RESEARCH ARTICLE

Changes in Woodland Cover on Prairie Refuges in North Dakota, USA

Todd A. Grant[1]
U.S. Fish and Wildlife Service
J. Clark Salyer National
Wildlife Refuge
681 Salyer Road
Upham, ND 58789 USA

Robert K. Murphy
U.S. Fish and Wildlife Service
Des Lacs National Wildlife
Refuge Complex
8315 Hwy 8
Kenmare, ND 58746 USA

ABSTRACT: Detailed case histories of long-term successional changes in vegetation are crucial for assessing ecological integrity and developing restoration objectives on prairie preserves in North America's northern Great Plains. Such documentation generally is lacking, however. We used aerial photo measurements plus records from land surveyors and other sources to document change in extent of woodland across four National Wildlife Refuges in northern North Dakota during the 1800s and 1900s. Woodlands were rare when Europeans settled the region in the early 1900s, except green ash (*Fraxinus pennsylvanica* Marsh.)-American elm (*Ulmus americana* L.) woodland occurred within the floodplain of the Souris River, and stunted copses of quaking aspen (*Populus tremuloides* Michx.)-bur oak (*Quercus macrocarpa* Michx.) occurred along fire-protected scarps of sandhills prairie in north central North Dakota. Ash-elm woodland expanded in the Des Lacs and Souris River valleys especially along adjoining, intermittent tributaries (coulees) of the Souris River, mainly during the early- to mid-1900s. During the mid- to late-1900s, aspen woodland expanded in sandhills of the Souris Lake Plain and in the Missouri Coteau, changing much of the mixed-grass prairie to parkland. With settlement by people of European descent, large herbivores were extirpated from the region and natural and anthropogenic fires were suppressed. These changes are implicated in expansion of woodland into native prairies.

Index terms: aspen parkland, fire suppression, mixed-grass prairie, plant succession, restoration, woodlands

INTRODUCTION

Northern mixed grass prairie has declined by 61-99% across nearly all states and provinces where it once predominated (Samson and Knopf 1994). This trend continues, with the loss of at least 404,000 ha of native rangeland in North Dakota, South Dakota, and Montana since 1985 (Higgins et al. 2002). The quality of remaining prairie tracts is increasingly diminished by fragmentation, expansion of woody and exotic plants, and loss or misapplication of historic ecological processes, such as fire and herbivory (Samson and Knopf 1994).

Native prairie dominates National Wildlife Refuges (NWRs) and other publicly owned lands in the northern Great Plains. Conservation of native prairie is an appropriate goal on these refuges because the NWR system explicitly embraces ecosystem integrity and the conservation of biological diversity (Gergely et al. 2000). To understand ecosystem integrity and to develop defensible objectives for prairie restoration, managers of NWRs and other preserves in the region should understand the local, historic prairie landscape to determine to what extent its biotic communities have been altered or degraded (Noss 1985). The relationship between plant succession and formative ecological processes (e.g., fire, drought, or herbivory) is poorly understood in the mixed-grass prairie, based often on speculation or generalized accounts from closely related grassland systems. Northern mixed-grass prairie dominates four major NWRs scattered across northern North Dakota. However, woodlands also are a conspicuous component of the contemporary refuge landscapes. Our study objectives for these NWRs were to: (1) approximate the extent of woodland at the time of settlement by persons of European descent (circa 1900), (2) identify types of woodlands and quantify the extent of each following settlement to the establishment of NWRs (circa 1930s) and at subsequent intervals through 1985-1997, and (3) provide a temporal and spatial context for reconstructed woodland vegetation patterns and discuss ecological processes that influenced these patterns.

STUDY AREA

We confined our quantitative analysis to four NWRs (8000 to 24,000 ha) located in north central and northwestern North Dakota (Figure 1). All NWRs lie within the Northern Mixed-grass Prairie Physiographic Region (Coupland 1992). Refuge prairies are within a needlegrass-wheatgrass (*Stipa-Agropyron*) association but are heavily invaded by Eurasian grasses, especially smooth brome (*Bromus inermis* Elyss.) and Kentucky bluegrass (*Poa pratensis* L.). The climate is continental, with short summers and long, cold winters. Annual precipitation, although highly variable, averaged 42 cm across the study

[1] Corresponding author:
todd_grant@fws.gov

Natural Areas Journal 25:359–368

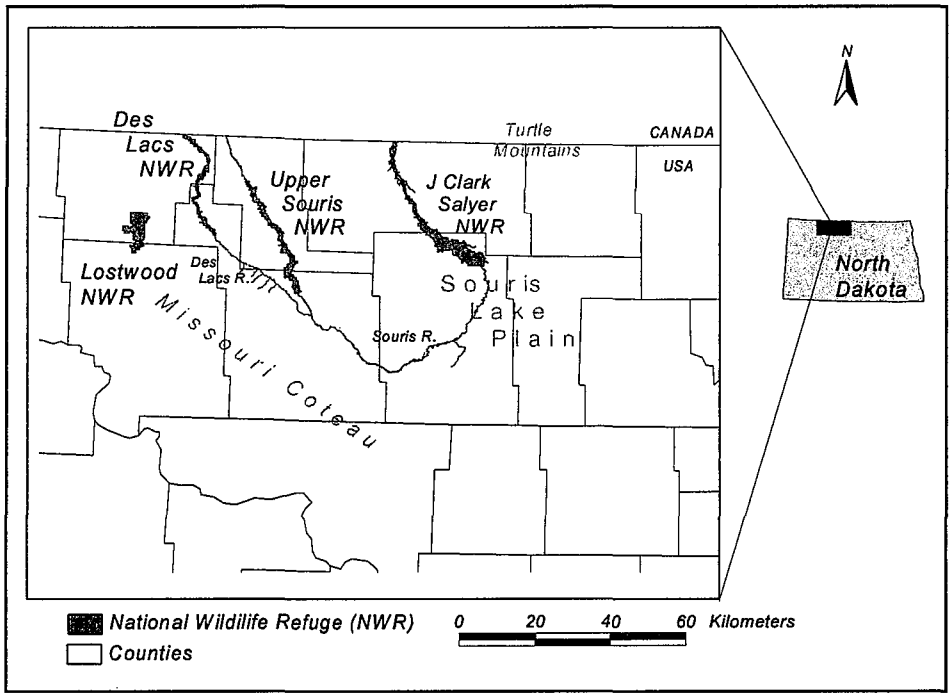

Figure 1. Study area including four National Wildlife Refuges located in north central and northwestern North Dakota.

area from 1936-1990. The geology (i.e., mainly soils and topography) of each refuge was uniquely shaped by the Wisconsin lobe of the Laurentide Ice Sheet during the end of the Pleistocene Epoch (Bluemle 1991). Des Lacs, Upper Souris, and J. Clark Salyer NWRs are associated with the Souris River (Figure 1). The Des Lacs River and upstream portion of the Souris River (encompassing Des Lacs and Upper Souris NWRs) were formed by catastrophic meltwater release from sudden drainage of two large glacial lakes (about 10,000 years ago). Des Lacs and Upper Souris NWRs formed as spillways from these glacial lakes and are characterized by steep, high-relief (1 km wide and 50 m deep) valleys (Lord and Kehew 1990). Soils are mostly well-drained, level to steep loams formed in glacial till. The Souris Lake Plain characterizes the downstream portion of the Souris River drainage (east of Minot, North Dakota, including J. Clark Salyer NWR), and is the remnant of Glacial Lake Souris (Lord and Kehew 1990). The contemporary Souris Lake Plain is a flat, deltaic outwash plain, bordered to the south and east by sandhills formed from wind and wave action of historic Glacial Lake Souris. Soils are mostly sand, gravel, and clay; water drainage is poor near the Souris River and the water table can be close to the surface in sandy soils, especially during years of above average precipitation. Lostwood NWR lies within the 20-km to 30-km wide Missouri Coteau, a physiographic region, chiefly of moderate relief (30-90 m), dead ice moraine deposited by the Wisconsin glacier over a previously occurring escarpment (Bluemle 1991). Surface material is glacial till, composed of thin, gravely, mostly loam soils.

Excluding planted woodlands, four distinct woodland types occur within the study area: (1) **Riparian woodlands** are contained within a narrow (0.2-0.5 km wide) band that borders the meandering Souris River beginning at Upper Souris NWR and ending at J. Clark Salyer NWR. Dominant tree species are green ash (*Fraxinus pennsylvanica* Marsh.), American elm (*Ulmus americana* L.), bur oak (*Quercus macrocarpa* Michx.) and eastern cottonwood (*Populus deltoides* Marsh.); (2) **Coulee woodlands** are contained within numerous intermittent tributaries of the Souris and Des Lacs rivers, on Upper Souris and Des Lacs NWRs. Dominant tree species are green ash, American elm, and box elder (*Acer negundo* L.); (3) **Parkland woodlands** occur within the sandhills complex of J. Clark Salyer NWR and are dominated by aspen (*Populus tremuloides* Michx.) and bur oak. Parkland woodlands also occur at Lostwood NWR and are composed of scattered, small (mean 0.4 ha) aspen copses, often associated with wetland margins (Murphy 1993); (4) **Meadow woodlands** predominate the low, poorly drained soils of J. Clark Salyer NWR and are composed of aspen, balsam poplar (*P. balsamifera* L.), green ash, and willow (*Salix* spp.). Plant nomenclature follows Great Plains Flora Association (1986).

METHODS

We estimated the historical occurrence of woodland within the region from many sources and partitioned our analysis into the following eras: presettlement (1730's to circa 1880), settlement-to-refuge establishment (circa 1880 to 1930's), and refuge era (1930's to present).

Presettlement and settlement-to-refuge establishment eras

We compiled presettlement histories primarily from the published journals and expedition narratives of early naturalists, explorers, and military personnel. We reconstructed settlement-to-refuge establishment histories from Government Land Office Survey (GLO) records on landscape features from the 1880-90s, U.S. Biological Survey (USBS) notes, landscape photographs, narratives from early naturalists, and interviews of local residents.

Refuge era

Aided by a stereoscope, we used a dot-grid to measure the number and extent (ha) of woodland patches on refuge era black and white aerial photographs (1:7,920 and 1:15,840). We quantified the total change in percent woodland, by type, for each refuge from 1938 through 1985, 1991, or 1997. Except, we used a random area sample of 3,277 ha for Upper Souris NWR (i.e., we randomly selected five legal townships which, in total, comprised about 25% of the refuge). We also sought to compare and contrast rates of change among woodland

types that increased or decreased during this 50- to 60-year period and also to comprehend possible effects associated with local edaphic factors and/or influences of refuge management practices. Thus, we quantified rates of change among consecutive, 10- to 15-year intervals using the following methods: (1) At Lostwood NWR, we assessed woodland change among years 1938, 1953, 1969, and 1985 for the entire refuge. We did not sample woodlands at Lostwood after 1985 because prescribed fire was used widely by the late 1980s to reduce parkland woodlands and facilitate restoration of native prairies. (2) At Des Lacs NWR, we compared woodland change for the entire refuge among years 1938, 1953, 1969, 1979, and 1991. (3) At Upper Souris NWR, we selected a random area sample (3277 ha) and compared changes in woodland by type among years 1938, 1953, 1969, 1979, and 1997. (4) At J. Clark Salyer NWR, we assessed the rate of change among years 1938, 1953, 1969, 1979, and 1991. We selected a random sample of 10 legal quarter sections (64 ha; total 650 ha) each for meadow and parkland woodlands. Again, because our focus was to identify periods when woodlands changed significantly, our sample for J. Clark Salyer NWR included only quarter sections with at least 10% increase in woodland coverage during 1938-1991. Differences in sampling among refuges reflect the availability of photos, personnel to adequately document woody vegetation coverage and trends, and management needs of individual refuges.

RESULTS

Presettlement era

General descriptions for north central and northwestern North Dakota suggest a landscape generally bereft of trees, except for luxuriant growth of riparian woodland along the Souris River, and scattered brush and stunted trees in the sandhills of J. Clark Salyer NWR. During 1872-74, a commission surveyed the boundary between Canada and the U.S. Territories; the astronomer for the survey reports, "West of the Turtle Mountains, there is no timber to be found near the line, except along the Mouse (Souris) River. The [boundary] line actually cuts no growth of trees, or even brush of any kind for 600 miles" (Twining 1878:52). Qualitative evidence suggests a nearly treeless landscape in the Missouri Coteau around present day Lostwood NWR. Alexander Henry in his 1806 travels (about 40 km southeast of Lostwood NWR) describes the Missouri Coteau as hills covered with large stones where "there is no wood of any kind" (*in* Coues 1897:315). Captain Featherstonhaugh, in 1872-74, described the Coteau near Lostwood NWR as "this remarkable range of hills runs for some hundreds of miles across the plains from south-east to north-west... perfectly bare of trees" (Featherstonehaugh 1876:38).

In 1853-55, an expedition was commissioned to survey a route of the Pacific Railroad (Stevens 1860). This expedition is particularly useful because engineers and naturalists kept specific records on the occurrence and abundance of trees for use in building track and bridges for the railroad, and their route traversed lands within or near each of the four NWRs in our study. In travel from the Sheyenne River to the Souris River (near present day J. Clark Salyer NWR), they reported, "There is a general destitution of wood throughout this interval, and it is only rarely that one finds a growth of wood on numerous small lakes" (Stevens 1860:21). Traveling upstream toward present day Upper Souris NWR, they reported the "Mouse River is liberally wooded, and I think may be depended upon to furnish 200 miles with sleepers [crossties]" (Stevens 1860:23). Continuing upstream along the Souris River just south of present day Upper Souris NWR, they described the Souris River valley as "wooded, and sometimes heavily wooded, with a growth of elm, oak, ash, and probably with other woods. Its high steep banks are cut by deep coulees, extending back from the river ten and fifteen miles having generally a fertile soil and scattered trees." Moving west, the expedition crossed the Des Lacs River and reported the river "wooded for only a small extent" (Stevens 1860:22). The expedition then headed northwest across the Missouri Coteau where daily journal entries are punctuated with entries of "no wood" (Stevens 1860:362).

A well-traveled trading route extended between the Assiniboine River (southwest Manitoba) and the Manadan and Hidatsa Indian villages along the Missouri River (near Mandan, North Dakota). Traders David Thompson and Alexander Henry, in winter 1797 and summer 1806, respectively, described "Woods End" (a prominent camping spot near the confluence of Willow Creek and the Souris River within present day J. Clark Salyer NWR) as the downstream termination of riparian woodland along the Souris River. Their descriptions of riparian "Aspin [sic], Oak, and Ash all along the River" (*in* Wood and Thiessen 1985) are corroborated by Stevens (1860) and others. Thompson described the sandhills complex as a "range of sandhills with patches of small wood extendg [sic] from the River" (*in* Wood and Thiessen 1985). Henry, returning from the Missouri River, camped at a prominent butte (Buffalo Lodge Lake) 24 km southwest of present day J. Clark Salyer. Looking northeast (across the present day refuge), he stated that "to the N. lies an extensive plain, bounded by a ridge that runs E. and W., over which the Turtle mountain appears. On the left is a level plain, with many small lakes about which numerous herds of buffalo feed. On the right, the plain is also level for about three leagues, where it rises into many high sandy hills; stunted willows and poplars grow in the valleys, but the summits display only white sand" (*in* Coues 1897:410).

Settlement-to-refuge era

Lands that comprise the four NWRs were surveyed by the GLO during the 1890s at the advent of settlement by persons of European descent. GLO surveyors more carefully described occurrences of trees in the western part of our study area where woody vegetation apparently was scarce and thus more noteworthy. For example, surveyors indicated the Lostwood area was treeless prairie, e.g.: "The land in this township is all prairie." Some tall shrub occurred, as on a steep slope above a lakeshore (a place where shrubs still persist despite frequent prescribed fire in the 1980s and 1990s): "Brush on E. shore, cherry [chokecherry, *Prunus virginiana*] and thorn [hawthorn,

Crateagus spp.]." Surveyor references to trees on townships in and around present-day Lostwood NWR were confined to a single area covered with elm: a steep (30°), north-facing slope above a lakeshore that apparently was uniquely invulnerable to fire and allowed establishment of elm and, apparently aspen. Surveyor's notes in the Lostwood area also indicated prevalence of aspen suckers or saplings around wetland borders in the 1890s; accompanying the observation was the notion that, at least through the 1800s, aspen never approached tree size because of recurrent fire.

Settlement of the Lostwood area by people of European descent occurred during 1904-15. The major lake chain on the area, as well as a township and nearby town, were named Lostwood about 1906 because of incidents involving the scarcity of firewood (Williams 1966). R. Kellogg, USBS, examined the area during 10-20 August 1910 (Smithsonian Inst. Archives, Record Unit 7176) and described it thusly: "This region is high prairie country... The only timber in this region was formerly on S.E. corner of Lostwood Lake but this was cut off by the homesteaders and now there is nothing left but small oak [sic; probably elm] and poplar brush, with a clump of willows here and there." F. Uhler explored the "Lostwood Chain of Lakes" for USBS in August 1929 (U.S. Fish and Wildlife Service, unpubl. data). Uhler described uplands as "rolling hills covered with grass and occasional patches of buck brush [western snowberry, *Symphoricarpos occidentalis* Hook.], rose bushes, and silverberry [*Elaeagnus commutata* L.] or a few clumps of stunted trees" (U.S. Fish and Wildlife Service, unpubl. data). LNWR was resurveyed in spring and summer 1935 (U.S. Fish and Wildlife Service, Denver Regional Office, unpubl. data). There were many references to disturbance from settlement such as tilled soils, wagon trails, and fences, but especially striking in this survey was that aspen trees and brush obstructed section lines where no mention of woody vegetation occurred in 1890s survey notes.

Notes from early naturalists and explorers suggested trees were scarce in the valley of present-day Des Lacs NWR during the early to mid-1800s. However, the September 1895 GLO survey of the area indicated that trees were scattered in the deepest coulees – on some steep, north- or northeast-facing slopes and along lakeshores. For example, when crossing deep coulees "in scattering brush... some timber elm, ash and box alder [sic, box elder]" or "a few cottonwoods and elms." And, along a north-facing slope, "Timber on south bluff, elm, ash, and willow, some plum and cherry brush." The description for the township surrounding the "Middle Lake" at Kenmare stated: "The land in this township is all prairie... the bluffs on the S.W. side of the valley are covered in places with poplar and elm brush." And for the next township north: "The land in this township is all prairie... Upper Des Lacs Lake.... [is] generally fringed with a narrow strip of timber, elm ash, oak [sic?], box-alder and cottonwood, with willow brush." Surveyors occasionally used green ash or American elm, reported as "4 inches" to "7 inches" (10-18 cm) in diameter, to mark section corners and reference lines along this valley. In July 1913, R. Kellogg surveyed the Des Lacs area biota and noted: "Numerous coulees and steep gulches cut down into this valley from both sides and many of these are densely wooded or full

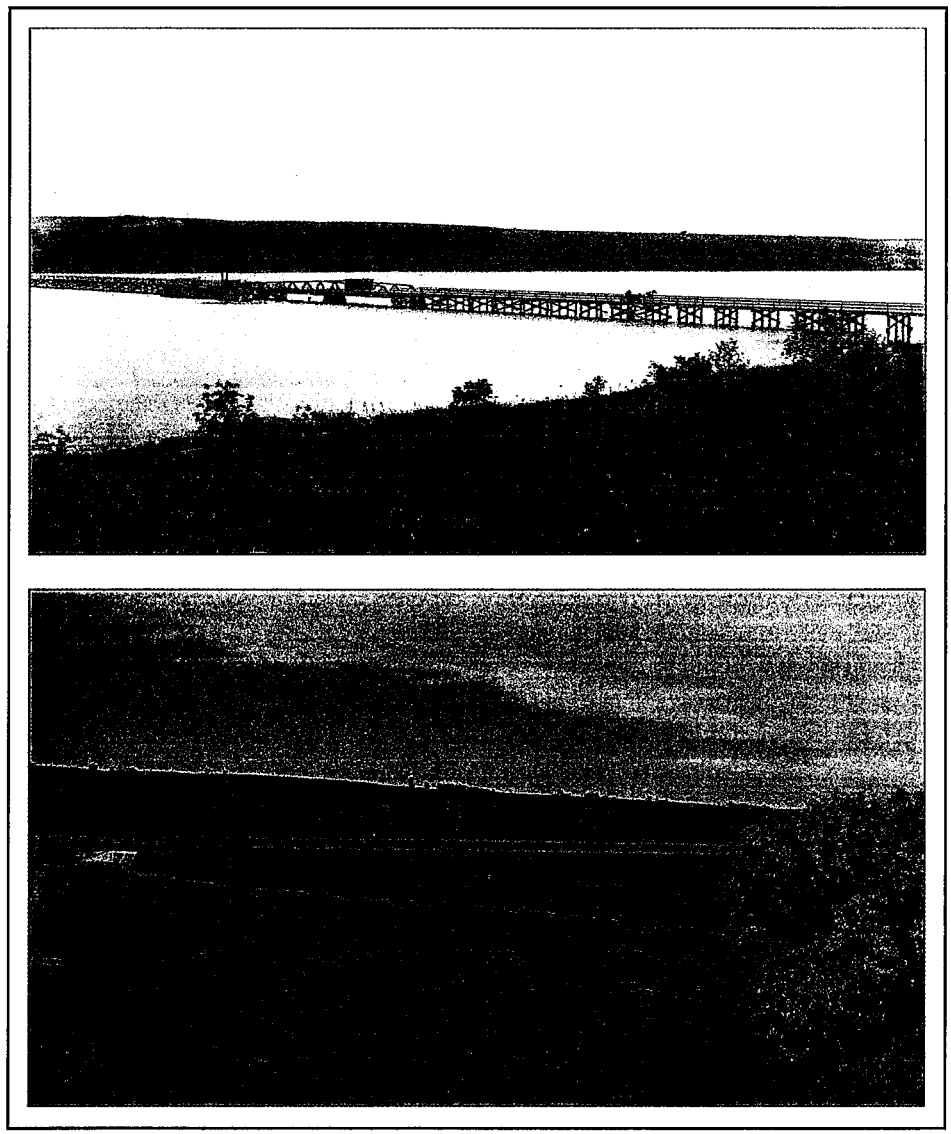

Figure 2. Example of 20th century change in prairie landscapes of north central and northwestern North Dakota: green ash-American elm woodland development along the Upper Des Lacs Lake, viewing from southeast to northwest across state highway 5 at Des Lacs National Wildlife Refuge: top photo, circa 1910; bottom photo, 2004.

Table 1. Changes in percent woodland and total woodland area (ha) on four National Wildlife Refuges in north central and northwestern North Dakota, based on aerial photos.

	J. Clark Salyer		Upper Souris		Des Lacs		Lostwood	
Woodland Type	**1938**	**1991**	**1938**	**1997**	**1938**	**1991**	**1938**	**1985**
Riparian	3.1	3.7	2.3	1.8	--	--	--	--
Coulee	--	--	0.9	3.8	1.7	5.9	--	--
Meadow	0.6	1.9	--	--	--	--	--	--
Parkland	5.4	9.7	--	--	--	--	0.1	0.7
Total % Woody	9	15.3	3.3	5.6	1.7	5.9	0.1	0.7
Refuge Area[a]	23,771	23,771	3,277	3,277	5,850	5,850	10,890	10,890

[a] Data for Upper Souris NWR is based on a sample of 3,277 ha.

of bushes" (Smithsonian Inst. Archives, Record Unit 7176). An early photographer captured the relatively treeless character of the Des Lacs valley during this early 1900s period of settlement (e.g., Figure 2).

Woodlands were more prominent in GLO descriptions of the western part of the Souris River on lands covered by present-day Upper Souris NWR. Surveyors constructed township maps that roughly depicted the extent of woodland along the meandering river channel, which was corroborated by detailed line descriptions in the surveyors' field notes. From the maps and survey notes, it appeared that woodlands bordered roughly half of the length of the river channel, typically on both sides of the river and more extensively around oxbows. There was, apparently, was very little riparian timber in a 22-km stretch of river that today lies north of Lake Darling Dam and is inundated by a reservoir. Bearing trees were used routinely as survey references along the river, including 25-cm to 50-cm diameter American elm.

Coulees along this part of the Souris River are broader than those along the Des Lacs River, and the river valley is more gently sloping. Surveyors' notes indicated woodland cover in many coulees along the west side of the river, e.g.: "Enter brush and timber [at 10 chains]. Leave brush and timber [at 16 chains]." Although it is difficult to quantify the extent of this cover based on the surveyors' records, it appears there was at least one wooded coulee every 1-2 km along the west side of the valley, primarily in the north and south townships within the area now encompassed by Upper Souris NWR.

Significant areas of woodland occurred at J. Clark Salyer NWR by the time GLO surveys were initiated in the area (circa 1884). GLO survey notes for J. Clark Salyer NWR are, therefore, coarse and less useful than for other NWRs.

Refuge era

Percent Change in Woodland Cover

Across the four refuges, total percent woodland has increased drastically since refuge establishment circa 1934-36. Total percent woodland varies among refuges, with a general increase in coverage from west to east (Table 1). Parkland woodlands at Lostwood NWR increased 8-fold during 1938-1985, and were small but widely distributed (mean, 4.8 woodland patches/km^2; mean patch size 0.4 ha), such that three-fourths of the refuge changed from open mixed-grass prairie to aspen parkland (e.g., Figure 3). Parkland woodlands nearly doubled during 1938-1991 at J. Clark Salyer NWR, and account for the greatest percent landscape coverage (about 9%) of any woodland type in the study area. Meadow and coulee woodlands increased 3- to 5-fold during this period, but account

Figure 3. Example of 20th century changes in parkland woodlands (1 km^2) of the Missouri Coteau Landform at Lostwood NWR in northwestern North Dakota. Few aspen woodlands occurred in 1938 (top photo); by 1979 (bottom photo) aspen had established around wetland margins and in brushy draws.

for less than 6% coverage of the current landscape. Riparian woodlands increased marginally at J. Clark Salyer NWR but decreased at Upper Souris NWR due primarily to flooding following construction of Lake Darling Dam in 1936 (Table 1).

Rate of Change in Woodland Cover

Percent cover of parkland woodlands increased at near linear rates on both Lostwood and J. Clark Salyer NWRs (Figure 4). However, subtle differences exist between the two refuges. At Lostwood NWR, the rate of increase for parkland woodlands was less during 1969-1985 than during 1938-1969. Conversely, at J. Clark Salyer NWR, the rate of increase in parkland woodlands was greatest during 1969-1991. The greatest rate of change for coulee woodlands at Des Lacs NWR occurred during 1938-1969, whereas coulee woodlands at Upper Souris have increased at a near constant rate (Figure 4). Meadow woodlands on J. Clark Salyer NWR exhibit the greatest departure from linear growth, with little expansion during 1938-1956 and 1979-1991, but very rapid increases during 1956-1979 (Figure 4).

DISCUSSION

Woodland expansion in the northern Great Plains

One of the most striking features of the Great Plains is the widespread, but local occurrence of woodlands. Many woodlands in the Great Plains are relicts of what were once more extensive forests (Stewart 1953, Axelrod 1985). Woodland encroachment into grasslands is most common in ecotonal or transitional regions that separate major grassland and forest ecosystems. For example, the aspen parkland ecoregion covers a broad geographic area between the boreal forest of northern and eastern Canada and the grasslands of the northern Great Plains (Coupland 1961). Aspen, an early successional woodland species, is the most characteristic tree of the region. Except for lands cleared for agriculture, aspen woodland has expanded into grasslands of the northern Great Plains (e.g., Ewing 1924, Maini 1960, Bailey and Wroe 1974, Anderson and Bailey 1980, Archibold and Wilson 1980). Oak savanna was once widespread across the mid-continent region of North America, occurring as the transition between western prairie and eastern deciduous forest (Anderson 1983, Nuzzo 1986). Bur oak is the most characteristic tree species of savanna, especially in northern latitudes. However,

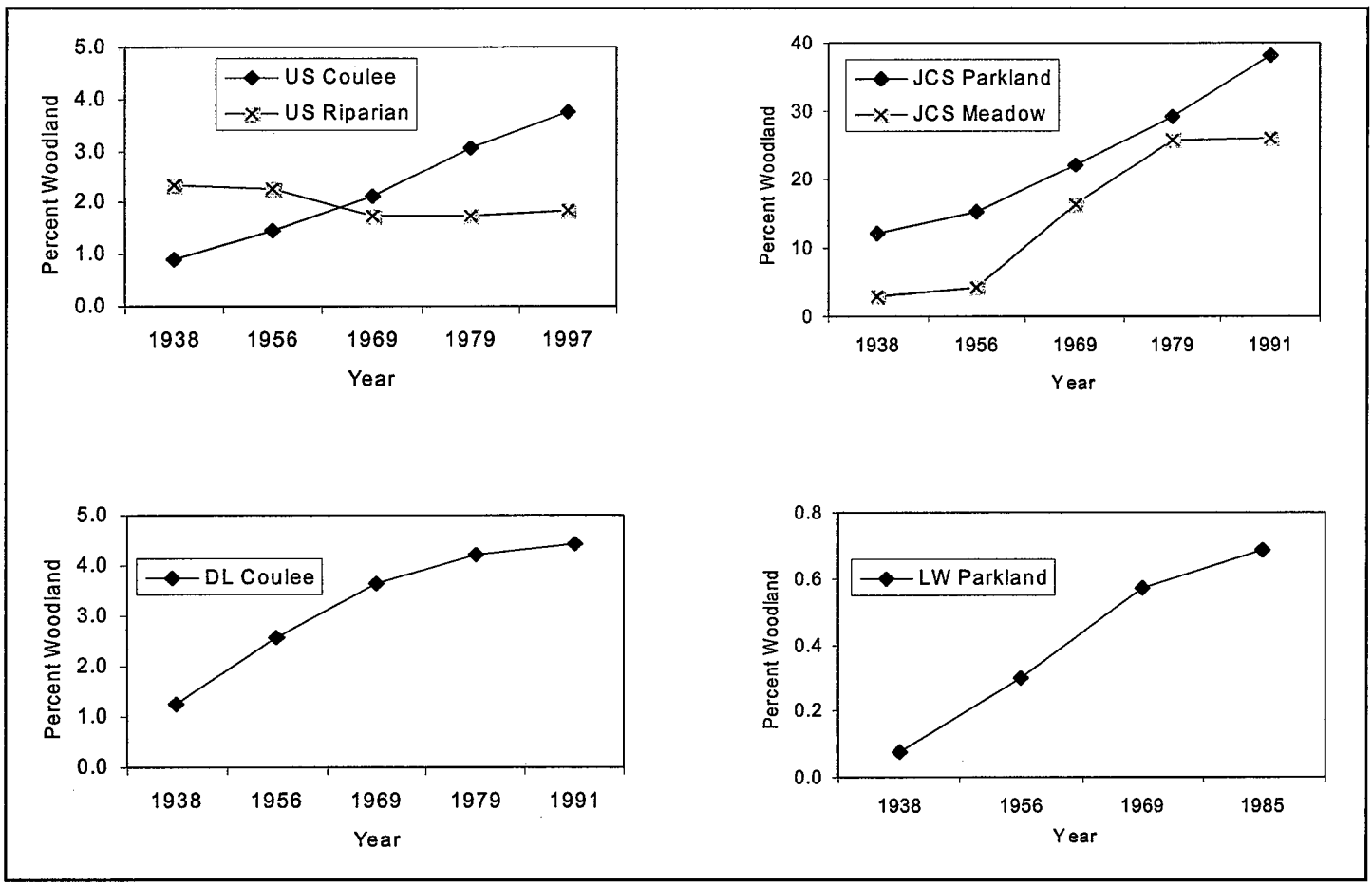

Figure 4. Rate of change in percent woodland during 1938-97 on four National Wildlife Refuges located in north central and northwestern North Dakota, based on the slope of each line between years when aerial photos were available. Upper Souris NWR (US) is based on a sample of 3,277 ha. J. Clark Salyer NWR (JCS) is based on a samples of 10 legal quarter sections (650 ha) each for meadow and parkland woodlands. Rates of change were calculated for the entire refuge for Des Lacs NWR (DL) and Lostwood NWR (LW).

less than 1% of relatively high-quality oak savanna remains (Nuzzo 1986), with losses due mainly to cultivation or through succession of grassland/savanna to closed-canopy, eastern deciduous forest (e.g., McClain and Anderson 1990, McClain et al. 1993, Faber-Langendoen and Davis 1995, Peterson and Reich 2001). Woodlands also have expanded into tallgrass prairies in Kansas (Bragg and Hulbert 1976, Briggs et al. 2002), mixed-grass prairies in Nebraska (Steinauer and Bragg 1987, Steuter et al. 1990), and mixed-grass/shortgrass prairies in western North Dakota (Potter and Green 1964) and Montana (Klement et al. 2001).

Reconstructed patterns of presettlement vegetation

The northern Great Plains are complex ecosystems, composed of plants associated with tallgrass, mixed-grass, and shortgrass prairies, eastern deciduous forests, northern and Rocky Mountain coniferous forests, and desert shrub communities (Axelrod 1985, Manske 1999). During the past 5000 years, woody plants and taller grasses increased during wet periods, but were then displaced by short-stature grasses during dryer periods (Bluemle 1991, Manske 1999). Because of the dynamic nature of Great Plains flora, we should be cautious of idealistic goals that focus only on a static moment in time (i.e., "presettlement conditions") when crafting a vision for the region (Noss 1985). Dynamic shifts in plant species composition may, in part, explain why early accounts offer disparate views of the Great Plains. For example, some accounts describe "tremendous areas of luxuriant grass" or "grass to a horses belly," while others report "a monotonous expanse...small arid hills, the greater part bare or covered with short grasses" or "our horses nearly starved" (see Hart and Hart 1997). More specifically, Higgins (1986a) cautions that accounts of the "treelessness" of the prairies are variable due to the subjectivity of some observers. Noss (1985) further cautions that not all early accounts may be reliable because authors sometimes exaggerated certain qualities of the land to encourage colonization. However, the survival of early explorers in the northern Great Plains required particular attention to three factors: (1) acquisition of food and water, (2) locating fuel for cooking and shelter, and (3) finding forage for horses. We, therefore, suggest that accounts that describe natural or anthropogenic fires, concentrations of (or lack thereof) bison (*Bos bison*), and acquisition of wood for fuel or building are among the more reliable of these early accounts.

As Europeans began to first explore and then settle the northern Great Plains, they gradually replaced natural ecological processes with new disturbances that have altered plant species composition and vegetation structure in grasslands. Chronologically, the first of these changes was the virtual extirpation of vast herds of native herbivores, particularly the bison, circa 1870 in North Dakota (Coues 1878, Hornaday 1889). Second was the suppression of natural and anthropogenic fires following settlement by people of European decent circa 1900. Campbell et al. (1994) proposed that aspen parkland in Alberta first increased following bison extirpation, but 10-20 years before European settlement, because bison inhibited tree expansion by browsing, trampling, wallowing, and toppling. The "scattered brush and timber" described in GLO surveys (10-20 years before homesteading) almost certainly was the progenitor of contemporary aspen-oak woodlands at J. Clark Salyer NWR (e.g., Macoun 1882:105-107, 296). As Campbell et al. (1994) suggest, scattered aspen copses may have expanded rapidly during 1860-1900 after bison were extirpated in the region. With homesteading, free-ranging bison were replaced by livestock restricted to fenced ranges. Cattlemen were particularly attracted to the expansive meadows adjacent to the Souris River (on and near J. Clark Salyer NWR). Frequent, reoccurring livestock grazing can facilitate the expansion of woody plants into grasslands by reducing the frequency and intensity of fires and by altering competition between woody and herbaceous species (Bachelet et al. 2000, Briggs et al. 2002). Fires initially increased in many grasslands of the northern Great Plains circa 1850-1900, probably due to excessive fuel accumulation following extirpation of the bison (Higgins 1986b, Umbanhower 1996). Soon thereafter, fires became less frequent as prairies were plowed, roads were built, and as fires were actively suppressed during settlement (Cutter and Guyette 1994, Umbanhower 1996). Within the context of long-term climatic fluctuations, fire is probably the most important factor in maintaining North American grasslands; recurrent fire shaped grasslands by limiting encroachment of semi-open forests and woodlands (reviewed in Axelrod 1985). Many early explorers recognized the potential for fire to limit the extent of woody plants in the northern Great Plains (e.g., Macoun 1882, Christy 1892, Hind 1969, Higgins 1986b). Recent studies more objectively demonstrate that decreased fire frequency and intensity can exacerbate woodland and forest expansion into northern grasslands (e.g., Bragg and Hulbert 1976, Anderson and Bailey 1980, Faber-Langendoen and Davis 1995, Bachelet et al. 2000, Peterson and Reich 2001, Briggs et al. 2002). Indeed, results of management during the late 1980s to present on Lostwood, J. Clark Salyer, and Des Lacs NWRs suggests that woodland expansion may be controlled by appropriately timed, repeat fires that mimic fire occurrence prior to European settlement (U. S. Fish and Wildlife Service, unpubl. data).

Geomorphology and woodland expansion

Parkland woodlands at Lostwood NWR initially developed in association with numerous wetland basins contained within the knob-and-kettle topography of the Missouri Coteau Landform (Murphy 1993). Once established, aspen expanded rapidly (Figure 4) due to reduced frequency and intensity of fires; expansion was further exacerbated by annual, season-long cattle grazing at light stocking rates. Under the current weather regime, aspen woodland could potentially occupy a significant portion of the Missouri Coteau landform. The Turtle Mountain (200 km northeast of Lostwood NWR; Figure 1) is a landform similar to the Missouri Coteau, with the exception that the former is forested (Bluemle 1991). Except for land cleared for agriculture, aspen-oak woodlands

dominate the contemporary vegetation of the Turtle Mountain, suggesting a similar potential vegetation community for the Missouri Coteau. Early explorers apparently drew similar conclusions. "The [Missouri] Coteau resembled the Turtle Mountain in its physical features and like that district would no doubt be thickly wooded but for prairie fires, which have sometimes run hundreds of miles in dry weather of autumn" (Macoun 1882:63). A similar narrative from 1858 in south-central Saskatchewan states "the Grand Coteau de Missouri. The country east of that natural boundary may be classified as Prairie Country, over the greater portion of which forests of aspen would grow if annual fires did not arrest their progress" (Hind 1969:372).

Establishment of coulee woodlands at Des Lacs and Upper Souris NWRs appear related to the geologic formation of the Souris River and adjoining intermittent tributaries. Before settlement, riparian woodlands were common, typically associated with natural firebreaks created by the meandering channel and oxbow wetlands of the Souris River (from portions of Upper Souris NWR to Woods Ends on J. Clark Salyer NWR) and in large coulees near the Souris and Des Lacs rivers. With fire suppression, environmental conditions favored establishment of taller grasses, brush, and trees in the bottom of deep, narrow coulees. Woodlands have since expanded upslope (away from the river), but remain largely restricted to the coulees, where the unique topography provides suitable microclimate and soil moisture for tree growth (Sieg 1997). The rate of woodland expansion at Des Lacs NWR, in particular, has declined as nearly all available coulee habitat has been occupied (Figure 4).

Parkland woodlands on J. Clark Salyer NWR became established first on the north- and east-facing slopes of sand ridges, and as successional woodlands replaced tall shrub communities (particularly willow) on poorly drained soils. Unlike coulee and riparian woodlands, aspen-oak woodlands in and around J. Clark Salyer NWR are not strongly associated with the Souris River, nor is expansion constrained by topographical features such as draws or coulees. However, parkland woodlands have an affinity for sandy soils, particularly choppy sandhills (e.g., Macoun 1882:105-107, Coupland 1961, Hind 1969:294, Higgins 1986a), or in areas where the water table is close to the surface; both of these features are characteristic of the Souris Lake Plain. Of the four woodland types we studied, parkland woodlands near J. Clark Salyer NWR may be the most invasive and may have exhibited the most dramatic fluctuations in extent prior to settlement (e.g., Hind 1969:308, 336-337, 437).

Herbaceous meadows of J. Clark Salyer NWR likely were maintained historically by fire, periodic spring flooding, and year-round grazing by bison and elk (*Cervus elaphus*; Hanson 1984). After bison were extirpated, meadows were still used as open range by early ranchers and were annually cut for winter livestock forage 10-15 years before the region was widely settled. On poorly drained soils, willow and aspen can quickly invade sedges and grasses in the absence of fire or grazing (Ewing 1924, Buell and Buell 1959, Coupland 1961). Since 1900, natural flows of the Souris River have been altered, first by drainage and channelization and later by construction of low-head dams. Changes in the peak and duration of spring river flows may have altered historic soil moisture in meadows, which could have affected establishment and expansion of meadow woodlands. From 1900 to 1940, annual haying largely replaced fire and grazing as dominant disturbances in meadows of the Souris River. Recurrent clipping of woody sprouts appears effective in limiting the expansion of willow and aspen into these meadows. However, rapid expansion of willow and aspen during the 1960s and 1970s (Figure 4) correspond to several years of high to extreme flooding (1956, 1960, 1969, 1974-76) as the Souris River overflowed its banks and inundated adjacent meadows, thus limiting access by haying equipment.

Management Implications

Herein we describe a landscape that generally was devoid of extensive woodlands prior to European settlement, but one in which woodlands have since increased. Considering the dynamic nature of northern grasslands, in what context should we consider the "presettlement" landscape described in this paper, and is this period appropriate to use when designing a long-term vision for managing natural areas such as NWRs in the northern Great Plains? We can avoid this dilemma by expanding our focus in space and time and, whenever possible, emulate (with management) the ecological processes that shaped northern prairies (Noss 1985, Sieg 1997). A process-oriented vision may best capture the natural range of variability in ecosystem form and function.

Northern mixed-grass prairies evolved with interacting grazing and fire disturbances (Higgins 1986b, Manske 1999), as well as climatic variability (Bragg 1995). Natural and anthropogenic fires occurred roughly every 5-6 years in our study area (Bragg 1995), and the Souris River basin was a significant year-round range for bison (Hanson 1984). Natural fire and grazing regimes (i.e., frequency of occurrence, season of occurrence, and range of variability) should provide a basis for managing native prairies to maintain biotic diversity (Bragg 1995, Sieg 1997), but more research is needed to understand specifically how fire, grazing, and drought interacted to shape northern prairies. Although trees were a minor feature in the historic North Dakota landscape (Higgins 1986a), our data indicate that contemporary woodlands on four NWRs extend beyond their natural limits shaped by climate, fire, and herbivory circa 1700-1870. These increases have been detrimental to grassland-dependent wildlife (e.g., Murphy 1993, Madden et al. 1999, Grant et al. 2004) and can compromise the floristic integrity of native prairies indirectly (e.g., by facilitating invasion by cool-season, Eurasian grasses such as smooth brome; Murphy and Grant 2005). The increases in woodland we documented across northern North Dakota coincided with significant but unquantifiable decreases in the extent and occurrence of fire and grazing disturbances that accompanied settlement of the area by Europeans, followed by management of the lands as NWRs. Reintroduction of fire and grazing on some grasslands within our study area already has resulted in reduc-

tions of woody vegetation and restoration of native prairie communities (Madden et al. 1999). However, some tracts on NWRs we studied may already be so extensively wooded that restoration may not be practical (Grant and Berkey 1999). Managers of natural areas, such as NWRs we studied, will be challenged to determine where such "thresholds" may have been crossed and, optimally, they will allocate their limited management assets to maximize restoration benefits elsewhere.

ACKNOWLEDGMENTS

Rachel Laubhan helped interpret aerial photos for J. Clark Salyer NWR and compiled historical management notes for J. Clark Salyer and Upper Souris NWRs. C. Rubin compiled historical management notes for Des Lacs NWR. K. Smith helped compile GLO surveys for Upper Souris NWR and historical notes for Lostwood NWR. K. Behrend and T. Collingwood assisted with woodland summations. P. Carlson provided access to the E. H. Gross historic photo collection for the Des Lacs NWR area. K. Higgins, C. Sieg, K. Smith, and L. Strong improved earlier drafts of the manuscript.

This project was supported by funding from the U. S. Fish and Wildlife Service, Department of Refuges and Wildlife, and by a grant from the Joint Fire Science Program.

Todd A. Grant and Robert K. Murphy are the Wildlife Biologists for the U.S. Fish and Wildlife Service's National Wildlife Refuges and Wetland Management Districts in northwestern and north central North Dakota, respectively. They have broad interests in the ecology, restoration, and enjoyment of native prairie-wetland communities in the northern Great Plains.

LITERATURE CITED

Anderson, H.G., and A.W. Bailey. 1980. Effects of annual burning on grassland in the aspen parkland of east-central Alberta. Canadian Journal of Botany 58:985-996.

Anderson, R.C. 1983. The eastern prairie-forest transition – an overview. Pages 86-92 *in* R. Brewer, ed., Proceedings of the Eighth North American Prairie Conference, August 1-4, 1982. Western Michigan University, Kalamazoo, Mich.

Archibold, O.W., and M.R. Wilson. 1980. The natural vegetation of Saskatchewan prior to agricultural settlement. Canadian Journal of Botany 58:2031-2042.

Axelrod, D.I. 1985. Rise of the grassland biome, central North America. Botanical Review 51:163-201.

Bachelet, D., J.M. Lenihan, C. Daly, and R.P. Neilson. 2000. Interactions between fire, grazing and climate at Wind Cave National Park, S.D. Ecological Modelling 134:229-244.

Bailey, A.W., and R.A. Wroe. 1974. Aspen invasion in a portion of the Alberta parklands. Journal of Range Management 27:263-266.

Bluemle, J.P. 1991. The Face of North Dakota, Rev.ed. Educational series 21. North Dakota Geological Survey, Bismarck, ND.

Bragg, T.B. 1995. The physical environment of Great Plains grasslands. Pp. 49-81 *in* A. Joern and K.H. Keeler, eds., The Changing Prairie. Oxford University Press, New York, NY.

Bragg, T.B., and C. Hulbert. 1976. Woody plant invasion of unburned Kansas bluestem prairie. Journal of Range Management 29:19-24.

Briggs, J.M., G.A. Hoch, and L.C. Johnson. 2002. Assessing the rate, mechanisms, and consequences of the conversion of tallgrass prairie to *Juniperus virginiana* forest. Ecosystems 5:578-586.

Buell, M.F., and H.F. Buell. 1959. Aspen invasion of prairie. Bulletin of the Torrey Botanical Club 86:264-265.

Campbell, C., I.D. Campbell, C.B. Blyth, and J.H. McAndrews. 1994. Bison extirpation may have caused aspen expansion in western Canada. Ecography 17:360-362.

Christy, R.M. 1892. Why are the prairies treeless? Proceedings Royal Geographic Society 14:78-100.

Coues, E. 1878. Field notes on birds observed in North Dakota and Montana along the forty-ninth parallel during the seasons of 1873 and 1874. Bulletin U.S. Geological Survey Territories 4:545-661.

Coues, E. 1897. New light on the early history of the great northwest: the manuscript journals of Alexander Henry and of David Thompson 1799-1814, Vol. 1, The Red River of the North. F. P. Harper, New York.

Coupland, R.T. 1961. A reconsideration of grassland classification in the northern Great Plains of North America. Journal of Ecology 49:135-167.

Coupland, R.T. 1992. Mixed prairie. Pages 151-182 *in* R. T. Coupland, ed., Ecosystems of the World: Natural Grasslands. Elsevier Press, New York.

Cutter, B.E., and R.P. Guyette. 1994. Fire frequency on an oak-hickory ridgetop in the Missouri Ozarks. American Midland Naturalist 132:393-398.

Ewing, J. 1924. Plant succession of the brush-prairie in north-western Minnesota. Journal of Ecology 12:238-266.

Faber-Langendoen, D., and M.A. Davis. 1995. Effects of fire frequency on tree canopy cover at Allison Savanna, eastcentral Minnesota, USA. Natural Areas Journal 15:319-328.

Featherstonhaugh, R.E. 1876. Narrative of the operations of the British North American Boundary Commission 1872-76. From the Professional Papers of the Corps of Royal Engineers, Volume XXIII.

Gergely, K., J.M. Scott, and D. Goble. 2000. A New Direction for the U.S. National Wildlife Refuges: the National Wildlife Refuge System Improvement Act of 1997. Natural Areas Journal 20:107-118.

Grant, T.A., and G.B. Berkey. 1999. Forest area and avian diversity in fragmented aspen woodland of North Dakota. Wildlife Society Bulletin 27:904-914.

Grant, T.A., E.M. Madden, and G.B. Berkey. 2004. Tree and shrub invasion in northern mixed-grass prairie: implications for breeding grassland birds. Wildlife Society Bulletin 32:807-818.

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

Hanson, J.R. 1984. Bison ecology in the northern plains and a reconstruction of bison patterns for the North Dakota Region. Plains Anthropologist 29:93-113.

Hart, R.H., and J.A. Hart. 1997. Rangelands of the Great Plains before European settlement. Rangelands 19:4-11.

Hind, H.Y. 1969. Narrative of the Canadian Red River Exploring Expedition of 1857, and of the Assinniboine [sic] and Saskatchewan Exploring Expedition of 1858. Vol. 1. Greenwood Press, New York.

Higgins, K.F. 1986a. Evidence of the historical occurrence of woody plants in areas of North Dakota grasslands. Proceedings North American Prairie Conference 9:115-117.

Higgins, K.F. 1986b. Interpretation and compendium of historical fire accounts in the northern Great Plains. Resource Publication 161, U.S. Fish and Wildlife Service, Washington, D.C.

Higgins, K.F., D.E. Naugle, and K.J. Forman. 2002. A case study of changing land use practices in the Northern Great Plains, USA: an uncertain future for waterbird conservation. Waterbirds 25:42-50.

Hornaday, W.T. 1889. The extermination of the American bison, Vol. 2, Pt. 2. Annual Report Smithsonian Institute (1887), Washington, D.C.

Klement, K.D., R.K. Heitschmidt, and C.E. Kay. 2001. Eighty years of vegetation and landscape changes in the Northern Great Plains: a photographic record. Conservation Research Report No. 45, U.S. Department of Agriculture, Agricultural Research Service, Miles City, Mont.

Lord, M.L., and A.E. Kehew. 1990. Geomorphology of the Souris River Valley, Saskatchewan, North Dakota, and Manitoba. Journal of the North Dakota Archaeological Association 4:8-16.

Macoun, J. 1882. Manitoba and the Great Northwest. World Publishing, Guelph, Ont.

Madden, E.M., A.J. Hansen, and R.K. Murphy. 1999. Influence of prescribed fire history on habitat and abundance of passerine birds in northern mixed-grass prairie. Canadian Field-Naturalist 113:627-640.

Maini, J.S. 1960. Invasion of grasslands by *Populus tremuloides* in the northern Great Plains. Ph.D. diss., University of Saskatchewan, Saskatoon.

Manske, L.L. 1999. Prehistoric conditions of rangelands in the northern Great Plains. Summary Range Management Report DREC 99-3015, North Dakota State University, Dickinson.

McClain, W.E., and E.A. Anderson. 1990. Loss of hill prairie through woody plant invasion at Pere Marquette State Park, Jersey County Illinois. Natural Areas Journal 10:69-75.

McClain, W.E., M.A. Jenkins, S.E. Jenkins, and J.E. Ebinger. 1993. Changes in the woody vegetation of a bur oak savanna remnant in central Illinois. Natural Areas Journal 13:108-114.

Murphy, R.K. 1993. History, nesting biology, and predation ecology of raptors in the Missouri Coteau of northwestern North Dakota. Ph.D. diss., Montana State University, Bozeman.

Murphy R.K., and T.A. Grant. Land management history and floristic integrity in mixed-grass prairie, North Dakota, USA. Natural Areas Journal, 25:351-358.

Noss, R.F. 1985. On characterizing presettlement vegetation: how and why. Natural Areas journal 5:5-19.

Nuzzo, V.A. 1986. Extent and status of Midwest oak savanna presettlement and 1985. Natural Areas Journal 6:6-36.

Peterson. D.W., and P.B. Reich. 2001. Prescribed fire in oak savanna: fire frequency effects on stand structure and dynamics. Ecological Applications 11:914-927.

Potter, L.D., and D.L. Green. 1964. Ecology of ponderosa pine in western North Dakota. Ecology 45:10-23.

Samson, F.B, and F.L. Knopf. 1994. Prairie conservation in North America. Bioscience 44: 418-421.

Sieg, C.H. 1997. The role of fire in managing for biological diversity on native rangelands of the Northern Great Plains. Proceedings of the symposium on Conserving Diversity of the Northern Great Plains, August 17, 1995. General Technical Report RM-298, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ft. Collins, Colo.

Stevens, Isaac I. 1860. Reports of explorations and surveys to ascertain the most practicable and economical route for a railroad from the Mississippi to the Pacific Ocean, 1853-55. 36th Congress, 1st Session, Ex. Doc. 46, Vol. XII, Book I. Washington, D.C.

Steinauer, E.M., and T.B. Bragg. 1987. Ponderosa pine (*Pinus ponderosa*) invasion of Nebraska Sandhills prairie. American Midland Naturalist 118:358-365.

Steuter, A.A., B. Jasch, J. Ihnen, L.L. Tieszen. 1990. Woodland/grassland boundary changes in the Middle Niobrara Valley of Nebraska identified by ^{13}C values of soil organic matter. American Midland Naturalist 124:301-308.

Stewart, O.C. 1953. Why are the Great Plains treeless? Colorado Quarterly 2:40-50.

Twining, W.J. 1878. Astronomers report: Survey of the boundary between the territory of the United States and the Possession of Great Britain from the Lake of the Woods to the summit of the Rocky mountains. Government Printing Office, Washington, D.C.

Umbanhowar, C.E., Jr. 1996. Recent fire history of the Northern Great Plains. American Midland Naturalist 135:115-121.

Williams, M.A.B. 1966. Origins of North Dakota Place Names. Bismarck Tribune, Bismarck, N.Dak.

Wood, W.R., and T.D. Thiessen (eds.). 1985. Early Fur Trade on the Northern Plains. University of Oklahoma Press, Norman.