You must be the change you wish to see in the world

-- Mahatma Gandhi

University of Alberta

WOODY PLANT ENCROACHMENT INTO GRASSLANDS WITHIN THE RED DEER RIVER DRAINAGE, ALBERTA

by

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ABSTRACT

Montane grasslands play a key role in supporting wintering elk in the Rocky Mountains of Alberta. To document change in grassland extent and patch sizes, I analyzed repeat aerial photography at 4 sites in the upper Red Deer River drainage between 1952 and 2003. Excluding the Ya Ha Tinda, grassland extent declined 52 ± 20%, shrubland 39 ± 41%, with an increase in mixedwood forest of 32%, and coniferous forest of 39 ± 10%. The rate of grassland loss differed among sites: West Lakes > Tyrrell Flats ≃ Scotch Camp. Grassland area at Ya Ha Tinda was the same in 1952 and 2003 due to shrub mowing. Grassland patch size increased on average, but decreased in WL as larger patches of fragmented with woody plant encroachment. From 100-m transects along grassland-shrub-forest ecotones, differences in herbaceous biomass and species richness existed within cover types, but no pattern in edge effects on herbaceous biomass could be detected between ecotone type or among sites, except at the Ya Ha Tinda.

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CHAPTER 1: INTRODUCTION

1.1 Background

Ecological integrity has been a central theme for Parks Canada since the concept was integrated into the *Canada National Parks Act* in 1989. Parks Canada defines an ecosystem as having integrity when the biological community composition, abundance, and rates of change are typical of its ecoregion, including natural processes that shape the ecosystem (Canada National Parks Act). Within Banff National Park (NP), indicators of ecological integrity (EI) were selected based on major groups of organisms and their known response to, or influence on, disturbances such as fire and herbivory (Parks Canada, 2008). An assessment of condition and trend is assigned to the indicator where possible, based on quantitative and qualitative data analysis, expert opinion and accumulated knowledge of the supporting measures. For instance, even though the 'area of disturbance by fire' measure was assessed to be in fair condition in Banff NP (Parks 2008), the restoration of fire has been largely limited to dry montane slopes in the Front Ranges (White et al. 2003), which would have historically experienced the highest frequency of burns (Kay et al. 1994, White 2001). Although prescribed burns have targeted these areas, concern for the future of montane grasslands persists (The Banff-Bow Valley Task Force, 1996), and an account of the extent of grassland loss in the montane of Banff NP is lacking.

An understanding of fire regimes within this region is required to direct management concerned with losses in EI. A discrepancy in lightning ignition rates between the eastern and western slopes of the Rockies (Van Wagner et al. 2006) has led to the hypothesis that aboriginal peoples actively lit fires in the east, largely to improve habitat for game. Examination of first hand and historical accounts (Kay et al. 1994), conducting dendrochronological (White 1985, White 2001) and paleoecological studies (Hallet and Walker 2000), the probability of historic human based ignition events has been determined to be high. In contrast, Parks Canada adopted fire suppression as a guiding management principle in 1909 (White 1985; Kay et al. 1999), which was not truly effective until the 1950's (White et al. 2001). The product of an era of suppression has been an elongated fire return interval and fire cycle within the eastern slopes of the Rocky Mountains (Rogeau 1994). A prescribed burning program to restore 50% of the long-term fire cycle (~14 sq. km/ year) to the Banff NP landscape has been in place since 1984 (Parks Canada, 2007).

Following a reduction in disturbance frequency or intensity, woody species may advance into herbaceous communities and species composition and productivity of the understory changes. This herbaceous community shift is typically due to an altered microclimate driven by decreased light and increased moisture retention associated with shading (Breshears et al. 1998, Peterson and Reich 2008). Intermediate encroachment (<75% shrub cover; Bork and Burkinshaw 2009) may increase herbaceous richness depopulate species assemblage forms under the encroaching woody canopy (Weiher et al. 2004, Anthelme et al. 2007, Treydte et al 2009), where productivity is lowered compared to open areas (between 12% and 33%; Bork and Burkinshaw 2009, Lukomska et al. 2010). Fescue dominance at the YHT appears to decrease from a rough fescue-sedge-junegrass *(Festuca campestris-Carex filifolia-Koeleria macrantha)* assemblage in open drier sites, or rough fescue-fringed brome-sedge *(Festuca campestris-Bromus ciliatus-Carex spp.)* at open moister sites, to bog birch/sedge-rough fescue *(Betula glandulosa/Carex spp.-Festuca campestris)* with encroachment of bog birch (Willoughby 2001). In the extended absence of fire, productivity declines and community shifts may limit the ability of a landscape to support ungulates that rely primarily on herbaceous forage, particularly during times of scarcity such as the winter months (Singer 1995). Where grazing pressure and bog birch cover were suspected to be increasing in rough fescue grasslands within provincial lands in the eastern slopes of the Rocky Mountains, summer biomass production indicated a limited potential carry capacity for elk over winter (Morgantini and Russell 1983). Forage production in BNP was nearly doubled by burning shrub communities containing willow and bog birch, with potential summer carrying capacity increasing from 8 to 28 elk/100 km^2 within burned areas, with most of the increase (73%) attributed to changes within burned Engelmann spruce (*Picea engelmannii*) stands (Sachro et al. 2005).

Herbivory also influences woody plant encroachment, though the effects may be species specific according to ungulate forage preferences (Kay et a2005, Maher et al. 2010) and vary with grazing pressure (Jurena and Archer 2003, Hagenah et al 2009, Jeffers et al. 2011). Under low herbivory, aspen (*Populus tremuloides*) increased in cover by 0.05% /year at the expense of fescue grasslands in the parkland region of south-central Alberta from 1907 to 1966 (Bailey and Wroe 1974). However, within Banff, high elk densities in the past had drastically altered the prevalence of preferred browse species such as aspen, severely limiting it's regrowth and fragmenting the age structure of this species. Regeneration of aspen could require low densities (1elk/km^2) of elk sensitive to predation risk (White 2001). While aspen and willow (*salix* spp) are highly valued as forage for elk, other woody plants such as lodgepole pine (*Pinus contorta*) and white spruce (*Picea glauca*) have low palatability (Cook 2002), or in the case of bog birch (*Betula glandulosa*) are basically avoided (Cook 2002, Sachro et al. 2005). Once they have grown out of the browse zone (~2m in height; Keigley and Frisina, 1998), tree species are largely tolerant of browsing although mature aspen may be subject to mortality via bark stripping by elk (Baker et al. 1997).

Encroachment of woody plants into grasslands may alter grassland productivity, richness and species composition within a certain distance to the shrub or tree community. If the process of encroachment of woody plants into grassland regions provides suitable conditions for forest species to establish within open grasslands, or microclimate is altered so as to lower productivity for a certain distance into grassland regions (Lett et al. 2004. Zarovali et al.2007), this 'edge effect' would markedly reduce the area of grassland within montane meadows, which are already limited in extent within Banff NP (< 3% by area; Holland and Coen 1983). Depending on the distance of this effect, small grassland patches may become entirely influenced by edge (Kiviniemi and Eriksson 2002), and the influence of woody plants on neighbouring grassland may extend further or become non-linear, depending on the ecotone in question (Vandvick 2004). In terms of management objectives, the shape and size of burn units could become important in the presence of distinct plant community responses at ecotones, especially where edge effect extends far into grasslands or is non-linear (Fletcher et al. 2007).

Both a reduction in fire frequency and the presence of dense elk herds in the Rocky Mountain parks have raised concerns as to the state of grasslands in these regions. Rhemtulla et al. (2002) observed in-filling of coniferous forests from 1915 to 1997, and loss of early seral vegetation such as grasslands and shrublands to coniferous cover in montane valleys of Jasper NP, attributed to the reduction in burn area and frequency over time. Shrubland dominated by bog birch regenerates very quickly following fire (Bork and Willoughby 1996); a 2-year fire interval may be required to reduce cover (de Groot 1998). In wet meadows of the foothills of Alberta, sufficient browsing and burning have been lacking and bog birch has spread to reduce grassland cover by 58% between 1958 and 1998 (Burkinshaw and Bork 2009). While grass competition in productive environments can limit tree establishment (Riginos 2009), high intensity grazing of herbaceous matter can facilitate woody plant encroachment by providing gaps in the herbaceous cover for shrubs and trees to establish in addition to reducing fine fuels for fire propagation (Van Auken 2000). Within the upper RDR drainage, the Ya Ha Tinda ranch (20km^2) serves as winter range for elk of Banff NP where densities had been >20 elk/km^2 in the recent past (White 2001). In areas protected from grazing for 7 years, an increase in fescue (*Festuca campestris*) basal area occurred, together with an 8-fold increase in litter and a 2 fold increase in living graminoid biomass across all exclosures (Merrill et al. 2007). However, an increase in standing biomass and abundance of species sensitive to grazing at Scotch Camp, west of the YHT within the upper RDR drainage, suggests that herbaceous species response may differ where herbivory has been low in the recent past (East Slopes Rangeland Seeds Ltd 2003).

Loss of montane grasslands in the upper Red Deer River (RDR) drainage due to altered fire regimes have been of interest because of their limited extent and their importance as wildlife habitat, particularly as seasonal (short-term fall and spring use) range to a migratory elk population (Morgantini and Hudson 1989, Hebblewhite et al. 2008). The upper RDR drainage contains fescue (*Festuca* spp.) grasslands, which are highly productive ecosystems and also considered threatened in Alberta. It is estimated that 5% of the plains rough fescue (*Festuca hallii*) assemblage remains in pre-settlement condition (Vujnovic 1998), in part due to the great demand for these areas for rangeland and agriculture uses (Bogen et al. 2003). Fescue (*Festuca campestris*) grassland complexes in the upper RDR drainage remain in the vicinity of Scotch Camp (SC) -Tyrrell Creek (TY) 12 km west of the Banff park boundary, and at Ya Ha Tinda (YHT)-West Lakes (WL) 10 km east of the park. The last wildfire at YHT occurred in 1936, representing a departure from the typically brief montane fire cycle of <50 years, (20-10 years for YHT from 1645 to 1936; White et al. 2001). From 1936 to 2009 YHT-WL has not been burned in part to ensure the safety of the ranch buildings, but also because of the lack of fine fuels needed to carry fire in grassland and possible negative grassland species composition and biomass responses to fire under heavy herbivory (Bogen et al, 2003). Prescribed burning treatments have been employed at SC and TY sites since 1994, and monitoring of grassland was initiated following an early 2000 spring burn (ESRS Ltd 2003). Plant recovery assessed in both 2001 and 2003 showed there were only small differences in canopy cover and biomass of fescue between burned and unburned treatments in 2001; however, both treatments exhibited increased herbaceous biomass and abundance over 2 years thought to be a product of a decline in grazing pressure (ESRS, Ltd 2003). Documenting changes in extent of vegetation types, or plant functional types (Dansereau 1951; Duckworth et al. 2000) provides context for future prescribed burns.

Thesis objectives

The objective of my research was to document small- and large-scale changes in grassland extent and plant composition. Specifically, within 4 sites in the Red Deer River (RDR) drainage, I

(1) used aerial photographs to quantify the rate of change in grassland extent and the shift in size of patches of grasslands over the period from 1952-2003, and

(2) quantified species composition, richness, and biomass during peak of the growing season within and along ecotones between 4 major cover types. Aerial photographs were not available earlier than the 1950s.

The 4 sites under study were chosen because they are major grassland complexes in the RDRV that are exposed to variation in fire as well as herbivory as seasonal migration routes for elk (Morgantini 1988). Knowing which vegetation types have expanded the most into grasslands under fire suppression could help direct management aimed at maintaining grasslands in the RDR drainage.

1.2 Study Area

The study area for both chapters is the Red Deer River drainage within the Canadian Rocky Mountains of Alberta and includes areas within Banff National Park (BNP) and adjacent provincial lands within the Rocky Mountain Forest Reserve (RMFR) (Fig. 1-1). The region is classified as Montane along valley bottoms and transitions to Lower Subalpine in areas above 1650 m (Holland and Coen 1983). Average annual precipitation for Banff National Park averaged from 1900-2007 is 475 mm. Total mean precipitation in summer (1 May to 31 August) is 285 mm and 190 mm in winter (1 November to 30 April) (Fig. 1-2, Environment Canada 1900-2007). Mean daily summer temperature is 12^{o} C and mean daily winter temperature is -5^{o} C. Combined with low precipitation, Chinook winds keep the grasslands at YHT mostly snow-free in winter (Stelfox 1981). During field sampling in July 2009, mean summer temperature was 11.5 ± 4.1°C; however, precipitation data are unavailable from Banff or the RDR drainage.

Soils in the Red Deer River Valley range include Brunisol and Luvisol under lodgepole (*Pinus contorta*) pine stands, with Humic Regosols, Melanic Brunisols (soils with > 10 cm of Ah horizon) or Chernozemic soil in open grassland regions within both BNP and provincial lands (McGillis 1977, Holland and Cohen 1983). Grasslands of the Red Deer River Valley are described as *Festuca-Stipa richardsoni* associations (Looman 1969). Common grasses include foothills rough fescue (*Festuca campestris*), junegrass (*Koeleria macrantha*), Hooker's oatgrass (*Helicotrichon hookeri*), and invasive smooth brome (*Bromus inermis*) (Willoughby 2001). Forested regions consist mainly of lodgepole pine, trembling aspen (*Populous tremuloides*), balsam poplar (*Populus balsamifera*) and white spruce (*Picea glauca*). Common shrubs include bog birch (*Betula glandulosa*), shrubby cinquefoil (*Potentilla fruticosa)* and willow (*Salix* spp.*)* (McGillis 1977).

Ungulates using the Red Deer River Valley in the recent past include elk (*Cervus elaphus nelsoni*), deer (*Odocoileus virginiana, O. hemonius),* bighorn sheep (*Ovis canadensis*), and moose (*Alces alces*). Mountain goats (*Oreamnus americanus*) and woodland caribou (*Rangifer tarandus caribou*) typically do not occur, preferring higher elevations (Stelfox 1993). Nineteenth century journals suggest that bighorn sheep and plains bison (*Bison bison bison*) were historically the most numerous species in the area, with elk and deer being encountered less frequently (Kay et al. 1994). Plains bison were extirpated by the 1870s (Soper 1941) before the government of Alberta put in place hunting restrictions to protect them in 1905 (Stelfox 1993). Historically, caribou in BNP numbered 30 to 40 in 1980s, but the herd dwindled to ~5 members and then effectively none following the death of 3 females in an avalanche in spring of 2009 (Decesare et al. 2011).

Rocky Mountain elk populations have increased within BNP and the Red Deer River Valley since the early 1900s. Early in the 20th century, elk populations were reduced to remnant herds in the Rocky Mountains and foothills (Millar 1916, Dwyer 1969). During a period of elk reintroductions from 1917-1920, 251 elk from Yellowstone National Park were translocated into BNP. The population in BNP grew and elk culls were initiated in 1941. Elk numbers in BNP prior to the 1940's awere low (Morgantini 1988). By 1969, a major migratory route had been established along the Red Deer River leading from BNP to the YHT (Morgantini 1988). Outside BNP, the first recorded observation of elk in the Panther-Red Deer-Clearwater region was reported on the Ya Ha Tinda Ranch in 1933 (Cowan 1943). Cowan (1943) estimated the BNP population to be 4000 wintering elk. McGillis (1977) reported 50-60 bulls on and adjacent to YHT in 1942-43 with the nearest band of cows wintering at the head of the James River northeast of the YHT. By 1950, Flook (1970) reported that approximately 100 cows wintered on the YHT, and by 1961 1400-1800 individuals were observed in late winter (Webb 1961). The elk population at the YHT in winter peaked in 1992 and has since declined (Fig. 1-3). The decline has been attributed to a number of causes including translocations (1994-1999) and the recovery of the wolf population (Hebblewhite 2006).

The elk herd wintering in the Red Deer River drainage was reported to migrate 25-50 km into BNP to summer (Gunson 1997), but no real population estimates of the number of migratory animals existed until 1973 when aerial surveys began (Fig. 1-3, Morgantini 1988; Skjonsberg 1993, Hebblewhite et al.

2006; unpublished data, A. Hubbs, Alberta Fish and Wildlife). The majority of elk summering in BNP were not found in the valley bottom, but widely dispersed over some 1,600 km^2 of terrain (Morgantini 1988). Elk were found mostly in high subalpine and alpine ranges at the headwaters of several creek tributaries to the Red Deer, Panther and Clearwater rivers. In the 1970s and 1980s there was intermittent and low to moderate winter use of low elevation meadows, such as Scotch Camp (SC) and Tyrrell Creek (TY) in the upper Red Deer River drainage with elk typically using these sites as staging areas en-route between summer and winter ranges (Morgantini 1988; Hebblewhite et al. 2006). Elk use of SC and TY meadows in BNP was markedly higher during the late season hunt in 1977 and 1978 (Morgantini and Hudson 1985). However, shortly after the hunting seasons, the same animals occupied their traditional winter range at YHT. Summer use of the YHT grassland complex has increased since the early 1990s with the ratio of resident to migrant elk increasing 4x since the late 1970s despite a decline in the overall population (Hebblewhite et al. 2006). In response, in 2005 Parks Canada initiated a daily aversive conditioning program during the critical spring growth period for fescue where elk were herded along the upper RDRV drainage toward Banff NP using riders on horseback. In response, grassland standing biomass in August? was 210 % with aversive conditioning in low precipitation conditions (100mm) and by 25% in higher precipitation conditions (375 mm) (Spaedtke 2009).

Predators within the study area include wolf (*Canis lupus),* grizzly bear (*Ursus arctos*), and cougar (*Felis concolour*) (Morgantini 1988). Wolves were considered abundant prior to European settlement at the turn of the 20th century. Poisoning and shooting of wolves for livestock protection and hunting bounties led to extirpation in southern regions of Alberta, as well as in BNP by the 1950s (Gunson 1992; Musiani and Paquet 2004). Recolonization of wolves in BNP first occurred in 1985. Cougars have also been persecuted historically but are now increasing in the region (Stelfox 1993; Knopff 2010). Another major predator on elk is the grizzly bear, whose predation is primarily limited to spring time (Stelfox 1993).

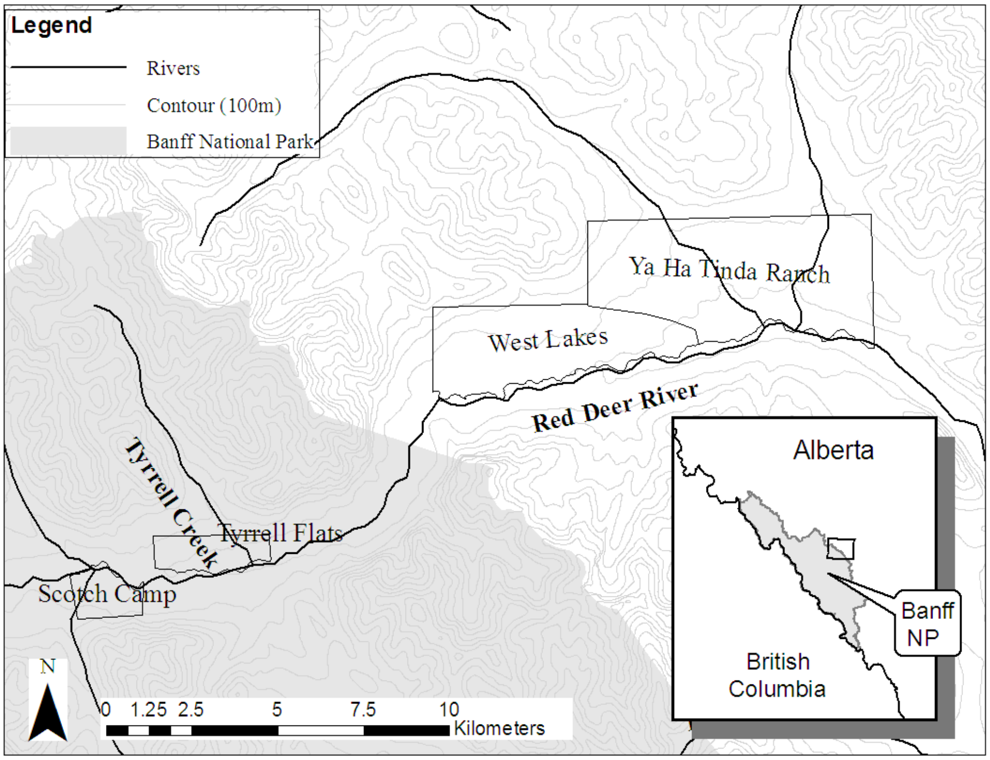

Fig. 1-1 Grassland study sites along the Red Deer River. Scotch Camp (SC) and Tyrrell Creek (TY) occur within in Banff National Park. West Lakes (WL) and Ya Ha Tinda (YHT) are east of Banff National Park in provincial lands of Alberta Canada. See Appendix I for site boundaries.

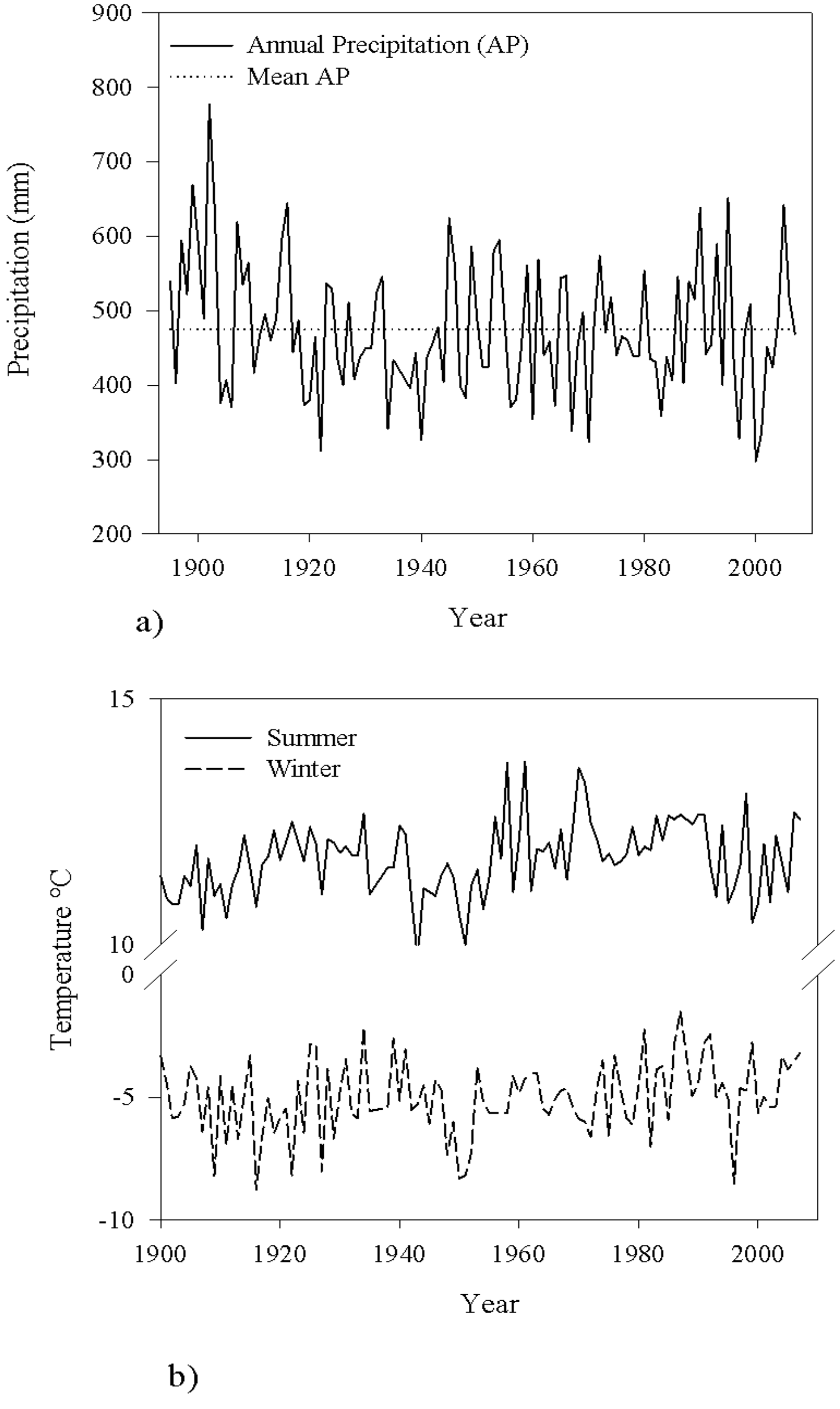

Fig. 1-2 (a) Annual precipitation and (b) mean daily summer (1 May – 31 August) and winter (November-April) temperature, recorded at the Banff CS weather station from 1900 to 2007.

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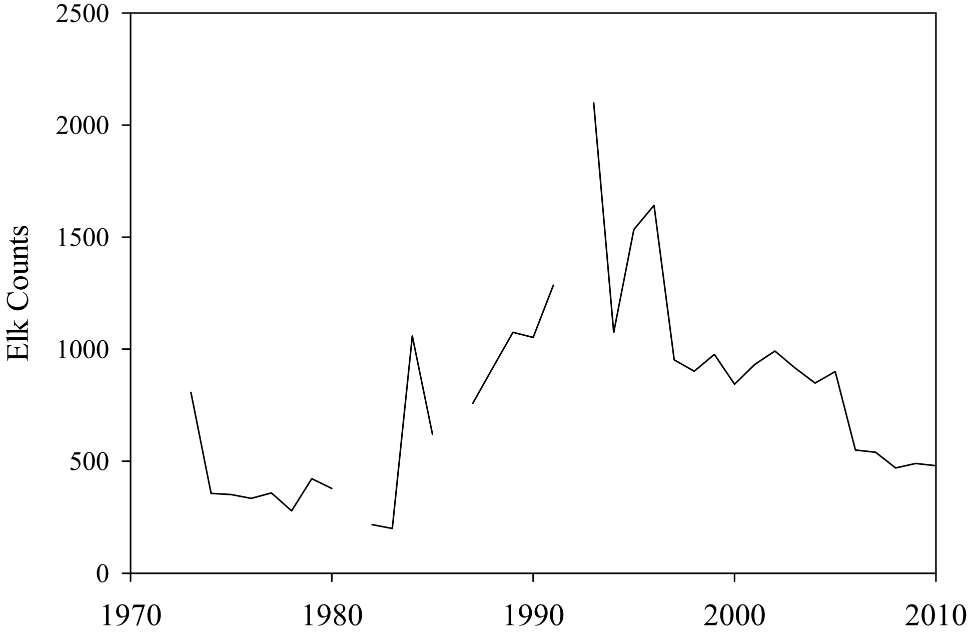


Fig. 1-3 Ya Ha Tinda elk herd winter elk counts (1973-2010) from the Ya Ha Tinda ranch.

1.3 Literature cited

Anthelme, F., Villaret, J.C., Brun, J.J., 2007. Shrub encroachment in the Alps gives rise to the convergence of sub-alpine communities on a regional scale Journal of Vegetation Science 18: 355-362

Banff-Bow Valley Study. 1996. Banff-Bow Valley: At the crossroads. Summary report of the Banff-Bow Valley Task Force (Robert Page, Suzanne Bayley, J. Douglas Cook, Jeffrey E. Green, and J.R. Brent Ritchie). Prep. For the Honourable Sheila Copps, Minister of Canadian Heritage, Ottawa, ON.

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

Baker, W.L., Munroe, J.A., Hessl, A.E., 1997. The effects of elk on aspen in the winter range in Rocky Mountain National Park. Ecography 20: 155-165

Bogen, A.D., Bork, E.W., Willms, W.D., 2003. Defoliation impacts on *Festuca campestris* (Rydb.) Plants Exposed to Wildfire. Journal of Range Management, 56: 375 – 381.

Bork, E., Smith, D., Willoughby, M., 1996. Prescribed burning of bog birch. Rangelands, 18:4–7

Bork, E.W., Burkinshaw, A.M., 2009. Cool-Season Floodplain Meadow Responses to Shrub Encraochment in Alberta. Rangeland Ecology and Management, 62: 44–52

Burkinshaw, A.M., Bork, E., 2009. Shrub encroachment impacts the potential for multiple use conflicts on public land. Environmental Management 44:493–504

Breshears, D.D., Nyhan, J.W., Heil, C.E., Wilcox, B.P., 1998. Effects of woody plants on microclimate in a semiarid woodland: Soil temperature and evaporation in canopy and intercanopy patches. International Journal of Plant Sciences, 159: 1010-1017

Cook, J.G., 2002. Nutrion and Food *in* North American elk ecology and management. Toweill, E.D., Thomas, W.J., (Eds). Washington, Smithsonian Instituion Press. 962 pp.

Cowan, I. M., 1943. Report on game conditions in Banff, Jasper and Kootenay National Parks. Canadian Wildlife Service, Edmonton. Unpublished, 72 pp.

Dansereau, P. 1951. Description and Recording of Vegetation Upon a Structural Basis. Ecology, 32: 172-229

Decesare, N. J., Whittington, J., Hebblewhite, M., Robinson, H., Bradley, M., Neufeld, L., Musiani, M., 2011. The role of translocation in recovery of woodland caribou populations. Conservation Biology, 25: 365-73

de Groot, W.J., 1998. Fire ecology of *Betula glandulosa* Michx. PH.D. Thesis Department of Forest Science, Univesity of Alberta.

Duckworth, J.C., Kent, M., Ramsay, P.M., 2000. Plant functional types: an alternative to taxonomic plant community description in biogeography? Progress in physical geography, 24:515-542

Dwyer, M.V., 1969. Ecological characteristics and historical distribution of the family Cervidae in Alberta. M.Sc. Thesis. University of Alberta, Edmotnon.158 pp.

Eastern Slopes Rangeland Seeds (ESRS), Ltd., 2003. Survey data collected and comparative analysis on pre-selected burn sites in Banff National Park 2001, 2003. Prepared for: Parks Canada, 24pp.

Fletcher, R.J. Jr., Ries, L., Battin, J., Chalfoun, A. D., 2007. The role of habitat area and edge in fragmented landscapes: definitively distinct or inevitably intertwined? Canadian Journal of Zooology. 85: 1017–1030

Flook, D. R., (ed.) .1970. Causes of implications of an observed sex differential in the survival of wapiti. Ottawa, ON, Canada: Canadian Wildlife Service Wildlife Service Report No. 11.

Gunson, J.R., 1992. Wildlife historical and present management of wolves in Alberta. Wildlife Society Bulletin, 20: 330-339

Gunson, J. R., 1997. Elk management plan for Alberta. Wildlife Management Division, Alberta Environmental Protection, Natural Resource Service, Edmonton, Canada.

Hagenah, N., Munkert, H., Gerhardt, K., Olff, H., 2009. Interacting effects of grass height and herbivores on the establishment of an encroaching savanna shrub. Plant Ecology 201: 553-566

Hallett, D.J., Walker, R.C., 2000. Paleoecology and its application to fire and vegetation management in Kootenay National Park, British Columbia. Journal of Paleolimnology 24: 401-414.

Hebblewhite, M., 2006. Linking predation risk and forage to ungulate population dynamics. University of Alberta. Edmonton, Alberta.

Hebblewhite, M., Merrill, E.H., Morgantini, L.E., White, C.A., Allen, J.R., Bruns, E., Thurston, L., Hurd., T.E., 2006. Is the migratory behaviour of montane elk herds in peril? The case of Alberta's Ya Ha Tinda elk herd. Wildlife Society Bulletin 34: 1280-1295.

Hebblewhite, M., Merrill, E. H., McDermid, G., 2008. A mutli-scale test of the forage maturation hypothesis for a partially migratory montane elk population. *Ecological Monographs* 78, 141-166.

Holland, W. D., Coen, G.M., Eds. 1983. Ecological (biophysical) land classification of Banff and Jasper National Parks. Volume II : Soil and Vegetation Resources. Alberta Institute of Pedology Publication No. SS-82-4 4

Jeffers, E.S., Bonsall, M.B., Brooks, S.J., Willis, K.J., 2011. Abrupt environmental changes drive shifts in tree–grass interaction outcomes. Journal of Ecology, 99: 1-8

Jurena, P. N., Archer, S., 2003. Woody plan establishment and spatial heterogeneity in grasslands, Ecology, 84: 907-919

Kay, C.E., Patton, B., White, C.A., 1994. Assessment of long-term terrestrial ecosystem states and processes in Banff National Park and the central Canadian Rockies. Banff National Park. Resource Conservation.

Kaye, M.W., Binkley, D., Stohlgren, T.J., 2005. Effects of conifers and elk browsing on quaking aspen forests in the central Rocky Mountains, USA. Ecological Applications, 15 (4): 1284-1295

Keigley, R.B., Frisina M.R., 1998. Browse evaluation by analysis of growth form. Montana Fish, Wildlife and Parks. Bozeman, MT

Kiviniemi, K., Eriksson, O., 2002. Size-related deterioration of semi-natural grassland fragments in Sweden. Diversity and Distributions 8: 21-29

Knopff, K.H., Knopff, A.A., Kortello, A. Boyce, M.S., 2010. Cougar Kill Rate and Prey Composition in a Multiprey System. Journal of Wildlife Management, 74 (7): 1435-144

Lett, M. S., Knapp, A. K., Briggs, J. M., Blair, J. M., 2004. Influence of shrub encroachment on aboveground net primary productivity and carbon and nitrogen pools in a mesic grassland. Canadian Journal of Botany, 82: 1363-1370.

Looman, J., 1969. The fescue grassland of western Canada. Vegetation 19: 128-145

Lukomska, N., Quaas, M.F., Baumgärtner, S., 2010. Bush encroachment control and risk management in semi-arid rangelands. University of Lu□neburg Working Paper Series in Economics ,191

Maher, K.A., Hobbs, R.J., Yates, C.J., 2010. Woody shrubs and herbivory influence tree encroachment in the sandplain heathlands of southwestern Australia. Journal of Applied Ecology, 47: 441–450

McGillis, J.R., 1977. Range management of the Ya Ha Tinda ranch. Prepared for Parks Canada, Canadian Wildlife Service, Edmonton. 75pgs

Merrill, E., McPhee, H., Robinson, B., 2007. Ya Ha Tinda exclosure study: Plant composition & fescue growth. Progress Report. Parks Canada, 27pgs.

Millar, W.N. 1916. The big game of the Canadian Rockies. Conservation of the fish, birds and game. Proceedings of committee meeting, Nov.1 and 2, 1915.

Morgantini, L.E., 1988. Behavioural adaptive strategies of wapiti (Cervus elaphus) in the Canadian Rocky Mountians. PhD thesis, University of Alberta, Edmonton 193 pg.

Morgantini, L.E., 1995. The Ya Ha Tinda: An Ecological Overview. Canadian Heritage, Parks Canada, Calgary

Morgantini, L.E., Hudson, R.J., 1985. Changes in diets of wapiti during a hunting season. Journal of Range Management, 38: 77-79

Morgantini, L.E., Hudson, R.J., 1989. Nutritional significance of wapiti (*Cervus elaphus*) migrations to alpine ranges in western Alberta, Canada. Arctic and Alpine Research 21: 288-295

Musiani, M., Paquet, P.C., 2004. The practices of wolf persecution, protection, and restoration in Canada and the United States. BioScience, 54: 50-60

Parks Canada, 2007. Banff National Park management plan. July 2007 amendment. Environment Canada, Parks Canada. ISBN: 978-0-662-05190-9, Government Catalog No.: R63-225/2007-MRC

Parks Canada, 2008. Banff Nation Park of Canada state of the park report.

Peterson, D.W., Reich, P.B., 2008. Fire frequency and tree canopy structure influence plant species diversity in a forest-grassland ecotone. Plant Ecology, 194: 5-16.

Rhemtulla, J., Hall, R., Higgs, E., MacDonald, E., 2002. Eighty years of change: vegetation in the montane ecoregion of Jasper National Park, Alberta, Canada. Canadian Journal of Forestry Research 32: 2010–2021

Riginos, C., 2009. Grass competition suppresses savanna tree growth across multiple demographic stages. Ecology, 90 (2): 335–340

Rogeau, M. P. 1996. Understanding age-class distributions in the southern Canadian Rockies. M.Sc. thesis. University of Alberta. Edmonton, Alberta. 139pp.

Rogeau, M. P., Gilbride, D., 1994. Forest stand origin mapping of Banff National Park. Resource Conservation. Banff National Park. Banff, Alberta. 69pp.

Sachro, L.L., Strong, W.L., Gates, C.C., 2005. Prescribed burning effects on summer elk forage availability in the Subalpine zone, Banff National Park. Environmental Management, 77: 183-193.

Singer, F.J.,1995. Effects of grazing by ungulates on upland bunchgrass communities of the northern winter range of Yellowstone National Park. Northwest Science, 69 (3): 191-203

Skjonsberg, T., 1993. Eastern slopes wildlife study 1984-1987. Final technical report. Banff National Park, 138pp.

Spaedtke, H., 2009. Aversive conditioning on horseback: A management alternative for grassland systems threatened by sedentary elk populations. M.S. thesis, University of Alberta.

Soper, J. D., 1941. History, range, and home life of the northern bison. Ecological Monographs, 11: 347-412

Stelfox, H.A., 1981. Ecological land classification. Red Deer-James. Energy and Natural Resources Report Number: T/11-No. 4. Edmonton, Alberta. 71 pp.

Stelfox, J.B., Adamczewski, J.Z., 1993. Hoofed mammals of Alberta. Stelfox, J.B. (Ed). Edmonton: Lone Pine Publishing. 241 pp.

Treydte, A.C., Grant, C.C., Jeltsch, F., 2009. Tree size and herbivory determine below-canopy grass quality and species composition in savannahs. Biodiversity & Conservation ,18: 3989–4002

Van Auken, O.W., 2000. Shrub invasions of North American semiarid grasslands. Annual Review of Ecological Systems, 31: 197–215.

Van Auken, O.W., 2009. Causes and consequences of woody plant encroachment into western North American grasslands. Journal of Environmental Management, 90; 2931–2942

Vandvick, V., 2004. Gap dynamics in perennial subalpine grasslands: Trends and processes change during secondary succession. Journal of Ecology 92: 86-96

Van Wagner C E., Finney, M. A., Heathcott, M., 2006. Historical fire cycles in the Canadian Rocky Mountain Parks. Forest Science, 52: 704-717

Vujnovic, K., 1998. Small-scale plant species composition and diversity in relation to environmental and disturbance factors in fescue grasslands of the aspen parkland of Alberta. M.S. Thesis. University of Alberta. 16p. Walter, W.D.,

Webb, R., 1961. Management suggestions for the Ya-Ha-Tinda and Corners elk winter ranges. Alberta Department of Lands and Forests, Fish and Wildlife Division, Edmonton. Unpublished 13 pp.

Weiher, E., Forbes, S. Schauwecker, T., Grace, J.B., 2004. Multivariate control of plant species richness and community biomass in blackland prairie. Oikos ,106: 151-157

White, C. A., 1985a. Wildland fires in Banff National Park 1880-1980. Occasional Paper 3. National Parks Branch, Parks Canada, Environment Canada. Ottawa, Ontario, Canada. 106pp.

White, C. A., 1985b. Fire and biomass in Banff National Park closed forests. M.Sc. thesis. Colorado State University. Fort Collins, Colorado. 205pp.

White, C.A., 2001. Aspen, elk and fire in the Canadian Rocky Mountains. PhD thesis, University of Alberta, Edmonton. 219 pp.

White, C.A., Feller, M.C., Vera, P., 2001. New approaches for testing fire history hypotheses. Proceedings of the International Conference on Science and Management of Protected Areas, 4: 398-411.

White, C. A., Pengelly, I. A., Rogeau, M.P., Zell, D., 2003. Landscape fire regimes and vegetation restoration in Banff Nation Park, Alberta. Parks Canada Occasional Paper BNP-2003-01. Parks Canada, Banff, AB. 39pp

Willoughby, M.G., 2001. Range plant community types and carrying capacity for the montane subregion. Edmonton, Alberta, Alberta Sustainable Resource Development Land and Forest Service. Pub. no.: T/003, ISBN: 0-7785-1792-6

Zarovali, M. P., Yiakoulaki, M. D., and Papanastasis, V. P., 2002. Effects of shrub encroachment on herbage production and nutritive value in semi-arid Mediterranean grasslands. Grass and Forage Science, 62: 355–363

CHAPTER 2: WOODY PLANT ENCROACHMENT INTO GRASSLANDS IN THE RED DEER RIVER VALLEY

2.1 Background

Over much of the past century, fire suppression in the eastern slopes of the Rocky Mountains has resulted in a longer mean fire return interval and fire cycle (Rogeau and Gilbride 1994). Intentional burning of montane grasslands had long been carried out by aboriginal peoples to initiate spring growth and promote grassland productivity (Christenson 1971, Arno 1980, Kay et al. 1994). The canopy cover of woody species has increased in areas dominated by herbaceous and grass species where they have not been periodically burned, changing the foothills landscape from pre-European settlement (Rhemteulla et al. 2002, Burkinshaw and Bork 2009). With canopy closure and woody invasion, forage production can be reduced by as much as 60% (Johnson and Smoliak 1968, Bork and Burkinshaw 2009); montane plant composition may shift to favour shade tolerant graminoids and forbs in the presence of shrubs such as bog birch and willow, or trees such as lodgepole pine and white spruce (Willoughby 2001) . The objective of Parks Canada is to maintain ecological integrity (Parks Canada 2007). In BNP, the alteration of landscape level processes such as the suppression of fire can result in shifts in plant communities that may pose a threat to ecological integrity unless there is additional management (Parks Canada 2007).

An ecologically important component of the upper RDR drainage are the montane fescue (*Festuca campestris,* Rydberg) grasslands. Fescue grasslands are highly productive ecosystems, which are now considered threatened in Alberta (Kemper 2009). It is estimated that 90% of fescue grassland has been greatly or moderately modified (Looman 1969), with more recent estimates indicating only 5% may be remaining in historical condition (Vujnovic 1998). Fescue grasslands provide important winter forage for herbivores due to its winter-hardy structure under snow and overall palatability (Willms et al. 1986). The cover of rough fescue can be reduced from one to three growing season after prescribed burning, with herbage production shifting in favour of perennial forbs (Bailey and Anderson, 1978; Antos et al 1983). The reduction in cover can occur when large bunches burn more severely, indicating a long fire return interval is not ideal for a maintaining rough fescue cover (Antos et al. 1983). However, annual burning has the potential to shift the graminoid community in favour of drought tolerant species (Anderson and Bailey 1980).

Loss of rough fescue grasslands at the YHT has been attributed to grazing and woody plant encroachment at the YHT (McGillis 1977). Fescue can be affected negatively by spring and summer grazing if there is little time for regrowth, resulting in shifts in dominance to other herbaceous species (Willms et al. 1985, ßWillms 1991, Merrill 2007). The increasing grazing pressure by a growing portion of the YHT elk herd, which now remain resident in summer was one of the major motivations for establishing exclosures at YHT (McInenly 2003, Merrill et al. 2007) as well as an elk aversive conditioning project (Spaedtke 2009). Prolonged heavy grazing in grasslands may also directly facilitate encroachment of shrubs. Once soil resources become limiting, both above and below-ground biomass will be reduced, along with the ability of grassland species to competitively exclude woody plants (Van Auken 2009). High herbivory also limits the litter available to act as fuel for fire propogation (van Auken 2009). Encroachment of shrubs and trees facilitated by grazing could further alter habitat capacity for grazers. Loss of grassland in this region has implications not only for extant populations of ungulates like elk, but for proposed reintroduction of a free-ranging bison (*Bison bison)* in the upper RDR drainage (Eleanor Luxton Historical Foundation, 2010).

The objective of this research was to use aerial photographs to quantify the change in spatial extent, rate of change, and shift in size of patches of grasslands over the period from 1952-2003 within the upper RDR drainage. Specifically, the questions addressed are a) has there been a loss in grassland area in the upper RDR drainage and if so what cover types have increased, b) is there a difference in rate of grassland loss between sites, and c) has there been a shift in grassland patch size distribution? It is predicted that while grassland loss has likely occurred, that mean patch size will increase as smaller patches are lost over time. The 4 sites under study are key secondary or primary winter range locations, providing forage for many ungulates in winter and along seasonal migration routes of elk from BNP to YHT (Morgantini 1988).

2.2 Methods

2.2.1 Study site background

The change in grassland characteristics was compared across 4 study sites along the Red Deer river (Fig. 1-1, Table 2-1, Appendix I). Sites were located along an east to west gradient decreasing in herbivory, shortened growing season (Hebblewhite 2006) and increasing gradient in moisture (Table 2-1). The Ya Ha

Tinda (YHT), which is the largest and most eastern site of the four study sites (Fig. 1-1, Table 2-1) is located 5 km east of the BNP boundary. West Lakes (WL) is contained within the YHT Ranch boundaries, but was considered a separate study site due to lower elk densities over time than the YHT site (Morgantini 1988:125-174, Hebblewhite et al. 2006: Fig. 1-3). By the late 1950s, Flook (1957) identified heavy grazing by the elk the population on YHT and predicted continued heavy use would result in rapid range deterioration. In 1970, there was an attempt to control shrubby cinquefoil at the YHT using Picloram (Scotter 1974) with use on bog birch to follow without promising results (McGillis 1977, Trottier and Milner 1978). Mowing of bog birch was initiated in 1982 (Parks Canada 1987). An attempt to reseed native grasses occurred during the 1980s in select high- elk use areas such as Scalp Creek, and in a formerly non-native grass pasture seeded to *Bromus* spp., but attempts failed (Walker 1984). By the late 1980s, Seel and Wiebe (1989) concluded the net effect of high elk and horse grazing at the YHT was likely altering grassland composition and productivity, although no direct comparisons to earlier studies were made. At the YHT, fescue communities where grazing was excluded had not begun to recover after two years (McInenly 2003); however fescue plants grew 2X as tall and had 7X larger basal diameters inside exclosures than outside, after 7 years (Merrill et al. 2007).

The WL site was not burned since 1929 and YHT site since 1936 until recently (Appendix II). In 2007 there was a prescribed fire that burned an area of 139 ha north of the YHT ranch buildings and up Hat Mountain in spring (April to

June), and a much larger burn starting in March of 2009 that burned a large portion (1774 ha) of the WL and YHT sites until mid July 2009 (Table 2-1, Appendix II). The aerial photo analysis did not contain these burns. The Scotch Camp (SC) and Tyrrell Creek (TY) meadows historically were spring and fall migration staging areas for elk migrating between winter range at YHT and BNP (Morgantini 1988, Skjonsberg 1993), and they have been described as low use areas for elk in winter (Morgantini 1988; Skjonsberg 1993). Prescribed burns have occurred periodically at SC and TY since 1983 (White 2001). There is also an east-west topographic and climatic gradient, which appears to influence grassland phenology (Hebblewhite et al. 2008).

2.2.2 Land cover classification scheme

I classified each study site using 6 vegetated land cover types (coniferous forest, mixedwood forest, shrubland, grassland, clearcut, and pasture) and 3 unvegetated land cover types (pond/river, road, and rock/bare ground). Vegetated land cover classes corresponded with the dominant canopy cover. Grasslands had sparse woody plant cover, except for shrubby cinquefoil, which was considered a grassland community co-dominant (Willoughby 2001). In addition, a pasture area (13 ha) that contained natural grasslands seeded with tame brome grass (*Bromus* spp.) was established at YHT prior to 1952 (Morgantini 1995, Willoughby 2001 Sumners and Archibold 2007) and classified as pasture thereafter. Shrublands were defined when woody cover comprised the majority of the area delineated. Woody shrub cover consisted largely of bog birch at YHT and WL and contained higher proportions of willow (*Salix* spp.) at the SC and TY sites (maximum ~50%

of shrub cover). The mixedwood forest cover type included areas with forest canopy and deciduous trees (trembling aspen, balsam poplar) comprising >20% of total tree canopy cover. Coniferous stands contained > 80% lodgepole pine and/or white spruce. One area (21.7 ha) at the YHT site that was clearcut in 1987 and seeded to creeping red fescue *(Festuca rubra*) post harvest (Morganitini and Eslinger 1994) and was classified as clearcut in 1992 and 2003.

2.2.3 Aerial photo imagery and pre-processing

Vertical aerial photographs of the study area were obtained from Alberta Sustainable Resource Development (ASRD) air photo library in Edmonton, AB for the years 1952, 1972, 1982, 1992, and 2003 (Table 2-1). Aerial photographs were not available earlier than the 1950s. The National Air photo Library of Natural Resources Canada (NRCan) in Edmonton provided images for 1962 and 1972. Imagery for 2003 was available only for YHT and WL, and so analyses for this date was restricted to these sites. The 1952, 1992, and 2003 images were taken on 31 July, 10 August and 30 September, respectively, and were at a scale of 1:40,000. The 1962 imagery was taken on 15 June at a scale of 1:25000, the 1972 photographs were taken on 5 October at a scale 1:21120 for the YHT and WL, and 27 August at 1:80000 for TY and SC. The 1982 imagery for all sites was taken on 2 September at a scale of 1:60000. Discrepancy in seasonality of photos could alter vegetation classification, therefore only photos with leaf cover were used. Time of day in which photos were taken influences shading, which is the most extensive with treed vegetation classes. Photos were selected to minimize shading effects by selecting photographs from the same time of day as best as possible although photo availability was limited. Although not corrected, shading effects associated with coniferous and deciduous forest were assumed to be consistent through time. Satellite imagery was not used as the resolution was poor compared to aerial photographs, making analysis of this data impractical. Introducing another image source at a lower spatial resolution would likely have lowered classification accuracy of already difficult to identify cover types such as shrub.

Because the imagery across years was of variable scale (1:25000 to 1:80000), it was scanned at a range of 600 to 2000 of dots per inch (DPI) to obtain the same pixel resolution (1 m^2) among years based on the conversion of: scale/DPI. The 1952, 1962, 1972, 1982, 1992, and 2003 photos were co-registered to 2003 orthorectified satellite images in ArcGIS using 6-10 ground control points (GCP) per photo, which was consistent with Rhemtulla et al. (2002) for similar studies in Jasper National Park (JNP). GCPs were distributed evenly across the photo surface to ensure good fit throughout the study area (Morgan et al. 2010). Ground control points included roads and trail intersections and buildings. Spline and polynomial transformations were used for photo sets depending on which transformation produced the best fit to the orthorectified 2003 image base on root mean square error (RMSE). All images regardless of transformation technique had an RMSE < 2 m, which is consistent with other high-resolution photo-interpretation studies (Bowman et al. 2001, Bai et al 2005, Fensham and Fairfax 2008)

2.2.4 Photo interpretation of land cover types

Classification of land cover types within the study area was completed using a supervised classification of the land cover types based on visual interpretation (Morgan et al. 2010). To maintain a consistent viewing distance for delineating cover types, the photo scale was set at a 1:4,000 for all photographs within the ArcGIS. Conducting the image classification at this scale produced a minimum mapping unit (MMU) of 500 m^2. A description of cover types and how they were identified using visual photo interpretation techniques is included in Appendix III. Because the focus of this study was on native vegetation change, anthropogenic features (roads, buildings), rocky bare surfaces and water bodies were lumped into a category called "Other". These types were relatively stable over time, with minor (~0.2%) increases the coverage of roads.

2.2.5 Classification accuracy

To provide an assessment of classification accuracy, the classification of the 2003 aerial photograph was compared to a classification based on 94 ground-truth locations visited in 2009 consisting of the 2 endpoints of a 100-m transect (Appendix IV). This assessment was conducted only at the WL and YHT sites because these were the only sites with 2003 imagery. While it would have been preferable to construct the error matrix using photographs taken closer to the sampling period of the ground-truth plots (i.e., 2009), these did not exist. Two types of accuracy assessment were derived. Producer accuracy (PA) is the probability that a pixel is classified correctly, while the user's accuracy (UA) is the probability that a pixel classified as a type on a map matches to what is on the ground (Pontius and Lippitt 2006).

2.2.6 Change in land cover extent and patch size

The total area of land cover types at each study site was calculated by summing the area of each polygon within a land cover type. The total area in land cover types was expressed as both extent (ha) and percent change in extent over time as [((ha$_{t+1}$ - ha$_t$)/ha$_t$) x 100] where t is the extent in 1952 and ha$_{t+1}$ is the extent in the year of interest. Differences in the rate of grassland change between study sites was examined by conducting ANCOVA and pair-wise comparisons at sites over time (Zarr 1999), where the trend in total extent of grassland (continuous dependent variable) was compared between sites (categorical independent variable) using year as a categorical covariate. For the ANVOCA, 2003 data was excluded because data for this year was not available for all sites (n=5). Differences in the distribution of sizes of grassland patches was tested using nonparametric Kolmogorov-Smirnov (K-S) distributions test. Within each site, grassland patch size distribution was compared between 1952 and the most recent year at a given study site. A record of all cover type shifts from 1952 to the most recent photo year available for each site is included in Appendix VI, a-d.

2.3 Results

2.3.1 Classification validation

Overall producer accuracy of vegetation classification was 76% with the most problematic vegetation class being shrublands (Table 2-2). Conifer forest (90%) and grassland (80%) cover types were most accurately identified from aerial photographs. Grasslands were most frequently misclassified as shrubland (14%). Mixed forest was moderately well classified (77%). Shrubland was correctly classified 58% of the time, most likely due to overlap of tone with moist meadows or conifer cover rather than shading, as most shrub fields encountered were low-growing (<2m in height). Shrubland was most often misclassified as conifer forest (28%) or grassland (14%). Overall user classification accuracy was 80%.

2.3.2 Change in extent of cover types

There was a relatively consistent change in vegetation types over time among sites with the exception of YHT (Fig. 2-1, Fig.2-2, Appendix V). Excluding YHT, grasslands declined on average 52.4+ 19.9% (range: 6.3 to -488.3ha) across sites between 1952 and 1992 with a corresponding increase of 38.6+ 10.4% (ha) in conifer forest (Fig. 2-2; Appendix V). WL exhibited the greatest relative loss of grassland within the upper RDR drainage since 1952 (73.7%, 488 ha by 2003). Grassland loss at WL was greatest between 1962-1982 and after 1992 (Fig. 2-2). At TY there was a steady increase in coniferous forest between 1952-1992 (35%, 50 ha) and decrease in grassland (49.2%, 67 ha) cover (Fig. 2-3). There was a decline (34.2%, 30 ha) in grassland area and increase in coniferous forest (30.4%, 36 ha) at SC over the same time period. In contrast, shrublands at both TY and SC remained relatively constant or declined only slightly, often transitioning to coniferous cover (Appendix VI, c-d).

At YHT there was a 8.8% (95 ha) decrease in grassland extent between 1952 and 1982 followed by an increase of 9.3% (101 ha) from 1982 to 2003. During the latter period there also was a 42.9% (172 ha) decline in shrubland cover and a 9.2% (93 ha) increase in conifer forest cover (Fig. 2-1). The pasture, which was established prior to 1952 at the YHT, comprised 0.5% (12.9 ha) of the area in the 1952 photograph but was reduced by 36.3% (8 ha) by 1972 when an established fence line became visible on the aerial photograph, increasing grassland area slightly as a result. Although there was an increase in conifer forest at YHT, there also was a 2% (12 ha) removal of coniferous forest within the study area due to timber harvest in 1987 along Bighorn Creek as part of a elk habitat improvement project (Burrington et al. 1986).

ANCOVA analysis indicated linear declines occurred in grassland extent over the 40-year period at each site ($P<0.02$) except at YHT. The rate of grassland loss from 1952 to 1992 was greater at WL ($\beta= -10.93 \pm 1.54$) than at TY ($\beta= -1.63 \pm 0.15$, $P =<0.001$) and SC ($\beta= -0.73 \pm 0.17$, $P<0.001$), whereas there was no difference in rate of grassland decline between TY and SC ($P = 0.80$).

Non-vegetated types became vegetated, and not vice versa. The largest change in a non-vegetated cover type was the development of grassland where roads or bare ground formerly occurred at YHT (Appendix VI). Ponds did not occur at all study sites, and where they were found, ponds had often become occupied by either grassland or coniferous cover by 2003. Many of these grassland ponds were small in extent, and the 2003 data represents the end of a period of drought that began in the mid-1990s (Fig. 1-2).

2.3.3 Changes in grassland patch sizes

Grassland patch distribution changed in a similar fashion across sites along the upper RDRV. At all sites except WL (Fig. 2-4), average patch size (ha ± SD) increased due to the loss of smaller patches (Fig. 2-3). From 1952 to 2003 patch distribution increased (K-S test: *D*= 0.15, *P*=0.05) from a mean of 4.99ha ± 45.29 (n=215) to 14.79ha ± 49.88 (n=146) at the YHT, which exhibited an increase in the number of larger patches as well as a loss of smaller patches (Fig. 2-3a). Grassland patch distribution changed from 1952 to 2003 at WL (*D*=0.27, *P*=0.028) representing a shift from a mean of 9.33ha ± 70.8, (n=71) to 3.29ha ± 7.41 (n=53), largely driven by an increase in number of small patches in the 0.1-1 ha category (Fig. 2-3b). At TY, grassland patch size increased from 1952 to 1992 (*D*=0.417, *P*= 0.02) from a mean of 3.77ha ± 11.9 (n=36) to 3.84ha ± 7.05, n=18, largely driven by a reduction in number of small patches (Fig. 2-3c). Grassland patch size distribution at SC changed from 1952 to 1992 (*D*=0.37, *P*=0.03) from a mean patch size of 2.03ha ± 11.5 (n=43) to 2.29ha ± 9.56 (n=25), reflecting the loss of patches in both larger and smaller size classes (Fig. 2-3d).

2.4 Discussion

From 1890 to 1983 Parks Canada maintained a fire suppression policy (White 1985) that has resulted in an increase in the extent and mean stand age of forests (Rogeau and Gilbride1994). As a result I found a loss of grassland extent at most sites within the RDRV over time with an increase in primarily conifers. Such increases in coniferous forest and shrub cover has been observed during the same period in valley environments of Jasper National Park (Rhemtulla et al. 2002) and the Rocky Mountains in the Alberta foothills (Burkinshaw and Bork, 2009). In the RDRV the average 47% decline in grassland between 1952 and 1992 was similar to Jasper National Park where grassland area was reduced by almost 50% over an 82-year period from 1915-1997 (Rhemtulla et al. 2002), and to portions of the Rocky Mountain Foothills Forest Reserve where there was a 58% loss in grassland between 1958-1998 (Burkinshaw and Bork 2009).

Although conifer encroachment occurred across all sites (6.8 to 29.2%), a higher rate of conifer encroachment at WL (29.2%) than other site may have occurred for a variety of reasons. Larger herds of elk have wintered at the WL and YHT sites than TY and SC since Alberta Fish and Wildlife and Parks Canada monitoring efforts began in 1972 (Hebblewite et al. 2006). An increasing portion of elk have become year long residents of the YHT and WL (Hebblewhite et al. 2008), grazing during the sensitive spring growth period for fescue (Branson 1953) and potentially reducing the ability of these grasslands to limit woody plant encroachment over time (van Auken 2009). Recently, prescribed fires were initiated to create a fireguard and restore 50% of the historic fire cycle in terms of area burned for stands of different origin years (Rogeau 1994). However, the 1929 fire in the WL area burned large tracts of coniferous forest, which has subsequently re-established resulting in the observed succession to conifer forest following that burn (Parks Canada data, unpublished). In addition, the conifers in this area consist primarily of lodgepole pine, a species that has been associated with faster establishment rates under warm spring temperatures and high fall (October–November) precipitation in the Cyprus Hills (Widenmaier and Strong 2010). Dry spring and moister winter climate could be prevalent at the WL, although fine scale climate data is unavailable. In general there has been an increase in mean summer temperatures (Fig 1-2, b) in Banff NP since 1952 possibly promoting lodgepole pine reestablishment, similar to the Cypress Hills.

The most likely reason for the higher rate of encroachment at WL is due to the steeper slope at this site. The rate of conifer encroachment depends on the dominant aspect and degree slope of the area in question (Bai et al 2002). With every 200 m rise in elevation per unit area, tree establishment can increase by 1.8 individuals/ha/year (Johnson and Miller 2006). Although grasslands in the upper RDR drainage were predominantly south facing and between 1600 to 1800m in elevation, the West Lake site was steeper on average (maximum slope ~ 50%) than the other sites in the RDR valley where sampling occurred.

Trends in shrub encroachment into grasslands were variable within the RDR drainage. SC and TY had lower rates of shrub encroachment, potentially due to browsing effects and the composition of the shrub community at these sites. Willow is currently dominant at SC and TY and is a highly palatable ungulate browse and where its distribution is limited, even moderate ungulate herbivory may arrest its growth (Tercek et al. 2010). Willow is currently a minor component of the shrub community at YHT and WL, while bog birch, which is not a palatable shrub (Toweill and Thomas 2002, Sachro et al. 2005), is the dominant shrub species in shrublands. Bog birch occurs in sites with precipitation as low as 109-230 mm (Blanken and Rouse 1994, Arri and Turkington 2002), and does not seem to be as moisture limited as willow. An increasing trend in bog birch-encroachment at YHT and WL similar to adjacent provincial lands (Burkinshaw and Bork 2009) might be expected due to (1) undesirable palatability, (2) lack of frequent fires, and (3) because grasslands can become susceptible to woody plant invasion with heavy grazing (Archer et al. 1995, Roques et al.2001, Jurena and

Archer 2003, Tremblay et al. 2006, Sasaki et al. 2008). Although shrubland increased from 1952 to 1972 at YHT, by 1982 this trend was reversed. Closer examination of the history of the YHT area indicated this was likely due to shrub mowing that was initiated in 1982, with an average of 0.25 km^2 of predominantly bog birch shrubland maintained by mowing every few years until 2003 (Parks Canada, 1987; Hebblewhite 2006). In addition, the moderate amount of shrub encroachment into grasslands that occurred in the upper RDR drainage (Appendix VI) was offset by tree encroachment into shrublands, such that shrubland extent appeared to change minimally through time.

Trends in grassland patch distribution reflect a general in-filling of grasslands by woody plants. Within the RDR drainage, large patches were not fragmented but simply reduced in extent, in addition to small remnant patches of grassland at SC, TY and WL converting to woody cover. However, encroachment at WL to a large extent reflected a fragmentation of the grasslands, with the larger central grassland reduced into smaller units over time. Rhemtulla et al (2002) found no change in mean patch size or number of patches from 1949 to 1997, proposing that much of the homogenization may have occurred prior to 1949. Within the RDR drainage the rate of encroachment has slowed only recently as available ecosites for colonization become limited. Without management intervention, further grassland patch shifts are likely to occur.

The montane ecoregion is estimated to occupy only 3% of the area within Banff, and grasslands occupy only portion of this area. My study indicated a general decline in grassland extent in the Upper RDR drainage has occurred. Most of the change is related to conifer encroachment directly into the grasslands, with grasslands less frequently converted to shrubland (2 – 15%, Appendix VI). Few burning programs have been conducted to ensure grassland maintenance by reducing conifer encroachment, but rather they have focused on the creation of fuel breaks and elk habitat (Parks Canada, 2005) and the maintenance of the 50% of the historical fire regime in forested areas (Parks Canada 2007). In contrast, intensive effort to control shrubs by mechanical means has been implemented. Mowing of shrubs in both shrublands and grasslands at the YHT was initiated in 1982 (Parks Canada, 1987) and appears to have limited the increase of shrubs at this site (Trottier and Milner 1978, Seel and Wiebe 1989). Shrub encroachment within the rest of the river valley has been minimal in the absense of mowing. Drastic fire schedule of 3-5 years may have been required to halt the progression (De Groot 1998, Bork et al. 1996). A burning frequency in the range of what is typically found in the montane ecoregion (50 year cycle; White et al. 2001) would be adequate to mitigate conifer encroachment. Given that the majority of encroachment has been from increases in coniferous cover, it would be logical to continue with a burn program designed to address the issue of conifer encroachment, as this would most likely be highly effective as well as address other management goals.

One of the difficulties with using natural variability as an approach to managing ecosystems (Parks Canada 2008) is determining the time frame of baseline conditions. Although conditions at the turn of the century could be viewed as benchmarks for restoration, the range in variability over a longer period may have been even greater. Some grassland patches in the current study were observed to be underlain by forest soils (Eutric Brunisols) suggesting that the current forest dominance may have been even more widespread in the past (Holland and Coen 1982). The current study simply provides insight into more complex vegetation dynamics over a brief period of time and may not extrapolate well on a broader time scale, but does reflect vegetation shifts over a period of fire suppression and increasing annual summer temperatures within BNP and adjacent areas.

Table 2-1 Physiographic and climatic characteristics of the 4 grassland study sites and their grazing and burn history, and years of the aerial photos used in analysis.

	SC	TY	WL	YHT	Source
Physiographic					
Area (ha)	249	329	1455	2634	7
Elevation (m)	1700-1800	1600-1700	1600- 1800	1600-1800	10
Soils	Brunisols Regosols	Brunisols Regosols	Regosols, Brunsisols	Brunisols Regosols	1, 2
Climatic					
Total annual precipitation (mm) (n=19) 1984-2007	375	375	610	610	8
Grazing history					
Pre 1890	Low	Low	Low	Low	3, 4
1890 to1940	Low	Low	Low	Low	3, 5
1940 to 2003	Moderate	Moderate	High	Very high*	5, 6
Recent Burning (Appendix II)	Prescribed burns	Prescribed burns	Suppression	Suppression	9
Shrub control	--	--	--	1974, 1982, 2000s*	
Photo dates	1952, 1962, 1972, 1982, 1992	1952, 1962, 1972, 1982, 1992	1952, 1962, 1972, 1982, 1992, 2003	1952, 1962, 1972, 1982, 1992, 2003	10

* >10elk/km^2 considered high for YHT (White 2001, White et al. 1995)
[1] McGillis (1977), [2] Holland and Coen (1983), [3] Gunson (1977), [4] Kay et al. (1994), [5] Morgantini (1988), [6] White et al. (1995), [7]Glines (2011). Hebblewhite 2005, [8]Alberta Environment stations at SC and WL, [9] Parks Canada, Government of Alberta, [10] Parks Canada, NAPL, Alberta SRD. *Incomplete records for 2000s.

Table 2-2 Classification accuracy matrix for 2003 images based on comparison with ground truth points (n=94) visited in 2009 at YHT and WL sites. Producer accuracy (PA) is the probability that a pixel is classified correctly, while the user's accuracy (UA) is the probability that a pixel classified as a type on a map matches to what is on the ground (Pontius and Lippitt 2006).

		Map Classification					
	Vegetation Class	Grassland	Shrubland	Coniferous Forest	Mixed Forest	Total	PA (%)
Ground Classification	Grassland	28	5	1	1	35	80.0
	Shrubland	4	15	7	0	26	57.7
	Coniferous Forest	0	2	18	0	20	90.0
	Mixed Forest	1	0	2	10	13	76.9
	Total	33	19	28	11	94	76.2
	UA (%)	84.8	78	64.2	90.9	79.5	

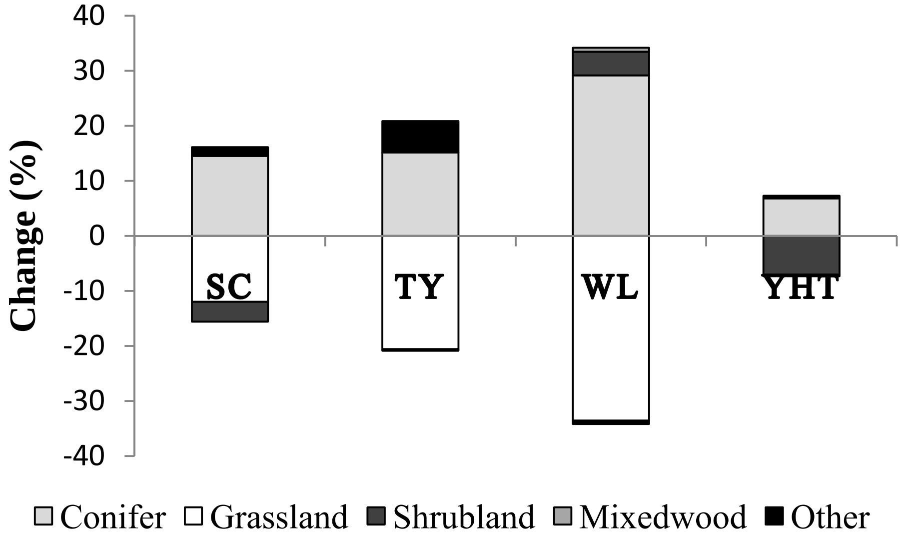


Fig. 2-1 Percent change in vegetative cover types relative to site area from 1952-1992 at SC and TY, and 1952-2003 at WL and YHT in the upper Red Deer River drainage, Alberta, Canada.

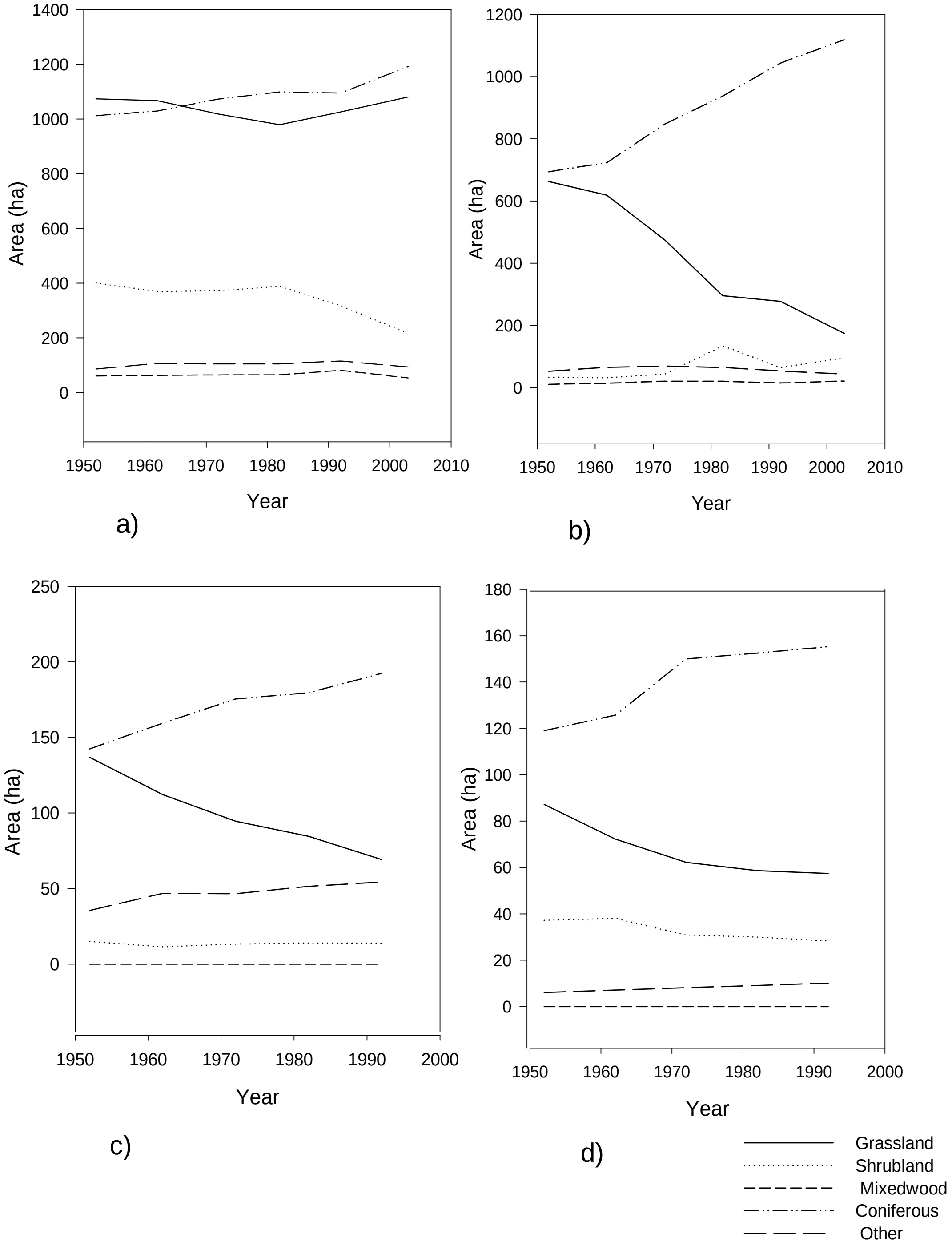


Fig. 2-2 Change in land cover within a) Ya Ha Tinda, b) West Lakes, c) Tyrrell Flats, d) Scotch Camp, spanning a 40yr period (1952 - 1992) and quantified at a decadal interval. Data from the upper Red Deer River valley in the central east slopes of Alberta, Canada

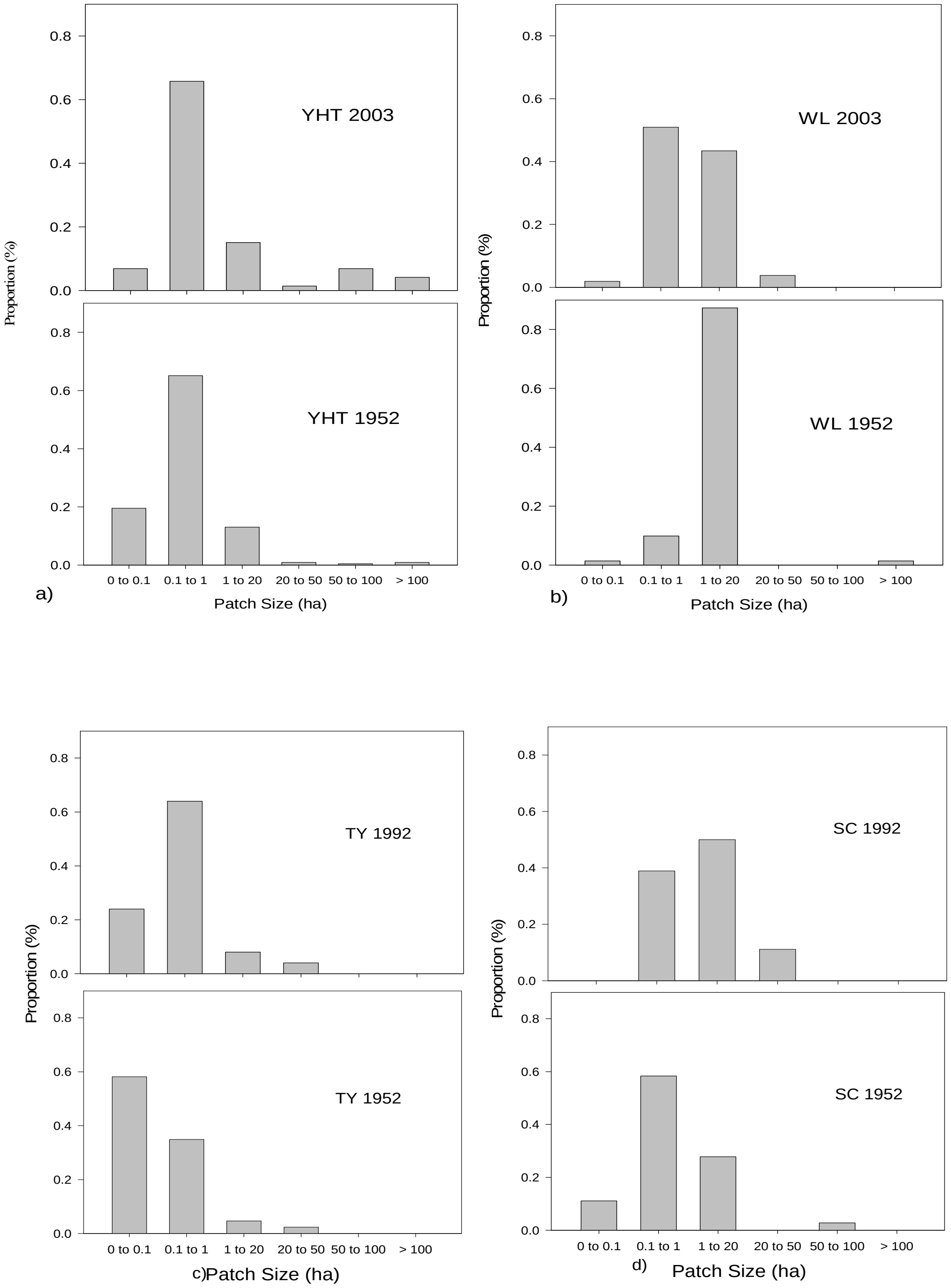
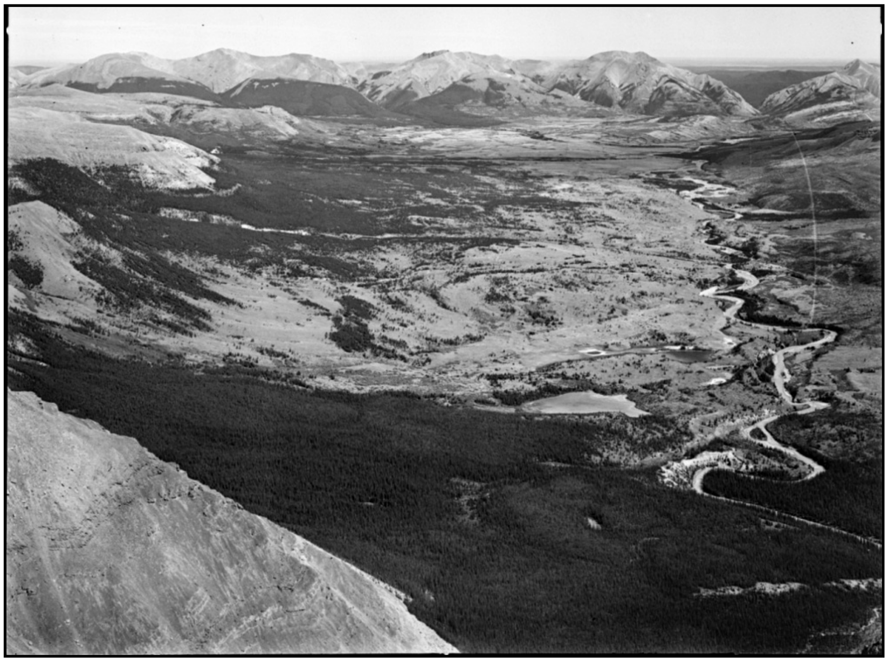
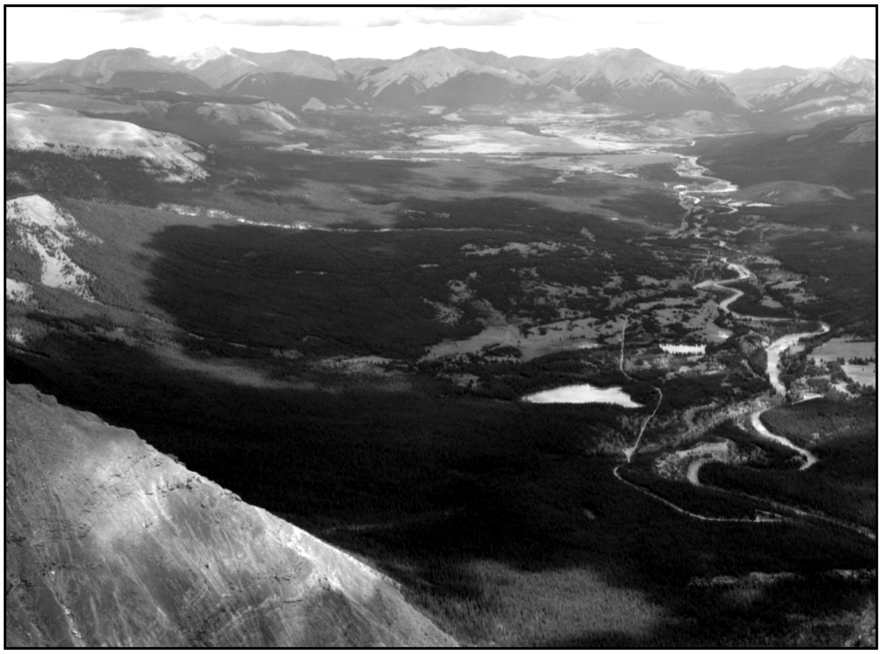


Fig. 2-3 Grassland patch distribution among the four study sites within the Red Deer River Valley: a)Ya Ha Tinda (YHT) b)West Lakes (WL), c) Tyrrell Creek (TY) and d) Scotch Camp (SC).



a)



b)

Fig. 2-4 Conifer encroachment in the WL, 1908 to 2008. These paired images indicated where the grassland was larger and continuous in extent in a) 1908, and has been fragmented into smaller meadows by b) 2008 (Photo sources: Dominion Land Survey and Mountain Legacy Project)

2.5 Literature Cited

Antos, J.A., McCune, B., Bara, C., 1983. The effect of fire on an ungrazed western Montana grassland. American Midland Naturalist, 110: 354-364

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

Arii, K., Turkington, R., 2002. Do nutrient availability and competition limit plant growth of herbaceous species in the boreal forest understory? Arctic Antarctic and Alpine Research, 34(3): 251-261

Arno, S.F., 1980. Forest fire history in the northern Rockies. Journal of Forestry, Vol. 78, 460- 465.

Archer, S., Schimel, D.S., Holland, E.A., 1995. Mechanisms of shrubland expansion: Land use, climate or CO_2? Climatic Change 29: 91-99.

Bai Y, Broersma K, Thompson, D., Ross, T.J., 2002. Landscape-level dynamics of grassland-forest transitions in British Columbia. Journal of Range Management 57: 66-75

Bai Y., Walsworth, N., Roddan, B., Hill, D. A., Broersma, K., Thompson, D., 2005. Quantifying tree cover in the forest-grassland ecotone of British Columbia using crown delineation and pattern detection, Forest Ecology and Management 212: 92-100

Bailey, A.W., Anderson, M.L., 1978. Prescribed burning of a *Festuca-Stipa* grassland. Journal of Range Management, 31: 446-449

Blanken, P.D., Rouse, W.R., 1994. The role of willow-birch forest in the surface energy balance at Arctic tree-line. Arctic and Alpine Research 26 (4): 403-411.

Branson, F.A. 1953. Two factors affecting resistance of grasses to grazing. Journal of Range Management, 6: 165-171.

Bork, E., Smith, D., Willoughby, M., 1996. Prescribed burning of bog birch. Rangelands 18: 4-7.

Bowman, D. M. J. S., Walsh, A., Milne, D. J., 2001. Forest expansion and grassland contraction within a *Eucalyptus* savanna matrix between 1941 and 1994 at Litchfield national Park in the Australian monsoon tropics, Global Ecology & Biogeaography 10:535-548.

Burkinshaw, A.M., Bork, E., 2009. Shrub encroachment impacts the potential for multiple use conflicts on public land. Environmental Management 44:493–504

Burrington, B., D. Eslinger, W. Gladstone, and M. Swan. 1986. Wildlife habitat improvement in the Bighorn Creek watershed. Alberta Energy and Natural Resources Tech. Rep. # T/118, Edmonton, Alberta.

Cook, J.G., 2002. Nutrion and Food. North American elk ecology and management. Toweill, E.D., Thomas, W.J., (Eds). Washington, Smithsonian Instituion Press. 962 pp.

Christenson, O.A., 1971. Banff prehistory: Prehistoric settlement and subsistence in Banff National Park, Alberta. MS Report No. 67. National Historic Parks and Sites Branch, Ottawa,Canada. 279 pp.

de Groot, W.J., 1998. Fire ecology of *Betula glandulosa* Michx. PH.D. Thesis Department of Forest Science, Univesity of Alberta.

Eleanor Luxton Historical Foundation, 2010. Banff bison restoration proposal summary. Websource: http://www.bisonbelong.ca/

Ferguson, C., Adams, I., Low, B., Pengelly, I., 2001. Environmental assessment of fire management in the Cascade/Bow ecological management area. Parks Canada, Banff National Park. 300 pp.

Fensham, R. J., . Fairfax, R. J., 2008. Effect of photoscale, interpreter bias and land type on woody crown-cover estimates from aerial photography. Australian Journal of Botany, 55: 457–463

Flook, D. R., 1957. Elk – Horse Grazing Situation, Yaha Tinda Ranch - Letter Report

Hebblewhite, M., 2006. Linking predation risk and forage to ungulate population dynamics. University of Alberta. Edmonton, Alberta.

Hebblewhite, M., Merrill, E. H., McDermid, G., 2008. A mutli-scale test of the forage maturation hypothesis for a partially migratory montane elk population. *Ecological Monographs* 78, 141-166.

Hebblewhite, M., Merrill, E.H., Morgantini, L.E., White, C.A., Allen, J.R., Bruns, E., Thurston, L., Hurd., T.E., 2006. Is the migratory behaviour of montane elk herds in peril? The case of Alberta's Ya Ha Tinda elk herd. Wildlife Society Bulletin 34: 1280-1295.

Holland, W. D., Coen, G.M., Eds. 1983. Ecological (Biophysical) Land Classification Of Banff andJasper National Park s. Volume II : Soil and

Vegetation Resources. Alberta Institute of Pedology Publication No. SS-82-4 4

Johnson, D.D., Miller, R.F. 2006. Structure and development of expanding western juniper woodlands as influenced by two topographic variables. Forest Ecology and Management 229, 7–15

Johnson, A, Smoliak S., 1968. Reclaiming brush land in southwestern Alberta. J. Range Management. 21: 404-406.

Jurena, P. N., Archer, S., 2003. Woody Plan Establishment and Spatial Heterogeneity in Grasslands. Ecology, 84: 907-919

Kay, C.E., Patton, B., White, C.A., 1994. Assessment of long-term terrestrial ecosystem states and processes in Banff National Park and the central Canadian Rockies. Banff National Park. Resource Conservation.

Kemper, J.T., 2009. Alberta natural heritage information centre vascular and non-vascular plant tracking and watch lists. Alberta Tourism, Parks and Recreation, Parks Division, Edmonton, Alberta.

Looman, J., 1969. The fescue grassland of western Canada. Vegetation 19: 128-145

McGillis, J.R., 1977. Range management of the Ya Ha Tinda ranch. Prepared for Parks Canada, Candian Wildlife Service, Edmonton. 75pgs

McInenly, L. E. 2003. Seasonal effects of defoliation on montane rough fescue (Festuca campestris Rydb.). University of Alberta, Edmonton, Canada.

Merrill, E., McPhee, H., Robinson, B., 2007. Ya Ha Tinda exclosure study: Plant composition & fescue growth. Progress Report. Parks Canada, 27pgs.

Morgan, J.L., Gergel, S.E., Coops, N.C., 2010. Aerial photography: A rapidly evolving tool for ecological management. Bioscience, 60: 47-59

Morgantini, L.E., 1988. Behavioural adaptive strategies of wapiti (Cervus elaphus) in the Canadian Rocky Mountians. PhD thesis, University of Alberta, Edmonton 193 pg.

Morgantini, L.E., 1995. The Ya Ha Tinda: An Ecological Overview. Canadian Heritage, Parks Canada, Calgary

Morgantini, L.E., Eslinger, D., 1994. Logging and elk in the Bighorn Creek Valley in western Alberta: The response of elk and important forage plants to forest harvesting (1988-1991). Department of Forest Science, University of Alberta in cooperation with Alberta Environmental Protection, Fish and Wildlife Services, 1994 - 114 pages

Parks Canada, 1987. Ya Ha Tinda ranch management plan. Environment Canada, Parks Western Region, Resource Conservation. 92pgs

Parks Canada, 2005. Ya Ha Tinda Ranch fuel break- prescribed fire- elk conditioning- elk proof fencing environmental assessment. October 14, 2005 version. Parks Canada, Box 900, Banff, Alberta T1L 1K2

Parks Canada, 2007. Banff National Park management plan. July 2007 amendment. Environment Canada, Parks Canada. ISBN: 978-0-662-05190-9, Government Catalog No.: R63-225/2007-MRC

Parks Canada, 2008. Banff Nation Park of Canada state of the park report

Pontius Jr, R.G., Lippitt, C.D., 2006. Can error explain map differences over time? Cartography and Geographic Information Science 33: 159-171

Rhemtulla, J., Hall, R., Higgs, E., MacDonald, E., 2002. Eighty years of change: vegetation in the montane ecoregion of Jasper National Park, Alberta, Canada. Canadian Journal of Forestry Research 32: 2010–2021

Rogeau, M.P., Gilbride, D., 1994. Forest stand origin mapping of Banff National Park. Resource Conservation, Banff National Park, 74 pg.

Roques , K.G., O'Connor, T.G., Watkinson, A.R., 2001. Dynamics of shrub encroachment in an African savanna: Relative influences of fire, herbivory, rainfall and density dependence, The Journal of applied ecology 38: 268-280

Sachro, L.L., Strong, W.L., Gates, C.C., 2005. Prescribed burning effects on summer elk forage availability in the Subalpine zone, Banff National Park. Environmental Management 77: 183-193.

Sasaki, T., Okayasu, T., Shirato, Y., Jamsran, U., Okubo, S., Takeuchi, K., 2007. Can edaphic factors demonstrate landscape-scale differences in vegetation responses to grazing? Plant ecology, 194: 51-66

Scotter, G. W., 1974. Effect of Picloram on shrubby cinquefoil and forage production at the Ya-Ha-Tinda ranch, Alberta. Canadian Wildlife Service, Edmonton. 18 pp.

Seel, K.E., Wiebe, A.P., 1989. Range improvement project, Ya Ha Tinda ranch West-Central Alberta. Third progress report. Natural Resource Conservation, Canadian Parks Service, Environment Canada. Western Regional Office, Calgary, Alberta. 99 pp.

Skjonsberg, T., 1993. Eastern slopes wildlife study 1984-1987. Final technical report. Banff National Park, 138pp.

Spaedtke, H., 2009. Aversive Conditioning on horseback: A management alternative for grassland systems threatened by sedentary elk populations. M.S. Thesis, University of Alberta.

Sumners, W. H., Archibold, O. W., 2007. Exotic plant species in the southern boreal forest of Saskatchewan, Forest Ecology and Management 251:156-163

Tercek, M T., Stottlemyer, R., Renkin, R., 2010. Bottom-up factors influencing riparian willow recovery in Yellowstone National Park. Western North American Naturalist, 70: 387–399

Trottier, G. C., Milner, B. J., 1978. Herbicied contro of dwarf birch (*Betula glandulosa*) at Ya-Ha-Tinda ranch. CAnadaian Wildlife Service, Edmonton, Alberta. 11 pp.

Tremblay, J. P., Huot, J., Potvin, F., 2006. Divergent nonlinear responses of the boreal forest field layer along an experimental gradient of deer densities. Oecologia 150:78–88

Van Auken, O.W., 2009. Causes and consequences of woody plant encroachment into western North American grasslands. Journal of Environmental Management, 90; 2931–2942

Vujnovic, K., 1998. Small-scale plant species composition and diversity in relation to environmental and disturbance factors in Fescue. M.S. Thesis. University of Alberta. 16p.

Walker, D., 1980. Assessment of the Ya Ha Tinda ranch elk winter range improvement by reseeding study. Alberta Energy and Natural Resources, Fish and Wildlife Department, Edmonton, Alberta. 43 pp.

White, C. A., 1985. Wildland fires in Banff National Park 1880-1980. Occasional Paper 3. National Parks Branch, Parks Canada, Environment Canada. Ottawa, Ontario, Canada. 106pp.

White, C.A. 2001. Aspen, elk and fire in the Canadian rocky mountains. PhD thesis, University of Alberta, Edmonton 219 pg.

White, C.G., Zager, P., Gratson, M.W., 2010. Influence of predator harvest, biological factors, and landscape on elk calf survival in Idaho. Journal of Wildlife Management 74: 355-369.

Widenmaier, K. J., Strong, W. L, 2010. Tree and forest encroachment into fescue grasslands on the Cypress Hills plateau, southeast Alberta, Canada, Forest Ecology and Management 259: 1870-1879

Willms, W.D., 1991. Cutting frequency and cutting height effects on rough fescue and Parry oatgrass yields. Journal of Range Management, 44: 82–86.

Willms, W. D., Smoliak, S., Bailey, A. W., 1986. Herbage production following litter removal on Alberta native grasslands. Journal of Range Management 39: 536-540

Willms, W.D., Smoliak, S., Dormaar, J.F., 1985. Effects of stocking rates on rough fescue grassland vegetation. Journal Range Management 38:220-225

Willoughby, M.G., 2001. Range plant community types and carrying capacity for the montane subregion. Edmonton, Alberta, Alberta Sustainable Resource Development Land and Forest Service. Pub. no.: T/003, ISBN: 0-7785-1792-6

Zarr, J.H., 1999. Biostatistical analysis. 4th Edition. Prentice Hall, New Jersey.

CHAPTER 3: FORAGE AVAILABILITY IN AND ALONG ECOTONES

3.1 Background

In Alberta, rough fescue (*Festuca campestris*) provides vital winter forage for herbivores. The well□developed sclerenchymatous layer in the leaves and the characteristic of leaf rolling provides high curability and hence improves the value of fescue for dormant season grazing (Willms et al. 1986). This results in a moderate losses of biomass over winter and retention of nutrients such as nitrogen, with Willms et al. (1998) report an average loss of 13% biomass over three years and a C:N ratio of 40:1 in southwestern Alberta. Recent studies have indicated that fescue grassland in the upper Red Deer River RDR drainage constitute important winter ranges for elk (Morgantini 1989, Hebblewhite 2006). Grasslands such as the Ya Ha Tinda (YHT) have been the focus of rangeland deterioration assessments, as early as the mid 1950s (Flook 1957). From anecdotal observations of shrub increase, subsequent efforts focused on chemically reducing shrubby cinquefoil (*Potentilla frusticosa*) (Scotter 1974), and bog birch (*Betula glandulosa*) (Trottier and Milner 1978). Recent examination of the grassland community at the YHT documented fescue response to summer and yearlong clipping compared to natural grazing (McInenly 2003) and a marked increase in fescue basal area and shifts in species dominance inside exclosures compared to areas immediately outside (Merrill et al. 2007). Alternatively, loss of fescue grassland could occur through encroachment of woody species. For example, under bog birch canopy herbaceous productivity is lowered and fescue loses dominance (Willoughby 2001, Bork and Burkinshaw

2009); lodgepole pine has also spread within fescue systems, increasing by 14.3 ha/year in Cypress Hills Provincial Park, Alberta (Widenmaier and Strong 2010). Woody plant encroachment leading to grassland loss has also occurred in the current study. Where mechanical clearing of shrub cover has not occurred, grasslands have been reduced by 52% on average, with a loss in shrublands as well (39%) and a marked increase in coniferous cover (39 %) (Chapter 2).

The effect of woody plant encroachment into grasslands on herbaceous productivity may vary by distance to the ecotone. An ecotone is an environmentally variable interaction zone between ecological systems with characteristics defined in space and time, and by the strength of the interaction (Hufkens et al. 2009). Plants in competition extend themselves on one side of the ecotone as far as their ability to maintain themselves allows; beyond this competitors of the adjacent community are more abundant. A peak in richness or biomass associated with an ecotone is known as an edge effect. As a result the ecotone represents a shift in dominance in species from one plant community to another, with a peak in biodiversity at these locations. Many studies examining the possible edge effect of forest extending into grasslands have used avian (Fletcher and Koford 2003; Jensen and Finck, 2004; Vander Haegen 2007; Koper et al, 2009) or insect (Magura et al. 2001; Bieringer and Zulka, 2003; Pryke and Samways, 2012) species as their response indicators. However, when focusing on herbaceous response across forest-grassland ecotones in a foothills landscape, Luczaj and Sadowska (1997) determined the strongest edge effects were recorded for bryophyte, shrub and tree species richness, with the weakest response from herbaceous plant species richness. Marozas 2003 found herbaceous species richness of herbs and mosses was maximum at the forest edge and decreased dramatically at 5-10 m into grasslands, and attributed this to penetration of grassland species in forest edge zones. Herbaceous productivity may experience an edge effect as well. Because the majority of sapling establishment (66%) may occur within 5 m of the forest-grassland boundary (Wearne and Morgan, 2001), it is expected that this region will fluctuate in herbaceous biomass depending on edge effects. Biomass in grassland exterior was higher than that in grassland interior with an edge effect width 60-90 m from forest where biomass peaked (Qing chun et al. 2007). Forest-meadow ecotones with variable topography maintained higher dry matter production at the forest canopy edge than open pasture at medium distances, regardless of aspect (Lopez-Carrasco and Roig, 2009).

The presence of an edge effect could alter estimates of forage availability for elk or any other herbivore of interest in the upper RDR drainage. If it is assumed that there is no transition zone between vegetation communities, then the potential to support any given ungulate species could be underestimated, assuming a peak in biomass production occurred at grassland edges. Additionally, if this potential peak in forage biomass were incorporated into nutritional carrying capacity (K) models, the species composition would be vital to accurate estimates. In nutrition-based models of K, model inputs include quantity (biomass) and quality (protein and nitrogen content) of plant material, animal nutritional requirements, season, and habitat (Hanley and Rogers, 1989). Such models can be constrained further by specifying a proportion of use for each species in the model (e.g., no more than 40% of dietary biomass), and a threshold at which an animal can no longer be supported (e.g., no less than 25 kg/ha). A given unit of grassland edge might not be equivalent in nutritive value as a given unit of grassland interior. Although the quantity of biomass produced at an edge may be greater, its quality may be lower.

In this Chapter, I assess forage availability with woody encroachment by quantifying species composition, richness, and biomass during the peak of the growing season within the ecotones of 4 major cover types (grassland, shrubland, mixed forest, conifer forest) whose long-term change in extent was delineated in Chapter 2. I also investigated whether or not there was a change in forage biomass with distance to the woody cover edge, (i.e., an 'edge effect') to determine how patterns in the distribution of grassland patch sizes over time might influence forage availability with edge: extent ratio. Specifically, I hypothesized (1) there was an increase and peak in herbaceous richness and biomass of elk forages with increasing distance from a woody edge, and (2) the rate of increase varied among ecotone types with a potential for the greatest change between open to woody cover (e.g., grass to conifer, grass to shrub) than shrubland to coniferous cover.

3.2 Methods

3.2.1 Sampling design

I sampled ecotone vegetation between 1 July to 25 July 2009, which was considered by previous studies to be peak biomass in this area (Sanchro et al.

2005, Hebblewhite et al. 2008). Sampling was first initiated at the lower elevation sites (YHT: 1-5 July; WL:5-10 July 2009) and extended to the higher elevation sites later in the season (TY: 14-19 July, SC: 20-25 July) following the phenological gradient in peak biomass, from east to west (Hebblewhite et al. 2008). The 5 types of ecotones were sampled by placing 100-m transects across an ecotone with the transect mid-point at the approximate transition point between cover types; as such a transect sampled an approximately equal portion or area into each cover type. With the exception of ecotones involving mixedwood forest, which was limited at most sites, at least 5 transects of each ecotone type were sampled at each site (Table 3-1). Transect placement avoided regions that were burned in 2009 at the YHT and WL (Appendix 1-e).

3.2.2 Ground cover

Plots of 0.25- m^2 (50cm X 50cm) were placed at 10-m intervals along each 100-m transect (n=10/transect) for visually estimating percent ground cover of bare ground, woody debris, rock, ground creeping woody shrubs, litter, standing dead grass, and moss (Bryohpyta). Woody debris included any tree or shrub deadfall (>2 cm diameter) within the plot. Ground creeping shrubs included bear berry (*Arctostaphylos uva-ursi*) and common and mountain juniper (*Juniperus communis* and *J. horizontalis*). Litter was defined as detached, compressed, partially decomposed vegetative matter. Standing dead grass included remnants of standing graminoids from the previous growing season.

3.2.3 Herbaceous biomass and species occurrence

Along each transect, I used a double sampling method to estimate dry biomass (g/0.25 m^2) of total graminoid and total forb species separately in each of the ten plots (Ahmed et al. 1983). The first and last plots along each transect were clipped to within 2 cm of ground height, graminoids and forbs separated, and oven dried for at least 24 hours at 100°C to derive relationships between visually estimated biomass and dry biomass by forage class (Appendix VII). In addition to visually estimating total biomass, I estimated the percent of the total graminoid biomass that each grass species, and percent of the total forb biomass for a subset of forb species found to be important elk forage species (Table 3.2). I recorded all graminoid and forbs species present in each of the 0.25-m^2 plot.

3.2.4 Woody cover and biomass

Shrub canopy was recorded by species along the 100-m transect using a line intercept method (Floyd and Anderson 1987) such that cover was considered continuous with gaps of $\leq$ 10 cm. When canopy of two shrub species overlapped, canopy intercept of each species was recorded separately. As a result, total shrub cover could exceed 100%. Because shrub cover was recorded along the sampling transect, shrub cover over each 0.25-m^2 herbaceous plot along the transect also could be determined. Tree canopy cover was estimated using a spherical densitometer directly over each of the 0.25 m^2 herbaceous plots. Densiometer measurements employed Strickler's (1959) modification, which uses 17 dots etched on the reflecting surface within a wedge-shaped portion of the densiometer grid. At each plot, 4 readings (number of dots covered by forest canopy) were taken, 1 in each cardinal direction. The 4 readings were summed and multiplied by 1.47 for percent canopy cover. This modification reduces sampling bias, although canopy coverage may still be overestimated.

Biomass of shrub species was estimated based on stem density, basal diameter (BD), and BD-biomass relationships. Stem density was counted by species within five 10-m^2 plot along the 100-m transect located at 10 m apart. A stem was considered an individual if it was rooted. BD of 5 stems of each species per plot were measured, averaged and used to estimate average shrub biomass/stem using BD-biomass relationships derived by Visscher et al. (2006). With the exception of willow < 7 mm in diameter, biomass for a species per plot was the product of stem density of a species and the average biomass/stem BD. For small willow (BD <0.7 mm) biomass was based on the BD-biomass relationship derived by harvesting stems at ground level within the YHT study site, oven-drying at 100 °C for 72 h, and weighing to the nearest 0.01 g. Following Visscher et al. (2006), I compared several model types (linear, power, exponential) and found the best regression model for predicting biomass of small willow was fit by:

$$Y = 0.0295\, x^{2.3291} \; (R^2=0.72,\ \mathrm{n}=48,\ P = 0.02)$$

where Y is biomass per stem (g) and x is the BD (Appendix VIII). Although several species of willow (*Salix geyeriana, S. candida, S. bebbiana, S. planifola, and S. scouleriana*) occurred in the study area, individuals were not identified reliably to species so measurements among species were pooled for this genus.

Because *Juniperus* spp., bog birch, bearberry, lodgepole pine and white spruce saplings (< 2m) are of low palatability (Cook 2002, Sachro et al. 2005), they were omitted from estimates of browse availability, but their cover was estimated along the line transect. These species did not have appreciable signs of browsing (Keigley and Frisina, 1998).

3.2.5 Edge effect on herbaceous biomass at grassland ecotones

From herbaceous biomass estimates along ecotones the appearance of any peak in productivity was assessed by constructing the line of best fit, leading from the beginning of woody cover (conifer or shrub) to 50m into grassland cover. I used distances from ecotones at 10-m intervals from 0 to 50m in the present study. I also included the mean of herbaceous biomass >100m from edge from Spaedtke (2009) in regression analysis. Data from Spaedtke (2009) was used to access an end point for variation in graminoid biomass by distance to edge for each ecotone (conifer to grassland, shrubland to grassland, or conifer to shrubland), for YHT and WL only due to data limitations. Mixedwood ecotones were not considered, as they occupied < 3 % of area within the study site (Chapter 2).

Biomass from Spaedtke (2009) that was included in regression analyses were collected in 0.25 m^2 quadrats, as in the current study. However a 'disc pasture meter' method was used to assess herbaceous biomass, whereby a flat disc covering the same area was placed on the quadrat, and the height at which it came to rest recorded. From clip plots, a regression between disc height and dry biomass was constructed for calibration. Full methodology is described in

Spaedtke (2009). Percent new growth of graminoids in clips plots was used to recalculate mean herbaceous biomass estimates from Spaedtke (2009) to be consistent with CAG biomass estimates of the current study, which omitted standing dead graminoids. July 2009 disc pasture meter data from Holger (2009) was used for comparison with the current study to ensure temporal overlap in data sets (Appendix IX).

3.2.6 Statistical Analysis

Analysis of variance (ANOVA) using mixed- effects linear models was used to contrast mean values of cover, biomass, and richness between vegetation types and between sites in order to control for the random effect of autocorrelation within transects. Where data was not normal, such as comparisons of species frequencies, data was square root transformed (Zarr, 1999). Bonferroni post-hoc tests were used for subsequent pair-wise comparisons between vegetations types using STATA 10. Pearsons's correlation was used for assessing the strength of relationships between canopy cover and species abundance or biomass. Regression analysis was conducted to determine the relationships between ground cover, herbaceous biomass, species richness and cover type, as well as overstory cover-understory biomass relationships. Akaike Information Criterion (AIC; Akaike 1974) was used to identify the most parsimonious regression model between linear, quadratic, power for biomass edge effects analysis for each of the ecotones, where significant models were obtained.

3.3 Results

3.3.1 Cover type ground cover, tree canopy cover, and understory biomass

Canopy cover differed between cover types (ANOVA; $F_{3, 86} = 28$, P <0.01) (Table 3-3). Tree canopy cover did not differ between mixed-wood (mean ± SD; 60.9 ± 17.7) and coniferous (57.4±19.0) forest stands (P = 0.15), but forest canopy cover in these types was greater than in grassland (0.2±3.4) and shrubland (0.5 ±5.5) areas (P<0.01) (Table 3-3). Bare ground was higher (ANOVA; $F_{3, 86}$ = 13, P <0.01) in grasslands (6.0 ±11.9) as compared to shrublands (P=0.02), mixedwood forest (P<0.01) and coniferous forest (P<0.01) forest. Woody debris cover was higher (ANOVA; $F_{3, 86} = 17$, P <0.01) in shrublands (32.6 ±28.6) compared to other cover types, but did not differ between mixedwood and coniferous forest stands (P =0.80), which in turn had more woody debris than grassland (P<0.01) and shrubland (P <0.02). Percent cover of dead grass (standing dead) was lower (ANOVA; $F_{3, 86} = 19$, P <0.01) in forested plots (coniferous and mixedwood forest) than shrubland and grasslands (P<0.01) (Table 3-3).

Graminoid and forb biomass both varied by cover type and study site (Table 3.3). Graminoid biomass was greatest (ANOVA; $F_{3, 86} = 14$, P <0.01) in grasslands (P <0.02) and mixedwood forest (P= 0.01), and lowest in shrubland and conifer forest. Between sites, graminoid biomass was lower (ANOVA; $\mathrm{F}_{3, 86}$ = 17, P <0.01) in grassland (P< 0.01) and conifer forests (P <0.01) at WL than YHT (P<0.01) (Fig 3-1).

Forb biomass differed among cover types (ANOVA; $F_{3, 86} = 21$, P <0.01) and across study sites (ANOVA; $F_{3, 86} = 7$, P <0.01). Forb biomass in grassland was equivalent to shrubland, which exceeed mixedwood forests and conifer forest, with conferous forest producing the least (Table 3-2). Between sites, forb biomass was similar in all cover types except grasslands, where the YHT was higher than WL (*P*<0.01).

Shrub biomass also varied between cover types (ANOVA; $F_{3,\,86} = 21$, P <0.01), and across study sites (ANOVA; $F_{3,\,86} = 7$, *P* <0.01). Shrub biomass was lowest in grasslands (*P*<0.02) and greatest in shrublands (*P* <0.01), however it was not different within shrublands across sites (*P*= 0.6). Shrub biomass overall was higher at WL compared to YHT sites only in mixedwood forest (*P*< 0.02), which comprised only 2% of the vegetative cover extent at both the YHT or WL site and was not present at the SC or TY (Fig, 3-1).

3.3.2 Species composition and richness

Composition of graminoid species based on visual estimates of percent of total biomass varied among communities (Table 3-4). With the exception of grassland, hairy wild rye (*Elymus innovatus*) was the most abundant graminoid species across cover types (ANOVA, $F_{3,86} = 21.3$, *P*=0.04), with no difference in percent biomass between conifer and mixedwood forests (*P*=0.14), and mixedwood and shrubland (*P*=0.06). Rough fescue was the most prominent species in grassland communities across sites, where hairy wild rye dominated in all others (Table 3-4).

Based on percent frequency of occurrence of species within 0.25-m^2 plots, Old man's whiskers (*Geum triflorum)* was the most common forb in grasslands across sites. Yarrow (*Achillea millefolium*) was common in shrubland and mixedwood forest (ANOVA , *df*= 3,87 *F*=7.3, *P*<0.001), and sweet vetch

(*Hedysarum alpinum*) did not differ between types (*P*=0.69).

Although shrub biomass did not vary between study sites (ANOVA, $F_{3,86}$ = 2.3, *P*=0.16) (Fig.3-1), shrub cover did vary among cover types (ANOVA, $F_{3,86}$ = 19, *P* <0.01). Shrubby cinquefoil (*Potentilla fruticosa*) dominated the shrub component of the grassland cover type (Table 3-4). Willow was the most abundant palatable shrub in shrublands (*P*<0.01), and buffalo berry (*Shepherdia canadensis*) was most abundant in mixedwood and coniferous forests (*P*=0.01). Bog birch, which was not considered a major browse species, had a higher proportion of shrub cover at YHT and WL, than SC and TY which instead had a larger willow component to shrub areas. Bog birch and willow dominated shrub areas, while other shrubs were less frequent (Fig. 3-2).

Mean herbaceous species richness among vegetation communities ranged from 4.1 to 9.0 species per $0.25m^2$, in coniferous and grassland plots, respectively. In total, 22 species of graminoids, 84 forbs and 6 shrub species were identified. Although forbs constituted only 10% to 23% of the biomass available within communities, forb richness was consistently greater (2X) than graminoid species richness across vegetation types (Table 4-5). Richness also varied between cover types (ANOVA; $F_{3,86}$ = 14.82, *P*<0.01) within the Red Deer River valley, but not by site. Between cover types Graminoid species richness was greatest in grasslands compared to all other types (*P* <0.01). However shrubland (*P*<0.02) and mixedwood (P<0.04) richness were greater than coniferous, with mixedwood having higher average richness than shrubland (*P*<0.02). Forb richness exhibited similar trends as graminoids, with richness being greater in grasslands, compared to all other habitat types except mixedwood forest ($P<0.01$). Shrubland was different than conifer ($P<0.02$), and mixedwood was also different than coniferous ($P<0.02$). Shrub richness did not vary between vegetation types.

3.3.3 Ecotonal shifts in species composition

A prominent shift in biomass of graminoid species occurred along ecotones (Fig. 3-3, a-c). Most evident was the decrease in rough fescue (n=140, R^2= - 0.3, $P < 0.01$) and increase in hairy wild rye (n=140, R^2= 0.53, $P < 0.01$) with increasing woody canopy cover as grassland transitioned into shrubland and conifer forest. The transition was more abrupt from grassland to conifer or shrublands than from shrublands to conifer communities. Total biomass and rough fescue decreased from early to later seral stages. While, the biomass of hairy wild rye was relatively constant along grassland to shrub transitions (n=220, R^2=0.01, P=0.6) but increased along the transition from grassland to shrubland (n=220, R^2=0.3, $P<0.01$) and shrubland to conifer (n=170, R^2=0.4, $P<0.01$).

Shifts in percent frequency of forbs varied by species (Fig. 3-4, a-c). For example, there was a decline in the frequency of old man's whiskers (*Geum triflorum*) from grassland to shrubland that was related to total shrub cover (n= 220, R^2 = -0.88, P <0.01) (Fig. 3-4b). A similar decline occurred from shrubland to coniferous forest in common yarrow (*Achillea millefolium*) with development of a tree canopy (n= 170, R^2 = -0.88, P<0.01). In contrast, occurrence of sweet vetch (*Hedysarum alpinum*) was highly variable (Fig. 4-4, c).

In terms of available shrub biomass, there was drop in shrubby cinquefoil as grassland shifted into shrubland (n= 220, R=-0.42, P <0.01), and little response in willow biomass at the transition in plots 4 and 5 (Fig. 4-5, b). As a tree canopy developed there was a decrease in shrubby cinquefoil (n=170, R= -0.6, P<0.01) and willow (r=-0.4, P<0.01), in addition to an increase in prominence of buffaloberry (r=0.71, P<0.01 Fig. 3-5, c).

3.2.4 Overstory-understory relationships

Because understory production differed among forest communities (*see* above), I derived understory-overstory relationships by vegetation community. In forested communities, herbaceous understory biomass was negatively related to both tree and shrub overstory, with graminoid biomass decreasing faster an increase in overstory cover in mixedwood forest than in conifer forests (Table 3-5, Fig. 3-6). There was no relationship between shrub cover and tree cover in either forested community (P> 0.29). As there was no difference in understory production among sites, one relationship was developed between shrub cover and understory biomass in shrublands. Shrub cover had a stronger negative relationship on graminoids than forbs (Table 3-5, Fig. 3-7).

3.3.5 Edge effect on richness at grassland ecotones

There was no relationship between graminoid or forb species richness in grassland and distance to woody cover. There was also no relationship between graminoid and forb richness in shrubland across varying distance to coniferous cover. However, there was a marked drop in forb richness across ecotones (Fig. 3-8), as reflected by previous differences in richness between cover types.

3.3.6 Edge effect on graminoid biomass at grassland ecotones

There was no relationship between graminoid biomass in grasslands and distance to woody cover (shrub or coniferous). There was also no relationship between graminoid biomass in shrublands and distance to coniferous cover, except for conifer to grassland transitions at the YHT (Fig 3-9). The relationship between graminoid biomass and distance to coniferous cover in grassland regions of the YHT was best described by a negative quadratic function (Table 3-6).

3.4 Discussion

The objectives of the current study were to assess changes in biomass and composition of herbaceous and woody species within cover types and across ecotones of the upper RDRV. It is important to note that current year annual growth of herbaceous and shrub species in econtone areas at YHT in July 2009 were within the range of annual estimates reported for graminoids (735 to 1018 kg/ha), forbs (250 to 403 kg/ha) and shrubs (41to 395 kg/ha) reported by Spaedtke (2009). Across the broader area of eastern Banff NP and the RDRV, Hebblewhite (2006: Appendix A, Fig. 2.5 a) incorporating data from Sachro (2003) reported generally lower graminoid (364 kg/ha), forb (230 kg/ha), and shrub (137 kg/ha) biomass in open herbaceous sites during 2001-2003, particularly given their measures reflect total standing biomass rather than CAG. These differences most likely reflect drought conditions during these years

Outside of grasslands, both Hebblewhite (2006) and Sachro et al. (2005) reported similar patterns in herbaceous understory biomass among other cover types. As in this study, both researchers reported the lowest total herbaceous biomass occurred in coniferous sites (< 325 kg/ha) with a similar decline in understory as canopy closure increased (Hebblewhite 2006: A2.5a). In contrast to Hebblewhite (2006), I found reduced (~33%) graminoid biomass in shrublands, that was related to the amount of shrub overstory (Fig. 3-2). Differences among studies may be due to the high variation in shrub abundance across sites, or time since encroachment at a given sample location. Even though shrub biomass was highest in both shrublands and mixed forests across studies, comparisons in shrub biomass values among studies is complicated by differences in methodologies.

Differences in soils rather than differences in climate may be responsible for variation in biomass between sites. Production in grasslands at YHT was similar to that at SC and TY located ~10 km up the Red Deer river, but was higher than the nearby WL site. Willoughby (2001) described two rough fescue-dominated community types within the Ya Ha Tinda ranch proper: the Rough fescue-Sedge-Junegrass *(Festuca campestris-Carex filifolia-Koeleria macrantha*) type occurring on steeper, morainal and colluvial slopes such as those found primarily in the WL region. This community type is found on drier microsites than the Rough fescue-Fringed brome-Sedge *(Festuca campestrisa-Bromus ciliatus-Carex spp.)* community type of the YHT where forage production tends to be higher (Willoughby 2001). In addition, the YHT contains a higher proportion of Black Chernozemic soils commonly known to be of high productivity (Krupenikov et al. 2011, see McGillis 1976 in Morgantini 1995). In contrast, soils of the WL are mostly represented by less developed and thin Orthic Regosols.

Results from the combined vegetation studies in the upper RDRV have important implications for changing availability of forages to ungulates. Because grasslands and shrublands provide the most forage for ungulates, long-term encroachment of coniferous forest into grassland since the 1950s indicates reduced carrying capacity for ungulates in the vicinity of these grassland systems. Winter forage loss with woody plant encroachment is exacerbated by a shift away from the predominance of rough fescue, whose winter-hardy structure and high palatability makes it an important forage. Periodic natural or prescribed burning by Parks Canada in the vicinity around the grasslands at SC or TY has not been sufficient to alter the long-term trajectory of tree encroachment based on our photo-interpretation studies (see chapter 2). This is consistent with the analysis of White (2001:67) who reported that fire history patterns around meadows did not support the hypothesis that meadows were specifically a focus for frequent cultural burns. However, short-term improvements in forage availability from prescribed burning by Parks Canada temporarily offsets grassland losses. For example, increased forage production occurred in 2001 (65 kg/ha increase) in the SC grasslands burned in 2000 but the benefit disappeared by 2003 (Eastern Slopes Rangeland Seeds Ltd 2003). A major improvement from burning may have been the removal of standing dead, limiting the shading effect and even providing a nutrient flush (Bork et al. 2002) as indicated by a large increase (27%) in litter on burned sites from 2001 to 2003.

Although total biomass in shrublands did not vary among sites, the palatability of shrub biomass differed greatly. Because bog birch was more abundant at WL and YHT compared to TY and SC where willow was most abundant, shrub encroachment at YHT and WL has provided little new browse while reducing the availability of herbaceous understory. At YHT mowing of shrub stands to enhance winter range started in the mid 1980s (Seel and Wiebe 1989, YHT Management Plan 1987) and continued through the early 2000s (E. Merrill pers. obs.). Initially, mowing likely reduced shrubs including willow. Because of high elk populations (800-2000 during winter) over the past ~15 years (Hebblewhite et al. 2006), it is probable that elk herbivory has altered shrub recovery to at least some degree due to selective grazing, as occurred with aspen (White et al. 2003). Willow is a preferred elk forage particularly in late summer while bog birch is not (Sachro et al. 2005, Hebblewhite 2006, van Beest et al 2010). With the recent (post 2005) reductions in elk densities, there was evidence for the resurgence of willow at YHT. Densities of willow shoots of stems < 0.7 mm diameter were greater than 97 shoots/m^2. Whether these plants escape herbivory under the lower current elk population remains to be seen.

The analysis of trends for herbaceous biomass, richness along ecotones did not indicate any significant ‘edge effect’ within grasslands adjacent to various forms of woody cover across the study sites. Edge effects are characterized by vegetation community shifts, sometimes reflecting shifts in resource availability and often resulting in distinct microclimate gradients near edge. Along an ecotone, the abundance of plants and animals reflects this change in the local abiotic conditions (Fletcher et al. 2007). Edge effects from logging may extend hundreds of meters into forest (Harper et al. 2005) but the influence of the convergence of a woody edge with grassland is less often examined (Beirenger and Zulka 2003). Kiviniem and Erikson (2002) focused on edge to interior relationships in fragmented semi-natural grasslands and found no relationship between size of fragment and species richness. If an edge effect were evident in the current study this would have implications for forage availability within open grassland areas and smaller grassland patches almost entirely classified as ‘edge’. The relative impact of patch size and edge extent on edge effects is ongoing and debated within the literature (Wuyts et al. 2009, Gonzalez et al. 2010).

Table 3-1. Transect types and number sampling within the Red Deer River Valley in summer, 2009. The 4 sites are Ya Ha Tinda (YHT), West Lakes (WL), Tyrrell Flats (TY) and Scotch camp (SC). Total transect across all sites = 87.

Transect type	YHT	WL	TY	SC
Grassland-shrubland	5	5	5	8
Grassland-coniferous forest	5	10	5	6
Shrubland-coniferous forest	5	5	6	7
Grassland-mixedwood forest	5	5	0	0
Shrubland-mixedwood forest	5	0	0	0
Total	25	25	16	21

Table 3-2. Percent of diet of top forbs consumed by the Ya Ha Tinda elk herd based on microhistological analysis of feces collected in summer 2002 (Hebblewhite 2006).

Species	Summer	Winter	Current study
Asteraceae spp.	0.29	0.76	*Achillea millefolium* *Aster alpinus*
Solidago spp.	0.41	0.26	*Solidago multiradiata*
Oxytropis spp.	0.42	0.38	*Oxytropis sericea* *Oxytropis monticola* *Oxytropis cuskii* *Oxytropis splendens*
Potentilla spp.	---	1.58	*Potentilla diversifolia* *Potentilla hookeriana* *Potentilla gracilis* *Potentilla anserina*
Astragalus alpinus	3.95	1.87	*Astragalus alpinus*
Equisetum	1.21	1.70	*Equisetum arvens*
Unknown	3.63	---	
Total	9.91	3.10	

Table 3-3 Mean and standard deviation (SD) of percent ground cover and total biomass by vegetation type along ecotone transects. Statistical differences ($P<0.05$) among cover types within a variable indicated by *a, b, c*…etc.

	Grassland (n=304)			Shrubland (n=238)			Mixedwood (n=80)			Conifer (n=248)		
	Mean		SD	Mean		SD	Mean		STD	Mean		SD
% Cover												
Tree canopy	0.2	*a*	3.4	0.5	*a*	5.5	60.9	*b*	17.7	57.4	*b*	19.0
Bare ground	6.0	*b*	11.9	3.4	*a*	8.7	1.0	*a*	5.5	2.1	*a*	10.1
Rock	1.1		4.3	0.7		4.8	0.0		0.0	0.7		3.4
Woody debris	6.6	*a*	15.4	32.6	*c*	28.6	17.4	*b*	16.8	15.2	*b*	18.3
Litter	28.8		19.2	27.5		17.1	35.1		22.8	43.4		27.8
Moss	13.4	*b*	19.9	7.3	*a*	12.8	3.9	*a*	13.3	21.0	*c*	26.7
Dead grass	6.7	*b*	9.7	3.4	*b*	7.1	0.8	*a*	3.3	0.6	*a*	2.9
Total	62.7		25.4	74.9		22.3	58.2		26.4	83.1		21.3
Biomass (kg/ha)												
Graminoid	880.0	*c*	530.5	593.2	*b*	494.4	735.3	*c*	562.5	164.0	*a*	183.3
Forb	99.5	*bc*	83.5	106.5	*c*	108.0	58.4	*b*	67.6	28.3	*a*	45.4
Shrub	260.7	*a*	96.0	1460.6	*c*	589.0	795.2	*b*	611.9	446.9	*b*	388.9
Total	1240.1		710.0	2160.4		1191.3	1588.9		1241.9	639.1		617.6

Table 3-4. Top 5 most abundant graminoid species based on percent of estimated biomass and the most common forbs based on percent frequency of occurrence along transects in the 4 major vegetation types within the Red Deer River Valley.

Grassland	Mean	SD	Shrubland	Mean	SD	Mixedwood forest	Mean	SD	Coniferous forest	Mean	SD
Graminoids	% biomass			% biomass			% biomass			% biomass	
Festuca campestris	41.2	32.0	*Elymus innovatus*	44.0	36.8	*Elymus innovatus*	55.9	43.0	*Elymus innovatus*	66.2	42.3
Elymus innovatus	21.9	23.8	*Festuca campestris*	23.5	30.2	*Festuca campestris*	10.8	18.8	*Bromus inermis*	8.6	24.4
Carex spp	11.5	20.6	*Carex* spp	10.1	19.3	*Carex spp*	8.9	25.4	*Festuca campestrix*	7.8	19.7
Bromus ciliates	5.4	14.1	*Bromus inermis*	7.8	18.7	*Muhelenbergia richardsonis*	4.2	16.8	*Carex spp*	5.0	18.1
Helictotrichon hookeri	2.9	8.5	*Juncus balticus*	3.7	12.4	*Agropyron trachycaulum*	1.4	6.7	*Muhelenbergia richardsonis*	2.2	12.3

Table 3-5. Top 5 most abundant forbs and shrubs based on percent of estimated biomass and the most common forbs based on percent frequency of occurrence along transects in the 4 major vegetation types within the Red Deer River Valley.

Grassland	Mean % occurence	SD	**Shrubland**	Mean % occurrence	SD	**Mixedwood forest**	Mean % occurence	SD	**Coniferous forest**	Mean % occurence	SD
Forbs											
Geum triflorum	0.5	0.5	*Achillea millefolium*	0.4	0.5	*Achillea millefolium*	0.4	0.5	*Hedysarum alpinum*	0.3	0.5
Astragalus alpinus	0.4	0.5	*Solidago multiradiata*	0.3	0.5	*Galium boreale*	0.4	0.5	*Solidago multiradiata*	0.3	0.4
Galium boreale	0.4	0.5	*Galium boreale*	0.3	0.5	*Vicia americana*	0.3	0.5	*Astragalus alpinus*	0.2	0.4
Anemone multifida	0.4	0.5	*Fragaria viriginiana*	0.3	0.5	*Hedysarum alpinum*	0.3	0.4	*Fragaria virginiana*	0.2	0.4
Solidago multiradiata	0.4	0.5	*Hedysarum alpinum*	0.3	0.5	*Fragaria virginiana*	0.2	0.4	*Achillea millefolium*	0.2	0.4
Shrubs	Mean % biomass	SD		Mean % biomass	SD		Mean % biomass	SD		Mean % biomass	SD
Potentilla fruticosa	0.9	1.0	*Potentilla fruticosa*	0.1	0.9	*Potentilla fruticosa*	0.4	0.4	*Shepherdia canadensis*	0.8	0.9
Salix spp	0.1	0.0	*Salix* spp	0.6	0.03	*Shepherdia canadensis*	0.4	0.4	*Potentilla fruticosa*	0.1	0.09
			Shepherdia canadensis	0.1	0.02	*Populus tremuloides*	0.2	0.1	*Salix* spp	0.1	0.01
			Populus tremuloides	0.1	0.02						
			Rosa acicularis	0.1	0.02						

Table 3-6 Mean and standard deviation (SD) of species richness by vegetation type within the Red Deer River Valley, Alberta. Statistical differences ($P < 0.05$) among grassland (n= 245), shrubland (255), mixedwood (n=75) and coniferous (n= 295) cover types indicated by a, b, c…etc. Note: plot sizes were different for herbaceous species ($0.25 m^2$) and shrubs ($10 m^2$).

	Grassland		Shrub		Mixedwood		Coniferous	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Graminoid	3.04^a	1.18	2.4^b	1.21	1.55^b	0.91	1.43^c	0.81
Forb	5.99^a	3.07	4.59^b	2.75	4.09^a	2.77	2.66^c	2.35
Shrub	1.23	0.56	1.79	0.61	1.66	0.78	1.47	0.83

Table 3-7 AIC best fit model comparison for quadratic, power, and linear regressions, where biomass was regressed with distance from conifer edge within grasslands at the YHT. The parameters (K), log likelihood estimates (LL), AIC value, change in AIC (Δ*i*) and weighted value of each model *(Wi)* is shown. The quadratic relationship is depicted in Fig. 3-9.

Form	Observations	K	LL	AIC	Δ*i*	*Wi*
Quadratic	30	3	-223.2	452.4	0	.95
Power	30	2	-227.6	459.2	6.8	.032
Linear	30	2	-228.2	460.3	7.9	.018

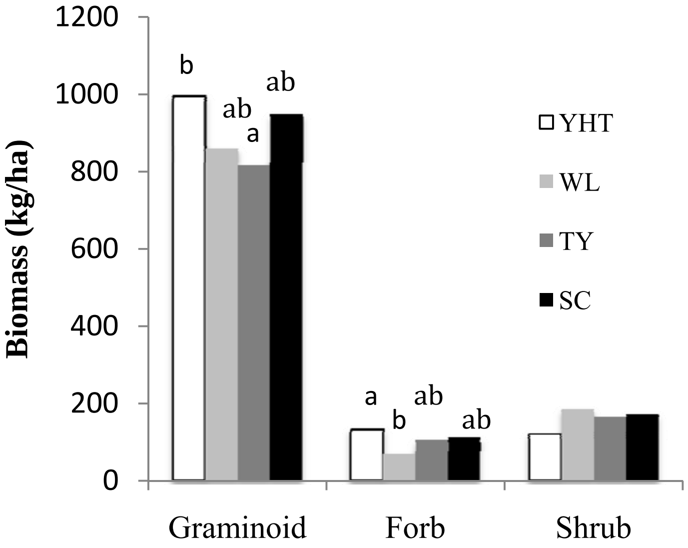


Fig. 3-1 Mean biomass within grassland study sites along the Red Deer River valley, Alberta. Letters indicate significant differences ($p < 0.05$) between sites within graminoid (n=870), forb (n=870), and shrubs (n=435).

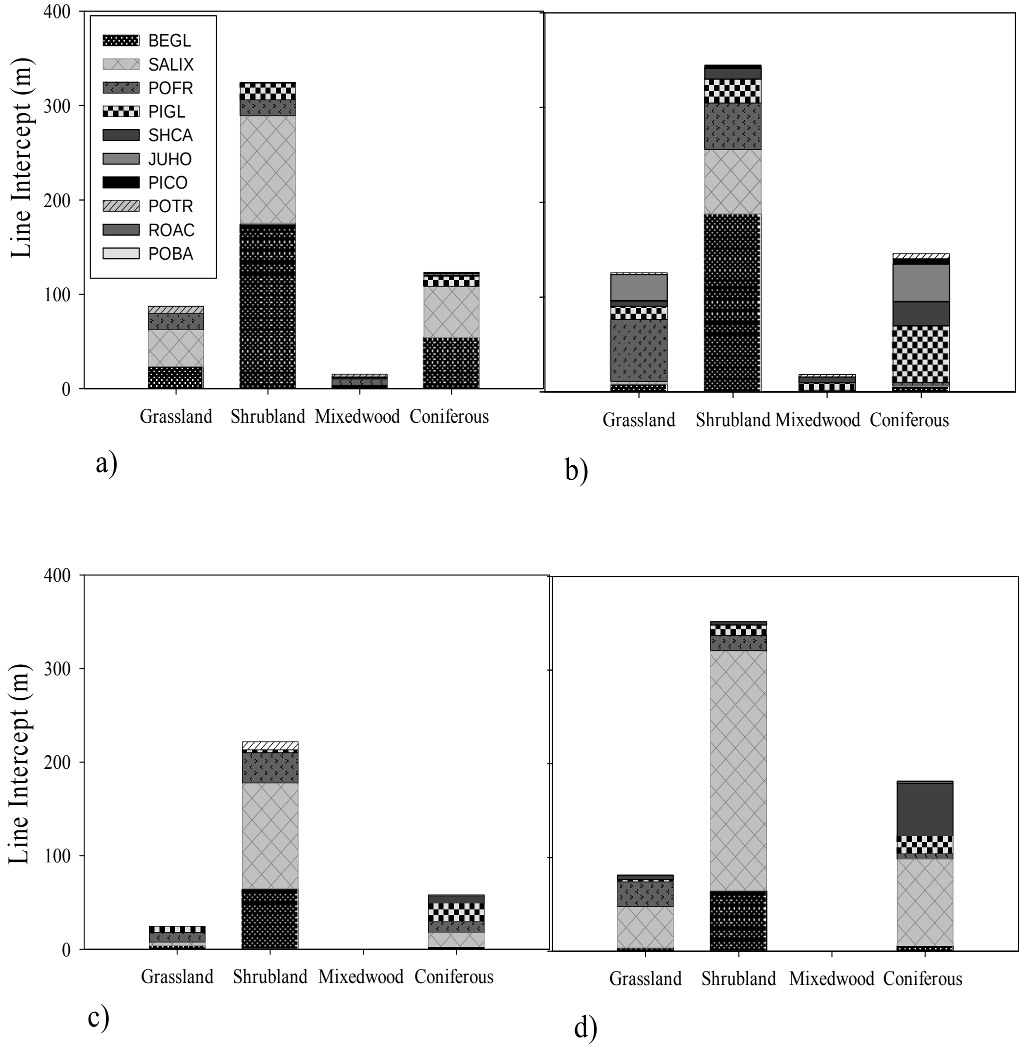


Fig. 3-2 Total shrub canopy cover based on line intersect along 100m transects, within vegetation types at a) Ya Ha Tinda b) West Lakes, c) Tyrrell Creek, and d) Scotch Camp study sites within the upper Red Deer River Valley, Alberta. Canopy cover is comparable within vegetation types. BEGL (*Betula glandulosa*) JUHO (*Juniperus horizontalis*), PICO (*Pinus contorta*) PIGL (*Picea glauca)* POFR (*Potentilla fruticosa*) POTR (*Populus tremuloides*) SHCA (S*hepherdia canadensis*) ROAC (*Rosa acicularis*) SALIX (*Salix spp*) POBA (*Populus balsamifera*).

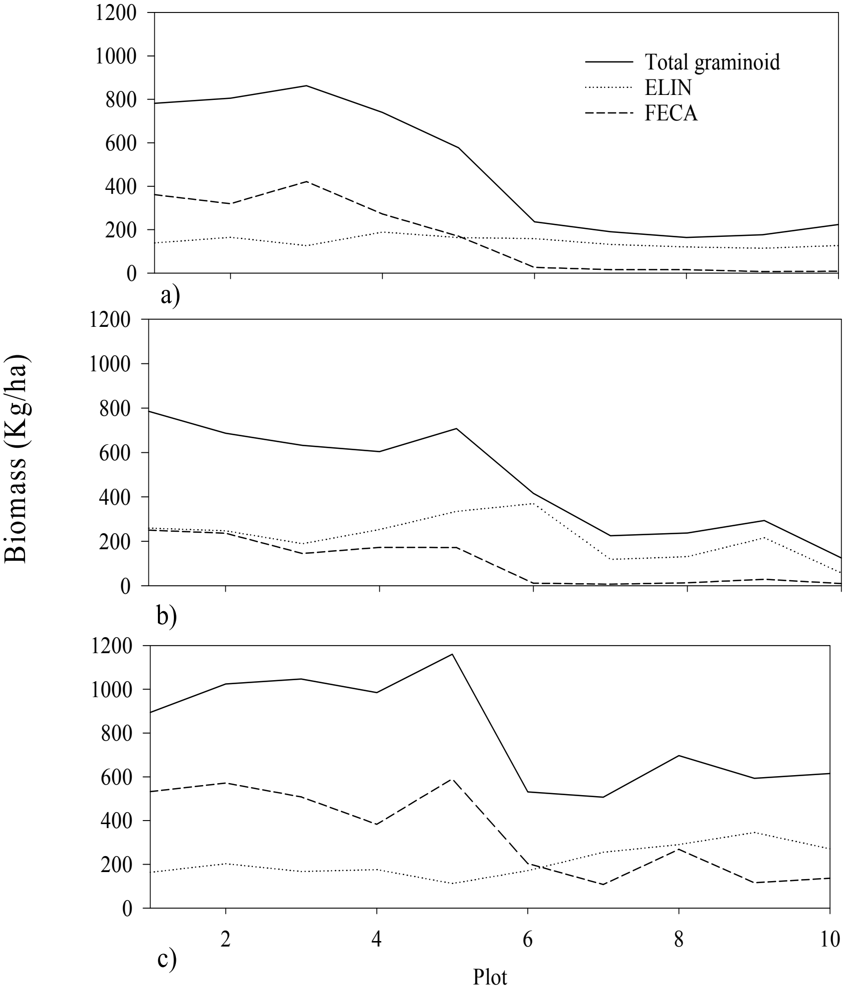


Fig. 3-3 Biomass of two prominent graminoid species, hairy wild rye (*Elymus innovatus*, ELIN) and rough fescue (*Festuca campestris*, FECA) and total graminoid biomass across a) grassland to coniferous forest, b) grassland to shrubland and c) shrubland to coniferous forest ecotones within the Red Deer River Valley, Alberta.

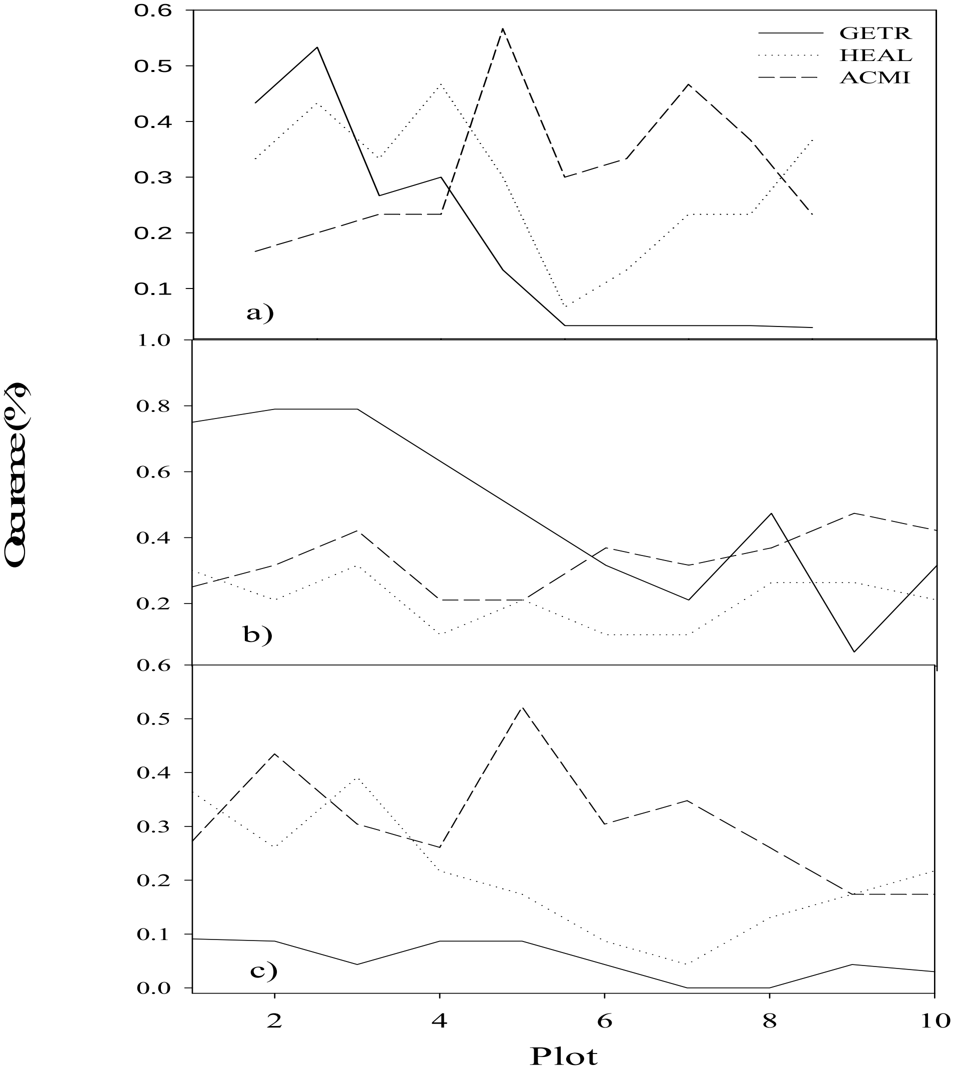


Fig. 3-4 Frequency of occurrence (%) of prominent forb species in 0.25 m^2 plots across a) grassland to coniferous, b) grassland to shrubland and c) shrubland to coniferous ecotones within the Red Deer River Valley, Alberta. HEAL= *Hedysarum alpinum,* ACMI= *Achillea millefolium*, GETR= *Geum triflorum.*

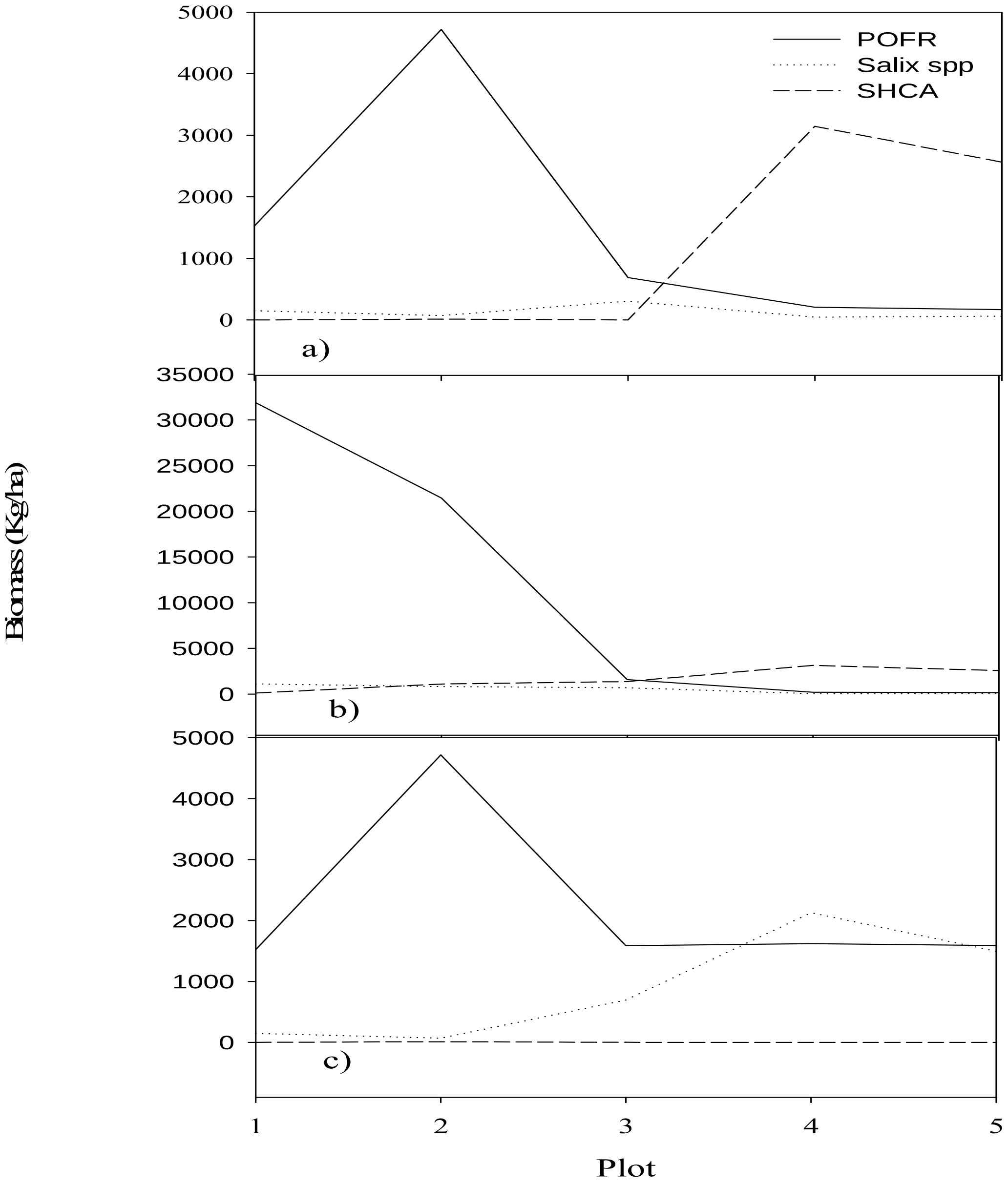


Fig. 3-5 Biomass for the most dominate shrub species (*Potentilla fruticosa* (POFR), *Shepherdia canadensis* (SHCA), *Salix)* within 10m^2 plots, averaged across 4 sites at the Red Deer River valley, AB. Plots spanned 100-m transects along a) grassland to coniferous, b) grassland to shrubland and c) shrubland to coniferous forest ecotones.

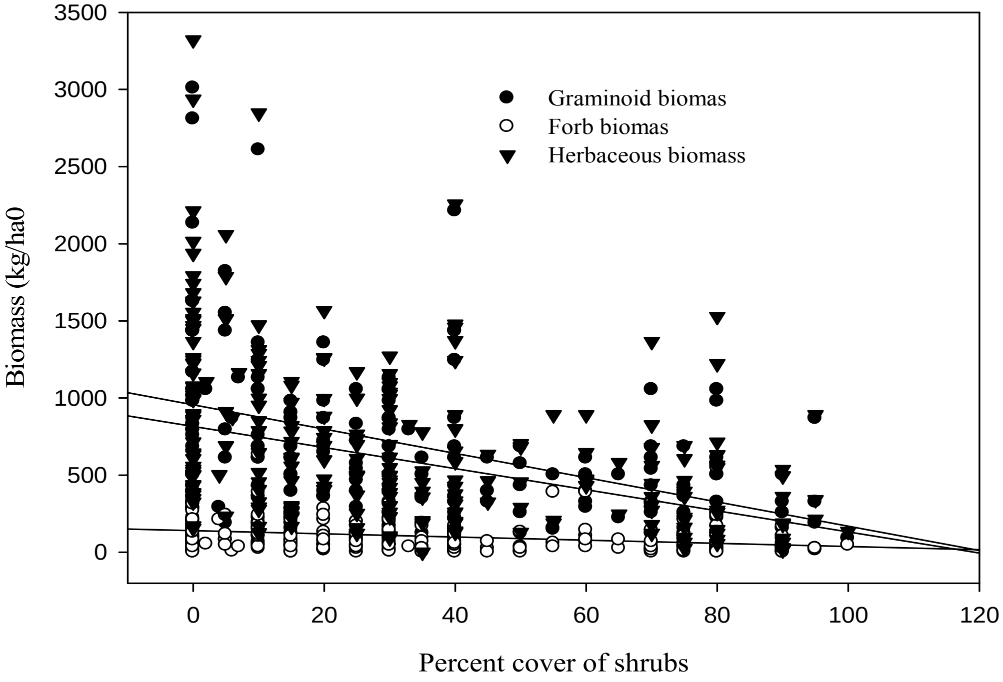


Fig. 3-6 Relationships between overstory shrubs (%) and understory graminiods, forbs and herbaceous biomass in shrubland transition across 4 sites in the RDRV in Alberta in July 2009.

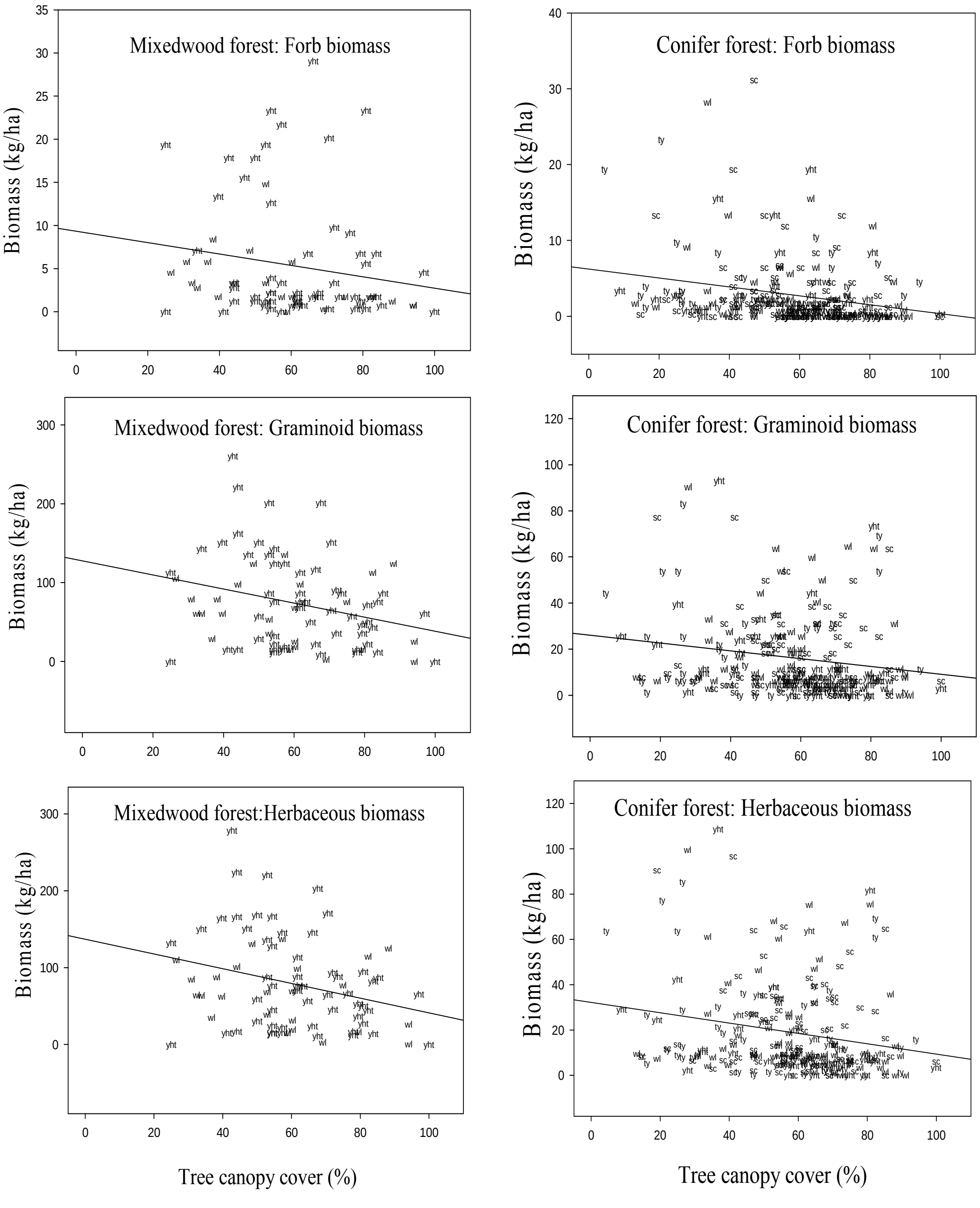


Fig. 3-7. Influence of overstory tree canopy cover on total herbaceous (forb plus graminoid), graminoid, and forb biomass (kg/ha) in the mixedwood and conifer forest type at the YHT, WL, TY and SC study sites. Herbaceous biomass (kg/ha) = 102.5 – 0.3909tree%cover - 60.93 forest type, r^2= 0.39, $P<0.001$, where forest type for mixedwood = 0)

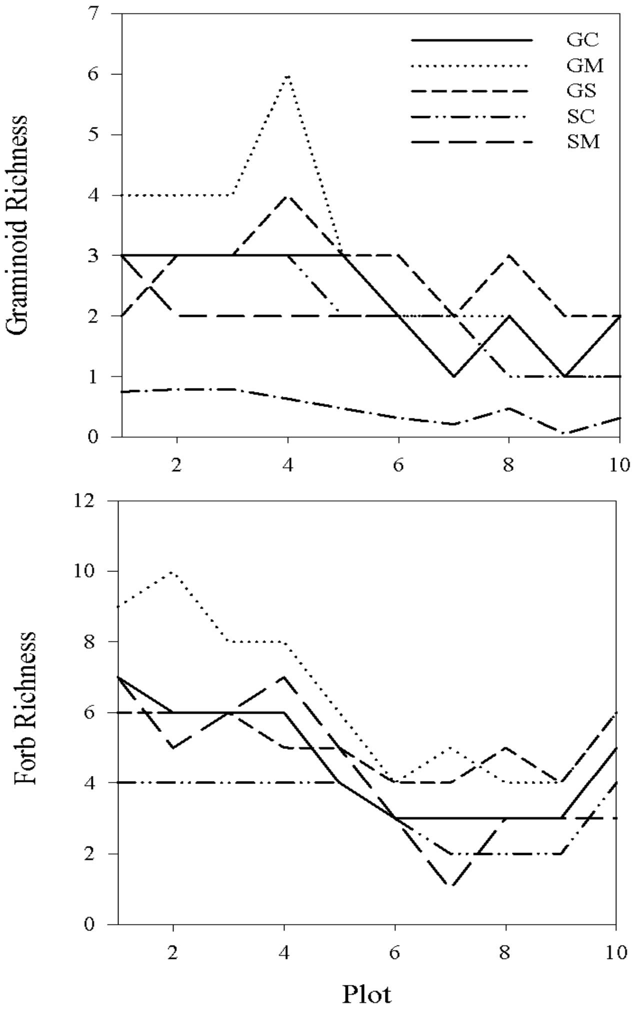


Fig. 3-8 Graminoid and forb richness across ecotones within the upper RDR drainage, Alberta. Several transitions were assessed here, including grass-conifer (GC), grass-mixedwood (GM), grass-shrub (GS), shrub-conifer (SC) and shrub-mixedwood (SM). Although there is an anomalous peak at plot 4 for GM transitions, there seems not to be an edge effect in richness across ecotones.

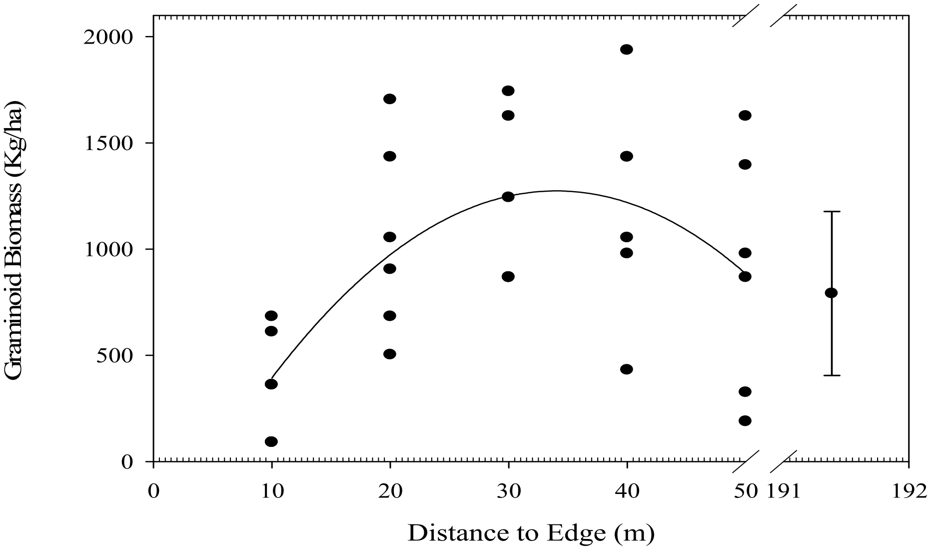


Fig. 3-9 Non-linear regression between distance to coniferous edge into grassland (m), and graminoid biomass (kg/ha) at the YHT study site. Second order (quadratic) polynomial regression proved to be the best fit to the data ($F_{2,27}$= 7.5 r^2= 0.36, *P* <0.01), with [graminoid biomass(kg/ha)] = -492.360 + (103.845 * [distance to edge(m)]) - (1.526 * [distance to edge(m)]^2). Mean graminoid biomass ± SD for regions >100m (average 191.5) away from edge is also denoted.

3.4 Literature Cited

Ahmed, J., Bonham, C.D., Laycock, W.A., 1983. Comparison of techniques used for adjusting biomass estimates by double sampling. Journal of Range Management, 36(2): 217-221

Akaike, H.,1974. A new look at the statistical model identification. IEEE Transactions on Automatic Control, 19 (6): 716–723.

Bieringer, G., Zulka, K.P., 2003. Shading out species richness: Edge effect of a pine plantation on the Orthoptera (Tettigoniidae and Acrididae) assemblage of an adjacent dry grassland. Biodiversity and Conservation, 12 (7): 1481 – 1495

Breshears, D D., Nyhan, J. W., Heil, C. E., Wilcox, B.P. 1998. Effects of woody plants on microclimate in a semiarid woodland; soil temperature and evaporation in canopy and intercanopy patches. International Journal of Plant Science 159 (6): 1010–1017

Bork, E. W., Adams, B.W., Willms, W. D., 2002. Resilience of foothills rough fescue, *Festuca campestris*, rangeland to wildfire. **:** Canadian Field Naturalist, 116: 51-59

Cook, J.G., 2002. Nutrion and Food *in* North American elk ecology and management. Toweill, E.D., Thomas, W.J., (Eds). Washington, Smithsonian Instituion Press. 962 pp.

Darrouzet-Nardi, A., D'Antonio, C. M., Berlow, E. L. Effects of young Artemisia rothrockii shrubs on soil moisture, soil nitrogen cycling, and resident herbs. Journal of Vegetation Science, 19: 23-30

Eastern Slopes Rangeland Seeds (ESRS), Ltd., 2003. Survey data collected and comparative analysis on pre-selected burn sites in Banff Bational Park 2001, 2003. Prepared for: Parks Canada, 24pp.

Eastern Slopes Rangeland Seeds (ESRS), Ltd., 2006. Survey data collected and comparative analysis on pre-selected burn sites in Banff Bational Park 2001, 2003, 2005. Prepared for: Parks Canada, 15pp.

Fletcher, R.J. Jr., Koford R. R., 2003. Spatial responses of Bobolinks (*Dolichonyx oryzivorus)* near different types of edges in northern Iowa. Auk, 120: 799-810.

Fletcher, R.J. Jr., L. Ries, J. Battin, and A. D. Chalfoun. 2007. The role of habitat area and edge in fragmented landscapes: definitively distinct or inevitably intertwined? Canadian Journal of Zooology. 85: 1017–1030

Floyd, D.A., Anderson, J E., 1987. A comparison of three methods for estimating plant cover. The Journal of Ecology, 75: 221-228

Flook, D. R., 1957. Elk – Horse Grazing Situation, Yaha Tinda Ranch - Letter Report

Gonzalez, M., Ladet, S., Deconchat, M., Cabanettes, A., Alard, D. Balent, G., 2010. Relative contribution of edge and interior zones to patch size effect on species richness: An example for woody plants. Forest Ecology and Management, 259: 266-274.

Harper, K.A, MacDonald, S.E., Burton, P.J., Chen, J. Brosofske, K.D., Saunders, S.C., Auskirchen, E.S., Roberts, D., Malanding, J.S., Esseen, P., 2005. Edge influence on forest structure and composition in fragmented landscapes. Conservation Biology, 19(3): 768-782

Hanley, T.A., Rogers, J.J., 1989. Estimating carrying capacity with simultaneous nutritional constraints.United States. Department of. Agriculture. Forest Service. Pacific Northwest Research Station. Research Note PNW-RN-485. 31pp.

Hebblewhite, M., 2006. Linking predation risk and forage to ungulate population dynamics. University of Alberta. Edmonton, Alberta.

Hebblewhite, M., Merrill, E.H., Morgantini, L.E., White, C.A., Allen, J.R., Bruns, E., Thurston, L., Hurd, T.E., 2006. Is the migratory behaviour of montane elk herds in peril? The case of Alberta's Ya Ha Tinda elk herd. Wildlife Society Bulletin, 34: 1280-1295.

Hebblewhite, M., Merrill, E. H., McDermid, G., 2008 A mutli-scale test of the forage maturation hypothesis for a partially migratory montane elk population. Ecological Monographs ,78: 141-166.

Hobbs, R. J., Mooney, H. A., 1986. Community changes following shrub invasion of grassland, Oecologia, 70(4): 508-513.

Hufkens, K., Scheunders, P., Ceulemans, R., 2009. Ecotones in vegetation ecology: methodologies and definitions revisited. Ecological Research, 24: 977–986

Jensen, W., Finck, E., 2004. Edge effects on nesting dickcissels (Spiza americana) in relation to edge type of remnant tallgrass prairie in Kansas. The American midland naturalist, 151:192-199

Kiviniemi, K., Eriksson, O., 2002. Size-related deterioration of semi-natural grassland fragments in Sweden. Diversity and Distributions 8: 21-29

Keigley, R.B. and M. R. Frisina. 1998. Browse evaluation by analysis of growth form. Montana Fish, Wildlife and Parks. Bozeman, MT.

Koper, N., Walker, D. J., Champagne, J., 2009. Nonlinear effects of distance to habitat edge on Sprague's pipits in southern Alberta, Canada. Landscape Ecology, 24: 1287- 1297

Krupenikov, I. A., Boincean, B. P., Dent, D., 2011.The Past, Present and Future of the Chernozem *in* Black Earth: Ecological Principles for Sustainable Agriculture on Chernozem Soils, 131-138

Luczaj, L., Sadowska, B., 1997. Edge effect in different groups of organisms Vascular plant, bryophyte and fungi species richness across a forest grassland border. Folia Geobotanica et Phytotaxonomica, 32(4): 343-353

Lopez-Carrasco, C., Roig, S., 2009.Effect of tree spatial distribution on herbaceous pastures in a Dehesa in Toledo (Spain): dry matter production. Eds. Reine, R., Barrantes, O., Broca, A., Ferrer, C. La multifuncionalidad de los pastos: produccion ganadera sostenible y gestion de los ecosistemas. XLVIII Reunion cientifica de la Sociedad Espanola para el Estudio de los Pastos, Huesca, Spain, 15-18 junio 2009 Pages: 565-571 Published: 2009

Magura, T., Tothmeresz, B., Molnar, T., 2001. Forest edge and diversity: Carabids along forest-grassland transects. Biodiversity and Conservation, 10: 287-300

Marozas, V., 2003. Effect of the lime forest - grassland edge on ground vegetation. Acta Biologica Universitatis Daugavpiliensis, 3: 41-48

McGillis, J.R., 1977. Range management of the Ya Ha Tinda ranch. Prepared for Parks Canada, Candian Wildlife Service, Edmonton. 75pp.

McInenly, L.E., 2003 Seasonal effects of defoliation on montane rough fescue (Festuca campestrisRydb.). MSc thesis. University of Alberta, Edmonton. 142 pp.

Merrill, E., McPhee, H., Robinson, B., 2007. Ya Ha Tinda exclosure study: Plant composition & fescue growth. Progress Report. Parks Canada, 27pgs.

Morgantini, L.E. 1988. Behavioural adaptive strategies of wapiti (Cervus elaphus) in the Canadian Rocky Mountains. PhD thesis, University of Alberta Edmonton, Alberta.

Morgantini, L.E., 1995. The Ya Ha Tinda: An Ecological Overview. Canadian Heritage, Parks Canada,Calgary

Pryke, J. S., Samways, M. J., 2012. Conservation management of complex natural forest and plantation edge effects. Landscape Ecology, 27: 73–85

Qing-chun, W., Xiu-zhen, L., Hong-shi, H., Li-guang, L., Yue-hui, L., Meng, Y., 2007. Edge effects of forest landscape in upper reaches of Minjiang River. Yingyong Shengtai Xuebao,18(10): 2202-2208

Sachro, L.L., Strong, W.L., Gates, C.C., 2005. Prescribed burning effects on summer elk forage availability in the Subalpine zone, Banff National Park. Environmental Management, *77*: 183-193.

Scotter, G. W., 1974. Effect of Picloram on shrubby cinquefoil and forage production at the Ya-Ha-Tinda ranch, Alberta. Canadian Wildlife Service, Edmonton. 18 pp.

Seel, K.E., Weibe, P., 1989. Range improvement project, Ya Ha Tinda, West-Central Alberta. First progress report. Natural Resource Conservation, Canada Parks Service, Environment Canada western regional office, Calgary, Alberta.

Spaedtke, H., 2009. Aversive Conditioning on horseback: A management alternative for grassland systems threatened by sedentary elk populations. M.S. Thesis, University of Alberta.

Strickler, G. S. 1959.Use of the densiometer to estimate density of forest canopy on permanent sample plots. U.S. Forest Services Resource Notes No. 180, 5pp

Trottier, G. C., Milner, B. J., 1978. Herbicied contro of dwarf birch (*Betula glandulosa*) at Ya-Ha-Tinda ranch. CAnadaian Wildlife Service, Edmonton, Alberta. 11 pp.

van Beest, F. M., Mysterud, A., Loe, L. E., Milner, J. M., 2010. Forage quantity, quality and depletion as scaledependent mechanisms driving habitat selection of a large browsing herbivore. Journal of Animal Ecology, 79: 910–922

Vander Haegen W. M., 2007. Fragmentation by agriculture influences reproductive success of birds in a shrub steppe landscape. Ecological Applications, 17: 934-947

Visscher, D. R., Merrill, E. H., Fortin, D., Frair, J. L., 2006. Estimating woody browse availability for ungulates at increasing snow depths. Forest Ecology and Management, 222: 348-354.

Wearne, L. J., Morgan, J. W., 2001. Recent forest encroachment into subalpine grasslands near Mount Hotham, Victoria, Australia. Arctic Antarctic and Alpine Research 33: 369-377

White, C. A., Olmsted, C. E., Kay, C. E., 1998. Aspen, elk, and fire in the Rocky Mountain national parks of North America: Wildlife Society Bulletin, 26(3): 449-492.

White, C.A. 2001. Aspen, elk and fire in the Canadian rocky mountains. PhD thesis, University of Alberta, Edmonton 219 pg.

Widenmaier, K.J., Strong, W.L., 2010. Tree and forst encroachment into fescue grasslands on the Cypress Hills plateau, southeast Alberta, Canada. Forest Ecology and Management 259 (10): 1870 – 1879.

Willoughby, M.G., 2001. Range plant community types and carrying capacity for the montane subregion. Edmonton, Alberta, Alberta Sustainable Resource Development Land and Forest Service. Pub. no.: T/003, ISBN: 0-7785-1792-6

Willms, W. D., Smoliak, S., Bailey, A. W., 1986. Herbage Production following Litter Removal on Alberta Native Grasslands Journal of Range Management 39: 536-540

Willms, W. D. , King, J., Dormaar, J. F. Weathering losses of forage species on the fescue grassland in southwestern Alberta.Canadian Journal of Plant

Science 78: 265–272.

Wuyts. K.; De Schrijver, A. Vermeiren, F. 2009. Gradual forest edges can mitigate edge effects on throughfall deposition if their size and shape are well considered. Forest Ecology and Management, 257(2): 679-687

Zarr, J.H., 1999. Biostatistical analysis. 4th Edition. Prentice Hall, New Jersey.

CHAPTER 4: SYNTHESIS

The occurrence and patterning of vegetation within a landscape is subject to interacting processes. ‘Bottom-up’ effects from soils (Kulminski et al. 2008; Partel et al. 2008) as well as the prevailing macro and microclimate often limit the potential community types that can exist in a given location (Prider and Facelli 2004, Burchuk et al. 2005, Madrigal et al. 2008). Underlying hydrological features (Darrouzet-Nardi et al. 2006), and fire frequency and intensity (Bond and Keeley 2005) also determine where vegetation can establish and persist. ‘Top down’ processes shaping vegetation distributions include plant-animal interactions, involving nitrogen returns from defecation as well as herbivory (Hobbs 1996). In addition, disease can lead to a plant species becoming locally less abundant (Cudmore et al. 2011), and resource extraction such as logging and mining routinely alter vegetation composition as target species are harvested or removed from an area (Huago et al. 2010). One or more of these factors may also combine to structure the dominant vegetation in a landscape. For instance, herbivory and climate shifts have decreased fire frequencies in some areas (Briggs et al. 2002, Johnson and Larsen 1991), warming trends have increased the range of disease vectors (Huago et al.2010), and season and frequency of burning can alter nutrient cycling water infiltration of soils (Manson et al. 2007).

Woody plant encroachment into grasslands is occurring in many landscapes globally, a directional trend that has been observed since data have been available to analyze this change. With the aid of aerial photography, it was determined that grasslands have been lost to heathland, wetland and trees in

Australia since 1936 (McDougall 2003) with 29% of open savanna converted to shrubland since 1947 in areas of Swaziland, Africa (Roques et al. 2001), and 64% of grassland lost to cropland and saline wetland since 1954 in the open plains of West Songen, China (Wang et al. 2007). In the Americas, studies have documented increases in juniper cover in prairie regions since 1956 (Briggs et al. 2002) as well as woody plant encroachment in the montane since 1936 or earlier (Rhemtulla et al. 2002, Coop and Givnish, 2007).

Succession operates through small scales changes in plant community composition, which over time transforms landscape vegetation distribution. Following a change in disturbance regimes, woody species advance into herbaceous communities and species composition of the understory changes. This herbaceous community shift is typically due to an altered microclimate (light, moisture) driven by shading (Peterson and Reich 2008); however, this change in species composition with increasing woody cover can become decoupled across an ecotone according to past land use (Batllori et al. 2009). Although a reduction in frequency or intensity of fire through human intervention is often cited as a primary cause of woody plant encroachment (Watson et al. 2009, Burton et al. 2011, DeSantis et al. 2011), the role of herbivory in altering species interactions and litter accumulation for fire fuel is also significant (van Auken 2009). At the local scale, herbivory can be a sufficient disturbance to structure a herbaceous community experiencing encroachment. Over a complete range of canopy cover, Shrestha and Vetaas (2009) did not find a significant change in the understory richness along the leading edge of encroachment. The gradual change in species composition was attributed to presence of grazing, which determined the actual forest-line despite the abrupt change in light regime. However, many wild ungulates avoid these transitional areas due to a decrease in visibility resulting in an increase in potential risk of predation (citations). In this case even though cover, composition and richness of understory species maybe be negatively affected by woody canopy, ungulates react more strongly to predation risk (Riginos and Grace 2008) effectively removing the potential for grazing effects to occur within the ecotone.

Park managers and ecologists are concerned that the current extent, of the montane ecoregion of BNP is outside the historical range of variability for the area (Achuff et al. 1996). Montane grasslands in the RDRV are an important forage base for many wildlife species including ungulates (Morgantini 1988, Hebblewhite 2008). Long-term fire cycles in montane grasslands average <50 years but since the 1950s fires have been less frequent (White 1985a). While prescribed burning at SC and TY has occurred to maintain grassland communities, fires have not been sufficient to arrest conifer encroachment. A consequence of fire exclusion has been a steady encroachment of predominantly coniferous cover, that reduces both forage quantity and quality for large herbivores except where human manipulations such as mowing and prescribed burning have occurred.

At YHT and WL, it has been less feasible to burn grasslands because of low fuel conditions associated with high elk populations (Hebblewhite et al. 2006) and drought conditions (Environment Canada, 2011) in the recent past. Instead, mechanical mowing has maintained or slightly increased the extent of grasslands at YHT, but not at WL where conifer encroachment has been greatest. Recent burn programs at the YHT and WL have removed tree and shrub cover, and with the recovery of grassland litter, fires have spread into portions of the grasslands as well (Parks Canada, 2009). The Ya Ha Tinda prescribed fire treatments are a collaborative effort between Parks Canada and Alberta Sustainable Resource Development (AB SRD), which began in 2007 with the interagency Hat Mountain Prescribed Fire. The most recent YHT fire encompassed an area of 5030 hectares (ha) on federal lands. The most recent efforts within the Red Deer River drainage have targeted a 4800 ha area surrounding the SC and TY sites within the Park boundaries (Parks Canada, 2011).

While the results of recent burning in the RDR drainage remain to be seen, studies of fire and logging in the Banff NP and east slopes area may provide insight. Following fire in coniferous stands, Hamer (1995) observed productivity boosts in buffalo berry in areas known to be used by grizzly bears; similarly, following willow/ bog birch shrubland burns, fire resulted in > 6X increase in the digging density ratio compared to the pre-fire ratio, likely due to gains in root visibility (Pengelley and Hamer 2006). In terms of ungulate nutrition, burns in Engelmann spruce and lodgepole pine dominated sites more than doubled the forage base from an average graminoid content of 76kg/ha to 481 kg/ha; mixed shrub–herb communities increased from 336–747 kg/ha to 517–1104 kg/ha in response to burning (Sachro et al. 2005). Regardless of an increase in forage, elk selection may be altered by logging treatments and the subsequent effect on predation risk where logging has occurred (Hebblewhite and Merrill 2010). Managers should consider trophic consequences of postfire logging on the interactions among species when gauging possible logging effects where this practice may be viable, such as at the YHT.

Future work should look further into implications of grassland habitat loss for elk and other ungulates in this ecosystem. With a decrease in grassland patch extent there may be a loss in carrying capacity (Whitehead et al. 2011, Belisle 2005), both in winter range and seasonal range used during elk migration along the upper RDRV (Morgantini 1988, Hebblewhite 2006, Spaedtke 2009). Although preliminary assessments of carrying capacity have been undertaken for the YHT/WL (Spaedtke unpublished), these have not included competition with grazers that may be reintroduced into the park, such as bison.

If the aims of prescribed burns are to reduce coniferous forest extent, these targets may be met; however, the resulting landscape may not return to the grassland species composition that was once present. In this study there was a prominent increase in hairy wild rye with a decrease in fescue biomass along grassland ecotones, particularly at coniferous transitions. With mechanical clearing, variation occurred in the level of recovery of montane grassland species four years following pine clearing, based on the density of invasive trees before control; however a typical grassland species assemblage did develop over time (Cuevas and Zalba 2010). In other areas with poor seedbanks, this kind of recovery is not typical and areas are replanted with native graminoids (Page and Bork 2005). Tree and shrub establishment can result in shifts in nitrogen cycling

(Darrouzet-Nardi et al. 2008) and result in soil conditioning (van de Voorde et al. 2011) that does not favour the re-establishment of herbaceous species following woody plant removal. If it is assumed colonization of newly burned coniferous stands in the upper RDR drainage will occur from neighbouring fescue grasslands, and a moderate level of browsing should limit deciduous regrowth. However, rough fescue germinates less frequently under the same conditions than does the aggressive fescue prairie invader which was found in the upper RDRV, smooth brome (*Bromus inermis*) (Grilz et al. 1994). Following fire, ungulate species such as deer preferentially browse fast growing pioneer species that thrive following disturbance (Royo et al. 2010). If a moderate browsing pressure is maintained as evidenced by wildlife enclosures (White et al. 1998), then areas identified as open landscapes in 1952 within the upper RDR drainage will once again be following the recent prescribed burns, and develop a fescue community similar to the neighboring grassland community (Willoughby 2001).

4.1 Literature Cited

Achuff, P.L., I. Pengelly and J. Wierzchowski. 1996. Vegetation: Cumulative effects and ecological futures outlook. Chapter 4 in: Green, J., C. Pacas, L. Cornwell and S. Bayley (eds). Ecological Outlooks Project. A CumulativeEffects Assessement and Futures Outlook of the Banff Bow Valley. Prepared for the Banff Bow Valley Study. Department of Canadian Heritage, Ottawa, ON. 47pp.

Banff-Bow Valley Study. 1996. Banff-Bow Valley: At the crossroads. Summary report of the Banff-Bow Valley Task Force (Robert Page, Suzanne Bayley, J. Douglas Cook, Jeffrey E. Green, and J.R. Brent Ritchie). Prep. For the Honourable Sheila Copps, Minister of Canadian Heritage, Ottawa, ON.

Batllori, E., Blanco-Moreno, J.M., Ninot, J.M., Gutierrez, E., Carrillo, E., 2009. Vegetation patterns at the alpine treeline ecotone: the influence of treecover on abrupt change in species composition of alpine communities. Journal of Vegetation Science, 20: 814–825

Bond, W. J., Keeley, J. E., 2005. Fire as a global ‘herbivore’: the ecology and evolution of flammable ecosystems. Trends in Ecology and Evolution, 20: 387- 394

Briggs J. M. ,Knapp A. K. , Brock B. L. 2002. Expansion of woody plants in tallgrass Prairie: A fifteen-year study of fire and fire- grazing interactions. American Midland Naturalist, 147: 287-294

Burchuk , A.H., Valiente-Banuet, A., Diaz, P. 2005.Effect of shrubs and seasonalvariability of rainfall on the establishment of *Aspidosperma quebracho-blanco* in two edaphically contrasting environments. Austral Ecology, 30: 695–705

Burton, J. A., Hallgren, S. W., Fuhlendorf, S. D., Leslie, D. M, Jr. 2011. Understory response to varying fire frequencies after 20 years of prescribed burning in an upland oak forest. Plant Ecolology, 212:1513–1525

Cook, J.G., 2002. Nutrion and Food *in* North American elk ecology and management. Toweill, E.D., Thomas, W.J., (Eds). Washington, Smithsonian Instituion Press. 962 pp.

Coop, J.D., Givnish, T.J. 2007. Spatial and temporal patterns of recent forest encroachment in montane grasslands of the Valles Caldera, New Mexico, USA. Journal of Biogeography, 34: 914–927

Cowan, I. M., 1943. Report on game conditions in Banff, Jasper and Kootenay National Parks. Candian Wildlife Service, Edmtonon. Unpublished, 72 pp. Ecology, 30: 695–705

Cudmore, T. J. , Bjo¨rklund, N. ,Carroll, A. L. , Lindgren, B. S. 2010. Climate change and range expansion of an aggressive bark beetle: evidence of higher beetle reproduction in naı¨ve host tree populations. Journal of Applied Ecology, 47: 1036–1043

Darrouzet-Nardi, A. , C. M. D’Antonio, T.E. Dawson. 2006. Depth of water acquisition by invading shrubs and resident herbs in a Sierra Nevada meadow. Plant and Soil, 285:31–43

Decesare, N.J., Whittington, J., Hebblewhite, M., Robinson, H., Bradley, M., Neufeld, L., Musiani, M., 2011. The role of translocation in recovery of woodland caribou populations. Conservation Biology, 25(2):365-73

DeSantis, R.D., Hallgren, S. W., Stahle, D. W., 2011. Drought and fire suppression lead to rapid forest composition change in a forest-prairie ecotone. Forest Ecology and Management, 261:1833–1840

Dwyer, M.V., 1969. Ecological characteristics and historical distribution of the family Cervidae in Alberta. M.Sc. Thesis. University of Alberta, Edmotnon. 158 pp.

Eastern Slopes Rangeland Seeds (ESRS), Ltd., 2003. Survey data collected and comparative analysis on pre-selected burn sites in Banff Bational Park 2001, 2003. Prepared for: Parks Canada, 24pp.

Fletcher, R.J. Jr., L. Ries, J. Battin, and A. D. Chalfoun. 2007. The role of habitat area and edge in fragmented landscapes: definitively distinct or inevitably intertwined? Canadian Journal of Zooology. 85: 1017–1030

Flook, D. R., (ed.) .1970. Causes of implications of an observed sex differential in the survival of wapiti. Ottawa, ON, Canada: Canadian Wildlife Service Wildlife Service Report No. 11.

Gunson, J.R., 1992. Wildlife Historical and Present Management of Wolves in Alberta. Wildlife Society Bulletin, 20: 330-339

Gunson, J. R., 1997. Elk management plan for Alberta. Wildlife Management Division, Alberta Environmental Protection, Natural Resource Service, Edmonton, Canada.

Hebblewhite, M., 2006. Linking predation risk and forage to ungulate population dynamics. University of Alberta. Edmonton, Alberta.

Hebblewhite, M., Merrill, E.H., Morgantini, L.E., White, C.A., Allen, J.R., Bruns, E., Thurston, L., Hurd., T.E., 2006. Is the migratory behaviour of montane elk herds in peril? The case of Alberta's Ya Ha Tinda elk herd. Wildlife Society Bulletin 34: 1280-1295.

Hobbs, N. T. 1996. Modification of Ecosystems by Ungulates. The Journal of Wildlife Management, 60:695-713

Holland, W. D., Coen, G.M., Eds. 1983. Ecological (Biophysical) Land Classification Of Banff andJasper National Park s. Volume II : Soil and Vegetation Resources. Alberta Institute of Pedology Publication No. SS-82-4 4

Haugo, R.D., Hall, S.A., E. Gray, Gonzalez, M.P., Bakker, J. D. 2010. Influences of climate, fire, grazing, and logging on woody species composition along an elevation gradient in the eastern Cascades, Washington

Johnson E. A., Larsen, C. P. S. 1991. Climatically Induced Change in Fire Frequency in the Southern Canadian. Ecological Society of America 72: 194-201

Kay, C.E., Patton, B., White, C.A., 1994. Assessment of long-term terrestrial ecosystem states and processes in Banff National Park and the central Canadian Rockies. Banff National Park. Resource Conservation.

Kiviniemi, K., Eriksson, O., 2002. Size-related deterioration of semi-natural grassland fragments in Sweden. Diversity and Distributions 8: 21-29

Knopff, K.H., Knopff, A.A., Kortello, A. Boyce, M.S., 2010. Cougar Kill Rate and Prey Composition in a Multiprey System. Journal of Wildlife Management, 74 (7): 1435-144

Kulmatiski, A., Beard, K. H. , Stevens, J. R., Cobbold S. M., 2008. Plant soil feedbacks: a meta-analytical review. Ecology Letters, 11: 980–992

Lett, M. S., Knapp, A. K., Briggs, J. M., Blair, J. M., 2004. Influence of shrub encroachment on aboveground net primary productivity and carbon and nitrogen pools in a mesic grassland. Canadian Journal of Botany, 82:1363-1370.

Looman, J., 1969. The fescue grassland of western Canada. Vegetation 19: 128-145

Madriga, J., Antonio, J., Rodriguez, G., Julian, R., Puerto, A., Fernandez-Santos, B. 2008. Exploring the influence of shrubs on herbaceous communities in a Mediterranean climatic context of two spatial scales

Manson, A.D., Jewitt, D , Short, A.D. 2004. Effects of season and frequency of burning on soils and landscape functioning in a moist montane grassland. African Journal of Range and Forage Science, 24: 9–18

McGillis, J.R., 1977. Range management of the Ya Ha Tinda ranch. Prepared for Parks Canada, Canadian Wildlife Service, Edmonton. 75pgs

McInenly, L. E. 2003. Seasonal effects of defoliation on montane rough fescue (Festuca campestris Rydb.). University of Alberta, Edmonton, Canada. 142pp.

Millar, W.N. 1916. The big game of the Canadaian Rockies. Conservation of the fish, birds and game. Proceedings of committee meeting, Nov.1 and 2, 1915.

Morgantini, L.E., 1988. Behavioural adaptive strategies of wapiti (Cervus elaphus) in the Canadian Rocky Mountians. PhD thesis, University of Alberta, Edmonton 193 pg.

Morgantini, L.E., 1995. The Ya Ha Tinda: An Ecological Overview. Canadian Heritage, Parks Canada, Calgary

Morgantini, L.E., Hudson, R.J., 1985. Changes in Diets of Wapiti during a Hunting Season. Journal of Range Management, 38: 77-79

Musiani, M., Paquet, P.C., 2004. The practices of wolf persecution, protection, and restoration in Canada and the United States. BioScience, 54: 50-60

Page, H. N., Bork, E. W., 2005. Effect of planting season, bunchgrass species, and neighbor control on the success of transplants for grassland restoration. Restoration ecology, 13:651-658

Parks Canada, 2007. Banff National Park Management Plan. July 2007 ammendment. Environment Canada, Parks Canada. ISBN: 978-0-662-05190-9, Government Catalog No.: R63-225/2007-MRC

Partel, M., Laanisto, L. Wilson, S. 2008. Soil nitrogen and carbon heterogeneity in woodlands and grasslands: Contrasts between temperate and tropical regions. Global Ecology and Biogeography, 17: 18-24

Peterson, D.W., Reich, P.B., 2008. Fire frequency and tree canopy structure influence plant species diversity in a forest-grassland ecotone. Plant Ecology, 194: 5-16.

Prider, J.N., Facelli, J.M. 2004. Interactive effects of drought and shade on three arid zone chenopod shrubs with contrasting distributions in relation to tree canopies. Functional Ecology, 18: 67–76

Rhemtulla, J., Hall, R., Higgs, E., MacDonald, E., 2002. Eighty years of change: vegetation in the montane ecoregion of Jasper National Park, Alberta, Canada. Canadian Journal of Forestry Research 32: 2010–2021

Riginos, C., Grace J.B.,2008. Savanna tree density, herbivores, and the herbaceous community: bottom-up vs. top-down effects. Ecology 89:2228–2238

Rogeau, M. P. 1996. Understanding age-class distributions in the southern Canadian Rockies. M.Sc. Thesis. University of Alberta. Edmonton, Alberta. 139pp.

Rogeau, M. P., Gilbride, D., 1994. Forest stand origin mapping of Banff National Park. Resource Conservation. Banff National Park. Banff, Alberta. 69pp.

Roques, K.G., O'Connor, T.G., Watkinson, A.R. 2001. Dynamics of shrub encroachment in an African savanna: relative influences of fire, herbivory, rainfall and density dependence. Journal of Applied Ecology, 38: 268–280

Sachro, L.L., Strong, W.L., Gates, C.C., 2005. Prescribed burning effects on summer elk forage availability in the Subalpine zone, Banff National Park. Environmental Management *77*, 183-193.

Shrestha, K. B., Vetaas, O. R. 2009. The forest ecotone effect on species richness in an arid trans-Himalayan landscape of Nepal. Folia Geobot, 44: 247–262

Singer, F.J.,1995. Effects of grazing by ungulates on upland bunchgrass communities of the northern winter range of Yellowstone National Park. Northwest Science, 69 (3): 191-203

Skjonsberg, T., 1993. Eastern slopes wildlife study 1984-1987. Final technical report. Banff National Park, 138pp.

Spaedtke, H., 2009. Aversive Conditioning on horseback: A management alternative for grassland systems threatened by sedentary elk populations. M.S. Thesis, University of Alberta.

Soper, J. D., 1941. History, range, and home life of the northern bison. Ecological Monographs, 11: 347-412

Stelfox, J.B., Adamczewski, J.Z., 1993. Hoofed mammals of Alberta. Stelfox, J.B. (Ed). Edmonton: Lone Pine Publishing. 241 pp.

Stelfox, H.A., 1981. Ecological land classification. Red Deer-James. Energy and Natural Resources Report Number: T/11-No. 4. Edmonton, Alberta. 71 pp.

Van Auken, O.W., 2009. Causes and consequences of woody plant encroachment into western North American grasslands. Journal of Environmental Management, 90; 2931–2942

Vandvick, V., 2004. Gap dynamics in perennial subalpine grasslands: trends and processes change during secondary succession, Journal of Ecology 92:86-96

Van Wagner C E., Finney, M. A., Heathcott, M., 2006. Historical Fire Cycles in the Canadian Rocky Mountain Parks. Forest Science, 52: 704-717

Wang, Z., Kaishan, S. Zhang, B. Liu, D., Ren, C., Luo, L. Yang, T. Huang, T., Hub,L. Yang, H. Liu, Z. 2009. Shrinkage and fragmentation of grasslands in the West Songnen Plain, China. Agriculture, Ecosystems and Environment 129: 315–324

Watson, P. J., Bradstock, R.A, Morris, E. C., 2009. Fire frequency influences composition and structure of the shrub layer in an Australian subcoastal temperate grassy woodland. Austral Ecology*,* 34: 218–232.

Webb, R. 1961. Management suggestions for the Ya-Ha-Tinda and Corners elk winter ranges. Alberta Department of Lands and Forests, Fish and Wildlife Division, Edmonton. Unpublished 13 pp.

White, C. A., 1985a. Wildland fires in Banff National Park 1880-1980. Occasional Paper 3. National Parks Branch, Parks Canada, Environment Canada. Ottawa, Ontario, Canada. 106pp.

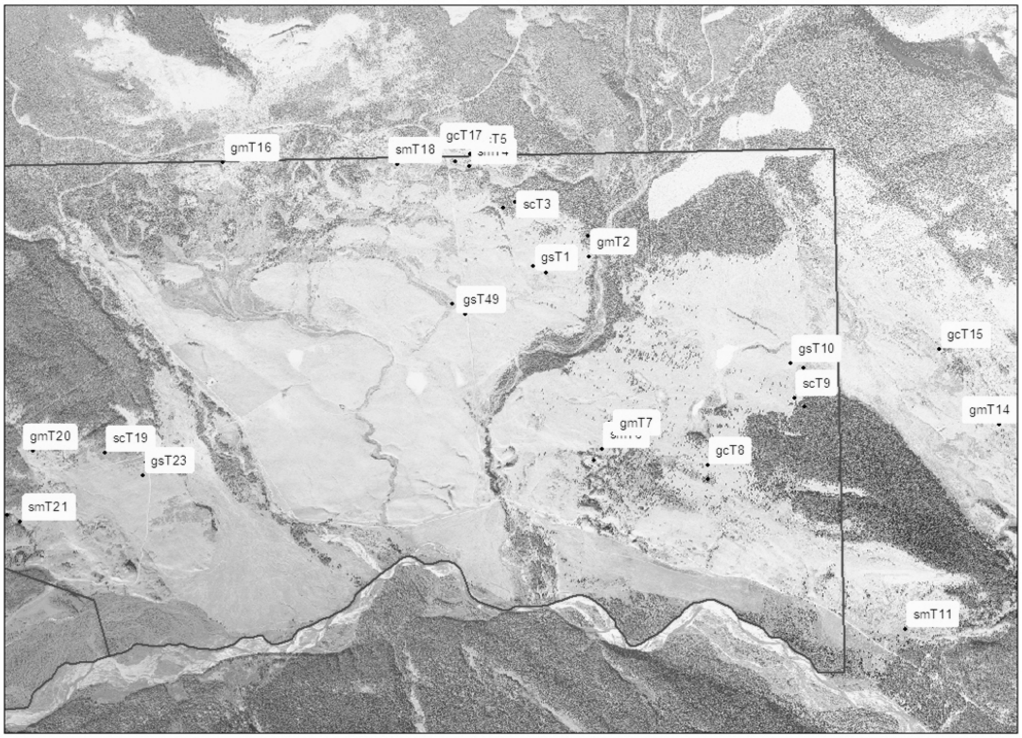
White, C. A. 1985b. Fire and biomass in Banff National Park closed forests. M.Sc. thesis. Colorado State University. Fort Collins, Colorado. 205pp.

White, C.A. 2001. Aspen, elk and fire in the Canadian rocky mountains. PhD thesis, University of Alberta, Edmonton 219 pg.

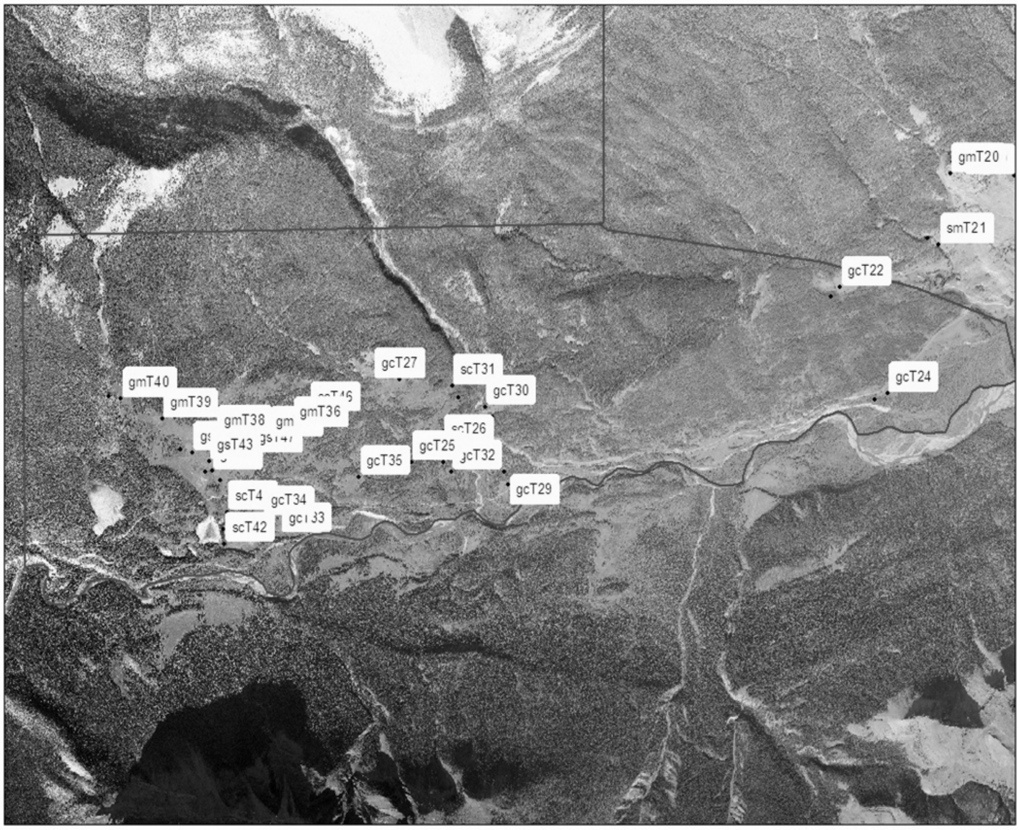
Willoughby, M.G., 2001. Range plant community types and carrying capacity for the montane subregion. Edmonton, Alberta, Alberta Sustainable Resource Development Land and Forest Service. Pub. no.: T/003, ISBN: 0-7785-1792-6

Zarovali, M. P., Yiakoulaki, M. D., and Papanastasis, V. P., 2002. Effects of shrub encroachment on herbage production and nutritive value in semi-arid Mediterranean grasslands. Grass and Forage Science, 62: 355–363

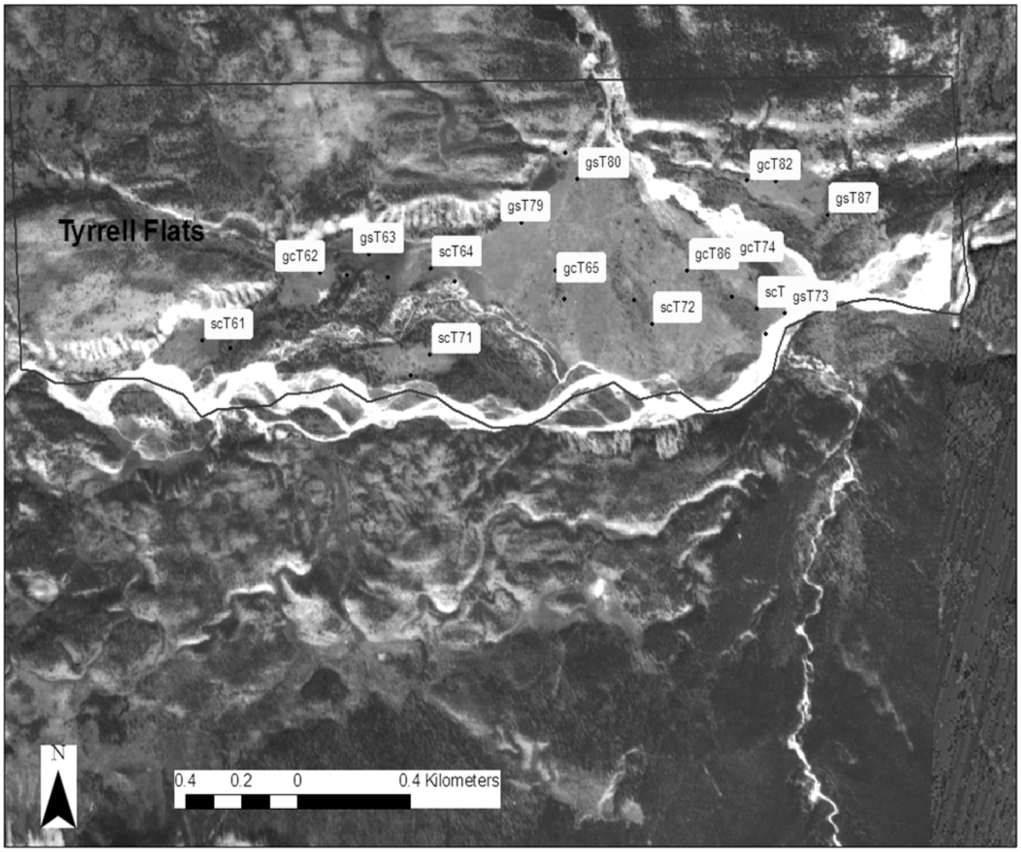
APPENDICES



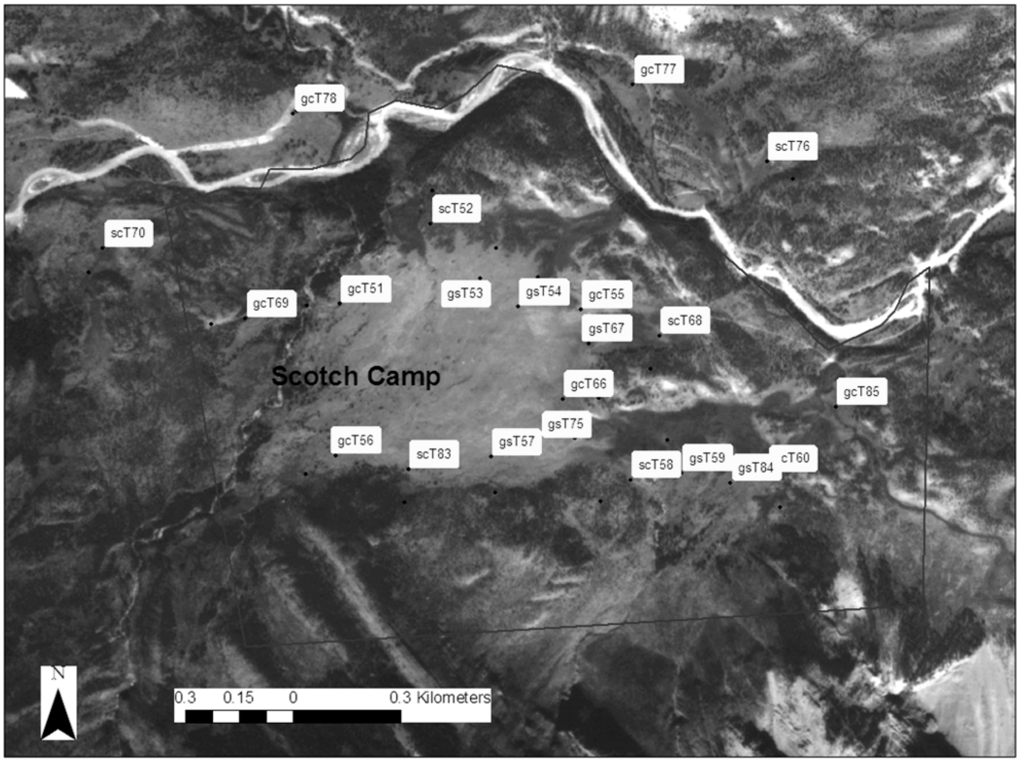
Appendix I-a. Transect locations within the Ya Ha Tinda used to ground truth classified 2003 cover map and collect biomass data.



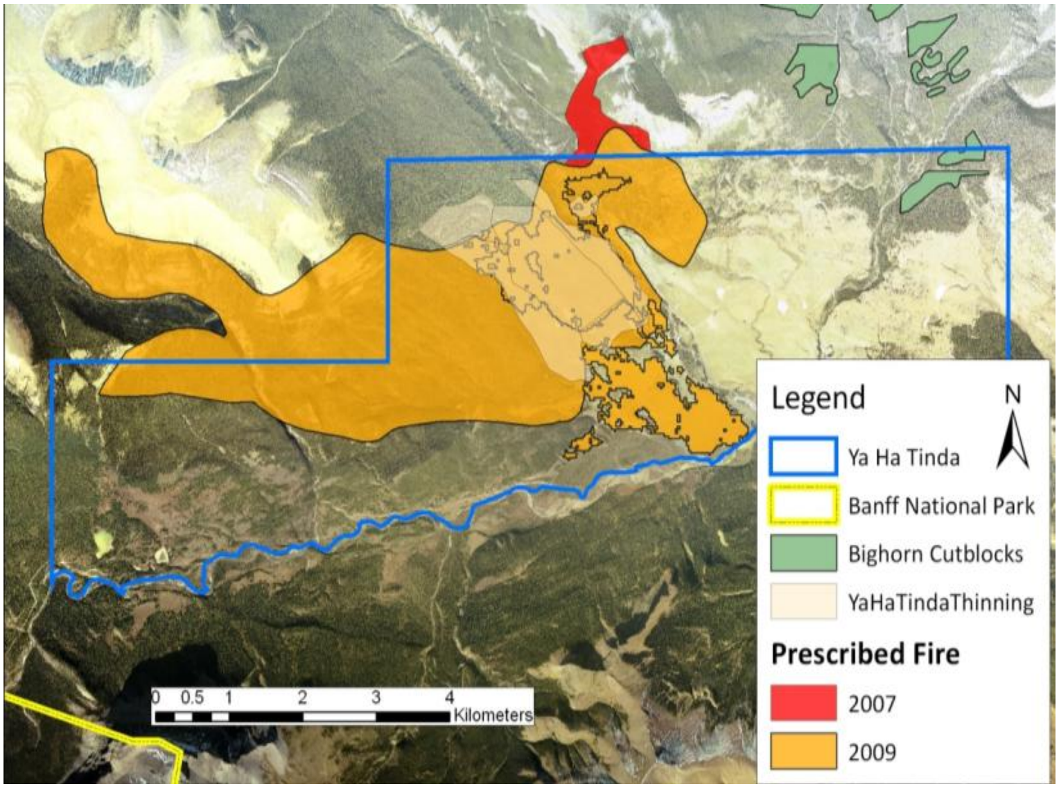
Appendix I-b. Transect locations within West Lakes used to ground truth classified 2003 cover map and collect biomass data.



Appendix I-c. Tyrrell Flats transect locations used to collect biomass and species data.



Appendix I-d. Scotch Camp transect locations used to collect biomass and species data.



Appendix I-e. Prescribed fire at the Ya Ha Tinda Ranch and West Lakes, 2007-2009. Thinned areas were burned following fuel reduction in overlap areas. The Bighorn cutblock treatments (from the 1980's) areshown for reference (Parks Canada progress report, Glines et al. 2011).

Appendix II. Fire occurrence within study sites of the upper Red Deer River Valley, Alberta reconstructed from fire scar and stand origin studies (White et al. 2001, White et al. 1985). Marked (*) years indicated prescribed burns

Scotch Camp	Tyrrell Flats	West Lakes	Ya Ha Tinda
2005*	2005*	2009*	2009*
1999*	1994*	1929	2007*
1994*	1921	1910	1936
1931	1881	1899	1929
1921	1875	1889	1910
1879	1859	1879	1899
1859	1700	1864	1889
1849	1675	1846	1879
1831	1660	1839	1864
1808		1817	1846
1795		1700	1839
1778		1645	1817
1771			1787
1754			1779
1720			1769
1700			1754
1627			1730
			1700

Appendix III. Characteristics of types used to classify aerial photographs to study the change through time of vegetation types in 4 study sites within the upper Red Deer River Valley.

Classification Type	**Description
Grassland	Typically circular; size ranges with few large, many small patches Light tones (varies between images), but among the lightest; only bare ground or rock is lighter. No shadows cast Smooth texture Associated with low elevations
Shrubland	Moderate patch size, typically smaller then coniferous patches Moderate height discernible when next to grassland or forest patches Medium tone, between grassland and coniferous Shadows not distinctive Fine texture; slightly ruffled Associated with low-lying wet areas, also with coniferous forest edge
Mixedwood	Uniform, circular, Patches smaller then shrubland typically 'Salt and pepper' tone due to mix of deciduous (light) and coniferous(dark) species Shading leads to cloudlike texture of canopy Bottom or sides of slopes
Coniferous	Matrix. Edges may be convoluted or gradually blend; especially sharp where logged Often tell height due to shadow Darkest vegetation tones, only water & shadow is darker Slight texture of zig-zag waves where canopy peaks and shadows fall Usually higher in elevation, bordering grasslands
***Logged**	Formerly coniferous in a previous time period, now bare (see road & bare ground) Only logged patch in 1982, in YHT and present in subsequent years
***Pond (water)**	Circular . Small (>8 ha each) Darkest tones Smooth texture in grassland areas (typically)
***River (water)**	Thin corridors running west to east and north to south Sinuous, braided pattern Wider then roads Darkest tones Associated with bare ground (gravel) from former channels
***Building**	Rectangular. Very small (>.35 ha each) Tone is very light (similar to bare) Shadows not visible Associated with each other and pasture

***Road & bare ground**	Bare patches smaller then shrubland patches, usually longer then wide Roads long and narrow; narrower and straighter then rivers Lightest tones Roads along valley bottoms highest peaks and area of sudden elevation change are bare
***Pasture**	Areas reserved for horse grazing and recently made inaccessible to elk/deer/wild ungulates with fencing Stable over time; appear the same as grassland except tone similar to shrublands , possibly because of increased watering or species monoculture Identified from literature, seeded with brome grasses

* grouped into 'Other' category for spatial extent summary

** General principles of air photo interpretation: Shape, pattern, size, tone, shadow, texture, and association.

Appendix IV. Reference points for comparison with 2003 photo set vegetation classification. Reference points were obtained from start and end points along 100-m transect spanning several ecotone types. Ecotones either began or ended in the following types depending on letter order, respectively: (G)rassland, (s)hrubland, (m)ixedwood, or (c)oniferous. Transects were also labeled in order sampled, eg) T1, T2, etc.

Transect	Start UTM x	Start UTM y	End UTM x	End UTM y
gsT1	601009	5734371	601098	5734324
gmT2	601392	5734444	601388	5734597
scT3	600881	5734844	600795	5734800
smT4	600563	5735112	600467	5735143
gcT5	600566	5735202	600583	5735296
smT6	601485	5733022	601433	5732943
gmT7	601556	5733111	601534	5733218
gcT8	602223	5732906	602223	5732802
scT9	602824	5733402	602895	5733334
gsT10	602797	5733657	602888	5733619
smT11	603595	5731699	603666	5731762
gsT12	604688	5731985	604588	5731996
scT13	605090	5731998	605184	5732021
gmT14	604253	5733205	604335	5733257
gcT15	603836	5733758	603920	5733812
gmT16	598848	5735138	598908	5735209
gcT17	600349	5735225	600275	5735285
smT18	600064	5735121	600058	5735220
scT19	598024	5732994	598051	5733095
gmT20	597525	5733008	597539	5733091
smT21	597436	5732489	597346	5732538
gcT22	596668	5732175	596596	5732108
gsT23	598292	5732832	598308	5732927
gcT24	597034	5731402	596939	5731358
gcT25	593326	5730899	593232	5730895
scT26	593573	5731120	593657	5731166
gcT27	593234	5731503	593237	5731616
gcT29	594081	5730732	594051	5730830
gcT30	593897	5731302	593954	5731227
scT31	593642	5731456	593690	5731372
gcT32	593633	5730829	593576	5730900
gcT33	592321	5730611	592425	5730611

gcT34	592169	5730498	592067	5730493
gcT35	592917	5730790	593009	5730818
gmT36	592397	5731145	592393	5731245
gmT37	592209	5731076	592190	5731181
gmT38	591800	5731085	591845	5731178
gmT39	591383	5731213	591480	5731229
gmT40	591062	5731363	590964	5731375
scT41	591890	5730535	591908	5730436
scT42	591867	5730301	591858	5730404
gsT43	591748	5730908	591722	5730829
gsT44	591614	5730969	591528	5730991
gsT45	591800	5731085	591744	5731172
scT46	592534	5731257	592556	5731346
gsT47	592075	5730960	591980	5730963
gsT48	591769	5730831	591838	5730767
gsT49	600535	5734018	600443	5734092
scT50	600234	5735167	600142	5735181

Appendix V. Change in spatial extent of vegetation types (ha) in 4 study sites within the Red Deer River Valley from 1952- 1992 for SC and TY, and 1952-2003 for WL and YHT.

Area of Vegetation Types (ha)

Site	Class	1952	1952 to 1962	1962	1962 to 1972	1972	1972 to 1982	1982	1982 to 1992	1992	1992 to 2003	2003	Total	
SC	Grassland	87.2	-14.9	72.3	-10.1	62.2	-3.5	58.6	-1.3	57.3	*		-29.8	(-34.2%)
	Shrubland	37.2	0.8	38.0	-7.2	30.8	-0.8	30.0	-1.7	28.2			-9.0	(-24.2%)
	Coniferous	119.0	6.7	125.7	24.3	149.9	2.5	152.4	2.8	155.2			36.2	(30.4%)
TY	Grassland	136.8	-24.7	112.1	-17.6	94.5	-10.0	84.5	-15.3	69.2			-67.7	(-49.4%)
	Shrubland	14.9	-3.5	11.4	1.9	13.2	0.7	13.9	0.0	13.9			-1.0	(-6.8%)
	Coniferous	142.5	17.0	159.4	16.0	175.4	4.1	179.5	12.8	192.3			49.9	(35.0%)
WL	Grassland	662.7	-43.4	619.3	-144.0	475.3	-179.3	296.0	-18.2	277.7	-103.3	174.4	-488.3	(-73.7%)
	Shrubland	33.8	-1.6	32.2	11.5	43.7	90.9	134.6	-70.0	64.7	31.7	96.3	62.5	(184.9%)
	Mixedwood	11.3	3.1	14.4	7.0	21.5	-0.8	20.7	-5.5	15.1	6.7	21.8	10.5	(31.8%)
	Coniferous	694.2	29.2	723.4	123.6	847.0	90.1	937.1	106.3	1043.4	75.4	1118.7	349.2	(61.1%)
YHT	Grassland	1073.9	-7.4	1066.6	-48.5	1018.1	-39.0	979.0	46.6	1025.7	54.5	1080.2	6.2	(0.6%)
	Shrubland	400.6	-31.4	369.2	3.2	372.4	15.9	388.2	-71.0	317.2	-101.5	215.7	-185.0	(-46.2%)
	Mixedwood	60.8	2.4	63.2	1.3	64.5	0.2	64.6	16.8	81.4	-28.1	53.3	-7.5	(-12.3%)
	Coniferous	1011.9	17.2	1029.1	43.6	1072.7	25.8	1098.5	-3.8	1094.6	96.7	1191.4	179.5	(17.7%)

* Images to derive land cover change from 1992-2003 not available for SC and TY

Appendix VI-a. Transition matrix showing change (%) in land cover type between 1952 and 2003 for the Ya Ha Tinda, Alberta

	2003									
1952	Grassland	Shrubland	Mixedwood	Coniferous	Logged	Pond	River	Building	Road/ Bare	Pasture
Grassland	40.7	15.2	2.3	38.5	0	0.3	2.1	0.002	0.4	0.5
Shrubland	47.1	30.2	2.9	18.6	0	0.15	0.55	0.02	0.3	0.14
Mixedwood	24.1	10.1	33.5	30.7	0.04	0	0.3	0.05		0
Coniferous	2.4	1.1	0.7	92.0	2.1	0	0.6	0	1.2	0.002
Logged	0	0	0	0	0	0	0	0	0	0
Pond	36.6	0.06	0	0.003	0	63.2	0	0	0	0
River	19.0	4.0	0.9	40.0	0	0	31.7	0	4.4	0
Building	0	0	0	0	0	0	0	0	0	0
Road/Bare	47.0	5.4	0.02	37.3	0	0	0	0	10.3	0
Pasture	36.0	0.5	6.3	0.5	0	0	0	0.3	3.6	53.9

Appendix VI-b. Transition matrix showing change (%) in land cover type between 1952 and 2003 for the West Lakes, Alberta.

	2003						
1952	Grass-land	Shrub-land	Mixed-wood	Coniferous	Pond	River	Road & Bare
Grassland	23.1	9.7	1.4	63.5	0.05	0.02	1.9
Shrubland	14.6	25.4	0.95	57.2	0.12	0	1.7
Mixedwood	17.8	17.8	28.8	52.0	0	0	0
Coniferous	1.5	1.7	1.23	94.3	0.2	0.07	1.04
Pond	4.23	3.2	1.06	23.5	68.0	0	0
River	8.2	24.4	37.5	4.2	0	0	25.7
Road/Bare	11.4	14.8	0	22.3	0	13.3	38.1

*logged areas and buildings not present

Appendix VI-c. Transition matrix showing change (%) in land cover type between 1952 and 2003 for the Tyrrell flats, Alberta.

	2003				
1952	Grassland	Shrubland	Coniferous	River	Road/Bare
Grassland	47.9	1.8	33.6	0.4	13.8
Shrubland	3.5	68.8	19.4	3.8	4.5
Coniferous	1.6	0.8	93.4	0.8	3.3
River	2.2	0.1	20.0	72.7	5.1
Road/Bare	2.1	0	19.0	8.5	70.4

*logged areas, buildings, and mixedwood not present, ponds exhibited 0 change

Appendix VI-d. Transition matrix showing change (%) in landcover type between 1952 and 2003 for Scotch Camp, Alberta.

	2003				
1952	Grassland	Shrubland	Coniferous	River	Road/Bare
Grassland	58.7	10.4	29.2	0.1	1.5
Shrubland	9.4	42.1	46.7	1.1	0.7
Coniferous	0.22	2.2	92.6	0.7	2.2
River	0	13.7	35.4	50.9	0
Road/Bare	0	0	0	0	0

*logged areas, buildings, mixedwood and ponds were not present

Appendix VII. Model selection and comparison for estimating dry biomass from visual estimates. Candidate models were fitted using least squares analysis and include the covariates of visual biomass (visual), percent tree canopy cover (canopy), habitat type(shrub or conifer), and percent cover of litter as annual accumulated plant debry (lit). Models follow either the multiple linear regression (L) function of y= $a+bx_1+cx_2$….or power regression (P) of y=ax^b…and are shown with their corresponding rank, log-likelihood(LLi), Akaike information criterion (AIC), change in Akaike (ΔAICi), and Akaike weight(wi).

Class	Form	Rank	Variables	r^2	LL	AIC	ΔI	wi
Graminoid	L	1	Log(visual) + (conifer)	0.88	-81.88	169.75	0.00	0.99
	L	2	Log(visual)	0.87	-88.28	180.57	10.82	0.00
	L	3	null	0.00	-260.90	523.81	354.05	0.00
	P	4	x*(visual^lit) + (conifer)+x	0.90	-419.64	847.28	677.53	0.00
Forb	L	1	Log (visual) + (shrub)	0.84	-131.97	269.94	0.00	0.90
	L	2	Log (visual) + (canopy)	0.83	-134.45	274.89	4.95	0.08
	L	3	Log (visual)	0.83	-136.43	276.86	6.92	0.03
	P	4	x* (visual)	0.92	-276.46	556.92	286.98	0.00
	L	5	null	0.00	-278.06	558.12	288.18	0.00

Appendix VIII. Regression equations (Visscher et al 2006) used to derive biomass for browse species within the Red Deer River Valley. The equation for <7mm BD salix was derived from willow collected in the study area

Form	Species	Equation	R^2
E	*Potentilla fruticosa*	y=11.156*(x)^(0.155*x)	0.83
L	*Salix* spp	y=2.981*(x)+1.075	0.73
P	*Salix* spp <7mm BD	y=0.0295*(x)^2.3291	0.72
E	*Shepherdia canadensis*	y=12.238*(x)^(0.129*x)	0.86
E	*Rosa acicularis*	y=12.668*(x)^(0.089*x)	0.8
E	*populus tremuloides*	y=12.668*(x)^(0.089*x)	0.89
E	*Ribes spp*	y=12.668*(x)^(0.089*x)	0.51

E= exponential, P= power, L= linear form for the regression equation

BD= basal diameter

y= g/twig, where a twig is <7mm in diameter

x= basal diameter

Appendix IX. Calibration linear regression from Spaedtke (2009), derived from subset of July 2009 data (n= 37). The equation ($F_{1,35}$=77, P<0.01) states that [dry biomass (kg/ha)] = -244.012 + (119.880 * drop disc height).