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Historic Distribution and Ecology of Tall-Grass Prairie in Western Canada

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ABSTRACT Rapid settlement and agricultural development of Western Canada in the late 1800s and early 1900s nearly eliminated the tall-grass prairie, and pre-empted a detailed description by ecologists. A combination of literature review and historical ecological analysis of soils, climate, and composition data are applied to estimate the historic distribution, and area occupied by tall-grass prairie in southern Manitoba and south-eastern Saskatchewan, Canada. The resulting area estimate of 20,830 km^2 is more than three times any previously reported value. Some confusion of terms from the first half of the 1900s, and the impact of invasive species on vegetation patterns observed in the past 50 years, likely disguised the original distribution of tall-grass prairie. Protection and conservation efforts should now cast their nets wider to seek remnant prairies beyond the Red River valley, particularly westward along the Assiniboine, Qu'Appelle, and Souris rivers. Prospects are limited for managing these small fragments in a way that emulates the former natural disturbance regime of floods, fires, and bison grazing, but conservation and restoration efforts should continue.

KEY WORDS biogeography, conservation, historical ecology, tall-grass prairie

Tall-grass prairie occupies a wedge-shaped area in the middle of North America, over a 2,500 km distance north-south, from Texas to Manitoba (Risser et al. 1981). East-west, tall-grass prairie occupies a narrow area at the northern and southern extremes, but extends up to 500 km in width between Kansas and Illinois (Transeau 1934). Tall-grass prairie in Western Canada exists only as a small remnant of the former distribution (Fig. 1), and land use practices on those remnants impose new and different disturbance patterns compared to historical conditions. The rapid decline of tall-grass prairie pre-empted an opportunity to fully describe the distribution and ecology of this ecosystem (Ralston 1968), and a forensic reconstruction of either has not yet been undertaken. Future conservation and restoration efforts can apply this knowledge to help survey for, discover, and protect remnant prairies and to design management approaches that simulate natural patterns to the extent possible (Samson and Knopf 1994, Swetnam et al. 1999).

We took several approaches to reconstruct the distribution and ecology of tall-grass prairie in Western Canada. With a historical ecology approach (Egan and Howell 2001), we reviewed archived maps, land survey records, farm census data, soil survey maps and reports, as well as published literature prior to 1960 to determine the original distribution and rate of decline. Taking a biogeographic approach, we reviewed available species occurrence, frequency, and cover data sampled after 1960 to illustrate what remains. Our synthesis integrates climate data and ecological land classifications, with the historical and recent data sources to produce a map with associated tabular data of the likely distribution and variation in Western Canada's tall-grass prairie. Combined with conceptual models of grazing and fire variation within the core area, this review should help guide future conservation and restoration efforts in the region.

WHAT IS TALL-GRASS PRAIRIE?

Tall-grass or "true" prairie was most comprehensively described by Weaver (1954) who distinguished two main associations of "lowland" and "upland" prairie, with big bluestem (*Andropogon gerardii* Vitman) and little bluestem (*Schizachyrium scoparium* Michx.) both ubiquitous and co-dominant. Those community types, or slight variants thereof, have become entrenched in ecological classification schemes used in Canada (Wiken 1986, Smith et al. 1998) and the United States (Kuchler 1964, Bailey 1978, Omernik 1987, USEPA 1996). Nearly all species listed as principal components by Weaver (1954) and Risser et al. (1981) also occur in Western Canadian tall-grass prairie. Weaver notes that Indian grass (*Sorghastrum nutans* [L.] Nash) is progressively less abundant in the north, whereas two other grasses represent dominants along a moisture gradient, with switchgrass (*Panicum virgatum* L.) along the mesic portion, and prairie cord grass (*Spartina pectinata* Bosc ex Link) in more hydric environments, relative to big and little bluestem. Ralston (1968) described similar upland and lowland community types within the confines of the Red River valley, east of the Manitoba Escarpment (Fig. 1).

Lowland tall-grass prairies are dominated by these few, C_4 tall-grasses, and transition towards a wet-meadow community common to boreal fens (Warner and Rubec 1997) and prairie marshes (Walker and Coupland 1970, Stewart and Kantrud 1972). Mixtures with tall C_3 grasses like small reed grass (*Calamagrostis inexpansa* A. Gray), common river grass (*Scholochloa festucacea* [Willd.] Link), slender wheatgrass (*Elymus trachycaulus* [Link] Gould ex Shinners),

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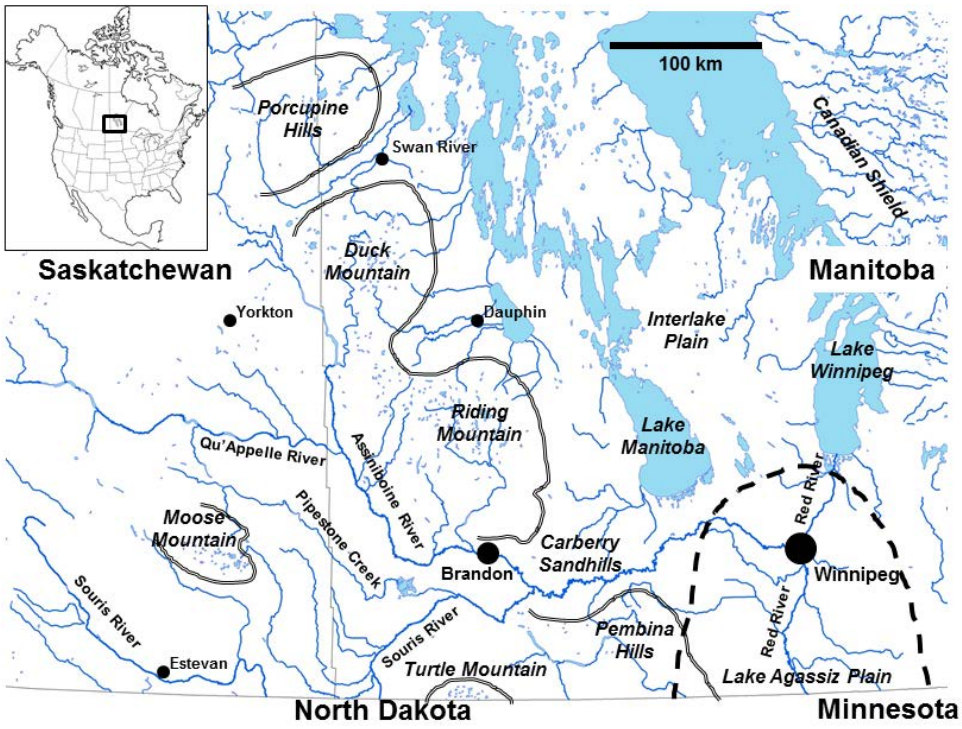

Figure 1. Major cities, uplands, escarpments, plains, water bodies and streams mentioned in the text, and the boundary of tall-grass prairie in Manitoba (bold dashed line) previously estimated by Joyce (1989).

and tufted hair grass (*Deschampsia caespitosa* [L.] P. Beauv.) along with sedges (*Carex*) and rushes (*Juncus*, *Eleocharis*, *Scirpus*, *Typha*) are common in lowland prairie. Where salinity increases, the C_4 mat muhly (*Muhlengergia richardsonis* [Trin.] Rydb.) becomes more prevalent (Ralston 1968). Conversely, upland tall-grass prairies are increasingly dominated by little bluestem, porcupine grass (*Hesperostipa spartea* [Trin.] Barkworth), and/or prairie dropseed (*Sporobolus heterolepis* [A. Gray] A. Gray), with a sub-dominant presence of big bluestem or side-oats grama (*Bouteloua curtipendula* [Michx.] Torr.; Weaver 1954). Risser et al. (1981) did not consider the latter upland prairie to be "true" tall-grass prairie, but some hybrid with mixed-grass prairie. However, Ralston (1968) described the Red River valley as a mosaic of both upland and lowland communities, separated on the basis of soil texture and duration of inundation following flooding. All of these upland species are also present and sometimes frequent in remnant prairies of south-western Manitoba (Wilson and Shay 1990, Mansell and Moore 1999, Kowalchuk 2003), but are absent from mixed-grass prairie to the west in Alberta and Saskatchewan (Coupland 1950).

Sandhill prairie in southern Manitoba appears to be a variant on tall-grass prairie, as multiple authors (Bird 1927, Ralston 1968, Ward 1980, Shay et al. 2000, Gorrie 2002) indicate big bluestem and little bluestem are among the dominant grasses, but further west in the Canadian prairies these species are not present in sand dune systems (Hulett et al. 1966). The bluestems are mixed with other C_4 tall grasses like sand reed grass (*Calamovilfa longifolia* [Hook.] Scribn.), and sand dropseed (*S. cryptandrus* [Torr.] A. Gray), and C_3 grasses like Indian rice grass (*Achnatherum hymenoides* [Roem. & Schult.] Barkworth), Canada wild rye (*E. canadensis* L.) and sand dune wheatgrass (*E. lanceolatus* [Scribn. & J.G. Sm.] Gould *ssp. psammophilus* [J.M. Gillett & H. Senn] Á. Löve).

A more specific, regional description for Western Canadian tall-grass prairie has evaded us for two reasons: 1) a limited area and sample of natural vegetation now remains, and 2) what does remain has been transformed by cumulative effects of land use and alien species invasions since the late 1800s. Little published research describes upland or lowland tall-grass prairie on uncultivated lands in southern Manitoba (Ralston 1968, Levin and Keleher 1969, Smeins and Olson 1970, Gorrie 2002, Faber and Markham 2011). Many authors in Manitoba, Saskatchewan, and North Dakota recognize the problem of alien invasive species altering the composition of remnant grasslands (Wilson and Belcher 1989, Mansell 1995, Thorpe 2007, Grant et al. 2009, Koper et al. 2010). Often what persists in a native state are biased examples of atypically wet and saline sites (Faber and Markham 2011), or rapidly-drained xeric sites (Wilson and Shay 1990), upon which whole regions may be mistakenly described without reference sites on more widespread soils. Because current

conditions and characteristics of tall-grass prairie differ dramatically from the historic conditions, it is difficult to understand or describe the expected composition and structure prior to severe anthropogenic disturbance.

The provincial agency, Manitoba Conservation, adopted a grassland classification system used by The Nature Conservancy in North Dakota, but even the adoptee (Greenall 1996) recommended that quantitative descriptions of Manitoba sites were needed to confirm whether those community types actually exist in Manitoba. Conversely, although detailed inventories have been conducted for most federally-managed Indian Reserves or Community Pastures in south-eastern Saskatchewan (Thorpe 2007), sampling tends to purposely avoid the atypical ecosites or community types, and may have overlooked smaller patches of tall-grass prairie at the western-most periphery.

THE DECLINE OF WESTERN CANADIAN TALL-GRASS PRAIRIE

Land survey records from the 1870s provide a broad overview of the past vegetation in southern Manitoba. Hanuta (2007) examined land survey records from 170 townships (16,000 km^2) south of Winnipeg and extending east to west 180 km from Steinbach to Portage la Prairie. At that time, there was a high proportion of forest (35%) and wetlands (10%), but still a dominance of prairie (55%) throughout this region. Of the forest cover, half was called "scrub" that appeared to be in various stages of recovery from fire, with significant windthrow and burned wood visible. Forest was unevenly distributed along the western sandhills and uplands between Portage la Prairie and Morris, or along the east side of the Red River where trees were protected from fires driven by prevailing westerly winds. Wetlands also were extensive in the level Red River valley, such that some were as large as several townships. Most of the Red River valley was open prairie and wetlands, extending 100 km wide along the U.S. border.

Cultivation began in small areas in the early 1800s, and a census of the Selkirk settlement indicated only 871 ha had been cultivated by 1831, and 3,564 ha by 1856 (Ehrlich et al. 1953). Once the railways were in place after the 1870s, the rate of cultivation greatly accelerated, and the area of improved land increased in farm census records (Fig. 2). Ex-

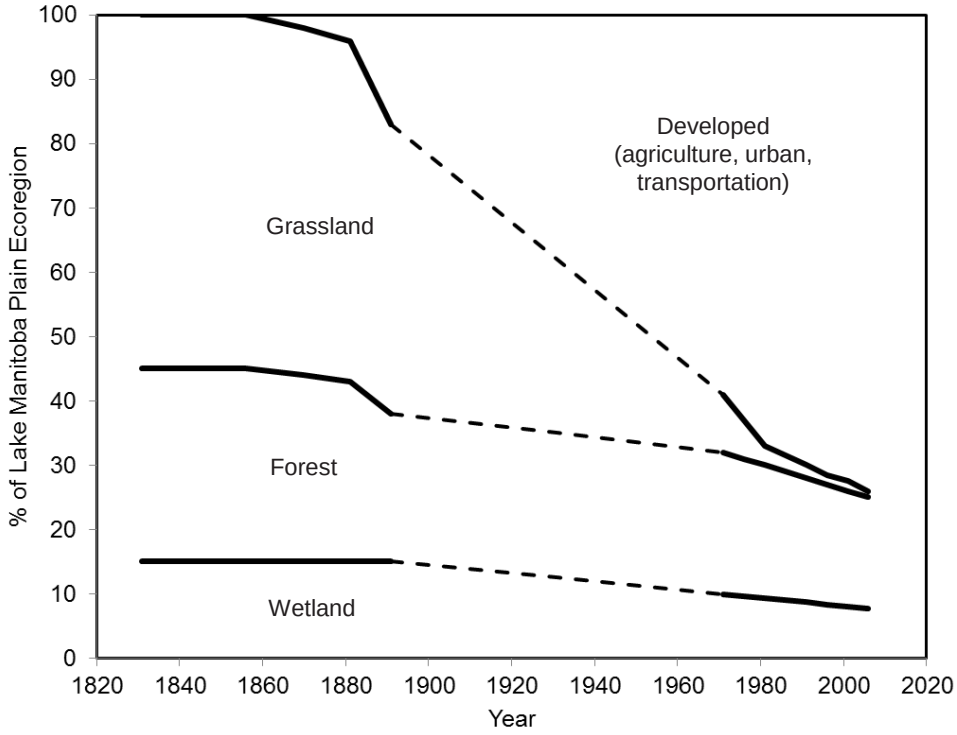

Figure 2. Estimated change in proportional cover of grassland, forest, wetland, and developed land in the Red River valley of southern Manitoba, 1830–2006. Farm census data from Statistics Canada was used to determine the total area of developed land in 5-yr increments (1881–1891 and 1971–2006). Data from 1901–1971 are aggregated by political and not natural boundaries, so dashed lines represent interpolation. Hanuta (2007) provides estimates of forest, wetland, and grassland cover in 1870 and 1995. Smith et al. (1998), Koper et al. (2010), Stunden-Bower (2011), and Bartzen et al. (2010) were used to estimate change in the proportional cover of grassland, forest, and wetlands.

tensive wetlands restricted access and agricultural capability in much of the area. That changed after The Land Drainage Act was created in 1895 along with the Manitoba Drainage Commission and associated Drainage Districts in 1919 to facilitate the conversion of the tall-grass prairie and wetland mosaic into cultivated farmland (Stunden-Bower 2011). By 1943, 60% of the Red River valley was under cultivation, while the remainder was forest, wetland and unimproved native grassland pasture (Ellis and Shafer 1943). A more detailed analysis in 1946 at the scale of individual sections (259 ha) indicated an average of 23% remained as unimproved pasture (Ehrlich et al. 1953).

Lowland prairie associated with wetlands held on longer than the drier uplands that were more arable for annual crop production. After wide-spread flooding of the Red River valley in the mid-1950s, renewed efforts into drainage projects helped reduce the remnants of tall-grass prairie even further (Stunden-Bower 2011). By the mid-1960s it was difficult for researchers to find representative prairie patches >0.04 ha upon which to base a description of the former vegetation (Smeins 1965, Ralston 1968, Levin and Keleher 1969). Once efforts began to systematically locate and document remnant tall-grass prairies for conservation in the late 1980s, it appeared less than 1% of the native vegetation remained (Joyce 1989). By 1995 the study area used by Hanuta (2007) had changed such that prairie now occupied <1%, wetlands 1%, and forest 9% of the landscape. This represents a 99.5% reduction in prairies, 90% reduction in wetlands, and 75% reduction in forested areas. Most of what does remain is invaded by alien invasive species (Mansell 1995), and some patches have vanished in response to invasion over the past two decades (Koper et al. 2010). Now some of the most frequently encountered species are smooth brome (*Bromus inermis* Leyss.) and Kentucky bluegrass (*Poa pratensis* L.).

WHERE WAS TALL-GRASS PRAIRIE IN WESTERN CANADA?

Previous Estimates

A number of sources delineate the boundary of tall-grass prairie in southern Manitoba as a semi-circle occupying the Lake Agassiz plain, with a straight-line base along the 49th parallel and the peak of the arch reaching northward to Lakes Manitoba and Winnipeg (Joyce 1989, Reaume 1993). In general, southern ecodistricts within the Lake Manitoba Plain Ecoregion are presumed to represent the tall-grass prairie in Western Canada. Current ecoregion classification schemes at national (Wiken 1986) and regional (Acton et al. 1998, Smith et al. 1998) scales reinforce that the Lake Manitoba Plain ecoregion was originally dominated by tall-grass prairie. The total area included in these descriptions ranges from 6,000 to 9,000 km^2, but also includes wetlands and forests.

The origin of popular descriptions for tall-grass prairie distribution in Manitoba appears to come from repeated use of a few sources. Shimek (1925) was first to document and outline the flora of the Red River valley consisting of tall-grass prairie dominants. Scoggan (1953, 1957) and Bird (1961) wrote that tall-grass prairies of the Lake Agassiz plain extended westward beyond the Manitoba escarpment, thinning out with increasing elevation or soil drainage further west and north; but neither author mapped the distribution of tall-grass prairie. Coupland (1961) illustrated the distribution of "true prairie" to include an area from Brandon to Winnipeg, south of the Assiniboine River to the U.S. border, presumably to align with the tall-grass prairie distribution mapped by Shantz (1923) south of the border. Coupland (1961) remarked that no quantitative description of the vegetation, or map of the distribution was available. Watts (1969) and Risser et al. (1981) outlined an area limited to the Red River Valley, east of the Manitoba Escarpment and northward to the shores of Lake Winnipeg. Joyce (1989) used this boundary to constrain surveys for remnant tall-grass prairie in the 1980s (Fig. 2), and few have looked for remnant prairies beyond those boundaries.

These previous estimates of tall-grass prairie distribution suffered from a lack of data and accessible remnant prairies from which to obtain data, and the problems of invasive species and land use altering the composition so as to be unrecognizable as tall-grass prairie. Since that time, both upland and lowland tall-grass prairie communities have been discovered outside the Lake Agassiz plain and Red River valley. The largest known remnants in the Manitoba Tall-Grass Prairie Preserve (MTGPP), or Carberry Sandhills in south-western Manitoba are actually outside the Lake Manitoba Plain Ecoregion (Hamel et al. 2006). Many adjacent landscapes with similar soils, precipitation and temperature regimes, could and apparently do support tall-grass prairie (see next section), but do not fall within the Lake Manitoba Plain Ecoregion. There are additional lines of evidence that can be used to frame, and actually map, a reconstruction of the historical distribution of tall-grass prairie.

Reconstructing Tall-grass Prairie Distribution

A cross-comparison of several U.S. based classification schemes (Kuchler 1964, Bailey 1978, Omernik 1987, USEPA 1996) indicates that upland and lowland tall-grass species become community dominants in North Dakota, immediately south of the Saskatchewan border in Kuchler Region 67 "Wheatgrass-Bluestem-Needlegrass", or USEPA Region 46 "Northern Glaciated Plains". At the eastern-most extreme, in Minnesota, tall-grass prairie gives way to forest vegetation in Kuchler Region 81 "Bur Oak Savanna", or USEPA Region 49. In between, and upon the Lake Agassiz plain is Kuchler Region 74 "Bluestem Prairie", or USEPA Region 48 "Lake Agassiz Plain". This broad east-west expanse indicates that tall-grass prairie should be present in the Aspen Parkland

Ecoregion westward into Saskatchewan, and Boreal Lowland Ecoregion eastward from the Red River valley.

Tall-grass indicator species such as big bluestem, Indian grass, switchgrass, prairie dropseed, and jerusalum artichoke (*Helianthus tuberosus* L.) are tracked as rare species by the Saskatchewan Conservation Data Centre (subnational conservation status S1-S3, based on Faber-Langendoen et al. 2009), and geographically correspond with the western distribution limits suggested by U.S. ecoregion classifications above. The specific locations of these indicator species in Saskatchewan are concentrated along major valley complexes like the Souris River, Antler River, Pipestone Creek, Qu'Appelle and Assiniboine Rivers, where crop production was restricted by steep topography or frequent flooding. Hamilton (2005) examined the distribution of leaf-hoppers restricted to feeding upon tall-grass prairie species, and suggested the range of this community type extends far westward along the Qu'Appelle River in Saskatchewan, and northward along the Manitoba escarpment to the Swan River.

Even the physiognomy of some species can be used to identify western boundaries, as Weaver (1954) remarked that isolated bunches of little bluestem can occur far to the west in mixed-grass prairie, but fail to take on the rhizomatous sod growth-form and co-dominance that charact erizes upland tall-grass prairie. Coupland (1950) described the semi-arid mixed-grass prairie, and Looman (1963) the fescue prairie, of Alberta and Saskatchewan, and indicate little bluestem was a rare bunchgrass in these communities.

Ecoclimatic zones have been described by Padbury et al. (2002) for the northern Great Plains, in which the core area of the Lake Agassiz plain was characterized by mean (30 year average) annual temperature (MAT) 2.5°–5.0° C, mean annual precipitation (MAP) 500–600 mm, and a frost-free season approximately 125 days. Padbury et al. (2002) also separated the Aspen Parkland Ecoregion south and east of the Qu'Appelle and Assiniboine River valleys as distinct from those areas north and west. The primary difference was warmer (MAT >1.5° C) and moister (MAP >450 mm) climate, with a longer growing season (>100 frost-free days) to the south and east. Tracking this pattern eastwards, several ecodistricts in the Boreal Upland Ecoregion become excluded, but several in the Boreal Lowland Ecoregion adjacent to the Lake Manitoba Plain become included. The distinctions made by Padbury et al. (2002) are relevant for identifying the distribution limits of crop varieties, and by association the tolerance limits of many C_4 species that would have otherwise dominated the natural vegetation. This region also corresponds with the north-western limit of bur oak (*Quercus macrocarpa* Michx.) in Saskatchewan (Acton et al. 1998).

Finally, the early soil surveys of southern Manitoba employed botanists who distinguished between "wet meadow", "meadow-prairie", "tall-grass prairie", and "mixed-grass prairie" types when describing vegetation associated with gleysolic (Aquoll), gleyed-black (Alboll), black (Udoll), and dark brown (Ustoll) chernozemic soils (Mollisols) respectively (Ehrlich et al. 1953, 1956, 1957, 1958, Ellis et al. 1943). In many cases these soil surveys include lists of indicator species for soil groups or landscapes, which makes possible a direct comparison with groupings by Weaver (1954) and Ralston (1968). It would appear that the "upland" association of Weaver (1954) is most similar to a combination of "tall-grass" and "mixed-grass" recognized by the soil surveyors, and the "lowland" association of Weaver is most similar to the "meadow-prairie" from the soil surveys. The relative coverage of these soil associations within ecodistricts helps to estimate the relative coverage of tall-grass prairie at the same scale (Table 1, Fig. 2). Any finer scale representation to individual soil polygons would imply greater precision than is warranted from the presence/absence data provided for larger landscape units in soil survey reports.

A synthesis of these various sources of information provides a broader view of the potential historic distribution of tall-grass prairie in Western Canada 150 years ago. Approximately 20,830 km^2 in Western Canada may have been dominated by tall-grass prairie. There were and are extensions of tall-grass prairie in a mosaic with deciduous woodlands, drier mixed-grass, fescue, and sandhill prairie, and moister fens and marshes to the north, west and east in the Lake Manitoba Plain (Bird 1961). Much of the western extension into the Aspen Parkland Ecoregion occupied mesic sites in the outwash plains of the Assiniboine delta and glacial Lake Souris between 400 and 500 m above sea level. Fingers of tall-grass prairie extended further west along the lower-slopes and floodplains of major melt-water valleys radiating into adjacent Saskatchewan and North Dakota, up to 600 m above sea level (Ehrlich et al. 1953, 1956, 1957, 1958, Ellis et al. 1943). Remnants within that area are now badly degraded and difficult to distinguish from mixed-grass prairie or tame pastures of Kentucky bluegrass (Mansell and Moore 1999, Kowalchuk 2003). Northern and eastern extensions blend into herbaceous marshes, fens, and deciduous forest glades of the Boreal Lowland Ecoregion of the Western Boreal Ecozone, at elevations between 250 and 400 m above sea level (Ewing 1924, Weaver 1954, Chapman et al. 1998).

RECONSTRUCTING THE HISTORICAL ECOLOGY OF TALL-GRASS PRAIRIE

Although wild fire and bison (*Bison bison*) grazing are recognized as important natural disturbances in tall-grass prairies elsewhere (Knapp et al. 1999), it is not clear how those disturbances operated at the northern extent of this ecosystem. Spring flooding was also a widespread, frequent, and intense disturbance across the Red River valley (Stunden-Bower 2011). Rapid snowmelt over frozen ground lead to significant runoff that may have set-back initial vegetation growth and perhaps provided an advantage to later-developing C_4 tall-grasses. How those three factors interacted on

Table 1. Estimated proportional distribution of historic natural land cover, including tall-grass prairie area and type (L= Lowland or U = Upland), by ecodistrict. Adapted from multiple sources (see text).

Ecoregion	Ecodistrict	Forest %	Meadow or Fen %	Fescue or Mixed %	Tall-Grass		
					%	km^2	Type
Lake Manitoba	Gladstone	30	7		63	646	L
Lake Manitoba	MacGregor	30	7		63	1,831	LU
Lake Manitoba	Winkler	30	7		63	537	LU
Lake Manitoba	Emerson	10	27		63	442	L
Lake Manitoba	Winnipeg	10	36		54	4,975	L
Aspen Parkland	Carberry	10	36		54	311	U
Lake Manitoba	Laungruth	30	28		42	152	L
Aspen Parkland	Oak Lake	30	28		42	1,764	LU
Interlake Plain	Steinbach	30	28		42	1,505	L
Lake Manitoba	Portage	30	28		42	357	L
Lake Manitoba	Dauphin	50	20		30	633	L
Lake Manitoba	Ste. Rose	50	20		30	277	L
Lake Manitoba	McCreary	50	20		30	434	L
Interlake Plain	Manitou	50	10		30	989	LU
Aspen Parkland	Stockton	10	5	58	27	928	U
Aspen Parkland	St. Lazare	30	5	44	21	423	U
Aspen Parkland	Shilo	30	5	44	21	558	U
Interlake Plain	Gimli	50	35		15	1,047	L
MidBoreal Upland	Hilton	50	10	25	15	202	U
Aspen Parkland	Gainsborough	10	10	71	9	632	U
Interlake Plain	Swan Lake	70	21		9	684	L
Moist Mixedgrass	Souris River	10	10	71	9	156	U
Aspen Parkland	Melville	30	10	53	7	684	U
Aspen Parkland	Killarney	30	10	53	7	361	U
MidBoreal Upland	Pembina Hills	50	15	30	5	77	U
Interlake Plain	Lundar	75	22		3	64	L
Interlake Plain	Alonsa	75	22		3	189	L
TOTAL						20,830	

this landscape of flat ridges and shallow swales shaped by glacio-lacustrine processes (see review in Ralston 1968) is of interest to those attempting to preserve remnants and their biodiversity.

Fire was perhaps the most important historical process for maintaining tall-grass prairie, by suppressing woody vegetation and encouraging the dominance of grasses and fire-tolerant forbs (Wright and Bailey 1980). It appears aboriginal peoples were responsible for most ignitions, and as such were responsible for creating and maintaining widespread tall-grass prairies (Higgins 1986, Boyd 2002). Fire return intervals had to be frequent enough to prevent the formation of forests (Briggs et al. 1992, Swetnam et al. 1999), but flooding and prolonged inundation of clay soils can also limit tree growth (Weaver 1954, Ralston 1968). Return intervals of 10 to 20 years are known to cause the most heterogeneity in vegetation structure and composition, while 1- to 5-yr intervals lead to increasing grass dominance (Gibson and Hulbert 1987, Collins 1992). Fire interacts strongly with large ungulates that preferentially graze burned areas free of litter and avoid unburned grasslands where litter has accumulated (Vinton et al. 1993, Coppedge and Shaw 1998). At

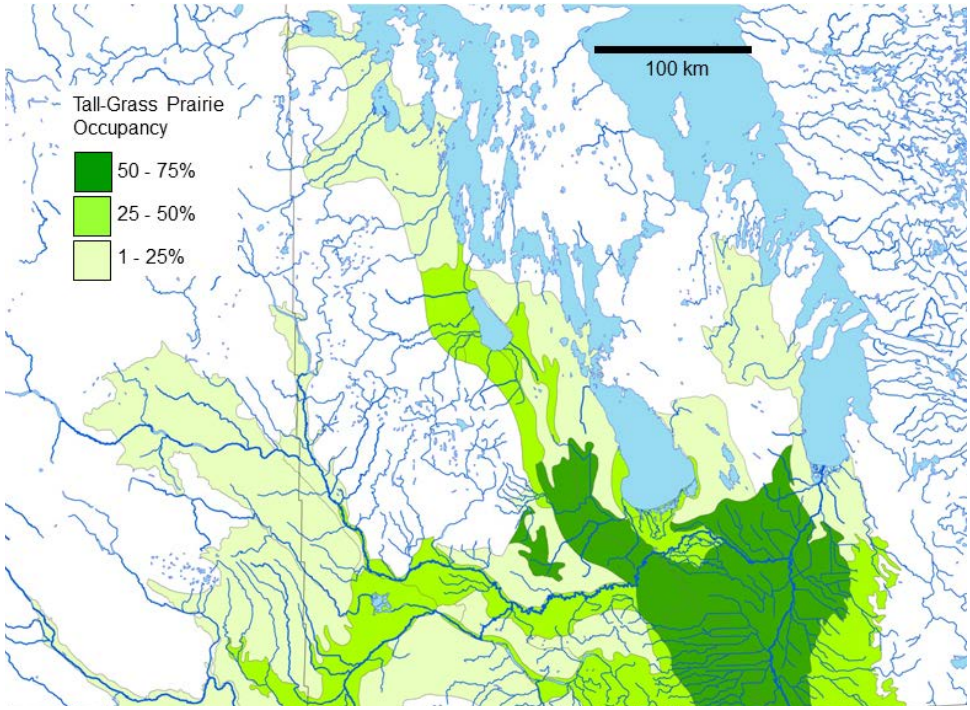

Figure 3. Estimated historic distribution and proportional coverage, or occupancy, of tall-grass prairie in Western Canada at the scale of ecodistricts. See Table 1 for a detailed description by ecodistrict.

a landscape scale, this combination of grazing and burning increased biodiversity through the development of many different plant community patches (Fuhlendorf et al. 2006).

Historic patterns of large ungulate grazing in northern tall-grass prairie remain a mystery, as the destruction of bison, elk (*Cervus canadensis*), and prairie was mostly complete before any scientific description was possible (Knapp et al. 1999). Further, most published literature regarding bison grazing patterns in tall-grass prairie is derived from studies in Nebraska, Kansas, and Oklahoma (Vinton et al. 1993, Hartnett et al. 1996, Coppedge and Shaw 1998), far from the edge of boreal forests and subarctic climates. Better analogues for Manitoba may occur where grasslands and forests meet in Saskatchewan and Alberta, and where small herds of wild or semi-wild bison still graze. In these cases, bison appear to prefer foraging in wet meadows dominated by sedges (*Carex atherodes* Spreng.) relative to upland fescue prairie or forests (Reynolds et al. 1978, Hudson and Frank 1987, Fortin et al. 2002, Courant and Fortin 2010). Forage quality analyses indicate *C. atherodes* is both productive and relatively more nutritious throughout the year (Courant and Fortin 2010). Conversely, tall-grasses, though very productive, contain large amounts of structural carbohydrates that decrease digestibility and palatability after curing in late fall (Bergman et al. 2000, Sedivic et al. 2009). Studies from tall-grass prairie in Nebraska, Kansas and Oklahoma indicate bison select upland patches with a high proportion of grasses, particularly for the first few years following a fire (Vinton et al. 1993, Hartnett et al. 1996), but will also seasonally shift preference to sedges in winter (Coppedge et al. 1998).

Taken together, this suggests that bison in southern Manitoba may have seasonally shifted between a preference for recently burned upland prairie of C_3 and C_4 grasses during spring and summer when lowland prairie was inundated, followed by local movement to sedge-dominated lowlands during the fall and winter as waters drew-down or froze. As a result, large areas of unburned upland or inundated lowland prairie may have remained ungrazed for years at a time. This mosaic of interacting disturbance would likely intensify the heterogeneity in vegetation structure already generated by the ridge and swale topography, like it has in other landscapes (see Collins and Smith 2006).

PROSPECTS FOR THE FUTURE OF TALL-GRASS PRAIRIE

Restoration of remnant tall-grass prairie must overcome problems with woody and alien invasive plant encroachment that occurred due to fire suppression. Prescribed fire has been used in Manitoba tall-grass prairie since settlement by Europeans to maintain hay meadows free from woody plants that could damage mechanical haying equipment, or to reduce mosquitoes and ticks that otherwise plague people and livestock (Chapman et al. 1998). More recently, conserva-

tion agencies like the Nature Conservancy of Canada, Ducks Unlimited Canada, and staff at the MTGPP have used fire as a conservation tool to maintain tall-grass prairie (Hamel et al. 2006). These latter management efforts have helped increase the area and quality of tallgrass prairies (Koper et al. 2010).

Grazing practices are perhaps the most difficult feature to change on remnant tall-grass prairies. The small fragments are most easily managed by grazing European-breed cattle, but those animals are only capable of grazing during the snow-free, growing season. Invasions of lowlands by canary reed grass (*Phalaris arundinacea* L.) or red top (*Agrostis stolonifera* L.), and uplands by smooth brome, Kentucky bluegrass, and sweet clover (*Melilotus officinalis* [L.] Lam.) has also altered the seasonal phenology and forage quality patterns, such that some sites cannot be grazed year round in a pattern similar to bison (Grant et al. 2009). However, to maintain diversity of both wildlife and vegetation, a combination of fire and grazing seems to be a useful management direction (Fuhlendorf et al. 2006).

The small remnant areas of tall-grass prairie are threatened by a number of factors, but isolation and high edge to area ratios of the small fragments make them susceptible to local extinctions and increasing competitive effects of alien invasive species that dominate the matrix surrounding the fragments (Koper et al. 2010). Some larger blocks do occur, and most are managed for conservation of wildlife or biodiversity by government agencies or the Nature Conservancy of Canada (Hamel et al. 2006). Now that a broader view of tall-grass prairie is available, perhaps those agencies will look beyond the Lake Agassiz plain to rediscover additional tall-grass prairie, and implement similar protective and restorative measures.

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