Bugs Reveal an Extensive, Long-lost Northern Tallgrass Prairie

K. G. ANDREW HAMILTON

Only tiny remnants of unplowed natural meadows remain in the eastern part of the state of North Dakota, and in Canada from eastern Saskatchewan to Manitoba. Those west of Lake Manitoba and the Red River Valley are characterized by their distinctive fauna of insects, principally leafhoppers and planthoppers (Homoptera: Auchenorrhyncha). These true bugs include hundreds of species invariably associated with North American grasslands. The distributions of those with the most limited dispersal abilities reflect long-term patterns of dominance and contiguity of native grass stands in prairies. These bug distributions indicate that bluestem-dominated grasslands in Canada, which usually are under 0.5 meter (20 inches) in height, are equivalent to tallgrass prairie from Illinois. This prairie once extended as much as 400 kilometers (250 miles) northwest of its previously known distribution. These bugs help differentiate tallgrass prairie from sites in southwestern Manitoba and adjacent North Dakota, which are more arid, and from sites east of Lake Manitoba and southward in the Red River Valley, which were formerly oak savanna.

Keywords: biodiversity, tallgrass prairie, oak savanna, leafhoppers, planthoppers

Tallgrass prairie is one of the most highly endangered ecosystems in North America. Rich soil, reliable rainfall, and extensive flatlands make it the most desirable cropland on the continent. Intensive farming and wildfire suppression by settlers have resulted in expanding fields and woodlands that have decimated the native grassland content of this ecosystem (Mlot 1990). Now only tiny fragments are left of what once seemed to be endless prairie.

Native grasslands west of the Red River Valley (on the border between the states of North Dakota and Minnesota), and in Canada from Lake Winnipeg west to Lake Manitoba and into eastern Saskatchewan, have been thought to be a mixed-grass understory in open aspen woods. However, these lands appear to include remnants of bluestem-dominated grasslands. These grasslands were mapped in 1737 by La Vérendrye (Combet 2001), who first used the word "prairies" for this area. La Vérendrye may have used that word, which is French for "meadows," because, like European meadows, mesic prairies in Canada have grasses that are rarely more than 0.5 meter (m) high. These extensive grasslands were "alternate wood and prairie" west of Lake Manitoba (Warkentin and Ruggles 1970, map 92) in 1859, possibly having become more heavily wooded after fire suppression by settlers. Only 50 years later, these grasslands had been virtually eliminated.

This article attempts to reconstruct this presettlement prairie using stable insect–plant associations. Broadscale subsets of the temperate grassland biome in North America can be discerned by faunas of insects that are restricted (endemic) to grasslands. Such faunas differentiate northwestern grasslands from other native grassland ecosystems to the west and to the east. The patterns of bug distributions show that tallgrass prairie once extended 400 kilometers (km) beyond its previously known distribution.

What and where is tallgrass prairie?

The preservation of biota and the effective management of native ecosystems require a sound working knowledge of what needs protection. For tallgrass prairie, this means characterizing remnants when they are found and determining from these remnants where grassland ecosystems were originally situated.

Ecosystems are most easily recognized and defined at the community level, where ecological interactions are strongest (Radenbaugh 1998). Modern efforts to group ecological communities into species "associations" seek to provide a comprehensive classification system suitable for geographical scales of tens to thousands of hectares, and for ecosystems that persist for 50 or more years (NatureServe 2004). Ecological associations on this scale are still too narrowly defined and too numerous for general reference. Ecological areas between the biome and the association scale are often cited and variously named but seldom rigorously defined. Such areas are usually on the order of hundreds of thousands of hectares or more and are presumed to persist for thousands of years.

K. G. Andrew Hamilton (e-mail: hamiltona@agr.gc.ca) is a research scientist working with the biodiversity of insects at Agriculture and Agri-Food Canada, Ottawa, Ontario K1A 0C6, Canada.

Table 1. Grasses and 58 associated monophagous or oligophagous short-horned bugs common to Minnesota and Wisconsin oak savanna or to tallgrass prairie.

Grass (by distribution)	Height	Common name	Associated short-horned bugs
Eastern distribution			
Andropogon gerardii	Tall	Big bluestem, turkeyfoot	**Caliscelidae:** *Bruchomorpha dorsata** **Cicadellidae:** *Flexamia graminea*, *Laevicephalus unicoloratus,* Stirellus bicolor** **Delphacidae:** *Delphacodes parvula**
[*Elymus canadensis*]	Tall	Canada wild rye	**Cicadellidae:** [*Commellus comma*]
Schizachyrium scoparium	Mid	Little bluestem, wiregrass, prairie beardgrass	**Caliscelidae:** *Bruchomorpha dorsata,* Bruchomorpha jocosa* **Cercopidae:** [*Philaenarcys killa, Prosapia ignipectus*] **Cicadellidae:** [*Chlorotettix spatulatus, Flexamia dakota*], *Flexamia delongi, Flexamia graminea, Laevicephalus unicoloratus,* Paraphlepsius lobatus, Polyamia caperata, Stirellus bicolor** **Delphacidae:** *Delphacodes parvula**
Sorghastrum nutans	Tall	Indian grass	**Caliscelidae:** [*Bruchomorpha extensa*] **Cicadellidae:** *Flexamia reflexa*
Sporobolus heterolepis	Mid	Prairie dropseed	**Cicadellidae:** *Aflexia rubranura, Memnonia panzeri*
Stipa spartea	Tall	Porcupine grass	**Cicadellidae:** *Commellus colon*
Widespread distribution			
Agropyron trachycaulum	Mid	Slender wheatgrass	**Cicadellidae:** *Athysanella attenuata, Attenuipyga minor, Commellus sexvittatus, Mocuellus americanus*
[*Bouteloua curtipendula*]	Mid	Side-oats grama	**Cicadellidae:** [*Flexamia albida, Flexamia pectinata*]
Bouteloua gracilis	Short	Blue grama	**Cicadellidae:** *Flexamia abbreviata,* Flexamia flexulosa,* [*Laevicephalus minimus*]
[*Bouteloua hirsuta*]	Short	Hairy grama	**Cicadellidae:** *Flexamia abbreviata,** [*Paraphlepsius altus*]
Calamovilfa longifolia	Tall	Sand grass	**Cicadellidae:** *Athysanella terebrans*
Distichlis stricta	Short	Alkali grass, salt grass	**Cicadellidae:** *Athysanella kadokana, Lonatura salsura*
Hordeum jubatum	Mid	Wild rye	**Cicadellidae:** *Psammotettix knullae*
Koeleria macrantha	Mid	June grass	**Cicadellidae:** *Amblysellus acuerus, Auridius helvus, Rosenus cruciatus*
[*Muhlenbergia cuspidata*]	Mid	Prairie muhly	**Caliscelidae:** [*Peltonotellus bivittatus*] **Cicadellidae:** [*Flexamia serrata, Lonatura megalopa*]
Muhlenbergia richardsonis	Mid	Mat muhly	**Cicadellidae:** *Flexamia decora, Flexamia serrata, Laevicephalus poudris, Lonatura teretis, Memnonia anthalopus*
[*Panicum virgatum*]	Tall	Switchgrass	**Cicadellidae:** [*Chlorotettix fallax*], *Flexamia atlantica,* [*Graminella mohri, Graminella oquaka*]
Puccinellia nuttalliana	Mid	Salt-meadow grass	**Cicadellidae:** *Deltocephalus serpentinus, Laevicephalus saskatchewanensis*
Spartina gracilis	Mid	Alkali cordgrass	**Caliscelidae:** *Aphelonema simplex** **Cicadellidae:** *Destria crocea,* Neohecalus magnificus** **Delphacidae:** *Megamelus metzaria,* Prokelisia crocea**
Spartina pectinata	Tall	Prairie cordgrass	**Caliscelidae:** *Aphelonema simplex** **Cicadellidae:** *Destria crocea,* Neohecalus magnificus,* Pendarus magnus* **Delphacidae:** *Megamelus metzaria,* Prokelisia crocea**

Asterisk (*), oligophagous (insects are monophagous unless otherwise designated).
Note: Brackets indicate grasses not common in the Manitoban prairie (Canada) and insects not known to occur there.

Tallgrass prairie is the most familiar of such broadscale subdivisions of the temperate grassland biome. Early subdivisions of North American prairies (reviewed in Scudder 1979) distinguished tallgrass, midgrass, and shortgrass areas. This "physiognomic" classification characterized western areas not only by relatively shorter vegetation, but also by reduced rainfall and grayer, more saline soils. More precise land-cover descriptors and accompanying ecological maps have a long and checkered history (Whittaker 1962) involving the rival merits of classifying by endemic plant species or by those plants that are dominant. Since 1964, North American grasslands usually have been defined by dominant grass species (Küchler 1964).

The dominant grasses themselves may be classified as relatively tall, short, or mid-height (table 1). Tallgrass prairie (figure 1) is dominated by a mixture of big bluestem (*Andropogon gerardii*), which grows up to 2 m high, and little bluestem (*Schizachyrium scoparium*), a midgrass of less than half that height. Shortgrass prairie is now defined as limited to areas where buffalo grass (*Buchloë*) and grama grass

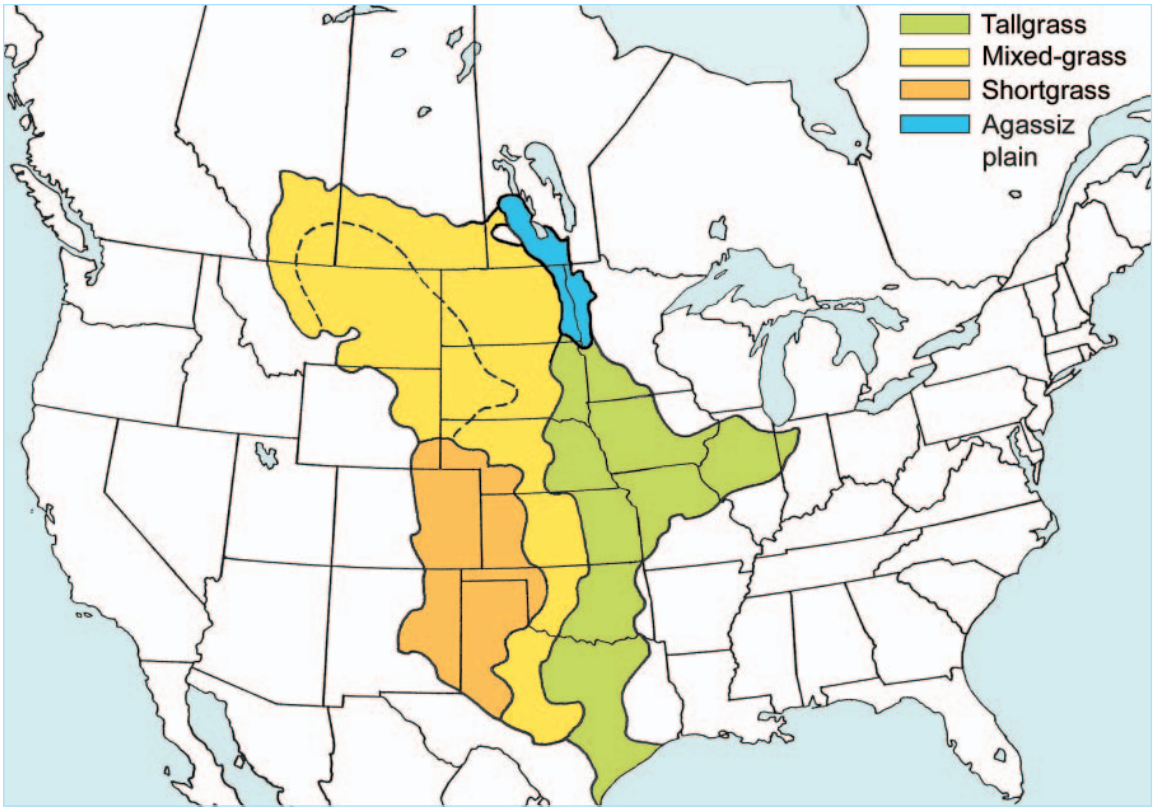

Figure 1. Traditional subdivision of the Great Plains into tallgrass (green), mixed-grass (yellow), and shortgrass prairie (orange), excluding oak savanna and aspen parkland. Reconstructed from Samson and colleagues (2004), with the Glacial Lake Agassiz plain (blue) segregated as "northern tall grasslands" (Ricketts et al. 1999). The northern part of the physiognomic "shortgrass" prairie extending into Canada (Scudder 1979), with short grasses represented by blue grama in the absence of buffalo grass, is indicated by a dashed line.

(*Bouteloua*) are co-dominant, growing to < 0.5 m high. Midgrass prairie, when defined by dominant species, is usually denoted "mixed-grass prairie" because the dominant species are various and include a wide range of growth forms. This grassland has also been called "steppe" (Coupland 1961) where the dominants are wheatgrass (*Agropyron*) and needlegrass (*Stipa*), as in central Asian grasslands. It also includes a northern extension of the prairie categorized as shortgrass in the earlier physiognomic system. There (figure 1), blue grama (*Bouteloua gracilis*) may be locally dominant, but buffalo grass is absent.

Each of these prairie grasslands can be subdivided by its associations of subdominant species. Such classifications are difficult to apply in northern grasslands, where there are few such species, with considerable local and temporal variation in their importance (Coupland 1961). Other subdivisions of tallgrass prairie have been proposed, based on corresponding zoological biodiversity. These suggest, for example, that the great north–south extent of tallgrass prairie has northern (Illinoian) and southern (Texan) "biotic provinces" (Dice 1943). These areas are roughly equivalent to Küchler vegetative regions 60, 66, and 73 (bluestem prairies and oak savanna) and region 75 (cross timbers), respectively. Such subdivisions are supported by studies of regional endemism of both plants and animals, including butterflies and beetles (Ricketts et al. 1999), and have been called "ecoregions."

Tallgrass prairie is widely recognized in much of the United States, but its extent in North Dakota is debatable (Küchler 1964, Sims 1988, Samson et al. 2004). The concept of tallgrass prairie is still more difficult to apply in Canada (Scudder 1979, Scott 1995). Farming changed the grasslands of Manitoba and eastern Saskatchewan so quickly and so completely after the coming of the first railway in 1870 that less than 5% of the prairie survives in eastern Saskatchewan (Coupland 1973, Samson et al. 1998) and only 0.017% has been identified in Manitoba (Joyce 1989). The extent of the original prairies and their dominant grasses is therefore highly debatable (Dice 1943, McAndrews and Manville 1987, Scott 1995). Most biologists concur that the warmest area of south-central Manitoba, near Morden, was originally tallgrass prairie. This area was sketched by Dawson (1875) when it was still open, unfarmed prairie with tussocks of tall grasses. This grassland may have extended as far as 100 km north of the US–Canadian border and east of the Pembina Hills in 1874

(Warkentin and Ruggles 1970), although its extent may have been magnified by fires set by aboriginals to produce fresh pasture to attract buffalo (Mlot 1990). By contrast, a careful painting of the Red River Valley of southeastern Manitoba in 1870 by W. G. R. Hind (Francis 1989) shows settlers clearing old-growth oak savanna. This vegetation extended in 1816 as "plains interspersed with tufts of woods" far beyond the 1- to 3-km-wide woods bordering the rivers (Warkentin and Ruggles 1970).

An alternative classification of Canadian prairies has been advanced through the study of soil types (Wiken 1986). The deep-soil plain of Glacial Lake Agassiz, including the Red River Valley and the area north of it around Lake Manitoba (figure 1), was designated a primary subdivision or "ecoprovince" without specified dominant vegetation. The rest of the Canadian prairies was designated as two additional soil types. These are now recognized as separate ecoprovinces, one dominated by aspen (aspen parkland) and the other by open grassland. The latter of these was subdivided by the aridity of its soils into secondary subdivisions, moist and arid ecoregions.

Aspen parkland is an ecotone (Pitelka 1941), an overlap of northern forest and grassland biomes. Oak savanna is also an ecotone (between tallgrass prairie and oak–maple forest), extending from the state of Minnesota to southern Ontario, Canada. Grassland classifications often include aspen parkland within mixed-grass prairie. More often, the oak savanna of northern Illinois and Wisconsin is excluded (figure 1), being relegated instead to the temperate deciduous forest biome.

The extent of ecotonal grasslands remains uncertain, because grasses characteristic of prairies may be found in woodlands far north of aspen parkland and oak savanna, along many northern rivers in Canada (Dore and McNeill 1980, Moss 1983), on sandy and rocky ridges, and on limestone plains (alvars). These localized populations may be relicts of the postglacial thermal maximum (6000 to 8000 years ago: Matthews 1979), when prairie extended much farther north and east than it does now. Some relictual grasslands may represent scour prairie, established by grass seeds washed down rivers or otherwise transported long distances beyond their native grassland habitats. Similar but short-distance spread of prairie vegetation follows roadsides and railroad rights-of-way where human activities, such as intentional fires, create suitable habitat for these plants.

Modern ecoregional classifications seek to resolve these conflicting views and indefinite boundaries by combining dominance data with sets of endemic plants, snails, beetles, butterflies, and vertebrates. Unfortunately, this has not improved the resolution of prairie habitats in Canada, which are mapped by Ricketts and colleagues (1999) merely as reiterations of the soil classification.

Obviously, greater clarity is needed for mapping the extent of the northern tallgrass prairie and for discriminating long-term patterns of grass dominance within it. How can these problems be resolved?

Bugs to the rescue

True bugs (Homoptera) of the subdivision Auchenorrhyncha, or short-horned bugs (so called because they have tiny antennae; figure 2), are the most speciose group that remains to be included in ecoregional analyses of prairie. They include hundreds of prairie-endemic species (Hamilton 2004). These are phytophagous insects whose lives are spent constantly on their host plants. They can occur in huge numbers even in tiny prairie remnants.

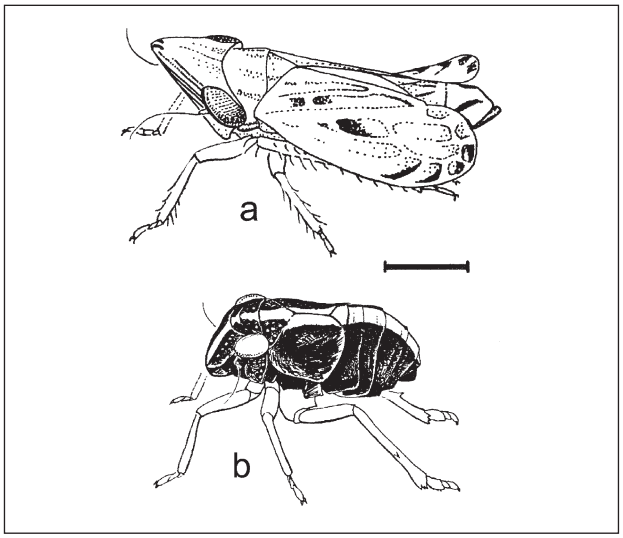

Figure 2. Flightless short-horned bugs (Homoptera: Auchenorrhyncha). (a) A leafhopper,* Flexamia huroni, *with aborted hind wings; (b) a planthopper,* Bruchomorpha dorsata, *with wings reduced to scales, exposing the abdomen. Scale line: 1 millimeter.

The largest diversity of prairie-endemic short-horned bugs is composed of leafhoppers, family Cicadellidae (Ross 1970, Hamilton and Whitcomb 1993). Smaller but significant numbers of prairie-endemic bugs are found in two families of planthoppers, Delphacidae and Caliscelidae. Other related bugs, such as treehoppers (Membracidae), cicadas (Cicadidae), and spittlebugs (Cercopidae), have fewer and scarcer grassland species (Hamilton 2004).

Leafhoppers and planthoppers in native grasslands range over many climate zones. Except for a few habitat specialists (Whitcomb et al. 1987), they do not track environmental conditions such as temperature regimes, unlike forest species (Hamilton 1997). Consequently, they persist in habitats that have been radically altered by many human activities, including deforestation, infrequent burning, and ditching, provided only that their hosts survive there. They are particularly good indicators of native grassland ecosystems (Whitcomb et al. 1994, Nickel 2003), because many of their endemic species have a very limited range of hosts (table 1). They are usually monophagous (feeding only on a single species of prairie grass) or oligophagous (restricted to a small group of related species). Furthermore, suites of four or more closely

related temperate-zone grassland species often share the same host (Whitcomb and Hicks 1988, Hamilton and Zack 1999, Nickel 2003). These intimate relationships suggest that insect–plant associations have persisted for hundreds of thousands of years or more. Monophagy on a particular host plant within northern latitudes thus appears to have survived the vicissitudes of Pleistocene glaciation.

Few experimental studies have focused on the biology of monophagous leafhoppers in grasslands. However, there is substantial circumstantial evidence that the intimate association of leafhoppers with perennial hosts results in the insects dispersing very slowly.

Bugs that are monophagous on common grasses and sedges frequently have flightless females to maximize egg production (Denno 1994). Species with entirely flightless females, which obviously have very limited mobility, are not uncommon. In an extreme case, the entire genus *Errhomus* has flightless females and has evolved essentially *in situ* on arid parts of the Columbia basin of the Pacific Northwest (Oman 1987). The distribution of 16 species is so rigidly maintained that one, *Errhomus praedictus,* was anticipated to be found in Washington State adjacent to the range of its sister species *Errhomus wolfei* before specimens were actually collected there (Hamilton and Zack 1999).

Even among fully winged species, it is not uncommon to find a monophagous leafhopper abundant in a relict grassland, although it is absent where its host grass has spread a kilometer or so further down an adjacent roadside. On a larger scale, leafhoppers that are common in some prairies may be completely absent from extensive intervening areas (figure 3), although their host may be abundant there. This suggests that monophagous leafhoppers in grasslands resemble polyphagous ones in seldom flying once the female becomes gravid (Waloff 1973).

The rate of grassland leafhopper dispersal has been measured in a "natural experiment" (Hamilton 1999) when leafhoppers reinvaded open tundra grasslands from a Yukon refugium following deglaciation. Two dozen leafhopper species have moved eastward across more than 2000 km of tundra over the last 12,000 years. Fully 50% of these leafhoppers have migrated much less than 1 km per year, and 30% have failed to cross the initial 10-km-wide ecological barrier, the Mackenzie River Valley. Only one was able to colonize offshore islands.

The low dispersal rate of some leafhoppers makes it possible to recognize biogeographic zones in Manitoba (Hamilton 1972) by simple historical data on leafhopper distribution, without further information on host associations and vagility. But much more can be deduced with these additional data. For example, two leafhoppers (*Aflexia rubranura* and *Memnonia panzeri*) specializing on prairie dropseed (*Sporobolus heterolepis*) have wingless females and inhabit alvars on islands in Lake Huron of known geological age. These show that grassland vegetation and its associated fauna became established in Ontario 9000 years ago, at least 1000 years before elevated temperatures brought prairies to their maximum extent (Hamilton 1994).

Insect–grass associations affirm that most isolated grasslands in fens or on sandy soil in forested areas are relicts from the time of maximum prairie expansion (Hamilton 1994, 1997) and may support a number of endemic species, such as *Flexamia beameri* (Whitcomb and Hicks 1988) in New York and *Flexamia huroni* (Bess and Hamilton 1999) in Michigan. By contrast, alvars in Ontario have a mixed leafhopper fauna represented by species that are restricted elsewhere to oak savanna, tallgrass prairie, or aspen parkland (Bouchard et al. 2001). Evidently, the alvar fauna represents relicts of a glacial-age fauna that survived in isolated situations and has become geographically realigned by the development of postglacial ecosystems, as have endemic bug faunas of far western areas (Whitcomb et al. 1987, Hamilton 2002).

Preliminary analysis of the entire short-horned bug fauna of the Canadian prairies strongly supports an east–west biotic zonation (Hamilton 2004). These eastern and western zones are roughly equivalent, respectively, to fire-maintained tallgrass prairie in central Manitoba and drought-maintained mixed-grass prairie in southwestern Manitoba, Saskatchewan, and Alberta, with aspen parkland being a subset of the latter. Analysis of the host associations of these species also confirms that little bluestem is the most important component of tallgrass prairie, as first proposed by Odum (1971), with far more specialist leafhoppers than any other grass (table 1). Similarly, the dominant and subdominant grasses in mixed-grass prairies also support diverse leafhopper faunas.

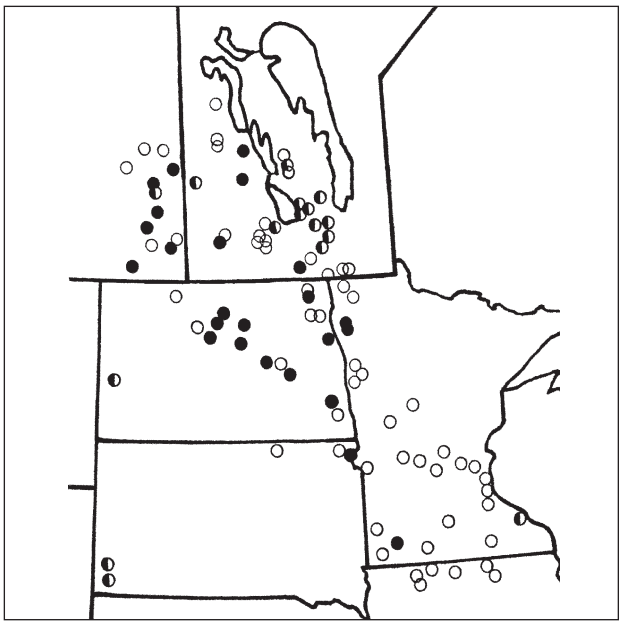

Figure 3. Limited dispersal of monophagous leafhoppers in stands of little bluestem from Iowa to Saskatchewan, Canada. Circles represent stands with monophagous leafhoppers* Flexamia graminea *(filled circles) or* Flexamia delongi *(split circles), or with neither leafhopper (open circles).

Searching for the lost prairie

The present study is an outgrowth of eight surveys, initiated in 1988, of the short-horned bug faunas of northeastern grasslands. More than 31,000 specimens have been collected from 232 grassland sites in Ontario, Manitoba, Saskatchewan, Alberta, and North Dakota and the northeastern states. These were compared with forest and wetland faunas of the same region. In all, 226 grassland-endemic species, including 168 leafhoppers, have been recorded from the Canadian plains (Hamilton 2004) and an additional 26 species from eastern grassland fragments (Hamilton 1995, Bouchard et al. 2001, Skevington et al. 2001).

Hosts of monophagous and oligophagous leafhoppers have been recorded from many of these sites. Together with similar data from elsewhere on the Great Plains, there are now 60 monocotyledonous hosts (mainly grasses) known for more than 150 leafhopper species (Hamilton and Whitcomb 1993). These bugs can be clustered roughly into three groups: (1) monophages with limited dispersal powers that feed on dominant or subdominant perennial grasses such as *Agropyron, Andropogon, Bouteloua, Muhlenbergia, Schizachyrium, Sorghastrum, Sporobolus,* or *Stipa;* (2) oligophages on such grasses; or (3) specialists on perennial grasses such as *Calamovilfa, Distichlis, Elymus, Hordeum, Koeleria, Puccinellia,* or *Spartina,* which grow in isolated patches in sloughs, in salt pans, and on sandhills. Bugs from the first group usually are reliable indicators of broadscale ecosystems defined by their hosts (e.g., bluestem prairie). By contrast, bugs from the third group are clearly adapted to longer-distance dispersal to find their hosts. They are indicators of specific local habitats within grassland landscapes. Oligophages also appear to disperse freely and might seem to belong within this latter group. However, oligophages of dominant and subdominant grasses may be found in various habitats or biogeographic zones, depending on the habitat requirements of their several hosts.

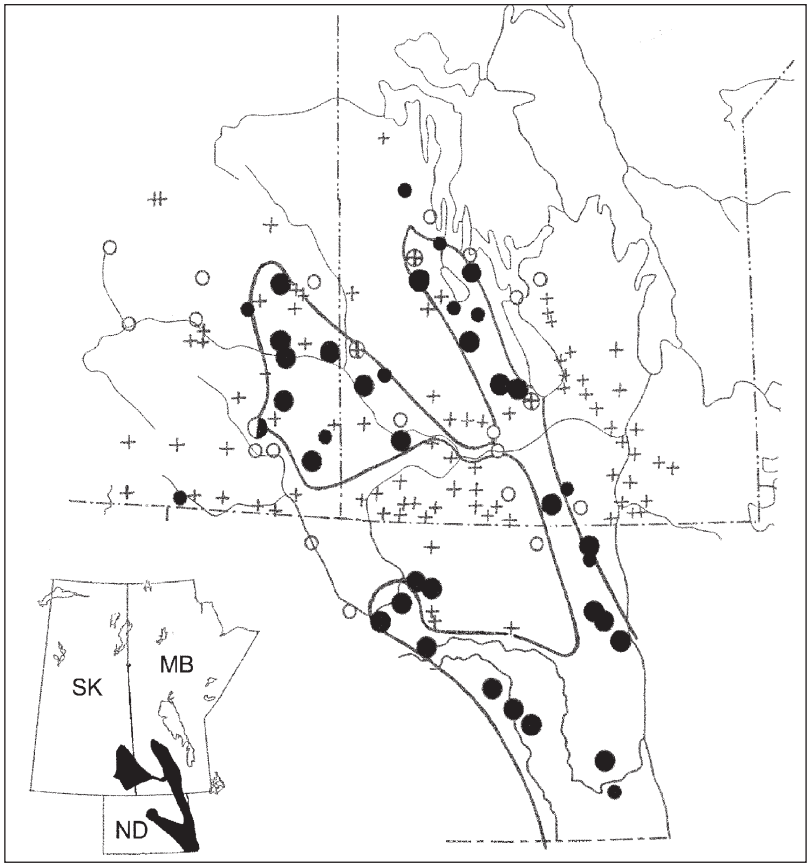

Figure 4. Area of 2003–2004 sampling in northeastern North Dakota (ND), and in southern Manitoba (MB) and adjacent Saskatchewan (SK), Canada, showing tallgrass area (bold outline), previously sampled sites (crosses), newly sampled sites (circles), and historical records of tallgrass leafhopper species (crosses in circles). Sites where tallgrass leafhopper species occur (filled circles) are shown as larger circles if two or more of these species were found. Sites with other faunas are indicated by an open circle, and a split circle is an ecotonal area where tallgrass prairie is found on the eastern slopes of arid hills. Inset: tallgrass prairie (black) relative to all three political areas.

Preliminary analysis of the distribution data of short-horned bugs on Canadian prairies revealed a comparative lack of records from the grasslands of eastern Saskatchewan and Manitoba, excepting only the southwestern corner of the latter province. This undersampled area included the area around the southwestern half of Lake Manitoba (south of The Narrows at a latitude of 51 degrees north), which was probably La Vérendrye's "Lac des Prairies." There, few grassland sites are known, and even fewer are under any kind of conservation management. I made transects across this area in 2003 (in August, when it was easy to spot the distinctive culms of bluestems). Sampling was extended into adjacent parts of Manitoba and Saskatchewan until a different fauna was encountered (figure 4). Further sampling in 2004 extended the search area farther south in Saskatchewan and west of the Red River in North Dakota (table 2) as far as the Missouri Coteau. This escarpment was once considered to be the western boundary for bluestem prairie (Küchler 1964), although the boundary is now thought to be farther east (Sims 1988, Samson et al. 2004).

Twenty grasses with 58 associated bugs are known to be characteristic of eastern prairies (table 1). Many of these grasses and bugs are found 5 km west of Morden, Manitoba, which is the only site in the province that we can be sure was truly tallgrass prairie. The distribution of these grasses and associated insects elsewhere in the search area proved to be quite unexpected. Bugs that were formerly known in Canada only from southernmost Manitoba, or were thought to be anomalous specimens, proved to represent a discrete and

Table 2. Tallgrass sites and their characteristic grasses, sampled 2003–2004, with the numbers of tallgrass-endemic short-horned bug species at each site and their percentage of the total grassland-endemic species found there.

Site (by province/state)	Grass genera characteristic of tallgrass prairie	Endemic short-horned bugs
Manitoba		
1. Ashville (11 km N)	*Andropogon, Schizachyrium, Sporobolus, Stipa*	4 (67% of 6)
2. Ashville (16 km N)	*Bouteloua, Schizachyrium, Sporobolus, Stipa*	3 (33% of 9)
3. Birtle (9 km W)	*Andropogon, Schizachyrium, Stipa*	3 (100% of 3)
4. Cowan (1 km N)	*Agropyron, Koeleria, Schizachyrium*	1 (20% of 5)
5. Dauphin †	[*Agropyron, Muhlenbergia, Sorghastrum, Spartina*]	1 (17% of 6)
6. Ethelbert †	[*Andropogon*]	1 (100% of 1)
7. Gladstone (1 km S)	[*Agropyron*], *Andropogon, Schizachyrium, Spartina*	3 (30% of 10)
8. Griswold (4 km W)	*Agropyron, Andropogon, Schizachyrium*	3 (60% of 5)
9. Kelloe	[*Distichlis*], *Muhlenbergia,* [*Puccinellia*], *Spartina, Sporobolus*	1 (13% of 8)*
10. McCreary (3 km E)	[*Agropyron*], *Andropogon, Schizachyrium, Spartina, Sporobolus*	4 (40% of 10)
11. Morden (5 km W)	*Andropogon, Distichlis, Schizachyrium, Spartina, Sporobolus*	11 (65% of 17)*
12. Myrtle (3.5 km E)	*Agropyron, Andropogon, Schizachyrium, Sorghastrum, Spartina, Stipa*	2 (25% of 8)
13. Ochre River (4 km N)	*Agropyron, Andropogon, Distichlis, Koeleria, Muhlenbergia*	1 (20% of 5)
14. Rorketon (6 km SE)	*Agropyron, Andropogon, Muhlenbergia, Schizachyrium*	4 (40% of 10)
15. Russell †	[*Stipa*]	1 (100% of 1)
16. St. Amelie (3 km N)	*Spartina*	1 (100% of 1)
17. Windygates (2 km N)	*Andropogon, Spartina*	3 (75% of 4)
18. Winnipegosis (1 km NW)	*Agropyron, Distichlis, Spartina, Sporobolus*	3 (38% of 8)
19. Woodside (5–6 km E)	*Agropyron, Distichlis, Puccinellia,* [*Schizachyrium, Sorghastrum*], *Spartina, Sporobolus*	5 (22% of 23)*
Saskatchewan		
20. Birds Point (6 km E)	*Agropyron, Andropogon, Bouteloua, Koeleria, Muhlenbergia,* [*Panicum*], *Schizachyrium, Stipa*	9 (47% of 19)
21. Craven (2 km NW)	*Spartina*	1 (100% of 1)
22. Duff (2–8 km E)	*Distichlis, Puccinellia, Schizachyrium, Sporobolus*	1 (13% of 8)*
23. Handsworth (11 km E)	*Bouteloua, Schizachyrium*	6 (50% of 12)
24. Redvers (15 km N)	*Schizachyrium, Sporobolus, Stipa*	1 (50% of 2)
25. St. Hubert (6 km SE)	*Agropyron, Andropogon, Koeleria, Muhlenbergia, Schizachyrium, Stipa*	7 (50% of 14)
26. Spy Hill (3.5 km NE)	*Agropyron, Muhlenbergia, Schizachyrium*	5 (71% of 7)
27. Stockholm (5 km W)	*Agropyron, Andropogon, Distichlis, Schizachyrium, Spartina, Sporobolus, Stipa*	7 (37% of 19)
28. Wauchope (4 km E)	*Andropogon, Schizachyrium, Sporobolus*	2 (67% of 3)
29. Willowbrook (12 km E)	*Agropyron, Koeleria, Muhlenbergia, Schizachyrium*	3 (33% of 9)
North Dakota		
30. Berwick	*Panicum, Schizachyrium, Spartina, Sporobolus*	2 (67% of 3)
31. Carrington (3 km S)	*Andropogon, Schizachyrium, Spartina*	3 (100% of 3)
32. Courtenay	*Distichlis, Schizachyrium*	6 (75% of 8)
33. Harvey (4 km NW)	*Agropyron, Andropogon,* [*Muhlenbergia*], *Panicum, Schizachyrium, Sorghastrum, Spartina, Sporobolus*	7 (78% of 9)
34. McLeod (5 km N)	*Bouteloua, Distichlis, Koeleria, Panicum, Schizachyrium, Stipa*	1 (14% of 7)
35. Melville (18 km E)	*Agropyron, Panicum, Schizachyrium, Spartina*	3 (43% of 7)
36. Rugby (6 km S)	*Panicum, Schizachyrium, Spartina*	2 (50% of 4)
37. Towner (16 km S)	*Agropyron, Andropogon, Koeleria, Panicum, Schizachyrium*	3 (50% of 6)
38. Voltaire (2 km E)	*Andropogon, Panicum, Schizachyrium, Spartina, Sporobolus, Stipa*	5 (71% of 7)
39. Red River Plain (6 sites)	*Agropyron, Andropogon, Muhlenbergia, Panicum, Schizachyrium, Sorghastrum, Spartina, Sporobolus, Stipa*	14 (61% of 23)

Asterisk (*), includes additional species found at a previous sampling; †, sites in the same area that have not been recently sampled and may no longer exist.

Note: Flora in brackets were not observed but are indicated on the basis of host-specialist Homoptera collected there.

consistent fauna (table 3). This fauna was found to extend along the western margins of the Glacial Lake Agassiz basin in Manitoba and also 400 km northwest (figure 4). Its northernmost known site in Saskatchewan is between Yorkton and Willowbrook. A shorter extension of tallgrass prairie in North Dakota lies north of the Missouri Coteau, but it terminates east of Minot after 200 km.

Over 30 bugs characteristic of tallgrass prairies were found in the sampled area (Hamilton 2004). Of these, 25 are widespread (table 3). One in particular, the leafhopper *Flexamia graminea* (on little bluestem), is ubiquitous in tallgrass sites (figure 5) and is not found in oak savanna. It was sampled at 41% of all bluestem stands (18 of 44) from North Dakota to eastern Saskatchewan (figure 5). Other bugs common on

Table 3. Total prairie distribution of 25 widespread species of short-horned bugs endemic to tallgrass prairies found in the study area.

Prairie bugs	Manitoba sites[a]	Saskatchewan sites[a]	North Dakota sites[a]
Tallgrass species (south to Texas)			
Leafhoppers			
Flexamia atlantica	0+	20	39 (3 sites)[b]
*Flexamia graminea**	8, 10, 11, 14	23, 25, 26, 27, 28	30, 31, 32, 33, 37, 38, 39 (2 sites)[b]
Flexamia prairiana	2, 6, 7, 11, 16+	–	39 (4 sites)[b]
Flexamia reflexa	5, 19	–	–
Graminella mohri	–	–	33, 39 (1 site)[b]
Laevicephalus vannus	18+	–	–
Stirellus bicolor	8, 11, 14, 19+	27, 29	–
Planthoppers			
Bruchomorpha jocosa	2, 10+	20, 25, 27, 29	38, 39 (1 site)[b]
*Delphacodes angulata**	11	–	–
Illinoian species (south to Oklahoma)			
Leafhoppers			
Chlorotettix fallax	–	–	35, 39 (1 site)[b]
Commellus colon	15+	20, 25	39 (1 site)[b]
Laevicephalus unicoloratus	3, 7, 8, 10, 11, 13, 14+	23, 25, 26, 27, 28	32, 36, 37, 38, 39 (1 site)[b]
*Neohecalus magnificus**	12+	–	33, 35, 36, 39 (1 site)[b]
Paraphlepsius hemicolor	11+	–	–
Paraphlepsius lobatus	1, 2, 3, 9, 11+	20, 22, 23, 24, 25, 27	–
Planthoppers			
Delphacodes parvula	1, 2, 4, 19+	23, 26	30, 34, 35, 37, 39 (3 sites)[b]
*Delphacodes n. sp.**	0+	–	–
*Megamelus metzaria**	18+	–	33
Prokelisia crocea	11, 12, 16, 18+	21	31, 33, 38, 39 (2 sites)[b]
Oak savanna species (east to Wisconsin)			
Leafhoppers			
*Aflexia rubranura**	0+	–	–
*Flexamia delongi**	3, 19+	20	–
*Memnonia panzeri**	0+	–	39 (1 site)[b]
Paraphlepsius umbrosus	11+	20, 27	–
Polyamia caperata	1, 3, 7, 10, 11, 16+	20, 23, 25, 26, 27	31, 32, 39 (1 site)[b]
Planthopper			
*Bruchomorpha dorsata**	11, 16	20, 25	38, 39 (2 sites)[b]

Asterisk (*), species usually found in tallgrass prairie or in oak savanna, but not in both; +, found on oak savanna.

a. Sites are numbered as in table 2.

b. Red River Plain (no. 39) includes six sites. For species that were found in Red River Plain, the number in parentheses indicates how many of these sites included the species.

little bluestem in the same area include three leafhoppers (at 25% to 41% of sites) and two planthoppers (at 14% to 32% of sites), all of which are widespread throughout both tallgrass prairie and oak savanna.

Leafhopper species occurring in sites east of Lake Manitoba and farther south along the Red River Valley are characteristic of oak savanna rather than true tallgrass prairie (table 3). In this region, two of the most common and characteristic oak savanna leafhoppers are specialists on prairie dropseed. Both have flightless females, yet their powers of dispersal are remarkable, since at least one of these two species occurs in 74% of all eastern grassland sites (figure 6) from oak savanna of Manitoba eastward to the alvars of Ontario, missing only the fens of south-central Michigan. Although prairie dropseed was sampled at 13 sites west of the Red River Valley in North Dakota, in western Manitoba, and in eastern Saskatchewan, and this grass was plentiful at five of these sites, neither of these insects was discovered. A similar disappearance of these two species occurs south of oak savanna in the United States. Clearly, prairie dropseed was never even a subdominant of true tallgrass prairie, or these two leafhoppers would be more widespread.

The oak savanna region of Manitoba has its richest leafhopper fauna north of Winnipeg (Hamilton 2004). There are both endemic leafhoppers, such as *Attenuipyga joyceae* (Hamilton 2000), and disjuncts, such as *Flexamia delongi* (figure 3). There is no such regional endemism within the tallgrass prairie of Manitoba west of the Red River Valley, with two pos-

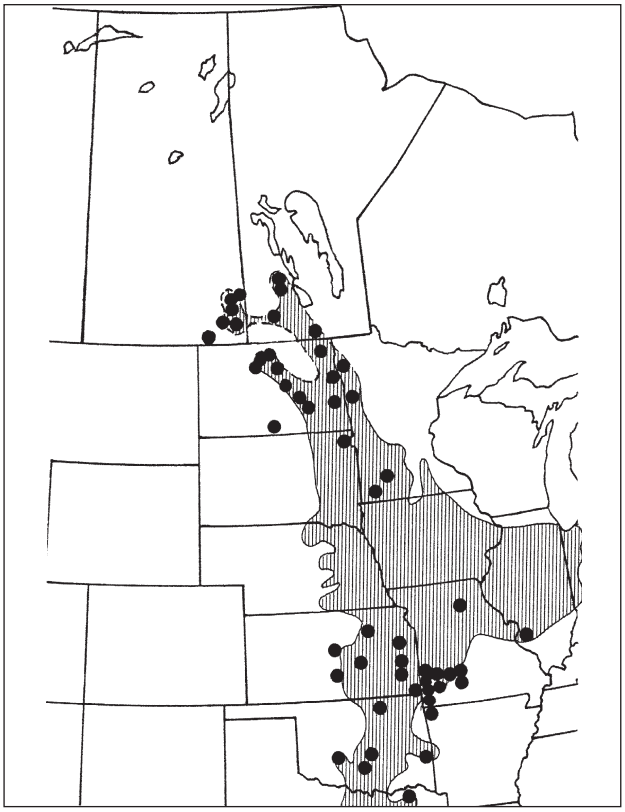

Figure 5. Distribution of tallgrass prairie (outline), based on US records (Dice 1943) and personal observations in Canada, and the distribution of its associated leafhopper **Flexamia graminea** *(filled circles).*

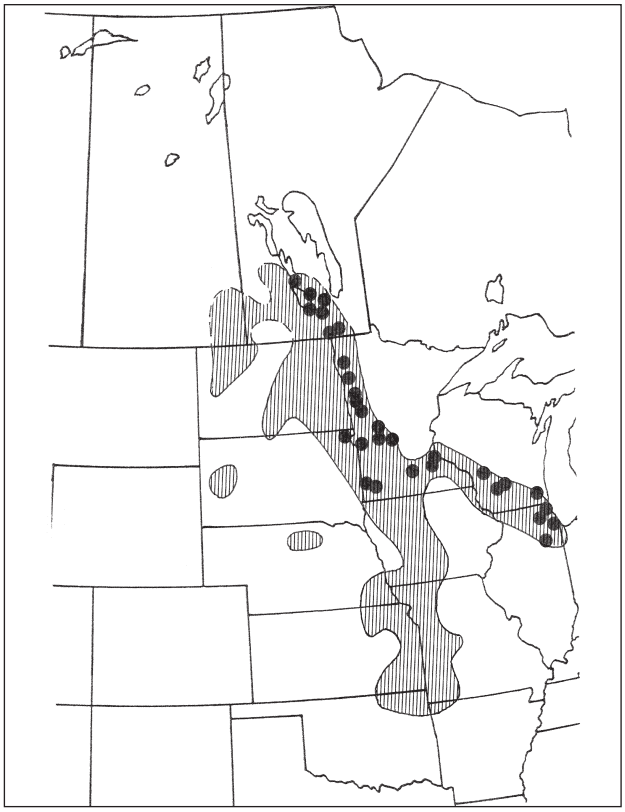

Figure 6. Distribution of prairie dropseed (outline) in eastern prairies, based on US records (Barkley 1977) and personal observations in Canada, and the distribution of its flightless leafhoppers **Aflexia rubranura** *and* **Memnonia panzeri** *(filled circles).*

sible exceptions. Both are known only from females; the discovery of associated males may show that these are undescribed endemics. One is a *Flexamia* with a distinctive facial pattern. It was taken in 1958 on an unknown host at Gladstone (possibly site 7 in table 2). The other is a *Laevicephalus* found in 2003 and 2004 on salt grass (*Distichlis stricta*) at Winnipegosis (site 18 in table 2).

Conclusions

The present distributions of leafhoppers that are specialists on dominant or subdominant prairie grasses reflect at least three processes of coevolution with modern grassland ecosystems. Suites of closely related species all feeding on the same host show that such a plant was an important part of an ecosystem even through the height of Pleistocene glaciation. Slow-dispersing species show that the grasslands they now inhabit were once contiguous, and flightless leafhoppers that are monophages demonstrate that their host plant once was at least a subdominant species wherever the leafhopper is still found.

The distributions of these insects also illuminate some of the poorly understood factors that constrained the presettlement extent of tallgrass prairies. For example, grassland elevation seems to be the chief factor in North Dakota and central Manitoba, where bluestem prairies were confined to lowlands associated with major rivers. In eastern Saskatchewan, these grasslands occur at much higher elevations, but still in river basins.

Biogeographic patterns spanning the US–Canadian border can be unified using such data. For example, insect evidence supports the usual opinion that southwestern Manitoba is an ecotone of northern mixed-grass plains (steppe) and aspen forest. Farther south, in north-central North Dakota, the land is more arid, with little evidence of aspen forest. This elevated area (the watershed between north- and south-flowing rivers) also has a fauna similar to that of the aspen parkland on the northern fringe of mixed-grass plains in Saskatchewan, but enriched with southwestern elements. This transborder area is therefore not part of the tallgrass ecosystem. Its extent has been estimated by elevation; the bug fauna has yet to be mapped.

Much of the tallgrass prairie in Canada is also an ecotone with aspen forest but is faunistically distinct from aspen parkland. It is a northwestern extension from the eastern Dakotas into central Manitoba, with a more or less isolated area in eastern Saskatchewan. The Assiniboine Valley and adjacent lowlands are the most likely connection between these two Canadian areas. Available sites to test this hypothesis are scarce. However, sampling to date suggests that Saskatchewan

tallgrass prairie has a leafhopper fauna similar to that of Manitoba, with common species such as *Paraphlepsius lobatus* that are dissimilar from those of the tallgrass extension in North Dakota.

Both aspen parkland and northern tallgrass prairie are ecotones of forest and prairie. Ecotones do not fit readily into a strictly hierarchal classification of ecosystems. For example, the oak savanna ecoregion belongs to the Illinoian ecoprovince within the ecozone of the Great Plains, which in turn is a major element of the North American section of the worldwide temperate grassland biome; but it is also a subsection of the temperate deciduous forest biome. Oak savanna cannot be considered to be only temperate deciduous forest, for it has both wide-ranging tallgrass prairie species and its own unique grassland bugs.

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