ABSTRACT: Opportunities for conserving native plant diversity in the northern Great Plains should be found on National Wildlife Refuges (NWRs), but floristics of these areas are largely undocumented. During 1998-2002, we used 25-m belt transects (n=713) to measure the general floristic makeup of a northern mixed-grass prairie on 4300 ha of glacial drift plain soils at Des Lacs NWR and J. Clark Salyer NWR in North Dakota. These prairies had been managed mainly by rest since the 1930s. For comparative purposes, we also measured about 1200 ha of nearby, privately owned prairies (n=154 transects), which had been annually grazed since at least the mid-1900s. Vegetation dominated by low (<1.5 m) native shrubs were common on both NWR prairies and on grazed prairies near Des Lacs NWR, occurring roughly in a 1:3 ratio with herbaceous-dominated vegetation. Nearly all prairies were moderately to severely invaded by introduced plant species, mainly smooth brome (Bromus inermis Leyss.) and Kentucky bluegrass (Poa pratensis L.) on NWRs, and Kentucky bluegrass, almost exclusively, on adjacent grazed prairies. Plant assemblages composed of native species were encountered rarely (3-6%), except when they occurred fairly often (16%) on grazed prairie next to J. Clark Salyer NWR. Our study demonstrates pitfalls of managing disturbance-dependent grasslands as relatively static, late-succession systems for many decades, without basic inventory and monitoring to comprehend and address associated ecological changes. A consequence of this course of action on NWR prairies we studied was a hastened invasion by introduced grass species, especially smooth brome.

Index terms: Bromus inermis Leyss., invasive species, mixed-grass prairie, Poa pratensis L., restoration

INTRODUCTION

Mixed-grass prairie has declined 70-90% in northern Great Plains states and provinces, mainly due to conversion to agriculture (Samson and Knopf 1994). Remnant tracts are mostly privately owned and likely will continue to decline in quantity and quality due to further conversion, certain livestock grazing practices and trends, suppression of wildfire, and invasions by woody and introduced plant species (Samson and Knopf 1994, Higgins et al. 2002). Conservation of representative mixed-grass prairie is a primary resource goal on most National Wildlife Refuges (NWRs) and other publicly-owned lands in the northern Great Plains. Key roles of the NWR system include contribution to ecosystem integrity and the conservation of biological diversity (U.S. House of Representatives 1997). Roughly 20,000 ha of mixed-grass prairie occurs on glacial drift plain soils on NWRs and other lands owned by the U.S. Fish and Wildlife Service in North Dakota (Figure 1). These prairies, like those of other NWRs in the Great Plains, should contribute to conservation of native plant assemblages unique to the region, but their floristic composition is undocumented. Our goal was to sample the general plant composition of native prairies on two of these NWRs to help identify opportunities and limitations for prairie conservation. For comparative purposes, we also sampled plant composition on nearby, privately owned prairies with a history of management that differed from that on the NWRs.

STUDY AREA AND METHODS

Our study sites are Des Lacs NWR and J. Clark Salyer NWR, located about 100 km apart within the Souris River basin of northwestern and north central North Dakota (Figure 1). “Drift prairie,” characterized by native sod in relatively deep (12-15 cm surface, 25-30 cm subsurface), level loams typical of the extensive Drift Plain physiographic region (Bluemle 1991), is a major component of the NWRs (2000 ha on 7900-ha Des Lacs NWR, 2300 ha on 23,900-ha J. Clark Salyer NWR). Drift prairies on each NWR consist of roughly 25-km long, 0.5-km to 2.0-km wide tracts along east and west sides of shallow river impoundments. Drift prairie on each NWR is bordered mainly by cropland (dryland farming for small grains) and by wetland impoundments of the Des Lacs or Souris rivers. Other bordering land includes scattered, 16-ha to 130-ha tracts of either annually grazed, privately owned drift prairie or cropland formerly seeded to introduced grasses and forbs for conservation purposes (e.g., to inhibit soil erosion, provide bird-nesting cover).
The Souris River basin is in the eastern (mesic) subregion of the northern mixed-grass prairie. Native flora is a cool-season (C₃)-dominated, needlegrass-wheatgrass (Stipa-Agropyron) association (Coupland 1992, Bragg 1995). Species characteristic of this association include other cool-season graminoids such as Junegrass (Koeleria pyramidata Lam.; nomenclature follows Great Plains Flora Association 1986), native Poa spp., and sedges (Carex spp.); several warm-season (C₄) grass species, mainly blue grama (Bouteloua gracilis H.B.K.), sideoats grama (B. curtipendula Michx.), and big bluestem (Andropogon gerardii Vitman); the low shrubs, western snowberry (Symphoricarpos occidentalis Hook.) and silverberry (Elaeagnus commutata Bernh.;) and many forb species, mainly Asteraceae and Fabaceae. The climate of our study area is semiarid to subhumid continental, with average monthly temperatures ranging from -15 °C in January to 20 °C in July (U.S. Fish and Wildlife Service, unpubl. data). The mean annual precipitation on Des Lacs NWR and J. Clark Salyer NWR were each established in 1935 “as a breeding and resting ground for migratory birds and other wildlife” (Executive Order 7154-A). Through the late 1960s, drift prairie on the NWRs typically was grazed season-long by cattle at light to moderate stocking rates (0.6-1.8 Animal Unit Months [AUMs]/ha), although at Des Lacs NWR, years of grazing often alternated with years of rest (i.e., no prescribed defoliations). To emphasize dense, undisturbed nesting cover for prairie ducks, a drift prairie on the refuges was rested with increasing frequency during the early 1970s through early 1990s, with long-range plans at J. Clark Salyer NWR to eliminate grazing (e.g., by the mid-1980s, total ha annually grazed on J. Clark Salyer NWR was 85-90% less than that grazed during the 1960s). Tracts totaling roughly two-thirds of the drift prairie on each NWR were prescribe-burned (spring or late summer), usually just once, during this 20-year period. About one-third of the prairie at Des Lacs NWR was grazed at moderate stocking rates (1.5-1.8 AUMs/ha) under rotation prescriptions (Stoddart et al. 1975;293) during an average of only two May-September seasons, and almost no grazing occurred at J. Clark Salyer NWR. In contrast, drift prairie on nearby, privately owned land generally was grazed season-long almost annually since at least the mid-1900s, at moderate to heavy (≥1.8 AUMs/ha) stocking rates, and had not been burned. Starting in the 1960s, herbicides were used to control localized infestations of the introduced forb, leafy spurge (Euphorbia esula L.), on both NWR and grazed drift prairies. Biological control with flea beetles (Apthona spp.) became the main method of managing leafy spurge on the NWRs by the late 1990s.

During late summer, we used 25-m belt transects to record frequencies of plant species or species groups (Grant et al. 2004) on drift prairie at each NWR and on privately owned, grazed drift prairies within 2 km of each NWR (total, about 1200 ha). We distributed 1 transect/5-8 ha of drift prairie, except on the grazed prairie near Des Lacs NWR, where we sampled half as intensively because the vegetation makeup within varied less than that on drift prairie elsewhere in our study area. Transects were distributed randomly, and each was oriented along a random compass bearing. We classified the dominant plant group at 50 successive, 0.5-m x 0.1-m belts along each 25-m long transect, using common plant groups of the region (Grant et al. 2004; Appendix A). Transect data were summarized by percentage frequency of occurrence according to plant species group, life form, or invasion class (i.e., mostly [≥50%] or somewhat [5-50%] invaded by introduced plant species, or devoid of introduced plant species). The data were averaged for the drift prairie of each NWR and for privately owned drift prairie adjacent to each NWR. We simply used 95% confidence intervals to discern significant differences between these means (Johnson 1999).

RESULTS

During 1998-2000, we collected frequency data from 252 transects on drift prairie at Des Lacs NWR and from 36 transects on nine nearby, grazed tracts of drift prairie. During 2002 we collected data from 461 transects on drift prairie at J. Clark Salyer NWR and from 118 transects on 17 grazed transects to record frequencies of plant species or species groups (Grant et al. 2004) on drift prairie at each NWR and on privately owned, grazed drift prairies within 2 km of each NWR (total, about 1200 ha). We distributed 1 transect/5-8 ha of drift prairie, except on the grazed prairie near Des Lacs NWR, where we sampled half as intensively because the vegetation makeup within varied less than that on drift prairie elsewhere in our study area. Transects were distributed randomly, and each was oriented along a random compass bearing. We classified the dominant plant group at 50 successive, 0.5-m x 0.1-m belts along each 25-m long transect, using common plant groups of the region (Grant et al. 2004; Appendix A). Transect data were summarized by percentage frequency of occurrence according to plant species group, life form, or invasion class (i.e., mostly [≥50%] or somewhat [5-50%] invaded by introduced plant species, or devoid of introduced plant species). The data were averaged for the drift prairie of each NWR and for privately owned drift prairie adjacent to each NWR. We simply used 95% confidence intervals to discern significant differences between these means (Johnson 1999).
tracts near the NWR. Our sampling was extensive; there was relatively little variation in transects across an NWR or across nearby, private lands, such that standard errors usually were within two percentage points of mean frequency values.

Makeup of general plant life forms was remarkably similar between Des Lacs NWR and J. Clark Salyer NWR, with a (roughly) 1:3 mixed occurrence of low shrub and herbaceous vegetation types (Figure 2a). Life form composition on the drift prairie at Des Lacs NWR closely resembled that on nearby, grazed drift prairie. At J. Clark Salyer, however, low shrubs occurred half as frequently on the grazed prairie as on the NWR. More significantly, drift prairie on both NWRs was invaded heavily by introduced plant species (Figure 2b). The range in magnitude of this invasion was similar between NWRs; vegetation dominated by introduced species was encountered frequently (>60%), while intact assemblages of native vegetation were encountered infrequently (3-6%). Grazed drift prairie near Des Lacs NWR exhibited a similar pattern of degradation, but the grazed drift prairie near J. Clark Salyer NWR had less extensive invasion.

We further examined degradation among herbaceous vegetation types (Figure 2c). Again, the pattern of degradation on Des Lacs and J. Clark Salyer NWRs was remarkably similar: Kentucky bluegrass (Poa pratensis L.) and smooth brome (Bromus inermis Leyss.) were the most common invasive species on both NWRs, although smooth brome-dominated types occurred almost twice as frequently as Kentucky bluegrass-dominated types. In contrast, vegetation dominated by smooth brome was rare (<3%) on nearby grazed prairies. Kentucky bluegrass accounted for nearly all invasion by introduced plants on privately owned drift prairie, and was overwhelmingly dominant on privately owned prairie near Des Lacs NWR. Weedy forb species were relatively uncommon except at J. Clark Salyer NWR, where they were fairly common (12%). Weedy forb-dominated vegetation on NWRs included leafy spurge (about 80% of weedy forb types), sweet clover (10%), and Canada thistle (Cirsium arvense Scop.: 10%). On nearby grazed drift prairies, weedy forbs were leafy spurge (85%) and Canada thistle (15%).

We also examined low shrub types (Figure 2d). In contrast to patterns of degradation observed in herbaceous types on NWRs, Kentucky bluegrass was at least as prevalent as smooth brome as an understory component of western snowberry stands on the NWRs. On grazed drift prairie, shrub understories almost always were dominated by Kentucky bluegrass, similar to invasion patterns in herbaceous types in the same prairies. Silverberry was conspicuous in the Des Lacs area, both on the NWR prairie and on adjacent, grazed prairie, but we recorded it infrequently because individual plant shoots of silverberry were widely dispersed.

**DISCUSSION**

The contemporary drift prairie vegetation at Des Lacs and J. Clark Salyer NWRs has badly deteriorated mainly through invasion by two introduced, cool-season grasses, smooth brome and Kentucky bluegrass. Prairie on the NWRs exhibited similar patterns of smooth brome and Kentucky bluegrass invasion in both herbaceous and low shrub communities, suggesting that the nature and extent of invasion are in part an unforeseen consequence of rest (i.e., non-disturbance), the chief management history common to drift prairie at both NWRs. Kentucky bluegrass tends to increase under prolonged rest or with grazing in northern prairies (Hulbert 1986, Bragg 1995, Biondini et al. 1998), but decreases with fire (Curtis and Partch 1948, Hill and Platt 1975, Gartner et al. 1986) especially when burning occurs during tiller elongation (roughly in mid-spring; Grace et al. 2001), in dry years (Engle and Bultsma 1984, Blakespoor 1987, Blakespoor and Bich 1991, Nagel et al. 1994), or on relatively dry sites (Zedler and Loucks 1969, Reader and Bonser 1993). Smooth brome also increases in northern prairies under rest (Romo et al. 1990, Blakespoor and Larson 1994, Bragg 1995) but, in contrast to Kentucky bluegrass, may be sensitive to repeated defoliation including grazing (Brown 1997) and likely is unaffected or may increase with prescribed burning (Grilz and Romo 1994, 1995; Willson and Stubbendieck 1995, 2000). Grazing and burning treatments on Des Lacs NWR and J. Clark Salyer NWR during the mid-1970s through mid-1990s were probably too infrequent, and perhaps not optimally timed with regard to phenology, to deter smooth brome and Kentucky bluegrass invasion.

Other factors probably contributed to widespread occurrence of Kentucky bluegrass and smooth brome on the drift prairie at Des Lacs NWR and J. Clark Salyer NWR. For decades, topsoil and nitrogen fertilizers have drifted onto boundaries of the drift prairie from adjacent, annually tilled croplands. These exposed soils overlie and shade native flora while providing germination sites for invasive plants (Grace et al. 2001). Nitrogen inputs from fertilizer drift can reduce the competitive ability of native grasses and thus favor introduced species invasion (Wedin and Tilman 1990). Smooth brome, in particular, tends to encroach into native prairie along an invasion front extending from boundaries (Blakespoor and May 1996). Brome also expands as islands in the interior, often from within patches of woody vegetation (Romo et al. 1990).

The influence of herbivory on smooth brome invasion in northern mixed-grass prairie is poorly documented. We observed smooth brome infrequently in annually grazed drift prairie near the NWRs, suggesting smooth brome is grazing sensitive. On the NWRs, smooth brome-dominated types were twice as prevalent as Kentucky bluegrass-dominated types, indicating that with little or no grazing and fire disturbance, smooth brome may be more competitive than Kentucky bluegrass in relatively rich loam soils of the Drift Plain physiographic region. Of the two introduced species, smooth brome seems more difficult to control and more significantly alters the quality and physiognomy of a prairie (Blakespoor 1987). In at least some northern prairies, however, reduction of one of these introduced grass species may simply mean an increase in the other (Brown 1997), particularly when either fire or grazing is used exclusively as the
Figure 2. Frequencies of drift prairie vegetation on Des Lacs and J. Clark Salyer National Wildlife Refuges (NWRs) and on nearby, annually grazed drift prairie in northwestern and north central North Dakota, based on data derived from randomly located, 25-m belt transects during 1998-2002 (n = 252, 461, 36, and 118 transects for Des Lacs NWR, J. Clark Salyer NWR, and privately owned, annually grazed drift prairies near the respective refuges): (a) frequencies by general life form; (b) frequencies of plant assemblages mostly (>50%) or somewhat (5-50%) invaded by introduced plant species, or devoid of introduced plant species (“pristine”); (c) frequencies of major herbaceous components; (d) frequencies of low shrub components. Error bars indicate 95% confidence intervals.
Vegetation dominated by low shrubs, principally western snowberry, occurred in roughly a 1:3 ratio with herbaceous-dominated vegetation on refuge prairie and on privately owned prairie near Des Lacs NWR. This frequency of low shrub vegetation probably is greater than that in northern mixed grass prairie under a natural (herbivore-fire) disturbance regime (e.g., an estimated 5% low shrub cover occurred on pristine mixed-grass prairie in northwestern and north-central North Dakota; U.S. Soil Conservation Service 1975). However, snowberry probably was more prevalent on drift prairies of the NWRs 20 to 30 years before our study (U.S. Fish and Wildlife Service, unpubl. NWR narrative reports), but has been largely replaced by smooth brome. The relatively cool, moist sites typically occupied by snowberry appear most vulnerable to smooth brome invasion (Romo et al. 1990). Concurrent with low shrub invasion on the NWRs’ drift prairies, woodland cover also encroached in the absence of fire and grazing for many decades (Grant and Murphy 2005).

Northern mixed-grass prairies evolved with interacting grazing and fire disturbances (Higgins 1986), as well as climatic variability (Bragg 1995). Through the mid-1800s the Souris River basin was a significant, year-round range for bison (Bison bison; Hanson 1984) and experienced a circa 5-year fire return interval characteristic of the region (Bragg 1995). These major, frequent disturbances ended by the early 1900s, however, after bison had been extirpated and most of the Souris River basin was being settled by homesteaders of European descent, who suppressed fires (Grant and Murphy 2005). During the following half-century, drift prairie on Des Lacs NWR and J. Clark Salyer NWR was managed mainly for late successional cover to attract nesting mallards (Anas platyrhynchos) and other duck species that prefer to nest in relatively tall, dense vegetation (Duebbert et al. 1986, Lokemoen et al. 1990). Predictably, avian species diversity also has diminished on the NWR drift prairies; only three to four species of breeding grassland passerines are common (Murphy and Sondreal 2003; T. Grant and E. Madden, U.S. Fish and Wildlife Service, unpubl. data), these associated with late successional prairie and/or tolerant of plant communities dominated by introduced grasses (Madden et al. 2000). At least six other grassland-dependent species of passerines occurred historically on the NWRs but now are uncommon or absent (Murphy and Sondreal 2003). These birds require shorter, sparser, more herbaceous prairie vegetation than that available on the NWRs’ extant drift prairie. In particular, the endemic Sprague’s pipit (Anthus spragueii) is associated with native bunchgrasses and avoids broad-leaved, introduced grasses, such as smooth brome (Wilson and Belcher 1989, Madden et al. 2000). Losses of floristic and avian diversity are not the only consequences when northern prairies are invaded by introduced plants. Nutrient pools, energy flows, soil invertebrate and mycorrhizal relationships, and the water cycle also can be altered significantly (Bragg and Steuter 1995, Seastedt 1995, Christian and Wilson 1999, Wilson 2002).

NWRs in our study were established 70 years ago in the northern prairie region, along with dozens of others. Nearly all of these NWRs have lacked staff, funding, and direction for basic inventory and monitoring of the integrity of upland vegetation. Without such fundamental assessments of status or risk, individual NWR managers apparently have been unable to appreciate the role of their relatively short tenure (generally, only 2-4 years) in influencing successive, incremental changes in prairie vegetation. This trend should be changing, however, following passage of the NWR Improvement Act of 1997, which calls for comprehensive management planning for individual NWRs (Gergely et al. 2000). Clearly, development of goals and appropriate habitat management objectives for drift prairie will be a challenge on publicly owned lands set aside for conservation purposes, such as Des Lacs and J. Clark Salyer NWRs and many other lands owned by the U.S. Fish and Wildlife Service in North Dakota (Figure 1). Goals could range from emphasizing nesting habitat for one group of birds, to attempting to restore largely indigenous biotic communities driven by more natural ecological processes. Relative to other northern mixed-grass prairies (e.g., Missouri Coteau), prairie on the relatively rich loam soils of the Drift Plain appears particularly vulnerable to invasion by smooth brome and Kentucky bluegrass as well as conversion to agriculture. Most northern mixed grass prairie has been destroyed (Samson and Knopf 1994, Samson et al. 2004), but losses have been particularly severe in the Drift Plain physiographic region (i.e., wheatgrass-bluestem-needlegrass type in Bragg and Steuter 1995). Drift prairie could thus be considered an endangered resource, underscoring urgency of refining goals appropriate for conserving remnant tracts of drift prairie on NWRs.

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APPENDIX A

Upland plant group types in northern mixed-grass prairies of North Dakota. One of the below types is recorded for each 0.1-m x 0.5-m segment along an outstretched 25-m tape, based on >50% dominance by canopy cover unless otherwise indicated. From Grant et al. (2004).

Low Shrub Types  (generally ≤1.5 m tall except in 1 to few post-disturbance years)
- western snowberrysdense (other low shrub spp. total 0-25%); other plants few or none
- snowberry (and other low shrub spp.); remainder mostly native grass-forb types
- snowberry (and other low shrub spp.); remainder mostly Kentucky bluegrass
- snowberry (and other low shrub spp.); remainder mostly smooth brome (or quackgrass a)
- silverberry prominent, remainder mostly native or invaded native grass-forbs
- silverberry prominent; remainder mostly Kentucky bluegrass
- silverberry prominent; remainder mostly smooth brome (or quackgrass)

Native Grass-forb and Forb Types  >95% dominance by native herbaceous plants
- dry cool season (sedges, green needlegrass, needle-and-thread, wheatgrass spp., prairie junegrass, forbs; often blue grama and some other C4 species)
- dry warm season (little bluestem, prairie sandreed, plains muhly, fescue spp., blue grama, forbs)
- mesic warm-cool mix (big bluestem, switchgrass, little bluestem, porcupine grass; mat muhly, prairie dropseed)
- subirrigated wet meadow microsite within upland (fowl bluegrass, foxtail barley, northern reedgrass, coarse sedge spp., baltic rush, dock, prairie cordgrass)

Exotic and Invaded Native Grass-forb Types
- Kentucky bluegrass >95%
- Kentucky bluegrass and native grass-forbs, bluegrass 50-95%
- native grass-forbs and Kentucky bluegrass, bluegrass 5-50%
- smooth brome (or quackgrass) >95%
- smooth brome (or quackgrass) and native grass-forbs, brome 50-95%
- native grass-forbs and smooth brome (or quackgrass), brome 5-50%
- crested wheatgrass >95%
- crested wheatgrass and native grass-forbs, crested wheatgrass 50-95%
- native grass-forbs and crested wheatgrass, crested wheatgrass 5-50%

Noxious Weed Types
- leafy spurge
- Canada thistle
- other noxious weeds (user-defined)
- tall exotic legume: sweet clover or alfalfa