away (more than 300 km) that past sympatry in the Valley can be postulated. Disjunct hybrids of *P. angustifolia* with *P. deltoides* (*P.* ×*acuminata*) are known in western North Dakota and western Nebraska (Eckenwalder, 1984). A disjunct hybrid of *Populus tremuloides* with *P. grandidentata* has recently been discovered in the Niobrara Valley (Fig. 8), more than 400 km from the nearest populations of *P. grandidentata* (Freeman & Churchill, in prep.). However, *P. grandidentata* occurred in the Sandhills 8900–3600 B.P. (Wright et al., 1985).

Further evidence of the restriction of once-wider ranges is given by Maze (1968), who showed that *Quercus macrocarpa* populations in the Black Hills and northeastern New Mexico show evidence of past introgression with *Q. gambelii*; we suspect that *Q. macrocarpa* in the Pine Ridge also shows such evidence. The two species are not now sympatric there or anywhere else and, in fact, are now so widely separated (about 300 km) as to preclude modern gene flow between them (Maze, 1968).

Van Haverbeke (1968) and Flake, Urbatsch, and Turner (1978) delineated the cline of morphological and chemical characteristics of *Juniperus scopulorum* to *J. virginiana* from west to east across the grasslands; Wells (1983) interpreted that cline to mean that once there were continuous populations of juniper across the grasslands (that are now discontinuous). In *Pinus ponderosa,* all grassland populations sampled have full genetic diversity, suggesting no founder effects or genetic bottlenecks, and indicating wider distribution in the past, according to Wells (1983, citing unpublished work of Hamrick, Mitton, and co-workers). Such uniformity could also be caused by gene flow among modern populations. Wells (1983) noted the lack of evidence of ponderosa pine in the central grasslands during the late Pleistocene.

The disjunct occurrence of many eastern and eastern-western woodland species in the Black Hills, and of a few eastern species in the Front Range

of the Rocky Mountains, suggests that those areas too are refugia. The Valley and the Black Hills do not share all woodland species, suggesting differential movements of the flora as well as unshared habitats.

Although most animals are more vagile than plants, the breeding distributions of terrestrial animals are strongly influenced by vegetation patterns. The distributional congruence of many mobile with less mobile animal species strengthens the case for the Valley as a glacial and postglacial refugium. Johnson (1975) described most of the western coniferous forest species of butterflies listed in Table I as postglacial relicts in the favorable escarpment habitats of the Niobrara Valley, and he emphasized the importance of this locale as a center of speciation in the evolution of the present butterfly fauna of the Rocky Mountains. In particular, Johnson (1977) attributed the allopatric subspecific status of *Pontia sysymbrii nordini* (Fig. 9) to the retreat of the post-Pleistocene coniferous forest and subsequent isolation of escarpment populations within a drier grassland biome. Likewise, Cardé et al. (1970) attributed the phylogenetic splitting of *Satyrodes eurydice* from its sibling species *S. appalachia* to Pleistocene glaciations that isolated proto-*eurydice* populations in the west from populations in eastern forests.

Mayden (1987) provided geological and faunal evidence for the former linkage of the Niobrara River system to the White River system of South Dakota. The separation of those systems could have restricted once-wider ranges of fish in the Niobrara Valley. The presence of spruce taiga in north-central Nebraska is indicated by discovery of Late Pleistocene fossils of tapir, musk-ox, stagmoose, and jaguar, all forest mammals (Schultz, Martin & Schultz, 1985). Although these particular species are now extinct or extirpated in Nebraska, other extant populations of mammals of northern affinity may well represent relicts left behind as this Pleistocene forest community retreated to the north. Such glacial and postglacial climatic events have been proposed (Hoffman & Jones, 1970) to account for discontinuous populations of several species of mammals now found in suitable habitats along several Great Plains rivers, including the Niobrara. These species were not included in our Tables I–III because they are not particularly restricted in the west to the Niobrara Valley, yet they support a refugial hypothesis for the Valley. Strongest support in the mammals comes from the presence in the Niobrara Valley of the endemic subspecies of the eastern woodrat, *Neotoma floridana baileyi.*

Birds, on the other hand, can readily take advantage of the mix of habitats to be found in the Niobrara Valley because of their great powers of dispersal, and most or all of the bird species in the Valley are undoubtedly postglacial immigrants. Although avian distributions may show least resemblance to historical patterns, they too support a refugial hypothesis. The Great Plains has constituted an ecological barrier to birds

and an isolating agent in avian speciation (Johnsgard, 1978; Mengel, 1970), but in the Niobrara Valley there is significant sympatry of eastern and western species (Brogie & Mossman, 1983; Mossman & Brogie, 1983). Hybrids of closely-related eastern and western entities are well-known in the Valley: indigo with lazuli buntings, Baltimore with Bullock's orioles, yellow-shafted with red-shafted races of the northern flicker, and possibly scarlet with western tanagers and eastern with western wood pewees (Ford, 1959; Johnsgard, 1979b; Sibley & Short, 1959, 1964; Short, 1965). Flicker, bunting, and oriole hybrids occur elsewhere in the Great Plains too, and therefore are not unique to the Valley (Johnsgard, 1979b). Thus the Niobrara Valley presently provides a "modern" faunal refugium from the aridity and treelessness of the surrounding grasslands, and it is not imprudent to suppose a similar role in the past.

The evidence presented here, we believe, strongly supports the case for a Niobrara glacial and postglacial refugium in the central plains of North America. The congruence of various extant plant and animal distributions, in addition to the macro- and microfossil data, strongly suggests historical factors rather than dispersal events to account for the observed distributional patterns of many species. Future studies of such patterns in other animal and plant taxa can provide more tests of the refugium hypothesis advocated for the Niobrara Valley in this study.

VIII. Acknowledgments

The Nature Conservancy owns a large tract of the Valley and adjacent Sandhills, and has encouraged studies there. The Bessey Herbarium of the University of Nebraska State Museum, Lincoln, has been an important source of data. We are grateful to Craig Freeman, A. T. Harrison, Anna Hermanson, Paul Johnsgard, Kurt Johnson, Steven Rolfsmeier, Richard Stasiak, and David Sutherland, who have kindly contributed data and advice. Two anonymous reviewers made helpful comments on an early draft. Of course we are indebted to earlier researchers, beginning with Bessey, whose works formed the nucleus and stimulus for this effort.

IX. Literature Cited

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

Axelrod, D. I. 1985. Rise of the grassland biome, central North America. Bot. Rev. **51:** 163–201.

——— **& P. H. Raven.** 1985. Origin of the cordilleran flora. J. Biogeogr. **12:** 21–47.

Beal, E. O. & P. H. Monson. 1954. Marsh and aquatic angiosperms of Iowa. State University of Iowa Stud. Nat. Hist. **19:** 1–95.

Bernabo, J. C. & T. Webb, III. 1977. Changing patterns in the Holocene pollen record of northeastern North America: A mapped summary. Quaternary Res. **8:** 64–96.

Bessey, C. E. 1887. A meeting-place for two floras. Bull. Torrey Bot. Club **14:** 189–191.

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

Bradbury, J. P. 1980. Late Quaternary vegetation history of the central Great Plains and its relationship to eolian processes in the Nebraska Sand Hills. U.S. Geol. Survey Prof. Paper **1120C**: 25–36.

Bragg, T. B. & L. C. Hulbert. 1976. Woody plant invasion of unburned Kansas bluestem prairie. J. Range Managem. **29**: 19–24.

Brogie, M. A. & M. J. Mossman. 1983. Spring and summer birds of the Niobrara Valley Preserve area, Nebraska: An annotated checklist. Nebraska Bird Rev. **51**: 44–51.

Brooks, R. E. & L. A. Hauser. 1978. Aquatic vascular plants of Kansas. I. Submersed and floating-leaved plants. State Biol. Survey Kansas, Tech. Pub. **7**: 1–70.

Brown, D. A. & P. J. Gersmehl. 1985. Migration models for grasses in the American midcontinent. Ann. Assoc. Amer. Geogr. **75**: 383–394.

Cardé, R. T., A. M. Shapiro & H. K. Clench. 1970. Sibling species in the *Eurydice* group of *Lethe* (Lepidoptera: Satyridae). Psyche **77**: 70–103.

Catalogue of American Amphibians and Reptiles. 1962 et seq. Amer. Soc. Ichthyologists and Herpetologists (1962–1971), Amer. Soc. for the Study of Amphibians and Reptiles (1971–).

Churchill, S. P. 1982. Mosses of the Great Plains, VI. The Niobrara River Basin of Nebraska. Trans. Kansas Acad. Sci. **85**: 1–12.

———. 1985a. Mosses of the Great Plains, X. The Niobrara Valley Preserve and adjacent area in Nebraska. Trans. Nebraska Acad. Sci. **13**: 13–19.

———. 1985b. A synopsis of the Kansas mosses, with keys and distribution maps. Univ. of Kansas Sci. Bull. **53**: 1–64.

Conover, W. J. 1971. Practical nonparametric statistics. Wiley & Sons Inc., New York.

Cooperrider, T. S. 1958. The ferns and other pteridophytes of Iowa. State Univ. Iowa Stud. Nat. Hist. **20**: 1–66.

Cross, F. B. 1970. Fishes as indicators of Pleistocene and Recent environments of the central plains. Pages 241–257 *in* W. Dort, Jr. & J. K. Jones, Jr. (eds.), Pleistocene and Recent environments of the central plains. University of Kansas Press, Lawrence.

Davis, M. B. 1983. Quaternary history of deciduous forests of eastern North America and Europe. Ann. Missouri Bot. Gard. **70**: 550–563.

Delcourt, P. A. & H. R. Delcourt. 1980. Vegetation maps for eastern North America: 40,000 yr B. P. to the present. Pages 123–165 *in* R. C. Romans (ed.), Geobotany **II**: 123–165.

Dorn, R. D. & J. L. Dorn. 1972. The ferns and other pteridophytes of Montana, Wyoming, and the Black Hills of South Dakota. Dept. of Botany, University of Wyoming, Laramie.

Eckenwalder, J. E. 1984. Natural intersectional hybridization between North American species of *Populus* (Salicaceae) in sections *Aigeiros* and *Tacamahaca*. II. Taxonomy. Canad. J. Bot. **62**: 325–335.

Ferris, C. D. & F. M. Brown. 1981. Butterflies of the Rocky Mountain states. University of Oklahoma Press, Norman.

Flake, R. H., L. Urbatsch & B. L. Turner. 1978. Chemical documentation of allopatric introgression in *Juniperus*. Syst. Bot. **3**: 129–144.

Ford, N. L. 1959. Notes on summer birds of western Nebraska. Nebraska Bird Rev. **27**: 6–12.

Freeman, C. C. & S. P. Churchill. 1983. Noteworthy pteridophyte records for Nebraska. Amer. Fern J. **73**: 29–30.

Gier, L. J. 1955. Missouri bryophytes. Trans. Kansas Acad. Sci. **58**: 24–49.

Gleason, H. A. 1913. The relation of forest distribution and prairie fires in the Middle West. Torreya **13**: 173–181.

———. 1922. The vegetational history of the Middle West. Ann. Assoc. Amer. Geogr. **12**: 39–85.

Great Plains Flora Association. 1977. Atlas of the flora of the Great Plains. Iowa St. University Press.

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

Grimm, E. C. 1983. Chronology and dynamics of vegetation change in the prairie-woodland region of southern Minnesota, U. S. A. New Phytol. **93**: 311–350.

Grüger, J. 1973. Studies on the late Quaternary vegetation history of northeastern Kansas. Bull. Geol. Soc. Amer. **84:** 239–250.

Hall, E. R. 1981. The mammals of North America. 2 vols. John Wiley & Sons, New York.

Hesse, L. W., Q. P. Bliss & G. P. Zuerlein. 1982. Some aspects of the ecology of adult fishes in the channelized Missouri River, with special reference to the effects of two nuclear power generating stations. Pages 225–276 *in* L. W. Hesse et al. (eds.), The middle Missouri River. Missouri River Study Group, Norfolk, Nebraska.

Hibbard, C. W. 1970. Pleistocene mammalian local faunas from the Great Plains and central lowland provinces of the United States. Pages 395–433 *in* W. Dort, Jr. & J. K. Jones, Jr. (eds.), Pleistocene and Recent environments of the central plains. University of Kansas Press, Lawrence.

Hoffman, R. S. & J. K. Jones, Jr. 1970. Influence of late-glacial and post-glacial events on the distribution of Recent mammals in the northern Great Plains. Pages 355–394 *in* W. Dort, Jr. & J. K. Jones, Jr. (eds.), Pleistocene and Recent environments of the central plains. University of Kansas Press, Lawrence.

Johnsgard, P. A. 1978. The ornithogeography of the Great Plains states. Prairie Naturalist **10:** 97–112.

———. 1979a. The breeding birds of Nebraska. Nebraska Bird Rev. **47:** 3–16.

———. 1979b. Birds of the Great Plains: Breeding species and their distribution. University of Nebraska Press, Lincoln.

Johnson, K. 1972. The butterflies of Nebraska. J. Res. Lepidoptera **11:** 1–64.

———. 1975. Post-Pleistocene environments and montane butterfly relicts. J. Res. Lepidoptera **14:** 216–232.

———. 1977. A new subspecies of *Pieris sisymbrii* (Pieridae) from western Great Plains relict forests. J. Lepidoptera Soc. **31:** 167–172.

——— **& G. Balogh.** 1977. Taxonomy and evolution of the Nearctic *Lycaena rubidus* Complex, with description of a new species. Bull. Allyn Mus. **43:** 1–62.

Jones, J. K., Jr. 1964. Distribution and taxonomy of mammals of Nebraska. Univ. Kansas Publ., Mus. Nat. Hist. **16:** 1–356.

———**, D. M. Armstrong, R. S. Hoffman & C. Jones.** 1983. Mammals of the northern Great Plains. University of Nebraska Press, Lincoln.

Kantak, G. E. 1983. Niobrara Preserve inventory. 1982 Annual Report. The Nature Conservancy, Minneapolis, Minnesota.

Kaul, R. B. 1975. Vegetation of Nebraska circa 1875. Map, 1:1,000,000, 13 colors. Conservation and Survey Division, University of Nebraska, Lincoln.

———**, Challaiah & K. H. Keeler.** 1983. Effects of grazing and juniper-canopy closure on the prairie flora in Nebraska high-plains canyons. Proc. VII Prairie Conf. **(1980):** 95–105.

Kohler, S. 1977. Revision of North American *Boloria selene* (Nymphalidae) with description of a new species. J. Lepidoptera Soc. **31:** 243–268.

Lakela, O. 1965. A flora of northeastern Minnesota. University of Minnesota Press, Minneapolis.

Larson, G. E. 1979. The aquatic and wetland plants of North Dakota. Ph.D. Dissertation. North Dakota State University, Fargo. 453 pp.

Lawson, M. P., K. F. Dewey & R. E. Neild. 1977. Climatic atlas of Nebraska. University of Nebraska Press, Lincoln.

Lee, D. S., C. R. Gilbert, C. H. Hocutt, R. E. Jenkins, D. E. Jenkins, D. E. McAllister & J. R. Stauffer, Jr. 1980. Atlas of North American freshwater fishes. North Carolina St. Mus. Nat. Sci., Raleigh.

Little, E. L., Jr. 1971. Atlas of United States trees. 1. Conifers and important hardwoods. U.S.D.A. Forest Serv. Misc. Publ. 1146.

———. 1976. Atlas of United States trees. 3. Minor western hardwoods. U.S.D.A. Forest Serv. Misc. Publ. 1314.

———. 1977. Atlas of United States trees. 4. Minor eastern hardwoods. U.S.D.A. Forest Serv. Misc. Publ. 1342.

Lynch, J. D. 1985. Annotated checklist of the amphibians and reptiles of Nebraska. Trans. Nebraska Acad. Sci. **13:** 33–57.

Madsen, T. I. 1985. The status and distribution of the uncommon fishes of Nebraska. M.A. Thesis. University of Nebraska at Omaha.

Mayden, R. L. 1987. Faunal exchange between the Niobrara and White River systems of the North American Great Plains. Prairie Naturalist **19:** 173–176.

Maze, J. 1968. Past hybridization between *Quercus macrocarpa* and *Quercus gambelii.* Brittonia **20:** 321–333.

McAndrews, J. H. 1966. Postglacial history of prairie, savanna, and forest in northwestern Minnesota. Mem. Torrey Bot. Cl. **22:** 1–72.

Melhus, I. E. 1936. Native ferns of Iowa. Iowa St. Coll. Extension Circ. 225.

Mengel, R. M. 1970. The North American Central Plains as an isolating agent in bird speciation. Pages 279–340 *in* W. Dort, Jr. & J. K. Jones, Jr. (eds.), Pleistocene and Recent environments of the central Great Plains. University of Kansas Press, Lawrence.

Miller, L. D. & F. M. Brown. 1981. A catalogue/checklist of the butterflies of America north of Mexico. The Lepidopterists' Society Mem. 2. Serbin Printing Inc., Sarasota, Florida.

Morley, T. 1969. Spring flora of Minnesota. University of Minnesota Press, Minneapolis.

Morris, J., L. Morris & L. Witt. 1972. The fishes of Nebraska. Nebraska Game and Parks Commission.

Moss, E. H. 1983. Flora of Alberta, second ed. rev. by J. G. Packer. University of Toronto Press, Toronto.

Mossman, M. J. & M. A. Brogie. 1983. Breeding status of selected bird species in the Niobrara Valley Preserve area, Nebraska. Nebraska Bird Rev. **51:** 52–62.

Nebraska Natural Resources Commission. 1976. Niobrara River Basin water quality management plan. Nebraska Environmental Control, Nebraska State Office of Planning and Programming, Lincoln.

Nixon, E. S. 1967. A vegetational study of the Pine Ridge of northwestern Nebraska. Southw. Nat. **12:** 134–145.

Opler, P. A. & G. O. Krizek. 1984. Butterflies east of the Great Plains. Johns Hopkins University Press, Baltimore, Maryland.

Perkins, S. G. & E. M. Perkins, Jr. 1967. Revision of the *Limenitis weidemeyerii* complex, with description of a new subspecies (Nymphalidae). J. Lepidoptera Soc. **21:** 213–234.

Petrik-Ott, A. J. 1979. The pteridophytes of Kansas, Nebraska, South Dakota, and North Dakota. Beih. Nova Hedwigia 61. J. Cramer, Vaduz.

Pound, R. & F. E. Clements. 1900. The phytogeography of Nebraska, 2nd ed. Univ. Nebraska Bot. Seminar, Lincoln.

Ritchie, J. C. 1976. The late-Quaternary vegetational history of the western interior of Canada. Canad. J. Bot. **54:** 1793–1818.

Rolfsmeier, S. B., R. B. Kaul & D. M. Sutherland. 1987. New and corrected records of the flora of Nebraska. Trans. Nebraska Acad. Sci. **15** (in press).

Rosche, R. C. 1986. Nebraska butterfly distribution maps. Privately published by the author. B & B Printing, Chadron, Nebraska.

Schaffner, J. H. 1926. Grasslands of the Central United States. Ohio State Univ. Stud., Contr. Bot. **178:** 5–56.

Schultz, C. B., L. D. Martin & M. R. Schultz. 1985. A Pleistocene jaguar from north-central Nebraska. Trans. Nebraska Acad. Sci. **13:** 93–98.

Scott, J. S. 1986. The butterflies of North America. Stanford University Press, Stanford, California.

Sears, P. B. 1935. Glacial and postglacial vegetation. Bot. Rev. **1:** 37–51.

Short, L. L., Jr. 1961. Notes on bird distribution in the central plains. Nebraska Bird Rev. **19:** 2–22.

———. 1965. Hybridization in the flickers (*Colaptes*) of North America. Bull. Amer. Mus. Nat. Hist. **129:** 307–428.

Sibley, C. G. & L. L. Short, Jr. 1959. Hybridization in the bunting (*Passerina*) of the Great Plains. Auk **76:** 443–463.

——— & ———. 1964. Hybridization in the orioles of the Great Plains. Condor **66:** 130–150.

Stasiak, R. H. 1986. New record of the lake chub (*Couesius plumbeus*) from Nebraska. Proc. Nebraska Acad. Sci. **1986:** 29–30.

Stebbins, R. C. 1985. A field guide to western reptiles and amphibians. Houghton Mifflin Co., Boston, Massachusetts.

Steinauer, E. M. & T. B. Bragg. Ponderosa pine (*Pinus ponderosa*) invasion of Nebraska sandhills prairie. Amer. Midl. Naturalist **118** (in press).

Steyermark, J. A. 1963. Flora of Missouri. Iowa State University Press, Ames.

Sutherland, D. M. & R. B. Kaul. 1986. Nebraska plant distribution. Trans. Nebraska Acad. Sci. **14:** 55–59.

Tolstead, W. L. 1942a. Vegetation of the northern part of Cherry County, Nebraska. Ecol. Monogr. **12:** 255–292.

———. 1942b. A note on unusual plants in the flora of northwestern Nebraska. Amer. Midl. Naturalist **28:** 475–481.

———. 1947. Woodlands in northwestern Nebraska. Ecology **28:** 180–188.

Transeau, E. N. 1935. The prairie peninsula. Ecology **16:** 423–437.

Tryon, R. 1980. Ferns of Minnesota, 2nd ed. University of Minnesota Press, Minneapolis.

Van Bruggen, T. 1985. The vascular plants of South Dakota, 2nd ed. Iowa State University Press, Ames.

van der Linden, J. O., D. R. Farrar & S. P. Churchill. 1985. Bryophytes of the loess hills of western Iowa. Proc. Iowa Acad. Sci. **92:** 193–195.

van Haverbeke, D. F. 1968. A population analysis of *Juniperus* in the Missouri River Basin. Taxonomic interrelationships between *Juniperus scopulorum* Sarg. and *J. virginiana* L. in the Missouri River Basin. Univ. of Nebraska Stud., new ser. **38:** 1–82.

Wagner, W. H., Jr. & F. S. Wagner. 1986. Three new species of moonworts (*Botrychium* subg. *Botrychium*) endemic in western North America. Amer. Fern J. **76:** 33–47.

Watts, W. A. & H. E. Wright, Jr. 1966. Late Wisconsin pollen and seed analysis from the Nebraska Sandhills. Ecology **47:** 202–210.

Wells, P. V. 1968. Historical factors controlling vegetation patterns and floristic distributions in the central plains region of North America. Pages 211–221 *in* W. Dort, Jr. and J. K. Jones, Jr. (eds.), Pleistocene and Recent environments of the central plains. University of Kansas Press, Lawrence.

———. 1970. Postglacial vegetational history of the Great Plains. Science **167:** 1574–1582.

———. 1983. Late Quaternary vegetation of the Great Plains. Trans. Nebraska Acad. Sci. **11** (special issue): 83–89.

Wiley, R. W. 1980. *Neotoma floridana.* Mammalian species no. 139, pp. 1–7. Amer. Soc. Mammalogists.

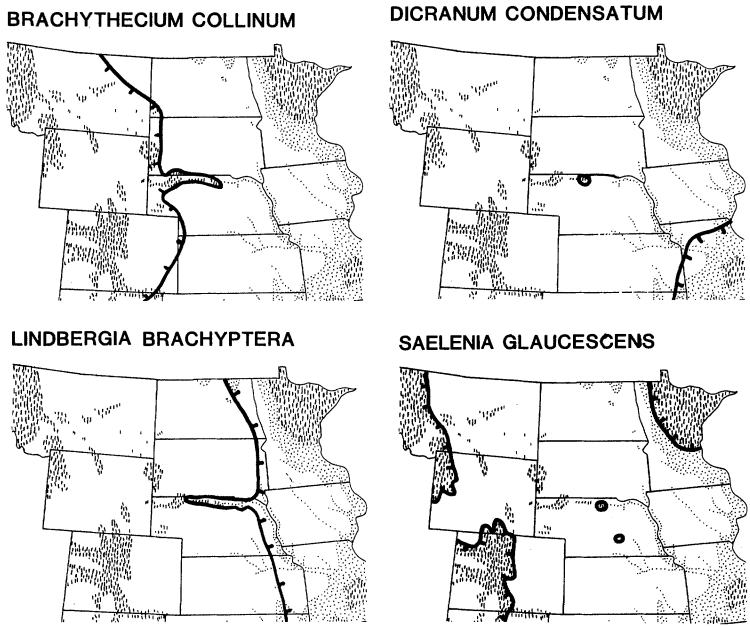
Wright, H. E., Jr. 1968. Vegetational history of the central plains. Pages 159–172 *in* W. Dort, Jr. & J. K. Jones, Jr. (eds.), Pleistocene and Recent environments of the central plains. University of Kansas Press, Lawrence.

———. 1971. Late Quaternary vegetational history of North America. Pages 425–464 *in* K. K. Turekian (ed.), The late Cenozoic glacial ages. Yale University Press, New Haven.

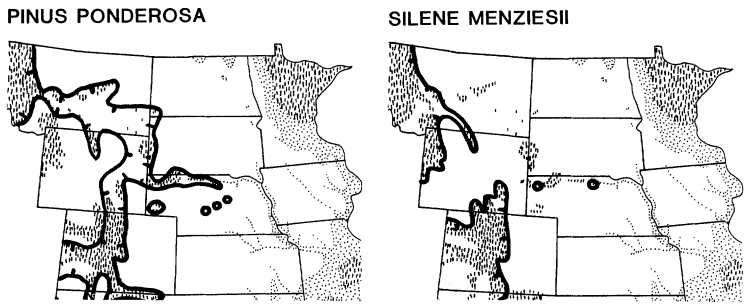
———. 1976. The dynamic nature of Holocene vegetation. Quaternary Res. **6:** 581–586.

———. 1981. Vegetation east of the Rocky Mountains 18,000 years ago. Quaternary Res. **15:** 113–125.

———, **J. C. Almendinger, and J. Grüger.** 1985. Pollen diagram from the Nebraska Sandhills and the age of the dunes. Quaternary Res. **24:** 115–120.

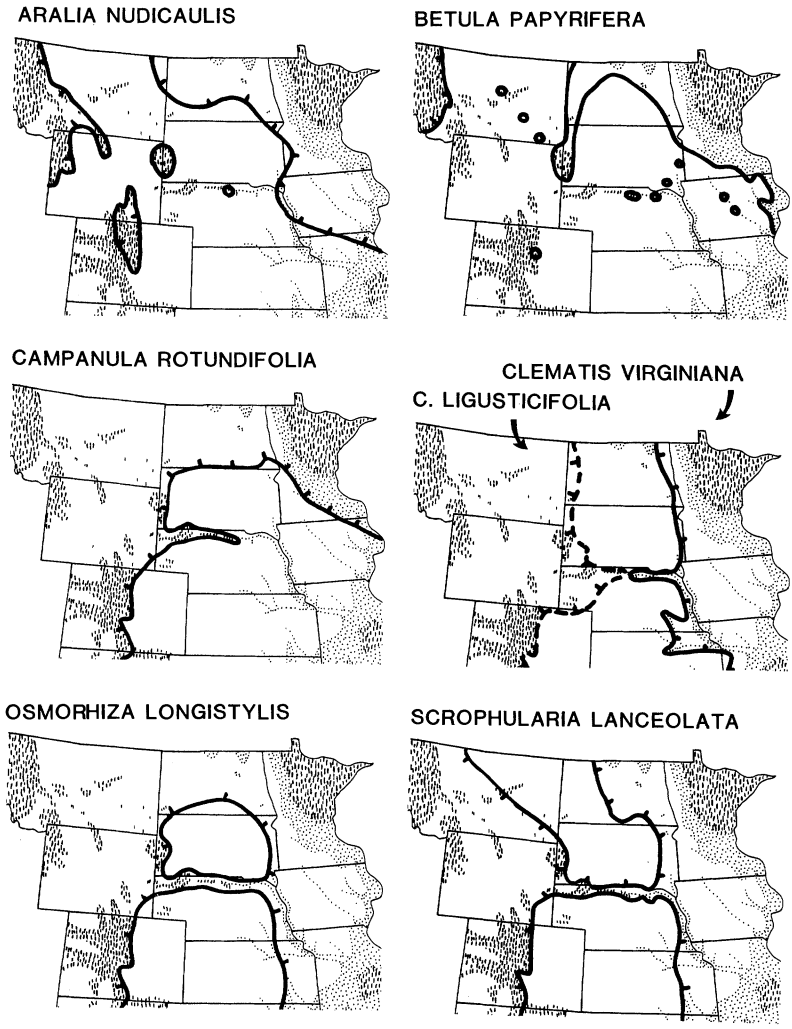


4 MOSSES



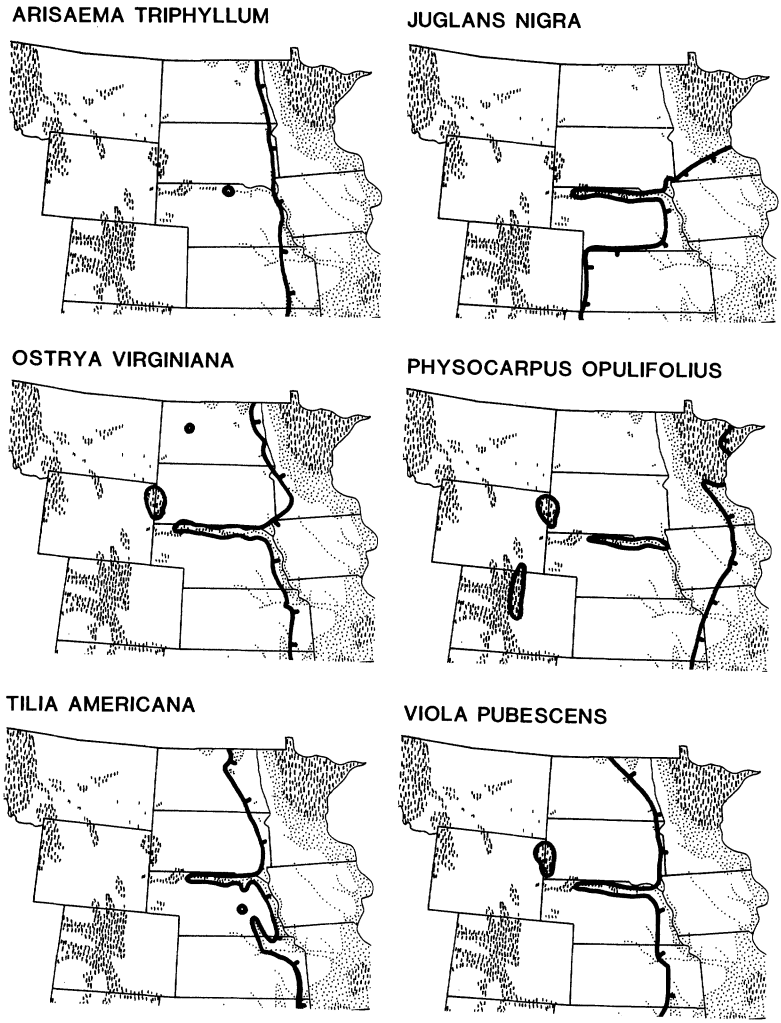
5 VASCULAR PLANTS (WESTERN)

Figs. 4, 5. Representative distributions of mosses and western vascular plants in the Niobrara Valley and central North America. **4.** Four distributional patterns of mosses: western peninsular (*Brachythecium*); eastern disjunct (*Dicranum*); eastern peninsular (*Lindbergia*); eastern-western disjunct (*Saelenia*). **5.** Vascular plants of western phytogeographical affinity, one with nearly continuous (peninsular) distribution (*Pinus*) and one with clearly disjunct distribution (*Silene*).



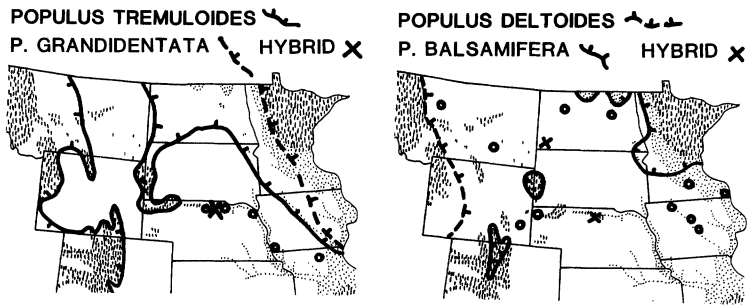
6 VASCULAR PLANTS (EASTERN-WESTERN)

Fig. 6. Representative distributions of vascular plants with main ranges both east and west of the central grasslands, but that are present in the Niobrara Valley: disjunct distributions (*Aralia, Betula*); peninsular distribution (*Campanula*); continuous distributions (*Clematis, Osmorhiza, Scrophularia*).

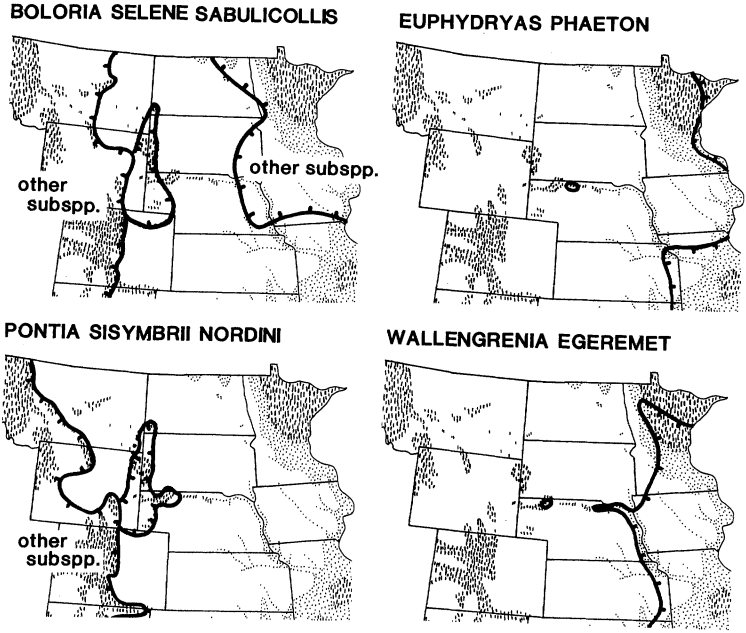


7 VASCULAR PLANTS (EASTERN)

Fig. 7. Representative distributions of vascular plants with main ranges east of the central grasslands, but that occur in the Niobrara Valley: disjuncts (*Arisaema, Physocarpus*); continuous (peninsular) distributions (*Juglans, Ostrya, Tilia, Viola*). *Physocarpus* has other disjunct populations in the Black Hills and Rocky Mountains, and *Ostrya* and *Viola* appear in the Black Hills.

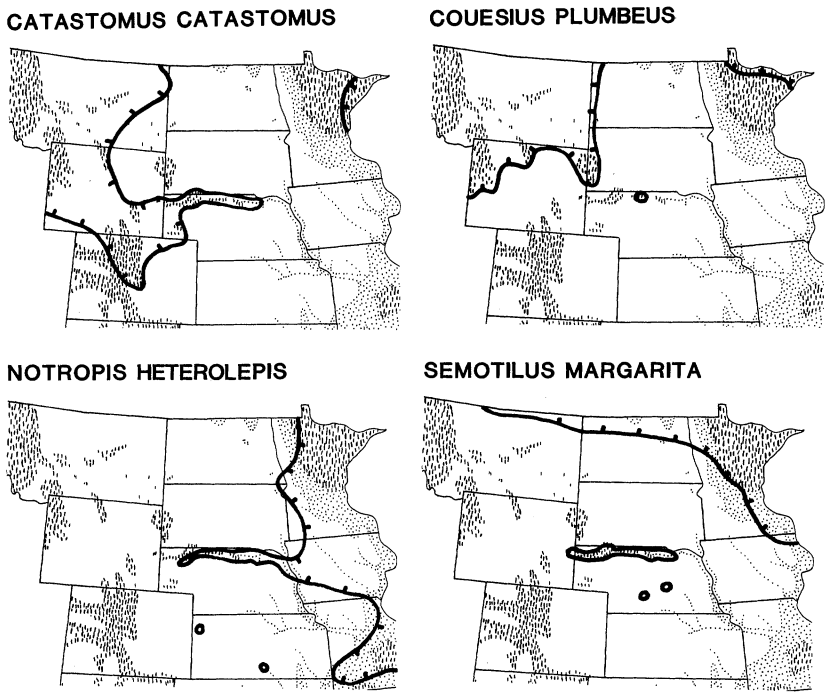


8 VASCULAR PLANTS (DISJUNCT HYBRIDS)



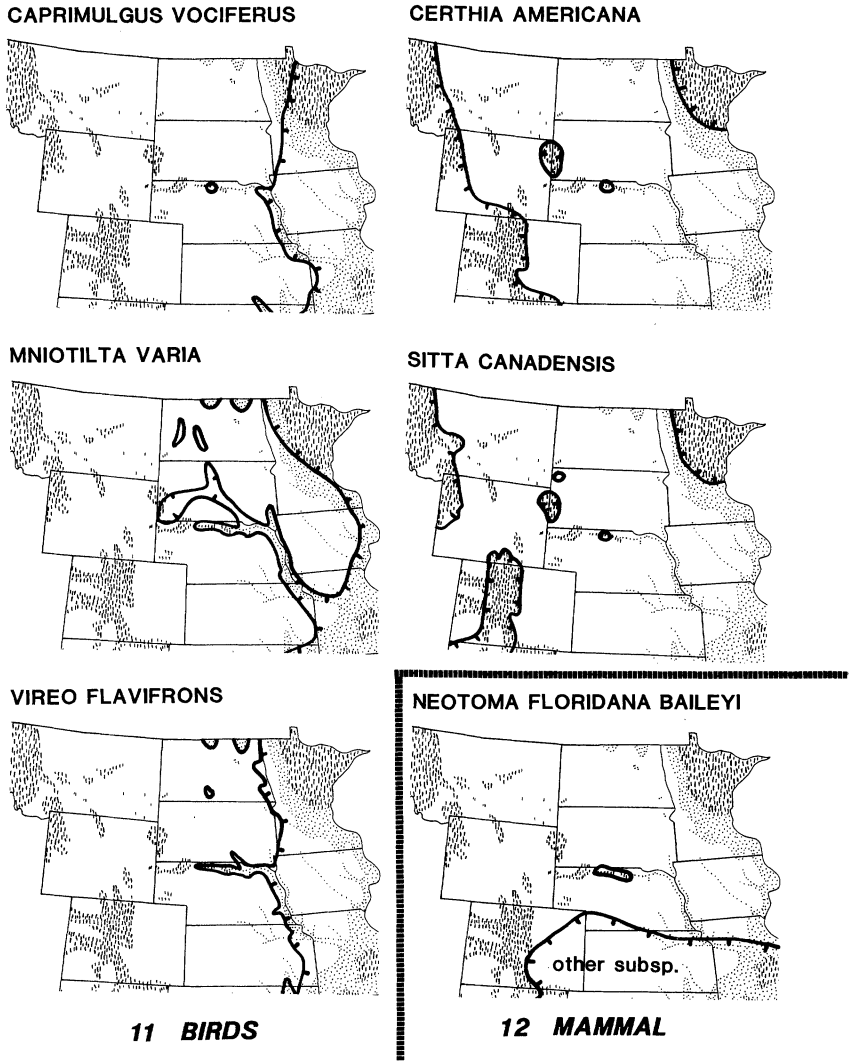
9 BUTTERFLIES

Figs. 8, 9. Distributions of disjunct hybrid vascular plants and of butterflies in the Niobrara Valley. **8.** Disjunct hybrids of vascular plants. *Populus tremuloides* × *P. grandidentata* is known from the Niobrara Valley, as is *P. tremuloides,* which is locally abundant there, but *P. grandidentata* does not now occur closer than central Iowa. *Populus* ×*jackii* (*P. deltoides* × *P. balsamifera*) occurs in the Valley, where one parent, *P. deltoides,* is common but the closest modern population of *P. balsamifera* is in the Pine Ridge northwest of the Valley. **9.** Representative distributions of butterflies. *Boloria* and *Pontia* have subspecies in the upper Niobrara Valley and adjacent Pine Ridge, Black Hills, and forested hills on the high plains. *Euphydryas* and *Wallengrenia* show disjunct occurrences in the Valley from their main ranges to the east.



10 FISHES

Fig. 10. Representative distributions of fishes in the Niobrara Valley. *Catastomus* and *Couesius* are distributed east and west of the Valley, but the former has nearly continuous (peninsular) distribution from the west, while the latter is clearly disjunct. *Notropis* is an eastern fish with continuous distribution westward through the Niobrara Valley. *Semotilus* is distributed both east and west of the Valley, and is disjunct in it and the Platte River Valley.



Figs. 11, 12. Representative distributions of birds and a mammal. **11.** Birds of eastern zoogeographic affinity are represented here by *Caprimulgus, Mniotilta,* and *Vireo.* Birds with breeding distributions both east and west of the Niobrara Valley, with disjunct breeding known from the Valley, are represented by *Certhia* and *Sitta.* **12.** The eastern wood rat is represented in the Valley by its endemic subspecies *Neotoma floridana baileyi,* the several other subspecies occurring well to the east and south of the Valley.