Cool-Season Floodplain Meadow Responses to Shrub Encroachment in Alberta

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Abstract

This study evaluated the impact of shrub encroachment within cool-season floodplain meadows in a portion of the Rocky Mountain Forest Reserve in southwestern Alberta, where nearly half of open grasslands have been lost since 1958. Sample transects situated in meadows, known formerly to be in open grassland, were assessed in 2001 ($n = 21$) and 2002 ($n = 33$) in areas ranging from 0% to 92% shrub cover. Shrub cover, density, and height were correlated to understory parameters, including herbaceous production, bunchgrass cover and density, and species richness and diversity. Additional data on soil horizon depths were obtained. Analysis was conducted using regression to assess empirical relationships between understory or soil characteristics and the overstory. Stronger empirical relationships (i.e., greater R^2) were found in 2002, coincident with larger sample sizes and greater rainfall. Among independent overstory variables, aggregate shrub cover for all species accounted for the greatest variation in understory characteristics. Significant ($P < 0.01$) negative nonlinear relationships were observed between shrub cover and herbage production, with the latter declining from 6 629 $kg \cdot ha^{-1}$ in meadows containing less than 12% shrub cover, to 2 797 $kg \cdot ha^{-1}$ in areas where shrub cover exceeded 35%. Negative linear trends were found ($P < 0.01$) for bunchgrass density and cover in relation to increasing shrub abundance in 2002. Understory diversity increased with shrub abundance, peaking at 64% shrub cover in 2002. Meadows with low and high shrub cover also coincided with thicker Ah and litter, fibric, and humic soil layer (LFH) horizons, respectively. Collectively, these results indicate shrub encroachment is threatening the sustainability of native bunchgrass communities and reducing forage availability. Meadow conservation in this area will require proactive management to protect or restore open grasslands.

Resumen

Este estudio evaluó el impacto de la invasión de arbustos dentro de la temporada fría de praderas inundables en una porción de la Reserva Forestal de las Montañas Rocallosas en el suroeste de Alberta, donde se han perdido cerca de la mitad de los pastizales abiertos desde el 1958. Los transectos de muestreos situados en praderas conocidas antiguamente como pastizales abiertos, fueron evaluadas en el 2001 ($n = 21$) y 2002 ($n = 33$) en áreas con rangos de 0% a 90% de cobertura arbustiva. La cobertura arbustiva, la densidad, y la altura fueron correlacionadas con varios parámetros del sotobosque que incluyen la producción de herbáceas, la densidad, y cobertura de pastos, y la diversidad y riqueza de especies. Adicionalmente se obtuvieron datos de la profundidad del suelo. El análisis se condujo usando regresión para evaluar las relaciones empíricas entre el sotobosque o características del suelo y el dosel. Las relaciones empíricas más fuertes (i.e., más grande R^2) fueron halladas en el 2002, coincidiendo con las muestras de mayor tamaño y con mayor precipitación. Entre las variables independientes del dosel, la cobertura agregada de arbustos para todas las especies representó la mayor variación en las características del sotobosque. Las relaciones negativas no-lineares significativas ($P < 0.01$) fueron observadas entre la cobertura arbustiva y la producción de herbáceas, con la disminución de este último desde 6 629 $kg \cdot ha^{-1}$ en las praderas que contenían menos del 12% de cobertura arbustiva, hasta 2 797 $kg \cdot ha^{-1}$ en áreas donde la cobertura arbustiva excedió el 35%. Las tendencias negativas lineares fueron halladas ($P < 0.01$) para la cobertura y densidad de la pastos en relación al aumento en la abundancia arbustiva en el 2002. La diversidad del sotobosque aumentó con la abundancia arbustiva, alcanzando un máximo de 64% en la cobertura arbustiva en el 2002. Las praderas con baja y alta cobertura arbustiva también coincidieron con los horizontes más gruesos de Ah y LFH, respectivamente. Colectivamente, estos resultados indican que la invasión de arbustos está amenazando la sustentabilidad de las comunidades nativas de pastos y reduciendo la disponibilidad de forraje. La conservación de praderas en esta área requerirá un manejo proactivo para proteger ó restaurar los pastizales abiertos.

Key Words: *Betula glandulosa*, biodiversity, bunchgrasses, fire suppression, forage production, shrub cover

INTRODUCTION

Expansion of woody species is a concern for land managers on rangelands worldwide (Archer et al. 1995). These increases have been attributed to many causes, including climate change (Emmanuel et al. 1985, Sturm et al. 2001), atmospheric CO_2 enrichment (Archer et al. 1988), overgrazing (Dunwiddie 1977; Van Auken 2000), nitrogen deposition (Köchy and Wilson 2001), and fire suppression (Cook et al. 1994; Kay et al. 1994; Bork et al. 1996).

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The ecological consequences of woody plant encroachment into grasslands are not thoroughly understood (Wessman et al. 2004). Although the community-based impacts of shrub encroachment have been documented within select warm-season grasslands of North America (e.g., Tallgrass Prairie, Briggs et al. 2005; subtropical grasslands, Archer et al. 1988; desert grasslands, Schlesinger et al. 1990), less is known about the impact of shrub encroachment in northern temperate grasslands dominated exclusively by cool-season vegetation. In these climatic zones, previous studies have focused heavily on the impacts of tree species such as trembling aspen (*Populus tremuloides* Michx.) expansion in the Parkland (Bailey et al. 1990) and the phenomenon of tree ingrowth and outgrowth in dry conifer forests (Bai et al. 2005; Page et al. 2005), rather than shrub encroachment.

In the Rocky Mountain Forest Reserve (RMFR) of southwestern Alberta, invasion of cool-season floodplain meadows on public land by shrubs is relatively widespread (Johnston and Smoliak 1968; de Groot 1998; Burkinshaw 2005), with rates of woody plant expansion occurring at 0.75% to 5.5% per year and highest on moister sites (Johnston and Smoliak 1968). Historically, low-intensity, high-frequency fires maintained these grasslands (Kay et al. 1994; Rogeau 1996) but with widespread fire suppression associated with regional fire exclusion policies throughout the 1900s (Rogeau 1996), many have become dominated by shrubs (Bork et al. 1996; Willoughby 2001).

Shrub and tree invasion into these grasslands is of particular concern in the RMFR due to the potential loss of forage for livestock and wildlife (Adams et al. 1992; Willoughby 2001), which is further complicated by policy to maintain baseline stocking levels for cattle along the eastern slopes (RMFR; Alberta Energy and Natural Resources Report 1984). Changes in vegetation from open meadows to shrublands is thought to reduce forage availability for wildlife and livestock (de Groot 1998), as well as its accessibility to herbivores by reducing the area of primary range (Bork et al. 1996; Burkinshaw 2005). Decreased forage, in turn, increases the risk of degradation in remaining meadows, particularly under current livestock stocking rates, stable or increasing wild ungulate populations (particularly elk), and increasing numbers of feral horses. The shrub species responsible for encroachment, primarily bog birch (*Betula glandulosa* Michx.), also is low in forage quality for many ungulates (de Groot et al. 1997) and is considered less preferable habitat (de Groot 1998). Collectively, these changes under encroachment have the potential to intensify land use conflicts, especially where competing land uses for these grasslands are high and this habitat is scarce.

Encroachment also has the potential to alter the basic ecology of floodplain meadows, and maintenance of remaining grasslands is important for conserving biodiversity (Watkinson and Ormerod 2001). Shrub-dominated communities are associated with changes in herbaceous composition, including a decline in species diversity (Willoughby 2001), reduced grass productivity (Stuart-Hill and Tainton 1989), and the loss of critical wildlife habitat (Adams et al. 1992). Decreases in the abundance of native bunchgrasses, such as rough fescue (*Festuca campestris* Torr.) and tufted hairgrass (*Deschampsia cespitosa* [L.] Beauv.), are of particular concern in the RMFR because these species are valued for forage (Johnston and Smoliak 1968; Willms et al. 1988), and thus are considered species indicative of healthy grasslands. Moreover, increased grazing pressure on remaining grasslands increases the likelihood of their degradation, typified by the loss of native species and replacement with introduced species (Willms et al. 1985).

In order to better understand the impacts of shrub encroachment on land use activities in the region and develop alternative management strategies for these communities, we employed a retrospective study to contrast characteristics of open meadows (grasslands) with those of adjacent plant communities having varied amounts of shrub cover. Previous work indicated the area under investigation had experienced a 49% decrease in grassland between 1958 and 1998 (Burkinshaw 2005), supporting the assumption of ongoing shrub encroachment.

The specific objectives of this study were to 1) determine the empirical relationship between shrub overstory abundance and important understory characteristics such as vegetational richness and diversity, bunchgrass density and cover, aboveground herbaceous primary production, and key soil characteristics; and 2) compare the utility of different shrub parameters (i.e., density, cover, height, and stand age) for predicting understory characteristics.

METHODS

Study Area

This research was conducted during 2001 and 2002 in floodplain meadows along the Clearwater River, a major tributary to the North Saskatchewan River within the northern portion of the RMFR in southwestern Alberta. The climate of the area is modified by the Rocky Mountains, with cool summers and ameliorated winters (Archibald 1982); temperatures average 11.5°C in summer and −6.0°C in winter. Although July is generally frost-free, June and August can receive up to 3 d of frost (Poliquin 1968).

Annual precipitation values at Nordegg, Alberta (the nearest primary weather station), in 2000 (501.2 mm), 2001 (391.4 mm), and 2002 (516.3 m) were below the 30-yr mean (596.3 mm) for the region. Local summer (April to August) precipitation collected by automated weather stations at the Clearwater Ranger Station, 13 km south of the study area, and Ram Falls, 11 km north of the study area, during 2001 (335.3 mm), also was less than in 2000 (404.3 mm) and 2002 (414.6 mm).

The study was conducted on primary ranges within the Elk Creek and Idlewilde Distribution Units (DUs) of the Clearwater (cattle) Grazing Allotment. Based on the 1989 range management plan, the permitted stocking rate for these DUs is 690 and 412 Animal Units Months, respectively, with the grazing season from late June to late August.

Local wildlife surveys conducted in the Idlewilde DU during the winter of 2002 indicated 54 elk, below the peak of 85 from 1995 (J. Allen, Alberta Sustainable Resource Development, Wildlife Biologist, personal communication). Elk are thought to have little impact on vegetation in the area during summer as they move out of valley bottoms and into the hills for calving. Deer and moose are frequent browsers and a small herd of feral horses roam the study area, the latter preferring revegetated pipelines and seismic lines. The surrounding coniferous slopes, mainly comprised of lodgepole pine (*Pinus contorta* Loudon), are actively logged as part of a 100-yr tenured forest management agreement.

Although many plant communities have been described within valley bottoms of the study area (Willoughby 2001), the two predominant grasslands are rough fescue-tufted hairgrass and tufted hairgrass–wetland sedge (*Carex* spp.) types, on well-drained and poorly-drained ecosites, respectively. In the absence of fire, both communities become dominated by bog birch and/or willow (mostly *Salix myrtillifolia* Anderss.; Willoughby 2001).

According to the Provincial Forest Fire Centre, only four fires, each less than 0.1 ha, have occurred in the study area since 1958, with the last major fire in the late 1800s (Rogeau 1996). Except for a 2-ha brush mowing project at the south end of the study area, no range improvements have occurred on this portion of the allotment since 1958. Approximately 8 km south of the study area, a series of experimental prescribed burns have been undertaken to reduce bog birch (Bork et al. 1996).

Experimental Design

Initially, a total of 21 30-m long transects were randomly placed in the spring of 2001 within meadow communities, which ranged from 0% to 65% shrub cover, throughout the study area. Transects were situated in areas known to be relatively open grassland in 1958 (based on aerial photographs) to assess the impact of shrub encroachment. As few transects sampled in 2001 represented shrub levels between 20% and 40%, 12 additional transects were sampled together with the original transects in 2002 to ensure a more continuous range from open grassland to closed shrubland. All 33 transects were positioned throughout 11 km of valley bottom across the study area, but a stratified random placement minimized variation in ecosite characteristics between shrub encroached and adjacent unencroached sites. Although elevations varied slightly from the south to north end of the study area (1 450–1 530 m), aspects were generally level. The location of all transects was determined using a Garmin 12XL GPS to facilitate relocation.

Along each transect, the canopy cover (%) of all grass and forb species, as well as moss and lichen, were estimated (Daubenmire 1959) within 15 0.1-m^2 quadrats. A larger 1-m^2 quadrat nested overtop was used to estimate shrub canopy cover. The minimum sampling area for all cover estimations was determined by preliminary analysis of changes in response values with incremental sample areas. Vascular species richness was determined for each transect and species diversity (H′) was calculated using the Shannon–Wiener index, using equation 1 (Bonham 1989):

$$H' = \sum (p_i \log[p_i]) \qquad [1]$$

where, p_i = the proportion of total plant composition for the transect consisting of species i, and H′ is the sum of values for all individual species on the transect.

The density of dominant native bunchgrasses, including rough fescue and tufted hairgrass, was determined for each transect by counting these plants within a 60-m^2 belted plot (2 m wide × 30 m long) centered along each transect. The stem density (no. per 60 m^2) and maximum height (cm) of individual shrubs (bog birch, willow, shrubby cinquefoil [*Potentilla fruticosa* L.]) and trees (lodgepole pine and white spruce [*Picea glauca* {Moench} Voss]) were also recorded within belted plots. Woody species considered to be encroaching were bog birch, willow, lodgepole pine, and white spruce, although tree encroachment was minimal across the area and proved insufficient for analysis.

Aboveground current annual grass and forb production along each transect was estimated for the plant community by sampling a 0.5-m^2 quadrat within each of two range production cages used to prevent herbivory by cattle and other ungulates. Biomass was harvested to ground level in mid-August after peak growth was attained. Samples were sorted to grasses and forbs, oven-dried at 50°C to constant mass and weighed ($g \cdot m^{-2}$). Where present, shrubs were aged along each belted plot by sampling three bog birch and three willow plants. Representative shrubs on each transect were selected based on their size to obtain a mean age of shrubs within each community. Shrub stems were cut at ground level, dried, sanded with No. 300 grit paper to burnish the wood, and rings counted using a hand lens (Stokes and Smiley 1968).

Adjacent to each transect, a 1-m-deep pit was dug and morphological information collected on the identity of surficial soil horizons, as well as their thickness. Horizons were assessed for texture and structure, and profiles were examined for rooting depths and any unique characteristics such as the presence of charcoal.

Statistical Analyses

Regression analysis (Proc REG; SAS Institute 1989) was used to assess relationships between the understory herbaceous community and shrub overstory. Varying levels of in situ shrub encroachment were considered treatments at each transect and examined for their association with the understory, with transects serving as experimental units. For nonlinear (i.e., quadratic) relationships, a polynomial regression was performed. All relationships were considered significant at $P < 0.01$, unless otherwise indicated.

The understory variables assessed included species diversity (H′), bunchgrass canopy cover, and density, as well as herbage production, because these parameters are important indicators of overall biodiversity and range health, the condition and demographic status of the bunchgrass population, and the amount of available forage, respectively.

Shrub cover, density, height, and age also were compared for their use in explaining understory responses. Overstory–understory relationships were assessed empirically using Goodness-of-Fit (R^2) criteria, and helped identify which overstory variables accounted for the most variation in the understory. A preliminary correlation analysis was performed to assess redundancy between variables. Data were assessed separately for 2001 and 2002 because of changes in growing conditions, particularly rainfall, between years.

Finally, to determine if shrub height reflected shrubland age, mean shrub height was regressed against mean shrub age (willow and bog birch) from each transect. Height is a relatively easy parameter to measure and a strong correlation would allow height to be used as a surrogate to assess the time elapsed since encroachment. In addition, soil litter, fibric, and humic soil layers (LFH) and Ah horizon thickness were regressed against mean shrub canopy cover for each transect to discern whether increasing shrub abundance led to a shift in the diagnostic grassland mineral horizon (Ah) toward the development of a surficial organic horizon (LFH).

RESULTS

Understory Species Composition

There was no relationship between species richness and the shrub overstory variables examined (except height; $P < 0.01$, $r^2 = 0.20$) in either year of the study. Similarly, species diversity in 2001 did not exhibit a significant relationship with mean shrub canopy cover, density, or height ($P = 0.65$), although diversity tended to increase to an absolute maximum of 2.86 under 75% shrub cover. In 2002, species diversity was related to shrub canopy cover ($P < 0.01$), increasing as shrubs rose from low to moderate canopy closure. Although mean species diversity within transects with no shrubs was low ($H' = 2.37$) during 2002, this increased to a maximum under 64% shrub cover ($H' = 3.0$).

Bunchgrass canopy cover and density exhibited marked declines ($P < 0.001$) in relation to increasing shrub canopy cover in both 2001 and 2002. Bunchgrass cover declined from 50% in open grasslands, to near 0% in transects with 80% shrub cover (Fig. 1A). Similarly, bunchgrass densities declined from a mean of more than 4 plants $\cdot$ m^{-2} on shrub free transects, to less than 2 plants $\cdot$ m^{-2} at 60% shrub cover, with no bunchgrass plants at 95% shrub cover (Fig. 1B).

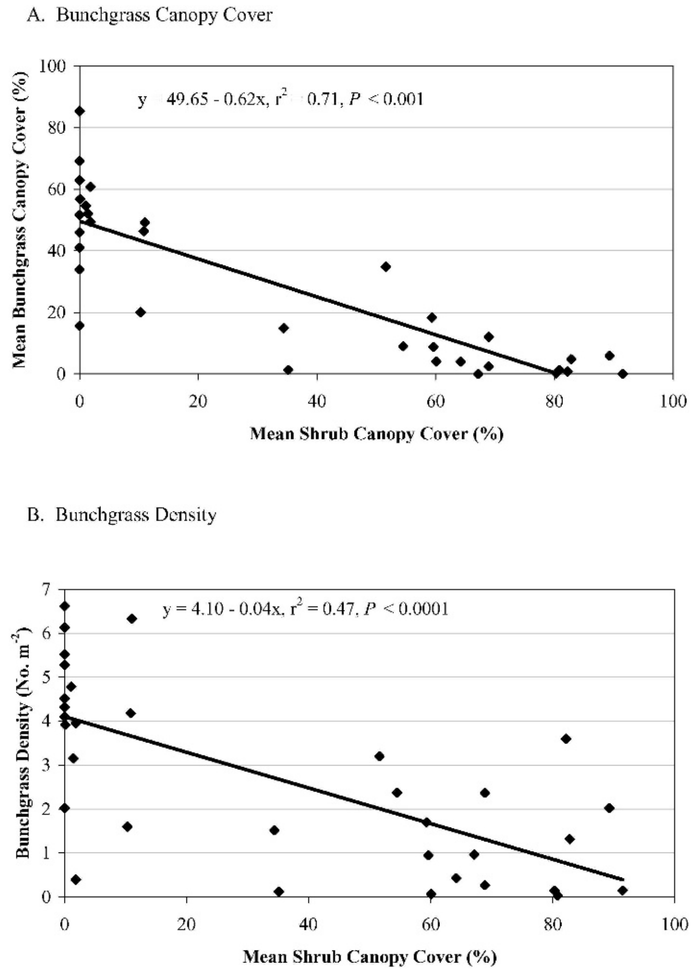

Figure 1. Relationship between mean shrub cover (%) in 2002 ($n = 33$) and **A**, bunchgrass canopy cover (%) or **B**, bunchgrass density (no. $\cdot$ m^{-2}).

Understory Production

Total herbage (grass plus forb) production within plots sampled during 2001 demonstrated a significant ($P < 0.01$) negative quadratic relationship ($r^2 = 0.63$) with increasing shrub canopy cover. Herbage production in 2001 (2 865 kg $\cdot$ ha^{-1}) was overall lower than one year later in 2002 (4 655 kg $\cdot$ ha^{-1}), coincident with lower growing season moisture in the first year of the study. During 2002, a similar but stronger negative relationship existed ($r^2 = 0.79$; $P < 0.01$) between shrub cover and total herbage production (Fig. 2A). Assessment of grass production alone in 2002 demonstrated only a small improvement in the curvilinear relationship ($r^2 = 0.82$; $P < 0.01$) with increasing shrub canopy cover (Fig. 2B), and was similar to that observed in 2001 (data not shown).

Total herbage production in 2002 decreased from a mean of 6 629 kg $\cdot$ ha^{-1} within relatively open grassland transects (< 12% shrub cover), to 2 797 kg $\cdot$ ha^{-1} in more closed shrubland transects (> 33% cover), representing a 58% decline. However, total herbage production in the absence of shrubs (i.e., 0% cover) also varied substantially in these floodplain meadows, with values ranging between 4 152 and 9 964 kg $\cdot$ ha^{-1}. Herbage–shrub relationships in 2002 (Fig. 2A) appeared to exhibit a threshold in shrub cover between 12% and 33%. Below 12%, production was variable (presumably due to ecosite variation) but relatively high (i.e., greater than 4 000 kg $\cdot$ ha^{-1}). In contrast, at shrub cover above 33%, maximum herbage production was much less than this value, reflecting the overriding negative influence of shrubs regardless of ecosite potential. Moreover, the nonlinear relationship between understory production and shrub cover indicates that greater production losses are likely with small increases in shrub abundance when the plant community was relatively open (i.e., < 12% shrub cover). Conversely, once shrub cover exceeded 33%, reductions in herbage occur at a lower rate with progressively greater shrub cover. For example, at 10, 40, and 70% shrub cover, estimated reductions in herbage production were 69, 48, and 33 kg $\cdot$ ha^{-1}, respectively, for each additional 1% increase in shrub cover.

Comparison of Shrub Characteristics and Soil Changes

The shrub variable with the strongest relationship to understory species diversity, as well as bunchgrass density and cover, was consistently shrub canopy cover ($r^2 = 0.27$, $r^2 = 0.47$, and $r^2 = 0.71$, respectively; Table 1). Similarly, mean shrub canopy cover ($r^2 = 0.79$) was a superior overstory variable compared to shrub density ($r^2 = 0.52$) and height ($r^2 = 0.42$) in accounting for the most variation in herbage production (Table 1).

The 2002 vegetation data revealed that the proportion of all shrub cover consisting of bog birch was 70%, with willow comprising most of the remaining 30%, and only trace amounts of shrubby cinquefoil. Among independent variables

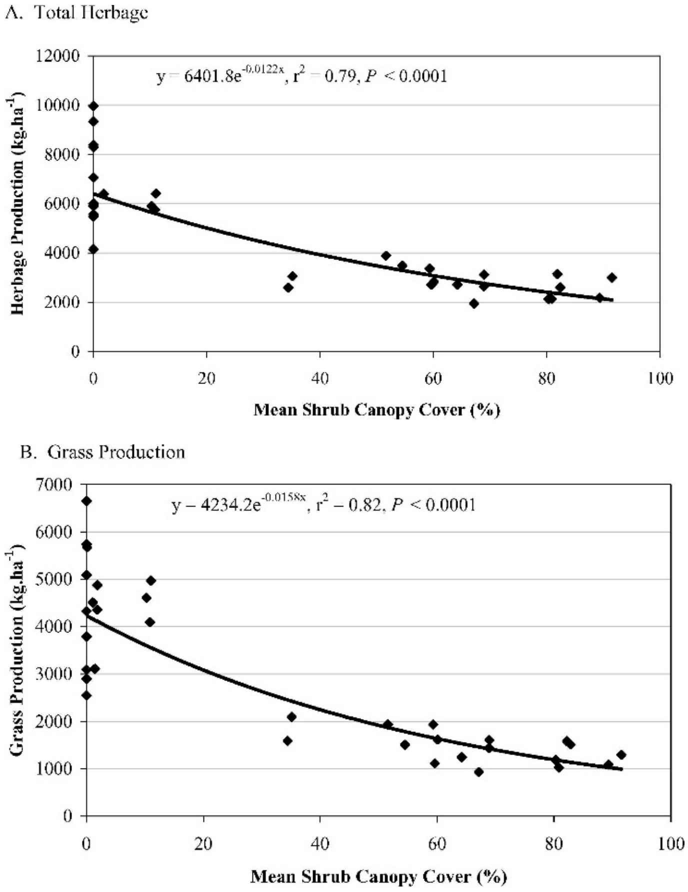

Figure 2. Relationship between mean floodplain shrub cover (%) in 2002 ($n = 33$) and **A**, total herbage (grass and forb) production or **B**, grass production alone.

comparing different shrub species, total mean shrub canopy cover (i.e., willow, bog birch, and cinquefoil combined) explained the most variation ($r^2 = 0.79$) in herbage production, and was greater than either the dominant or subdominant shrub species assessed alone.

Although the empirical relationship between mean shrub height and age was significant ($P = 0.05$), little variation in age was explained by height ($r^2 = 0.18$). Mean shrub age increased linearly with height but only to 15 yr of age, because shrubs older than this were generally absent within the communities sampled.

Soil profiles on each transect in this investigation were difficult to describe at depth due to the limited and inconsistent development of soil horizons, likely resulting from periodic flooding of these valley bottoms and intermittent sediment deposition. Nevertheless, the thickness of surficial LFH and Ah horizons had opposing relationships to increasing mean shrub canopy cover: LFH thickness increased with shrub cover and Ah thickness declined. Between the two, more variation in LFH ($r^2 = 0.51$; $P < 0.0001$) than Ah ($r^2 = 0.27$; $P < 0.01$) depth was explained by mean shrub canopy cover. In general, communities with shrub cover greater than 12% were associated with thinner Ah horizons (2.5 cm) and thicker LFH (3.7 cm) horizons compared to those communities with less than 12% shrubs (Ah and LHF horizons of 8.6 and 0 cm, respectively).

The influence of a high water table within these meadows was evident by the presence of mottling and gleying. Charcoal deposits were also noted in the soil horizons directly below the surface horizons in three soils at the south end of the study area, suggesting the historical occurrence of periodic fires between major floodplain accretion events.

Table 1. Comparison of overstory shrub cover, density, and height, following regression against various understory characteristics, within floodplain meadows of the Rocky Mountain Forest Reserve (RMFR) during 2001 and 2002.

		Overstory (Independent) shrub variables		
Understory response	Year	Total cover	Total stem density	Mean shrub height
Species diversity	2001	NS[1]	NS	NS
	2002	$r^2 = 0.27$	$r^2 = 0.22$	$r^2 = 0.23$
		$P = 0.002$	$P = 0.006$	$P = 0.004$
Bunchgrass canopy cover	2001	$r^2 = 0.48$	$r^2 = 0.31$	$r^2 = 0.20$
		$P = 0.0005$	$P = 0.0085$	$P = 0.04$
	2002	$r^2 = 0.71$	$r^2 = 0.23$	$r^2 = 0.52$
		$P < 0.0001$	$P = 0.004$	$P < 0.0001$
Bunchgrass density	2001	$r^2 = 0.34$	$r^2 = 0.21$	NS
		$P = 0.0069$	$P = 0.0344$	
	2002	$r^2 = 0.47$	$r^2 = 0.37$	$r^2 = 0.40$
		$P < 0.0001$	$P = 0.0002$	$P < 0.0001$
Grass production	2001	$r^2 = 0.55$	$r^2 = 0.40$	$r^2 = 0.24$
		$P < 0.0001$	$P = 0.0021$	$P = 0.0242$
	2002	$r^2 = 0.82$	$r^2 = 0.55$	$r^2 = 0.39$
		$P < 0.0001$	$P < 0.0001$	$P < 0.0001$
Herbage production	2001	$r^2 = 0.65$	$r^2 = 0.46$	$r^2 = 0.30$
		$P < 0.0001$	$P = 0.0007$	$P = 0.0009$
	2002	$r^2 = 0.79$	$r^2 = 0.62$	$r^2 = 0.42$
		$P < 0.0001$	$P < 0.0001$	$P < 0.0001$

[1]Indicates regression was nonsignificant ($P > 0.05$).

DISCUSSION

Meadow Understory Responses to Shrub Encroachment

In general, greater sample sizes for the 2002 data, together with the observed increase in rainfall, both might have contributed to the stronger relationships between understory variables and the overstory during the second year of sampling. Given that all transects were known to have little to no shrub cover as early as 1958, we are confident that these relationships are indicative of shrub-based influences on the understory, our first objective in this investigation.

The independence of species richness from shrub abundance likely occurred because as shrubs increased, plant species adapted to high light might have been replaced by more shade-tolerant ones (Knowles et al. 1999), resulting in no net change in richness. Our results contrast those summarized for the tallgrass prairie by Briggs et al. (2005), where herb richness declined markedly with increased shrubs. This discrepancy might be explained by the sampling methodology used to evaluate shrub encroachment impacts. Whereas the current study assessed aggregate changes across a mosaic of changing ratios of shrub and grassland patches, other studies have confined sampling to individual shrub clones or patches (e.g., *Cornus drummondii* C. A. Mey, Lett and Knapp 2005; *Morella cerifera* [L.] Small, Brantley and Young 2007), or their fringe ecotones (Briggs et al. 2002). However, our findings are consistent with the meta-study of Knapp et al. (2008) where species richness did not decline under shrub encroachment based on the assessment of study sites from across the North American continent.

The positive relationship between species diversity in 2002 and shrub cover through moderate levels of the latter likely arises from complex interspecific competitive forces within mixed communities, which depend on many factors, including the identity of neighboring species and environmental conditions (Van Auken 2000). The formation of an extensive shrub canopy previously dominated by grassland generally has a negative effect on the abundance of herbaceous species, because it reduces light and alters most microclimatic features (Hobbs and Mooney 1986; Briggs et al. 2005).

In the present study, given the absence of variation in species richness with shrub abundance, we hypothesize that increased diversity under moderate shrub canopies was due to greater species evenness arising from enhanced fine spatial-scale variation in microclimatic conditions along transects sampling each community. Whereas other studies have typically assessed the localized effect of shrub clones on understory responses, we assessed overall community level effects associated with variable shrub abundance. Thus, moderate shrub canopies might allow shade-tolerant plants to establish directly under encroaching shrubs, whereas the interspaces between shrubs are likely to be occupied by typical open grassland species. Briggs et al. (2005) indicate that in the tallgrass prairie, compositional changes are driven by shrub-induced low light levels rather than soil resource deficiencies. Although the cool-season grasslands assessed here appear more resistant to diversity changes than those in warm-season environments, moisture and nutrient constraints to plant growth (and hence, competition) were less likely to be factors limiting diversity in these floodplains under moderate shrub levels due to the shallow water table, periodic inundation, and associated deposition of nutrients during flood events.

The "leveling-off" of diversity as shrub canopy cover increased above 80% might be due to the eventual disappearance of open grassland species under excessive shading or root competition, both of which are more likely to occur when shrub height and rooting depth exceeds that of adjacent grasses (Knoop and Walker 1985). With abundant shrubs, lateral root extension would reduce gaps in the shrub interspaces to sizes unable to support grassland-dependent species. Although bog birch roots are known to be deep (de Groot et al. 1997), the roots of dwarf birch have been found to extend laterally less than a meter (Chapin et al. 1980). As a result, relatively high shrub cover would be required to close these gaps.

Although the results of this study indicate that moderate shrub presence was positively associated with understory herb diversity within these floodplain meadows, further investigations should be undertaken to determine the extent to which the increase in diversity is due to the inertia of grassland species. In other words, prolonged shading of the understory, even at moderate levels, might eventually overcome the tolerance of grassland species to this level of competition and result in a decline in their abundance and associated diversity. Consequently, specific information on the quantity of shrub cover likely to lead to short- and long-term changes in diversity would be beneficial to meadow conservation efforts. Species diversity is an important component of these ecosystems, and is an important attribute for which the RMFR is managed under the proposed government-sponsored biodiversity monitoring strategy. Less diverse plant communities also are generally less likely to recover from disturbances such as fire and grazing (Tilman and Downing 1994).

Bunchgrass Responses to Shrub Encroachment

Declines in bunchgrass abundance reflect deterioration in the range health of these meadows, because bunchgrasses are important indicators of lightly grazed, late seral meadows in the region (Willoughby 2001). The marked decline in bunchgrasses within well-established shrub communities might come about several ways. In northern mixed prairie, the response of grassland species is more strongly controlled by variation in the competitive effects from neighboring vegetation than differences in their competitive response ability (Peltzer and Köchy 2001). Although grasses initially are capable of inhibiting the growth of woody plants during their germination and early growth, this trend reverses once shrubs develop shoots that overtop grass canopies and root systems that extend below that of grasses (Van Auken 2000). Additionally, increased soil nitrogen under shrubs is thought to reduce native grasses by favoring shrub species that require greater nutrients (Brantley and Young 2008).

Alternatively, heavy grazing, particularly during the growing season when plants such as rough fescue are preferentially selected (Moisey et al. 2005), also is known to decrease the vigor and abundance of key bunchgrasses, including rough fescue (Willms et al. 1988). Two long-term exclosures maintained by Alberta Sustainable Resource Development in the study area indicate that grazing has reduced the abundance of bunchgrasses (Willoughby 1992), which further increases the grazing pressure on remaining plants. Moreover, it was noted during data collection that any remaining fescue plants in well-established shrub stands were often limited to the base of shrubs, where they had a small basal area and limited leaf area. Bunchgrasses at this location would be less likely to be grazed due to the protective shrub canopy, similar to that found for wolf willow (*Elaeagnus commutata* Bernh. ex Rydb.) in the Parkland of Alberta (Bailey 1970). This observation suggests that localized heavy grazing could play a role in the decline of bunchgrasses.

Shrub Impacts on Understory Production

Similar to species diversity and bunchgrass abundance, understory production was variable in open grasslands, presumably due to localized ecosite variation coupled with variation in disturbances such as grazing. Nevertheless, production in open areas generally remained high, only to decline sharply in those shrublands where cover rose over 33%, reflecting the overriding negative influence of shrubs, regardless of ecosite potential. Given that nearly half of the total herbage in these communities consisted of forbs, and the similar variation in total and grass biomass was accounted for by shrub abundance, these results suggest that both the grass and forb components of these meadow communities were negatively impacted by increasing shrub canopy cover. Thus, total herbage responses appear to be a superior indicator of shrub encroachment impacts in the area.

Decreases in grassland productivity found here (−58%) are more conservative than that observed in areas of tallgrass prairie encroached by red cedar (*Juniperus virginiana* L.) forest (−99%; Briggs et al. 2002) and rough leaved dogwood (*Cornus drummondii*) shrublands (−94%; Lett and Knapp 2005). However, as noted earlier, these and other studies often focus comparisons on local patches of woody species, rather than the collective matrix of grassland and associated woody species, which may inflate estimates of production loss. Alternatively, the grasslands assessed here consisted exclusively of cool- rather than warm-season plant species with markedly different ecophysiological limitations to growth, including a greater tolerance to low light under shrub encroachment. These differences might well contribute to increased resistance towards production declines.

Indicators used to estimate the availability of forage in shrub invaded meadow communities are a useful tool for land managers to make decisions quickly and easily regarding the status and sustainability of the range resource. Given that land managers can quantify shrub cover through ocular assessments more easily than through the measurement of understory biomass (i.e., through harvesting), landscape level information on the abundance of shrubs could be used to readily estimate forage production across large areas using the relationship established between these variables (2002; $y = 6\,401.80e^{-0.0122x}$, where x is shrub canopy cover [%] and y is herbage production [$kg \cdot ha^{-1}$]) in this investigation. However, we also acknowledge that the magnitude of herbage losses due to shrubs is likely to depend on growing conditions; below normal precipitation, particularly during 2001, and increased competition for soil moisture might have increased suppression of the understory relative to more normal growing conditions.

Shrubland Characteristics for Evaluating Understory Responses

Our second objective was to assess the comparative utility of different shrub variables for predicting understory responses. Shrub cover, rather than density or height, proved to be a superior variable for assessing understory responses because shrub canopy cover alters the microclimate in the understory and reduces light, nutrient, and water availability through competition, thereby affecting the ability of the understory to maintain growth, vigor, and ultimately, production (Hobbs and Mooney 1986). Although a larger shrub canopy is expected to be associated with a larger shrub root system, which in turn increases competition for soil water and nutrients, the latter were less likely to be limiting in the meadow environments examined here, both due to the restricted lateral rooting depth of dominant shrubs (Chapin et al. 1980) and the abundance of water in these floodplain environments. Thus, competition for light rather than soil resources is likely the key factor altering the understory. Although shrub cover might be the leading predictor for assessing shrub encroachment impacts, other considerations may necessitate the use of shrub density or height for monitoring ecological impacts on the understory. For example, it might be easier, quicker, and more precise to determine shrub density through field counts than ocular estimates of canopy cover.

Because bog birch is a dominant species within these floodplain meadows, it is not surprising that this species had the strongest relationship to the understory. Bog birch is a widespread species across North America from Alaska to northern Canada, and south into the United States (de Groot et al. 1997). Due to its abundance and the prominent understory responses assessed here, the overall regional impacts of encroachment by this species could be very significant.

Although the shrublands under study here were known to be up to several decades old (Burkinshaw 2005), the maximum age of individual shrub ramets did not exceed 15 yr. Bog birch produces abundant seed, but due to low seed germination and slow seedling establishment, most of the reproduction in this species, once established, is through vegetative layering (see review in de Groot et al. 1997). Although we initially hypothesized that shrub height would provide a useful, easy-to-measure parameter for quantifying the time period over which encroachment occurred, this was not true in our study. Instead, individual shrub stems appeared to grow and die back relatively quickly, with our stem ages therefore representative of individual ramet development due to resprouting rather than shrub community age. Given that both air photos dating back to 1958 and verbal accounts indicate that shrubs have been dominating many of these areas for much longer than that (Burkinshaw 2005), it appears the age of aboveground ramets does not represent stand shrub age or the length of time the understory has been subject to shrub encroachment.

Soil-Based Changes Due to Shrubs

Variation in soil LFH depth appears to be directly reflective of the time passed since shrub encroachment began and the associated extent of recalcitrant leaf and woody biomass deposition. Bog birch in particular produces abundant leaf litter that contributes to organic matter accumulation (de Groot et al. 1997), and should lead to a deeper LFH. Moreover, *Betula nana* L., a closely related species to that under examination here, has shown an ability to utilize organic nitrogen (Michelsen et al. 1996). Should *Betula glandulosa* be similar in adaptation, this would enhance its competitiveness over neighboring herbs. Nutrient enrichment has been cited as a mechanism driving woody plant expansion in arid (Schlesinger et al. 1990) and mesic (Brantley and Young 2008) regions, and might play a role here because bog birch litter decomposes relatively quickly (Moore 1984) and this species is known to respond positively to nitrogen fertilization (Turkington et al. 1998).

Observed variation in Ah depth in transects with little to no shrub cover can be attributed to the duration of soil development under deep, fibrous-rooted grassland vegetation following the last major deposition of sediment with flooding. Reductions in Ah depth with increasing shrub abundance might reflect the decline in fibrous root inputs from grasses and forbs, coupled with acidification brought on by shrub litter addition to the soil surface, a process similar to the relatively rapid biochemical changes seen in Black Chernozemic soils of Alberta exposed to aspen leaf litter (Dormaar 1971). The presence of subsoil charcoal confirms the historical importance of fire within this ecosystem, the suppression of which likely has exacerbated shrub abundance.

MANAGEMENT IMPLICATIONS

These results highlight the problems associated with shrub encroachment in cool-season grassland meadows of western Canada. It also provides land managers with tools to assess the health of this important resource and ensure its sustainability under increasing land use impacts and associated plant community change.

The negative relationship between herbage production and shrubs is of particular concern because it implies that the carrying capacity associated with the study area is decreasing. Concurrent research has indicated that nearly half of the open meadows in the area have experienced shrub encroachment between 1958 and 1998 (Burkinshaw 2005). Coupled with production declines of 58%, this sharply affects land use potential in the region, including livestock grazing, and might lead to increased conflict between livestock grazing and the maintenance of critical elk winter habitat. Moreover, continued encroachment likely will lead to even greater impacts on the health of floodplain meadows and necessitate changes to allowable stocking rates for domestic livestock and/or elk numbers in the region. Based on production responses in this study, managers should strive to maintain shrub cover below 12%, because this appears to be the level compatible for maintaining production, particularly of bunchgrasses, within these grassland habitats, and would minimize the requirement for more intensive restoration.

Finally, although not tested here, we acknowledge the potential importance of shrub encroachment on carbon dynamics in these cool-season grasslands, particularly given projections for climate change (Intergovernmental Panel on Climate Change 1995) and the positive response of the dominant shrub, bog birch, to increased temperatures at local (de Groot and Wein 1999) and coarse (Edwards et al. 2008) temporal scales. Because moisture is unlikely to be a limiting factor for plant growth in this mesic environment with its moderate rainfall and short growing season, shrub encroachment might actually enhance total community productivity based on the projections of Knapp et al. (2008).

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