UNIVERSITY OF ALBERTA

Prescribed fire and vegetation dynamics in northern boreal sedge-grass meadows of the Slave River Lowlands, Northwest Territories

BY

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ABSTRACT

Prescribed fire has been used since 1992 in sedge-grass meadows of the Slave River Lowlands (SRL), Northwest Territories, for the purpose of renewing and maintaining bison (*Bison bison*) habitat. A study of the meadows in the Hook Lake area of the SRL was conducted in the summer of 1998 to test for an effect of burn regime (unburned, burned once, burned three times) on herbaceous plant community composition and willow (*Salix* spp.) shrub vigor. In addition, image analysis of time-sequence aerial photographs was used to detect changes in shrub and tree cover in the meadows over a 24 year period.

Plant species abundance, plant litter biomass, soil pH, and depth of the organic (OH) soil horizon were measured from 300 1 m^2 quadrats, nested within 30 plots. Canonical Correspondence Analysis (CCA) was used to relate burn regime and microsite environmental conditions to plant community composition. Individual willow shrubs within the plots were assigned a shrub vigor score from I (dead) to IV (flourishing) and a G statistic was used to test for a relationship between burn regime and willow shrub vigor.

Ordination plots resulting from the CCA indicate that multiple prescribed burns influence plant community composition, and that less palatable species, *Carex aeana* and *Juncus balticus*, were favored strongly by a three spring burn regime. Burning had a negative effect on the survival of shrubs. Approximately 24% of sampled willow shrubs on meadows that had been burned three times were dead, compared to 12% on single burn meadows, and 0.08% on unburned meadows. Only slight differences were present in the relative proportion of shrubs in vigor classes II – IV between meadows burned once or three times.

Image-to-image registration of aerial photographs indicate moderate but variable shrub establishment in the Hook Lake area meadows between 1973 and 1997. Qualitative interpretation of the digital images suggests variable patterns of establishment, including the frontal advance of large patches, establishment along abandoned stream channels, and establishment of many "satellite" shrubs within meadows. Recommendations for the future management of northern boreal meadows are presented.

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CHAPTER 1

General Introduction

1.1 Background Information

Grassland communities are among the most threatened ecosystems in North America and globally (Sampson and Knopf, 1996; Frank *et al.*, 1998). In the above context grassland communities refer to a variety of herb-dominated communities including prairies, meadows, and savannas. Shrub expansion within grasslands is a major concern for both the maintenance of productive rangelands and for the conservation of natural areas and wildlife habitat (Yool *et al.*, 1997; Boren *et al.*, 1997). While the phenomenon of shrub encroachment may be common, the processes involved in shrub establishment and expansion within grasslands tend to be multiple and dynamic (Skarpe, 1992). Factors implicated in the balance of herbaceous to woody species can range from microsite conditions such as soil nutrient status (Skarpe, 1992), soil moisture (Williams and Hobbs, 1989), competition, grazing (McPherson, 1997) and seed dispersal by animals (Cook *et al.*, 1996), to larger scale influences such as fire (Howe, 1995), flooding, and climatic patterns (Timoney *et al.*, 1997).

A growing understanding of the variety of factors influencing shrub establishment and expansion in grassland systems has challenged traditional succession theory and has led to a major shift in the tenants of rangeland ecology. For instance, rangeland management has historically been based on Clements' theory of succession (Clements, 1916) that proposes a single, final vegetation state called the climax, which in the absence of disturbance, marks the endpoint of succession. Other vegetation states called "seres" progress along a single linear gradient toward the climax, unless drought, grazing or other disturbances such as fire, occur which shift the balance in favor of earlier seres. The appeal of this theory has resulted in long-held beliefs on how to manage rangeland systems to maintain a particular vegetation state. Over the past two decades experience in rangeland management has failed to support Clements' theory, reducing the number of grazers or applying fire does not always cause a direct return to a former vegetation state. Unfortunately, management practices have been slow to respond to the growing body of evidence that suggests more dynamic successional processes (Walker, 1993).

An alternative model of rangeland dynamics that proposes both multiple alternative states and transitions between the states (hence called the state-and-transition model), considers the combination and interaction of factors influencing vegetation structure and emphasizes timing and flexibility in management (Westoby *et al.*, 1989). In this model, transitions between states can be triggered by natural events or management actions or a combination of both. They can be rapid or slow and it is this catalogue of observed transitions and resulting states that represents the behavior of the system and that guides management actions. An example of shrub invasion into a grassland that conforms to the state-and-transition model is provided by Brown and Carter (1998). They describe how a rapid invasion of the shrub, *Acacia nilotica* into an Australian grassland, was triggered by a change from sheep to cattle grazers, and they heed the model's warning that transitions between states may be irreversible. Simply put, few generalizations can be made and a thorough understanding of the ecology of a particular grassland system is necessary for effective management.

The pattern of vegetation succession can also reveal information about the processes occurring. Species that serve as establishment centers (nuclei) by facilitating the establishment of other plants may be revealed by the structure and spatial pattern of plants in the landscape (Yarranton and Morrision, 1974). Whether nucleation is the predominant mechanism for shrub and tree establishment or another pattern prevails, such as frontal advance of large patches or establishment along waterways, can have important implications for controlling or manipulating vegetation succession.

Despite the range of processes that can influence vegetation structure in grasslands, the general management approach of prescribed fire is commonly employed to control shrub encroachment in a variety of grassland systems. Prescribed fire has been used to reduce shrub encroachment in systems as diverse as North American tall-grass prairie (Johnson and Knapp, 1995), subtropical savanna parkland, (Changxiang *et al.*, 1997), tropical wetlands (Cook *et al.*, 1996) and wetland prairies (Pendergrass *et al.*, 1998). The effect of fire on vegetation is highly variable. Controlled experiments have demonstrated the strong influence that a multitude of factors, *e.g.* season of burn, fire frequency and intensity, topography, fuel types, fuel load, size of area burned, fire history, and animal ecology, can have on post-fire vegetation (Lewis and Ferguson, 1988). Prescribed fire can be a cost-effective tool for grassland management, but its success depends largely on a thorough understanding of the ecology of the area being burned, a well-planned fire prescription, and on clearly defined management objectives.

In order to improve our ecological understanding of an area to be able to predict vegetation responses to fire, it is often necessary to proceed based on the information available and to conduct management actions as an experiment in progress. This process of learning by doing, is one of the basic principles of adaptive management (Walters and Holling, 1990). A prescribed fire project currently underway in the northern meadows of the Slave River Lowlands (SRL), Northwest Territories, provides such an opportunity.

The ten year Hook Lake Prescribed Fire Project was initiated in 1992 and involves springtime burning of sedge and grass meadows in the Hook Lake area of the SRL. The motivation for the project was partly a response to the diminishing bison (*Bison bison*) population in the Slave River Lowlands, which decreased from an estimated 1904 animals in the early 1970's (Van Camp and Calef, 1987) to ca. 600 animals in the 1990's (GNWT files, Ft. Smith). Maintaining productive bison habitat through semi-annual burning of the sedge meadows is one component of the larger goal of rejuvenating the bison population. The aim of the prescribed fire project is "to reverse the loss of meadow habitat caused by forest succession and possibly by a reduction in grazing related to lower numbers of bison" (Hook Lake Prescribed Burn Project, GNWT). Commensurate with the objective of enhancing bison habitat is improved productivity of important bison forage species such as *Carex atherodes* and *Calamagrostis* spp.. The aim of the present study is to determine the effect of the spring fires on both willow (*Salix* spp.) shrub vigor and on the composition of herbaceous plant communities, as well as to determine the extent and general pattern of shrub establishment in the Hook Lake area over the past couple of decades.

Implementing the prescribed fire project to decrease willow cover, presumes that willow cover within the meadows has increased in recent years. Change detection analysis of remotely sensed data provides a tool for assessing large scale changes in the landscape. Image analysis of time-sequence remote imagery is increasingly being used to examine changes in vegetation cover patterns through time (*e.g.* Mast *et al.*, 1997; Kitzberger and Veblen, 1999; Rutchey and Vilchek, 1999; Brown and Arbogast, 1999). Black and white aerial photographs of the Hook Lake area in 1973 (scale of 1:24,000) and 1996 (scale of 1:20,000) were used in this study to examine woody plant establishment and expansion within meadows. A better understanding of the rates, patterns and extent of landscape change will help to guide management.

1.2 Research Objectives

The objectives of the present study are 1) to determine whether plant community composition and *Salix* spp. shrub vigor differ between unburned meadows and meadows burned once or three times over a four year period (1992-1995), and 2) to determine the extent and general pattern of shrub establishment in the Hook Lake area meadows over a twenty-four year time period using change detection analysis and historic aerial photographs.

1.3 Description of Study Site

The Slave River Lowlands are located in southern part of the Northwest Territories, south of Great Slave Lake and bounded by the Talston River on the east and the Little Buffalo River on the west. The meadows in the study area lie north and slightly east of Hook Lake (Figure 1.1). The SRL area evolved out of the former basin of glacial Lake McConnell and the open meadows are believed to have originated and persisted as meadows following the drainage of post-glacial lakes (Raup, 1935). The general character of the land is flat, with many sloughs and abandoned stream channels. A history of periodic flooding has resulted in deep layers of alluvium overlying the glacial tills (Rowe, 1972).

1.3.1 Soils

The soils of the SRL are generally poorly drained. Day (1972) described nine soil series in the SRL, the most common Great groups being Humic Gleysols and Gleysols. The soils in the meadows near Hook Lake are Rego Humic Gleysols, belonging to the Grand Detour Complex (Day, 1972). These soils are characterized by a thick (*ca.* 15 cm) surface horizon of peat or muck, with a black clayey mineral horizon (Ah) over grayish calcareous clayey sediment, that is mottled at depth and underlain by fine sands (Day, 1972). Historically, permafrost was present in patches in open meadows of the nearby Wood Buffalo National Park (Raup, 1935) and may occur in the SRL meadows.

1.3.2 Vegetation

Meadow, shrubland, and forest, are the main vegetation types that occur in the SRL. The most commonly occurring trees in the low-lying forest bordering the river include white spruce (*Picea glauca*), balsam poplar (*Populus balsamifera*), and trembling aspen (*P. tremuloides*), while the shrublands are dominated by willows (*Salix* spp.) (Rowe, 1972). Both wet and dry meadows in the Hook Lake area of the SRL have been described by Reynolds *et al.* (1978). Sedges (*Carex atherodes, C. rostrata, C. aquatilis*) and grasses (*Calamagrostis* spp., *Scholochloa festucacaea, Glycerica* spp.) are dominant in wet meadows. While grasses (*Calamagrostis inexpansa*), rushes (*Juncus balticus*), and forbs (*Fragaria virginiana, Potentilla* spp., *Vicia americana, Solidago canadensis, Geum aleppicum, Thalictrum venulosum*, and *Rumex occidentalis*) are the dominant herbaceous vegetation of dry meadows. *Juncus balticus* and *Calamagrostis inexpansa* have been noted to cover large areas of semi-saline land in the nearby dry meadows of Wood Buffalo National Park (WBNP) (Raup, 1935). The small shrub *Ribes oxycanthoides*, which has been prominent in WBNP for many decades (Raup, 1935), is also relatively abundant in the dry meadows in the Hook Lake area.

The succession of woody plants into open meadow areas in the nearby WBNP has been documented throughout the past several decades. Raup (1935) observed that "Willow and poplar or spruce clumps seem to be encroaching slowly upon the open spaces, and appear to have done so within the memory of men". Raup (1935), described the first association of woody plants dominated by *Salix planifolia* and *S. myrtillifolia*, with *S. bebbiana* also invading the openings. Associated secondary species included: *Calamagrostis canadensis, alnus incana, Potentilla norvegica, Geum macrophyllum, Castillega raupii, Achillea millefolium, Agrostis scabra*, and *Erigeron acris*. Using historical maps and aerial photographs of the Peace Point area in WBNP, Jeffrey (1961), documented a prairie to forest succession over a 31 year period. The dominant species in the new shrub layer were *Salix bebbiana* and *Symphoricarpos occidentalis*. Declines in meadow habitat in WBNP continue to be reported and prescribed fire is often cited as a potential solution (Schwarz and Wein, 1997).

1.4 Research approach

1.4.1 Field sampling

A vegetation survey of dry meadows in the Hook Lake area was conducted in July 1998. Thirty sample plots were randomly selected from recent aerial photographs with the criterion that the site be a moderately dry meadow. Five plots were established on each of six prairies, two of which were unburned, two were burned in 1995, and two were burned in 1992, 1993, and 1995. Dry meadows were selected because wet sedge dominated areas are generally less combustible and the effects of fire would be expected to be less apparent on wet meadows (Jalkotzy and Van Camp, 1977). In a study of woody plant communities along a wet to dry gradient, and their response to prescribed fire, Liu *et al.* (1997), found that short term results were generally restricted to the drier plant communities.

Herbaceous vegetation and microsite environmental variables (soil pH, organic horizon soil depth, plant litter biomass), were collected from 300 $1m^2$ quadrats within the thirty plots. Cluster analysis and Canonical Correspondence Analysis were used to determine whether fire regime and the above site variables influenced the herbaceous plant community composition of these dry meadows. *Salix* spp. shrubs sampled in each of the thirty plots were compared and a G-statistic was used to test for a relationship between *Salix* spp. shrub vigor and burn regime.

1.4.2 Image analysis change detection

The second objective of this project, to determine the extent and general pattern of shrub establishment in the Hook Lake area meadows, was approached using digital change detection techniques on black and white panchromatic aerial photographs taken 24 years apart. This technique is based on differences in the spectral quality of a pixel at two different dates. Overlain images of the same location at two different dates revealed vegetation cover changes which were quantified and patterns of woody plant establishment were qualitatively interpreted from the change images.

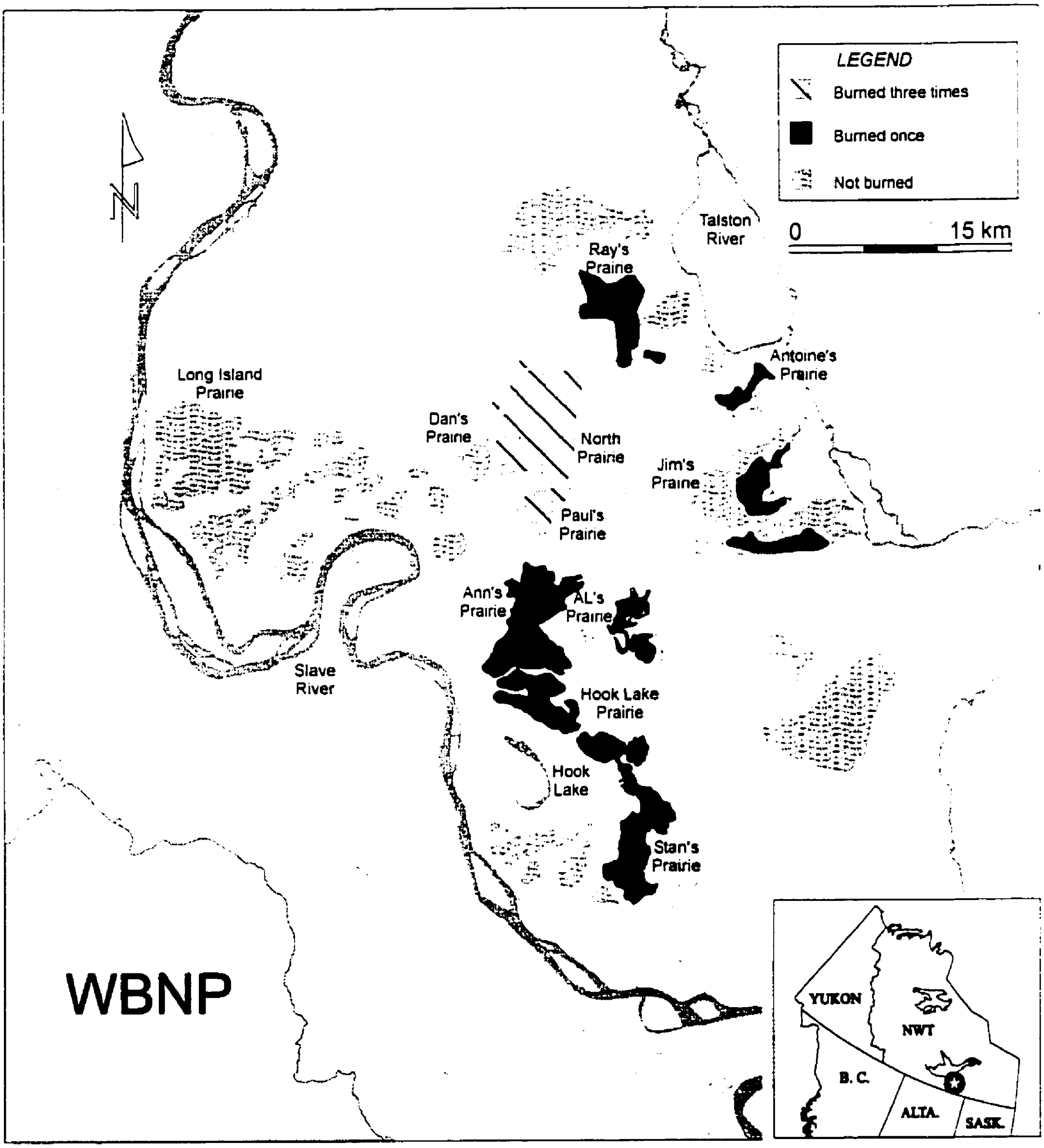

Figure 1.1 Map of the Hook Lake area meadows in the Slave River Lowlands, Northwest Territories. Meadows burned three times were burned in the spring of 1992, 1993, and 1995. Meadows burned once were burned in the spring of 1995.
(Map prepared by T. Ellsworth, GNWT)

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CHAPTER 2

Community composition and *Salix* spp. shrub vigor in burned and unburned northern boreal sedge - grass meadows

2.1 Introduction

2.1.1 Vegetation of northern boreal sedge - grass meadows

The sedge - grass meadows of the Slave River Lowlands (SRL) represent a northern outlier of the Great Interior Plains biome. The soils underlying meadows of the SRL have been described by Day (1972) as predominantly Humic Gleysols and Gleysols that developed under poorly drained conditions. Meadows of the SRL have been characterized as either wet or dry and their vegetation has been described by Reynolds *et al.* (1978). Wet meadows are dominated by sedges (*Carex atherodes, C. rostrata, C. aquatilis*) and grasses (*Calamagrostis* spp., *Scholochloa festucacaea, Glyceria* spp.). The vegetation of dry meadows is predominantly grasses (*Calamagrostis inexpansa*), rushes (*Juncus balticus*), and forbs (*e.g. Fragaria virginiana, Potentilla spp., Vicia americana, Solidago canadensis, Geum aleppicum, Thalictrum venulosum, and Rumex occidentalis*). Sedges (*Carex aenea, Carex foenea, Carex atherodes*) are present but are less abundant on dry meadows compared to wet meadows. Dominant shrubs on both wet and dry meadows belong to the genus *Salix*. In a *ca.* 7500ha study area in the Hook Lake area of the SRL, Reynolds *et al.* (1978) determined that 23% of the meadowland was wet meadow and 77% was dry meadow. *Carex atherodes* and *Calamagrostis* spp. account for

49% and 18% of wet meadow and 1% and 64% of dry meadow (Reynolds and Peden, 1987).

Vegetation of the SRL meadows is similar in composition to many of the semi-open prairies in Wood Buffalo National Park (WBNP), described by Raup (1935). The wetland communities in the Peace-Athabasca Delta (PAD), have in turn been shown to be similar in species composition and structure to marsh and meadow ecosystems in the Prairie provinces and north-central United States (Fuller and LaRoi, 1971). However, remnant grasslands in WBNP, described by Redmann and Schwarz (1986), are not similar in plant community composition to dry meadows in the SRL. The distinction between grasslands and meadows requires clarification because grasslands and meadows may not respond in the same way to prescribed burning. Timoney (1999), describes in detail the differences between "prairie", "dry grassland", freshwater and saline "marshes" and "meadows". He suggests that prairies and dry grasslands are generally well drained, upland, short-, mixed- or tall-grass communities, typically associated with Chernozemic soils, while meadows and marshes tend to be imperfectly to poorly-drained, azonal, communities associated with Gleysolic, Solonetzic, and Organic soils. This distinction is important because the majority of prescribed fire research in North America has focussed on grasslands, yet because grasslands and northern meadows differ, as described above, the response of vegetation to prescribed fires in northern meadows will not necessarily resemble that of more southern grasslands.

2.1.2 Prescribed fire in the SRL

Shrub and tree density has increased in the SRL meadows over the past few decades (see Chapter 3). Both long-term climate trends and flooding frequency have been suggested as important factors contributing to increased woody plant density in northern meadows and grasslands (Timoney *et al.*, 1996). It has also been speculated that the reduction of fire in the past few decades has lead to accumulations of plant litter and increased shrub establishment, predominantly by *Salix* spp., in SRL meadows (Jalkotzy and Van Camp, 1977). Maintaining open meadow habitat with lush sedge and grass growth in these meadows is desired by resource managers and local communities who wish to maintain viable bison populations in the SRL. The primary goal of a prescribed fire project in the Hook Lake area is to rejuvenate bison habitat, which is believed to be deteriorating in quality through natural successional processes from sedge/grass dominated meadows to shrub dominated meadows.

A reduction or end to fires being lit by Aboriginal People may have also influenced vegetation dynamics in northern meadows over the past few decades. Reports of Aboriginal People in northern Alberta burning wet meadows to improve muskrat habitat by removing accumulations of plant litter, suggest the burning continued into the early 1950's (Lewis and Ferguson, 1988). No specific evidence indicates burning of SRL meadows by Aboriginal People. Some meadows in the Hook Lake bison range were historically important muskrat trapping areas, which is reflected in the traditional names Big Rat Lake and Little Rat Lake (also called North Meadow). Prescribed fire has frequently been suggested as a tool to renew habitat in northern meadows, through the removal of plant litter and a reduction in woody plant density (Jalkotzy and Van Camp, 1977; Reynolds and Peden, 1985; Chowns *et al.*, 1997; Shwarz and Wein, 1997). However, little empirical information exists on the specific responses of northern meadow plant communities to prescribed fire.

2.1.3 Variable responses to prescribed fire

Plant species and community-level responses to prescribed fire exhibit a high degree of variability. Some of this variability in response to prescribed fire may be attributed to the season when a fire occurs. In tallgrass prairie, season (summer vs. spring burns), has been shown to influence strongly the relative abundance of plant species (Howe, 1994). Fire frequency has been shown to influence species diversity and relative abundance of individual species in wetland communities in tallgrass prairie (Johnson and Knapp, 1994). Other sources of variability might be: the life-history characteristics of species (Johnson and Knapp, 1995), fire interactions with physical environmental factors (Gibson and Hulbert (1987), age and size of plants (Wright *et al.*, 1976), as well as fire intensity, pre-burn vegetation composition, and site history (Whelan, 1995). In particular, fire intensity may interact strongly with the spatial heterogeneity of a landscape to increase the variability of plant response across the burned area.

In order to evaluate the effects of prescribed burning in the SRL, it is necessary to determine species and community-level responses to different burning regimes. The present study takes advantage of a ten year prescribed fire project in the Hook Lake region of the Slave River Lowlands. Two objectives of this prescribed burning project are to increase graminoid biomass by reducing dead plant litter build-up and to decrease total woody plant cover (Hook Lake Prescribed Burn Project, GNWT). Knowledge of the specific effects of prescribed fire on individual species, plant communities and shrub vigor will help managers to adjust the fire prescription to achieve desired results in the SRL, as well as contribute to our understanding of fire effects in northern boreal meadows.

2.1.4 Research Objective

My research objective is to determine whether vascular plant community composition and vigor of willow shrubs (Salix spp.) differs between unburned meadows and meadows burned once or three times between 1992 and 1995.

2.2 Methods

2.2.1 Field sampling

I sampled vegetation in July 1998 on six separate meadows in the Hook Lake area of the SRL. Two of the meadows had not been burned since 1992, another two meadows were burned once in May 1995, and the remaining two meadows were burned in May 1992, 1993, and 1995. I established five large plots (1000 m^2) on each meadow for a total of 30 sample plots. To select plot locations I used a stratified random approach using random numbers and a grid overlain on aerial photographs taken in 1997. I accepted a random plot location if it met the following criteria: moderately dry meadow, approximate shrub cover range 20-40%, evidence of burning at the base of shrubs (burned prairies), little obvious disturbance (e.g. bison wallows, recent grazing, and all-terrain vehicle tracks were avoided but occasionally a small portion of a plot had one of the above disturbance types).

Ten, 1 m^2 quadrats were placed within each of the thirty plots, for a total of 300 quadrats, in a similar manner to the Modified Whittaker plot sampling method described by Stohlgren *et al.* (1998). A random number was drawn to determine the distance to the next quadrat along each side of the plot (Figure 2.1). Within each 1 m^2 quadrat, herbaceous plant species abundance was estimated, using cover percentage charts from the Ontario Institute of Pedology (1985). Soil pH, at 10-15 cm depth and thickness of the OH horizon were also recorded. All dead plant litter within a 25 cm x 25 cm representative area within the quadrat was collected, bagged, and dried at 70°C for 72 hours. Upon removal from the oven, the dry weight of plant litter biomass was recorded. Within each 20 m x 50 m plot, all *Salix* spp. shrubs greater than 0.5 m height were identified to species, measured (maximum height and width), and assigned a "vigor" class on a scale of 1 - 4. A set of reference photographs aided classification of the shrubs according to the following criteria: I, standing dead shrub, II, resprouting at base of shrub, III, regrowth to approximately 80 % of its former height, and IV, robust (Figure 2.2).

2.2.2 Analytical methods-species composition

Canonical Correspondence Analysis (CCA) is a multivariate technique that directly relates community variation to environmental variation (ter Braak, 1986). A CCA was performed without data transformation or down-weighting of rare species, using the plant species abundance and environmental data collected in 300 quadrats at the $1m^2$ scale and using CANOCO version 3.12 (ter Braak, 1990). A second CCA was performed to test if the sample location explained some of the variation in the data by including the meadow from which the sample was taken, as a nominal environmental variable. A Monte Carlo permutation test (99 permutations) was used to test for statistical significance of the CCA. The ordination results were plotted using the weighted averages of the species and sample scores. Biplot scores of quantitative environmental variables and centroids of nominal environmental variables were included on the ordination plots.

Eight plant communities were identified by an agglomerative hierarchical cluster analysis (Ward's method), using the species abundance data from 300 1 m^2 sample quadrats. Ward's Minimum Variance clustering method uses squared Euclidean distances, and as the name suggests, it forms clusters by minimizing the sum of squares error with each merging of two objects in the stepwise procedure (Ward, 1963). Ward's method is commonly used and is considered among one of the best sorting strategies with similarity analysis (Kent and Coker, 1992). Hierarchical clustering is appropriate for looking for species associations but requires that the user select the level of partitioning that best corresponds to the ecological situation (Legendre and Legendre, 1998). The appropriate level of partitioning was determined by first selecting a threshold level high on the dendrogram chart and then cross-referencing the original cluster groups with the dominant species for each sample. Indicator species (occurrence in 80-100% of quadrats), frequent species (60-79% occurrence), and associate species (40-59%

occurrence), in each group were identified. The mean percent cover of species in each of the above categories aided in characterizing the eight plant community groups.

Discriminant function analysis was performed to test the hypothesis that the group centroids of species abundance in each of the three burn regime groups were significantly different. Burn regime was used as the grouping variable for the herbaceous species abundance data at the 1 m^2 scale. Wilks' λ was used to test the significance of the discriminant axes.

2.2.3 Analytical methods-shrub vigor

A multiple logistic regression with the binary response variable, shrub dead/alive, was used to test if burn regime, plant litter biomass, thickness of OH soil horizon, and shrub height had a significant effect on Salix spp. shrub mortality. A total of 1198 individual willow shrubs, from meadows within the three burn regime groups, were sampled and included in this analysis.

A G statistic was used in a test of independence between burn regime (0, I, III) and shrub vigor (class I – IV) with the *Salix* spp. shrub dataset ($\underline{N}$ = 1198). A separate test of independence between the two meadows within a burn regime and shrub vigor was performed for each of the three burn regimes.

2.3 Results

2.3.1 Vegetation Description

Seventy-two plant species were identified in the thirty sample plots (1000 m^2 scale), of which seven were shrub species of the genus *Salix* (see Appendix 1 for a complete listing). Forty-eight herbaceous plant species were identified within the 300 quadrats at the 1 m^2 scale; these herbaceous plant data were used in all of the following analyses. Analyses involving *Salix* spp. were performed using the shrub data collected from the 30 plots at the 1000 m^2 scale ($\underline{N}$ = 1198).

2.3.2 Description of eight vegetation groups determined by cluster analysis

An agglomerative cluster analysis using mean Euclidean distance and Ward's minimum variance method (Ward, 1963), resulted in eight plant community groups (A – H), based on species abundance within the 300 quadrats. Two groups, A (*Calamagrostis* spp.) and D (*Calamagrostis* spp., *Carex aeana*, *Juncus balticus*), account for 46% of the total 300 quadrat samples. Table 2.1 lists the indicator species (occurrence in 80 - 100% of quadrats), frequent species (60 - 79% occurrence), and associate species (40 - 59% occurrence), as well as the mean percent cover in the quadrats in which they occur, for each of the eight groups. The following description of the eight community groups reveals a large degree of overlap in dominant species, the relative proportion of the dominant species is the key distinguishing factor for many of the groups.

<u>GROUP A</u> - *Calamagrostis* spp.

Sixty-six quadrats (22% of total) belong to group A. *Calamagrostis* spp. is the dominant plant in this group with 100% occurrence and a mean percent cover value of 11%. *Carex atherodes* is a frequent species, occurring in 68% of the quadrats in this group, with a mean percent cover of 3.4%. *Stellaria longifolia* occurs less frequently at 44%.

<u>GROUP B</u> - *Agropyron trachycaulum & Achillea millefolium*

Thirty-four quadrats (11% of total) belong to group B. *Agropyron trachycaulum* and *Achillea millefolium* are the dominant species in this group with 85% and 88% occurrence and 6.1 and 1.8 mean percent cover respectively. Associate species include *Calamagrostis* spp., *Carex atherodes, Carex aeana*, and *Fragaria virginiana.*

<u>GROUP C</u> – *Carex aeana & Calamagrostis* spp.

Thirty quadrats (10% of total) belong to group C. *Carex aeana* and *Calamagrostis* spp. are the dominant species in this group, both with 100% occurrence and 4.8 and 6.3 mean percent cover respectively. *Carex atherodes* occurs in 60% of the quadrats in this group and has a mean percent cover of 2.7. *Achillea millefolium* occurs in 50% of the quadrats with a mean percent cover of 1.7.

<u>GROUP D</u> – *Calamagrostis spp., Carex aeana, Juncus balticus*

Group D comprised 24% of all sample quadrats making it the most frequently occurring community. *Calamagrostis* spp. occurs in 97% of the quadrats in this group and has a mean percent cover of 4.1%. *Carex aeana, Juncus balticus* and *Epilobium angustifolium* are associate species with mean percent cover values of 2.5, 3.8, and 2.0 respectively.

GROUP E – *Epilobium angustifolium*

Twenty-four quadrats belong to group E. *Epilobium angustifolium* is the dominant species with occurrences in 96% of the quadrats and a mean percent cover of 7.7 in the quadrats in which it occurs. Additional indicator species of this group include: *Calamagrostis* spp. and *Carex atherodes* with 92% and 88% occurrences and mean percent cover values of 4.1 and 4.5.

GROUP F – *Calamagrostis* spp. & *Carex atherodes*

Forty-five quadrats belonged to this group (15% of total), which is characterized by the presence of *Calamagrostis* spp. and *Carex atherodes* which both occur in 100% of all quadrats in this group. Mean percent cover of the above two species is 4.2 and 5.0. Associate species include: *Epilobium angustifolium* and *Achillea millefolium*.

GROUP G – *Poa* spp. & *Carex atherodes*

Only 3% of the 300 quadrats belonged to group G, which is characterized by 100% occurrence of *Poa* spp. and *Carex atherodes*. Mean percent cover of the above two species is 8.1 and 8.6. *Calamagrostis* spp. and *Epilobium angustifolium* occur frequently in these quadrats and *Achillea millefolium* is the only associate species in this group.

GROUP H – *Carex atherodes* & *Calamagrostis* spp.

Carex atherodes (100% occurrence) and *Calamagrostis* spp. (90% occurrence) were the dominant species in 6% of the 300 quadrats. *Carex atherodes* had a mean percent cover of 10.5 while *Calamagrostis* spp. had a mean percent cover of 4.6.

2.3.3 Canonical Correspondence Analysis

Canonical Correspondence Analysis (CCA) was used to evaluate the relative influence of burn regime and microsite environment factors on community composition at the 1 m^2 scale. The environmental variables included in the CCA were: burn regime (0, 1, 3), soil pH, OH soil horizon thickness, and plant litter biomass. The mean values for the quantitative variables were: soil pH 5.9 ± 0.4 s.d., OH horizon thickness 7.2 cm ± 2.1, and plant litter biomass 40.4 g ± 19.7 s.d.. An organic matter gradient, defined by plant litter biomass, was associated with the first axis, and a burn regime gradient was associated with the second axis (eigenvalues 0.213 and 0.099 respectively). The cumulative percent species variance explained by the CCA is low for both the first axis, 4.0%, and the second axis, 5.8% (Table 2.2). The strongest intra-set correlations between the environmental variables and individual ordination axes are 0.80 between litter biomass and axis 1, and 0.96 between Burn-0 (unburned meadow) and axis 2 (Table 2.3). A Monte Carlo Test with 99 permutations indicated that CCA-1 was significant on both the first canonical axis and the overall test ($p = 0.01$).

The CCA was repeated with the additional environmental variable, prairie location (CCA-2). The first and second axis eigenvalues for CCA-2 (0.253, 0.139), are comparable to those of CCA-1 (Table 2.4). The percent cumulative variance explained is only slightly higher in CCA-2 (4.7 % and 7.3 % on axes 1 and 2 respectively), which suggests that differences in species composition between meadows may account for only a very small portion of the variability that is not explained in CCA-1.

2.3.4 Ordination Plots

An ordination diagram (Figure 2.3), based on the results of CCA-1, contains the weighted average species scores, environmental biplot scores of qualitative variables, and centroids of nominal environmental variables. Figure 2.3 illustrates the relationship between individual species and the environmental gradients litter biomass (axis 1) and burn regime (axis 2). On the first axis, plant litter biomass increases from left to right on the ordination diagram. The second axis represents a burn regime gradient from unburned at the top of the ordination diagram to meadows burned three times at the bottom of the diagram. *Calamagrostis* spp., an important bison forage, is located near the center of the plot, indicating a low correlation between this species and either the burn regime (axis 2 gradient) or the plant litter biomass gradient (axis 1). *Carex atherodes*, also an important forage species, shows a low correlation to burn regime, but has a relatively strong correlation with high litter biomass. Conversely, *Juncus balticus* and *Carex aeana*, two species that are important in the ordination (*i.e.* both have a high weight), appear to be strongly correlated with the B–3 (burned three times) regime.

A second ordination diagram (Figure 2.4), illustrates the position of the 300 sample scores in two dimensional ordination space. The sample scores are labeled by plant community group, which reveals the strength of the association between the samples belonging to a particular group and the environmental gradients: burn regime (axis 2) and litter biomass (axis 1). The eight community groups (A – H) appear to be influenced by the environmental gradients to a variable degree. Community group D (*Calamagrostis* spp., *Carex atherodes, Juncus balticus*) is clustered in the bottom left side of the ordination diagram indicating a strong association of this community type with the B-3 regime. Group B (*Agropyron trachycaulum, Achillea millefolium*) is more diffuse and is generally associated with low litter biomass according to the ordination diagram, but group B also shows a cluster of sample plots in the B-3 region of the plot. Community group A (*Calamagrostis* spp.), the second largest group, forms a relatively tight cluster near the center of the ordination plot.

2.3.5 Discriminant Function Analysis (DFA)

DFA was used to test the hypothesis that the three burn regime groups were significantly different based on their species composition. The group centroids of B-0, B-1, and B-3 meadows were significantly different ($p < 0.001$) and 77% of the original grouped cases were correctly classified (Figure 2.5).

2.3.6 Logistic regression of Salix spp. shrub mortality

A total of 1198 *Salix* spp. shrubs, comprising seven species, were identified within the thirty 1000 m^2 plots. *Salix bebbiana,* was the most abundant willow followed by *S. petiolaris, S. maccalliana, S. pseudomonticola, S. planifolia, S. glauca* and *S. serrisima.* The results of a multiple logistic regression with the binary response variable, shrub alive/dead, indicate that burning had a significant negative effect on shrub survivorship ($\underline{N} = 1198$, $p < 0.05$). Single burns, multiple (three times) burns, litter biomass, thickness of OH horizon and shrub height were entered into the regression model as predictor variables. The stepwise procedure determined that the best model contained all of the above variables except shrub height. Single burns, multiple burns and OH horizon thickness all had a negative association with shrub survivorship ($p = 0.001$, $p = 0.001$, $p = 0.002$, respectively), while litter biomass was weakly positively associated with shrub survivorship ($p = 0.02$). The resulting model had 71.6% concordance.

2.3.7 Test of independence between shrub vigor and burn regime

The results of a G-statistic test of independence between shrub mortality and burn regime indicate a significant difference in shrub frequency among the four mortality classes and three burn regimes ($p < 0.001$) (Table 2.6). Shrub frequency in all four vigor classes on unburned meadows and shrub frequency in vigor Classes I and IV on meadows burned three times appear to contribute most to the differences detected by the G-statistic test according to the Freeman-Tukey standard residuals presented in Table 2.6. The more the Freeman-Tukey standard residual deviates from zero the more that cell of the contingency table contributes to the overall difference determined by the G-statistic. Of the total 1 198 shrubs sampled, 14% were standing dead shrubs with 10% occurring on meadows that had been burned three times and the remaining 4% on meadows that had been burned once. Within the single burn regime, 12% of the 398 shrubs sampled were standing dead. Within the multiple (three times) burn regime, 24% of the 507 shrubs in this group were standing dead, while only 0.3% of the 293 shrubs sampled from unburned meadows were standing dead shrubs.

The relative proportion of shrubs in each of the four vigor classes differed most between unburned meadows and burned meadows but within the B – 3 regime there were more shrubs than expected in Class I (*i.e.* more standing dead) and fewer than expected in

Class IV (*i.e.* fewer robust) (Figure 2.6). On unburned meadows, approximately 92% were healthy, flourishing shrubs in Class IV, compared to 29% in B – 3 meadows. The proportion of shrubs in Class I on unburned meadows was 0.3% compared to 24% on meadows burned three times.

2.3.8 Tests of independence between shrub vigor and meadows within a burn regime

The results of three separate tests of independence between the four shrub vigor classes and the two meadows within each of the three burn regimes, indicate significant relationships among shrub vigor and meadows within a burn regime (B – 0: G = 9.9, d.f. = 3, $p < 0.05$; B – 1: G = 13.7, d.f. = 3, $p < 0.01$; B – 3: G = 27.4, d.f. = 3, $p < 0.01$). The sum of the three within-meadow G-statistics is much less than the overall G-statistic (51.4 << 291.4) which suggests greater differences in shrub frequency among the four vigor classes between burn regimes compared to within burn regimes.

Table 2.1 Descriptive characteristics of eight plant communities based on species abundance in 300 1 m^2 quadrats from six northern boreal meadows in the Hook Lake area, Northwest Territories. Communities were determined by Ward's minimum variance cluster method.

Group	No. Members	Indicator species (80-100% occurrence)	Mean Percent Cover	Frequent species (60-79% occurrence)	Mean Percent Cover	Associate species (40-59% occurrence)	Mean Percent Cover
A	66	*Calamagrostis* spp. (100)	11	*Carex atherodes* (68)	3	*Stellaria longifolia* (44)	1
B	34	*Achillea millefolium* (88)	2			*Calamagrostis* spp. (53)	3
		Agropyron trachycaulum (85)	6			*Carex atherodes* (53)	3
						Carex aeana (47)	2
						Fragaria virginiana (44)	3
C	30	*Carex aeana* (100)	5	*Carex atherodes* (60)	3	*Achillea millefolium* (50)	2
		Calamagrostis spp. (100)	6				
D	71	*Calamagrostis* spp. (97)	4			*Carex aeana* (58)	3
						Juncus balticus (44)	4
						Epilobium angustifolium (41)	2
E	24	*Epilobium angustifolium* (96)	8			*Achillea millefolium* (54)	1
		Calamagrostis spp. (92)	4				
		Carex atherodes (88)	5				
F	45	*Calamagrostis* spp. (100)	4			*Epilobium angustifolium* (42)	4
		Carex atherodes (100)	5			*Achillea millefolium* (40)	2
G	9	*Poa* spp. (100)	8	*Calamagrostis* spp. (67)	5	*Achillea millefolium* (44)	2
		Carex atherodes (100)	9	*Epilobium angustifolium* (67)	2		
H	20	*Carex atherodes* (100)	11			*Epilobium angustifolium* (45)	2
		Calamagrostis spp. (90)	5			*Stellaria longifolia* (45)	2

Table 2.2 Summary of Canonical Correspondence Analysis (CCA - 1) based on plant abundance and environmental data measured in 300 1 m^2 quadrats from six northern boreal meadows in the Hook Lake area, Northwest Territories.

Axis	*1*	*2*	*3*	*4*	Σ
Eigenvalue	0.21	0.10	0.07	0.05	
Species/environmental correlation	0.70	0.61	0.45	0.41	
Cumulative % variance of :					
species data explained	4.0	5.8	7.2	8.0	
species/environmental relation explained	45.6	66.8	82.2	92.2	
Canonical eigenvalues					5.38
					0.47

Table 2.3 Intra-set correlations between environmental variables and ordination axes for CCA-1, based on plant abundance and environmental data measured in 300 1 m^2 quadrats from six northern boreal meadows in the Hook Lake area, Northwest Territories. (LIT = plant litter biomass, PH = soil pH, OH = thickness of OH soil horizon, B-0 = unburned meadow, B-1 = meadow burned once, B-3 = meadow burned three times)

Axis	*1*	*2*	*3*	*4*
LIT	0.80	0.33	0.06	-0.02
PH	0.09	-0.16	-0.44	0.83
OH	0.39	0.54	0.39	0.49
B-0	-0.06	0.96	0.01	0.10
B-1	0.46	-0.35	-0.43	-0.37
B-3	-0.43	-0.64	0.45	0.28

Table 2.4 Summary of Canonical Correspondence Analysis (CCA-2) based on plant abundance, meadow, and environmental data measured in 300 1 m^2 quadrats from six northern boreal meadows in the Hook Lake area, Northwest Territories.

Axis	*1*	*2*	*3*	*4*	*Σ*
Eigenvalue	0.25	0.14	0.11	0.06	
Species/environmental correlation	0.76	0.68	0.55	0.43	
Cumulative % variance of :					
species data explained	4.7	7.3	9.3	10.5	
species/environmental relation explained	36.4	56.4	72.0	81.2	
Canonical eigenvalues					5.38
					0.69

Table 2.5 Intra-set correlations between environmental variables and ordination axes for CCA-2, based on plant abundance, meadow, and environmental data measured in 300 1 m^2 quadrats from six northern boreal meadows in the Hook Lake area, Northwest Territories. (LIT = plant litter biomass, PH = soil pH, OH = thickness of OH soil horizon, B-0 = unburned meadow, B-1 = meadow burned once, B-3 = meadow burned three times, HK = Hook Meadow, AN = Ann's Meadow, PL = Paul's Meadow, NT = North Meadow, AL = Al's Meadow, DN = Dan's Meadow)

Axis	*1*	*2*	*3*	*4*
LIT	0.75	0.00	-0.19	0.15
PH	0.11	-0.03	-0.03	-0.78
OH	0.44	0.23	0.26	0.39
B-0	0.10	0.77	0.00	0.29
B-1	0.28	-0.49	-0.49	0.05
B-3	-0.40	-0.29	0.53	-0.35
HK	0.64	-0.09	0.04	-0.19
AN	-0.32	-0.53	-0.68	0.26
PL	-0.03	0.00	0.00	-0.36
NT	-0.49	-0.38	0.69	-0.09
AL	-0.15	0.65	-0.34	0.04
DN	0.27	0.33	0.32	0.31

Table 2.6 Summary of a test of independence between *Salix* spp. shrub vigor classes and burn regime (B-0 = unburned meadow, B-1 = meadow burned once, B-3 = meadow burned three times; Class I = standing dead, Class II = re-sprouting from base, Class III = re-growth to less than 80 % former height, Class IV = flourishing).
($G = 291.4$, d.f. = 6, $p < 0.001$)

Observed *Expected* *Freeman-Tukey*	*B-0*	*B-1*	*B-3*	*Total*
Class I	1 41.1 -10.5	48 55.8 -1.0	119 71.1 -5.0	168
Class II	1 26.7 -8.0	40 36.2 0.7	68 46.1 2.9	109
Class III	23 81.9 -8.4	139 111.3 2.4	173 141.8 2.5	335
Class IV	268 143.3 8.8	171 194.7 -1.7	147 248 -7.2	586
Total Frequency	293	398	507	1198

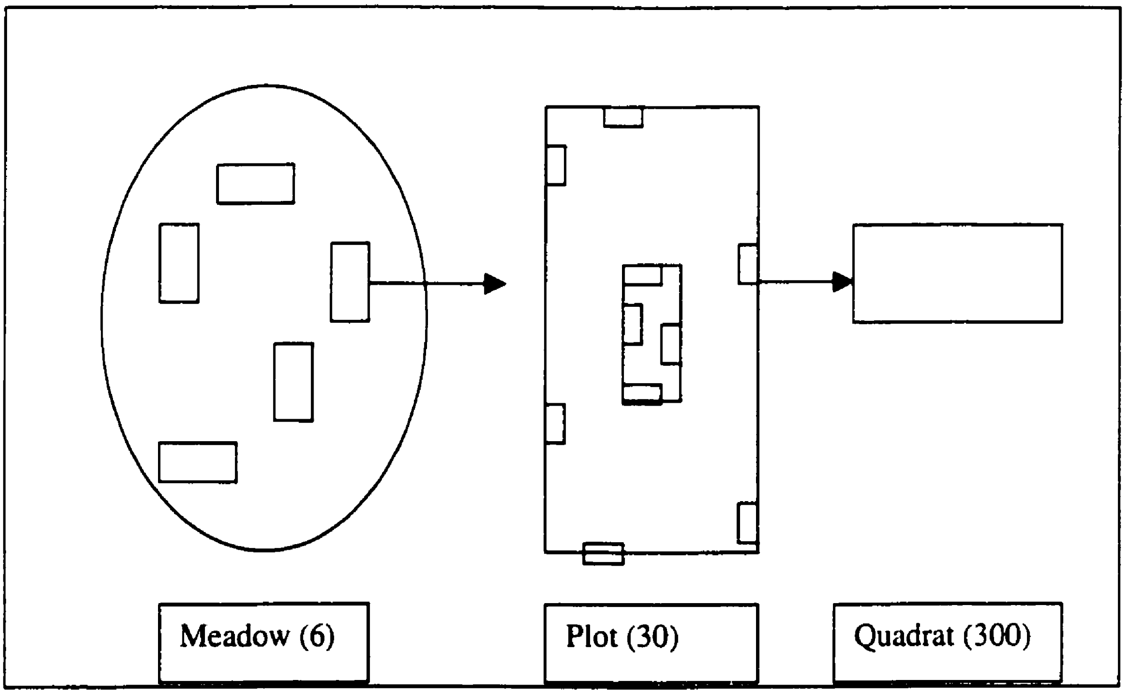

Figure 2.1 Schematic diagram of hierarchical vegetation sampling scheme in the Hook Lake area meadows. Within each of six meadows, five plots (20 m x 50 m) were established and each plot contained ten quadrats (2 m x 0.5 m).

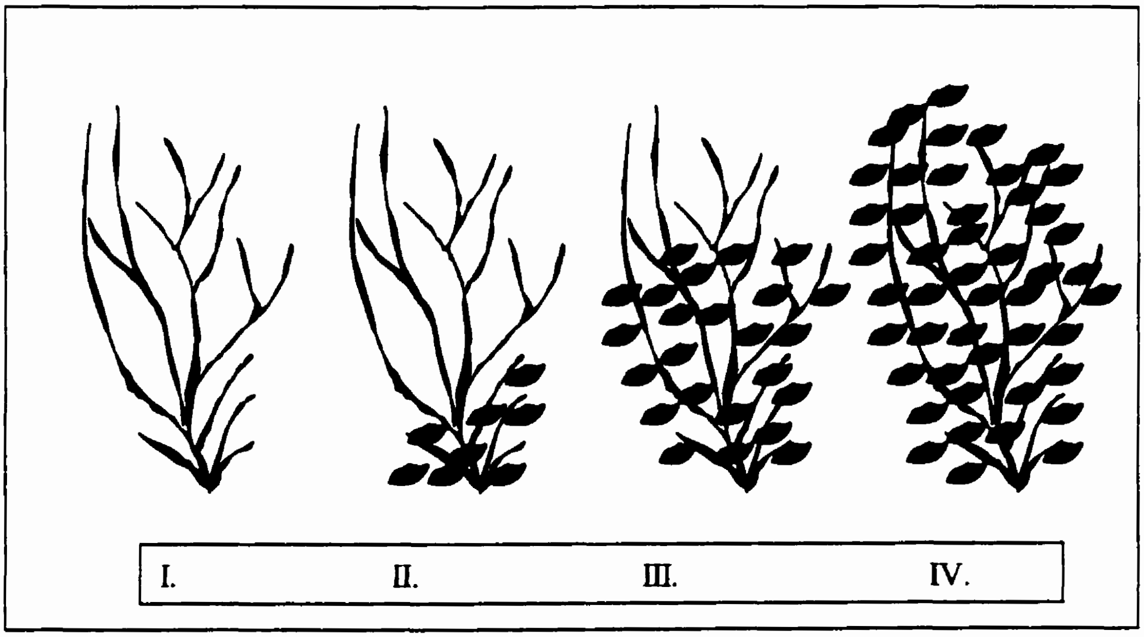

Figure 2.2 Schematic diagram illustrating the criteria for willow shrub vigor classification. Class I = standing dead, Class II = re-sprouting at base, Class III = maximum height of leaves is less than 80% former height, Class IV = very healthy, flourishing.

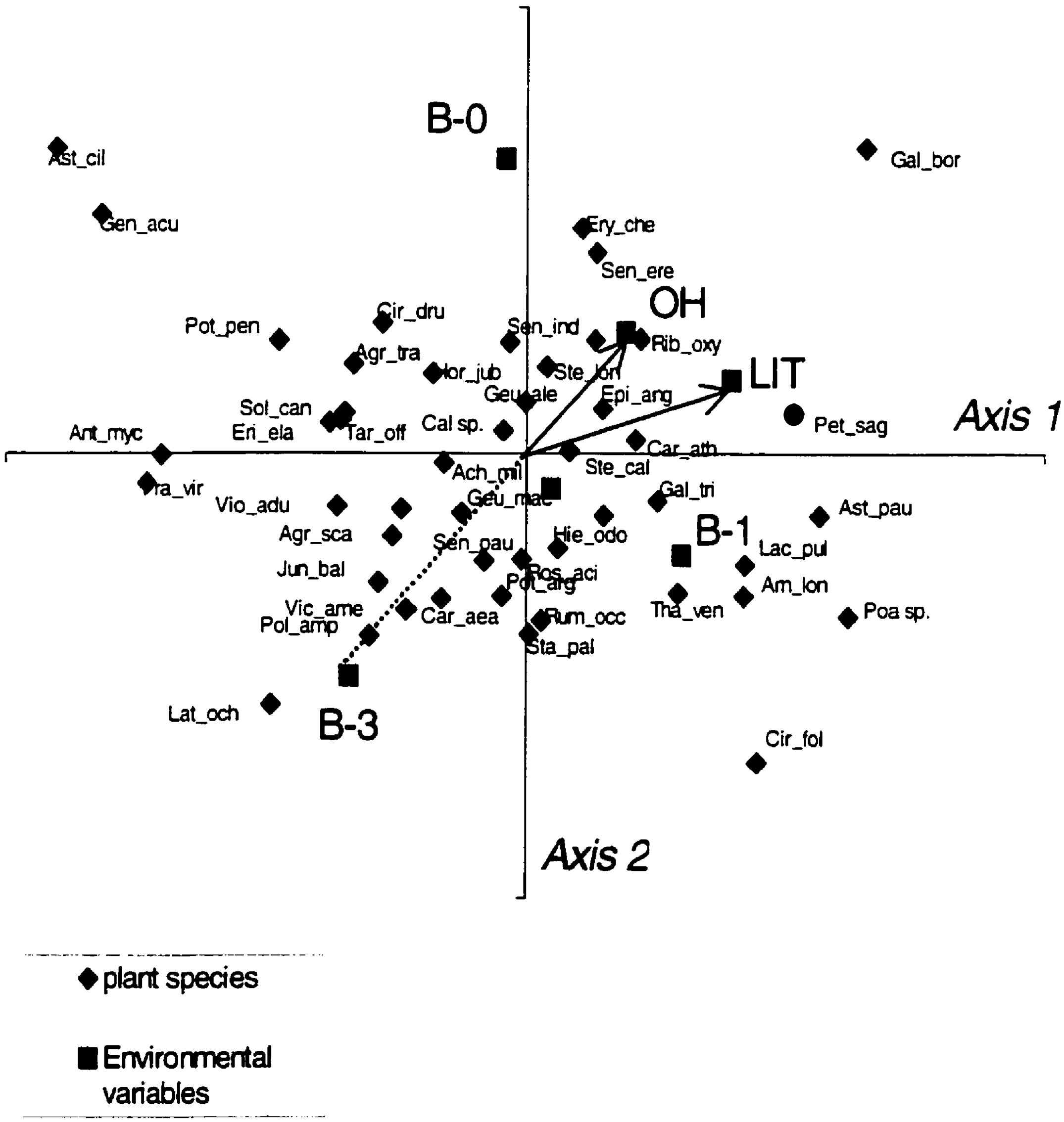

Figure 2.3 Ordination diagram of plant species based on CCA-1 of 300 quadrats from the Hook Lake area meadows, Northwest Territories. B-0 = unburned, B-1 = meadows burned once, B-3 = meadows burned three times, LIT = plant litter biomass, OH = thickness of the OH soil horizon.

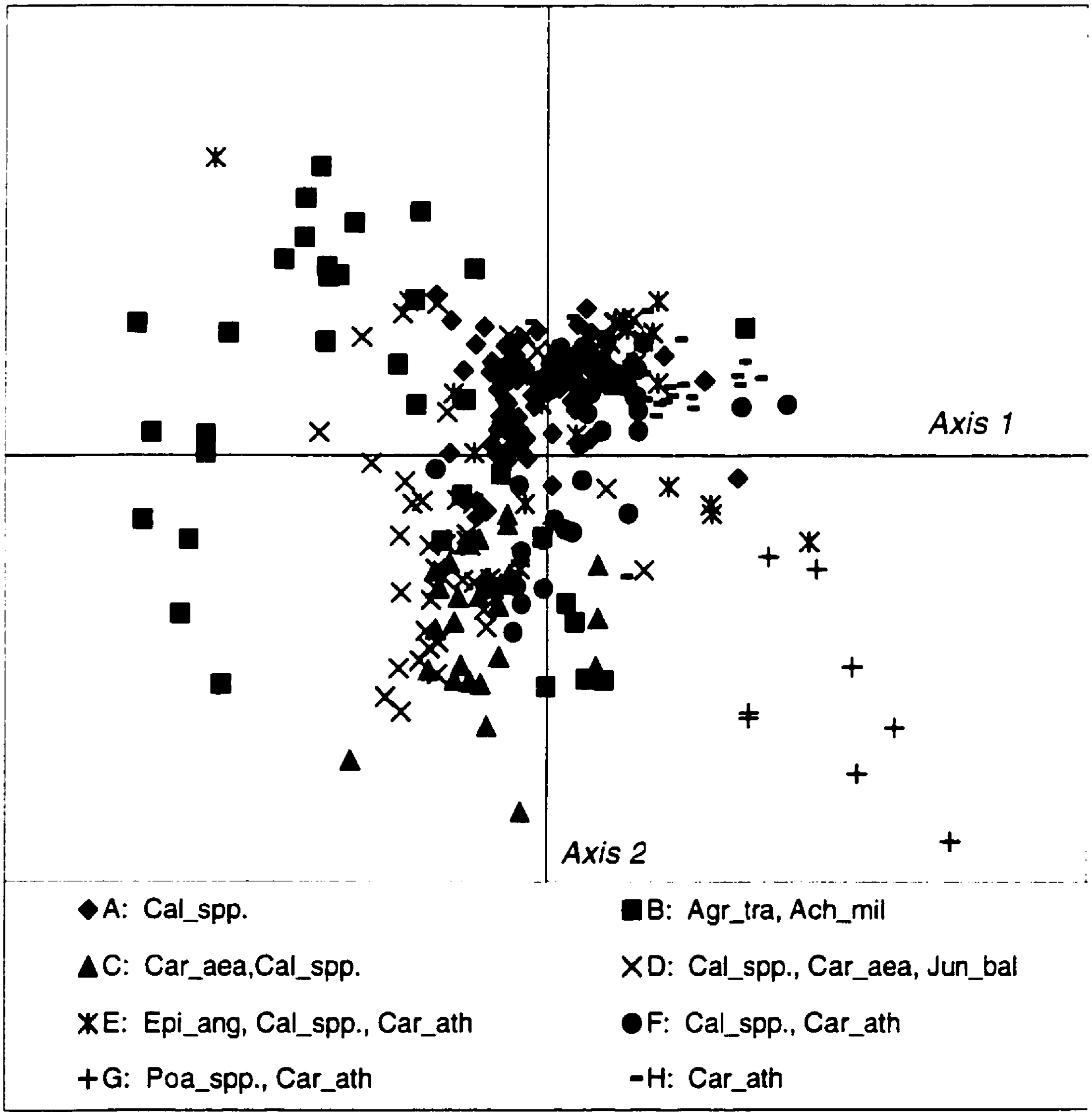

Figure 2.4 Ordination diagram of samples, based on CCA-1 of 300 1 m^2 quadrats from the Hook Lake area meadows, Northwest Territories. Samples are labeled according to community group (A-H) membership as determined by cluster analysis (Ward's method).

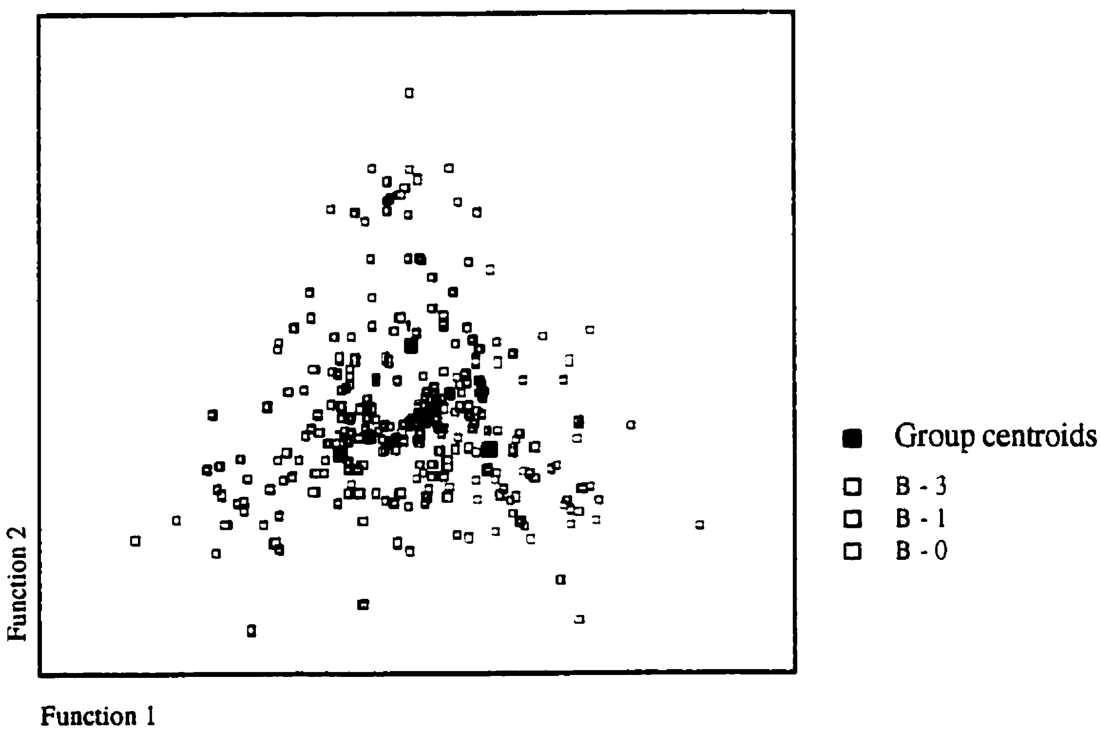

Figure 2.5 Ordination plot of canonical discriminant functions based on plant species abundance in 300 1m^2 quadrats in dry meadows of the Hook Lake area, Northwest Territories. Samples were separated by burn regime group. (B – 3 = meadows burned three times, B – 1 = meadows burned once, B – 0 = unburned meadows)

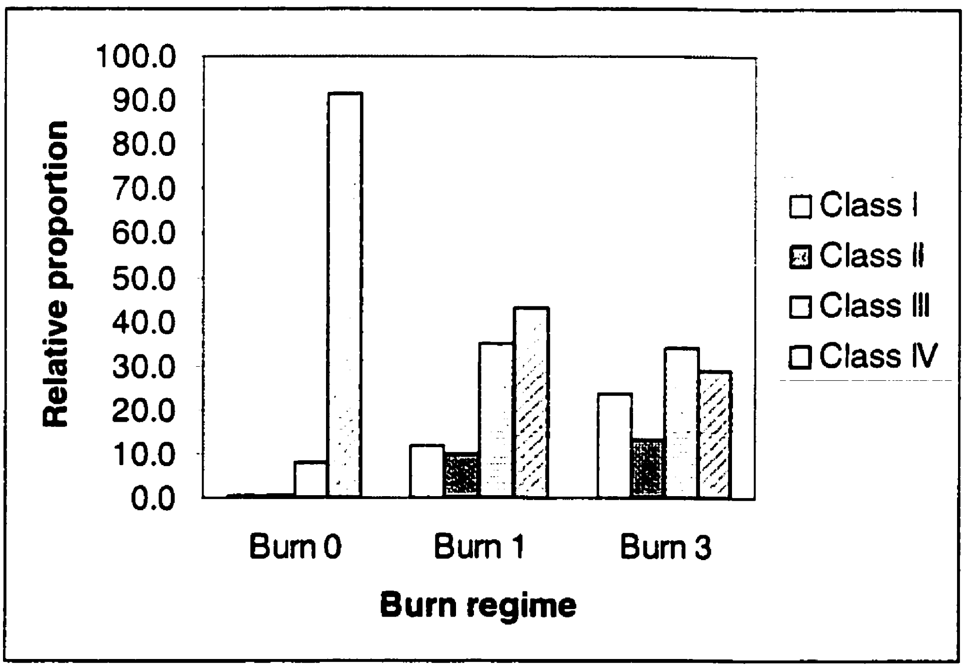

Figure 2.6 The relative proportion of shrubs (*Salix* spp.) in each of the four vigor classes, within each of the three burn regimes. Class I = standing dead, Class II = re-sprouting at base, Class III = re-growth to less than 80% former height, Class IV = flourishing.

2.4 Discussion

2.4.1 CCA and the relationship between herbaceous plant species and burn regime

I used Canonical Correspondence Analysis to describe and compare plant community composition between meadows in the Hook Lake area that were subjected to one of three prescribed burning regimes (unburned, burned once, burned three times). I also included environmental variables (plant litter biomass, OH soil horizon thickness, and soil pH) in the analysis to evaluate their relative influence on plant community composition. Plant litter biomass was most strongly correlated with the first axis, while burn regime was most closely correlated with the second axis. The cumulative percent species variance explained for the 1^{st} and 2^{nd} axes was low (4.0% and 5.8%) but low species variance explained is typical for abundance data analyzed with CCA (ter Braak, 1990). However, it is also possible that there were other important environmental variables (*e.g.* soil moisture, topography, fire intensity) that were not included in the analysis or there is a large amount of natural variability in community composition at the plot or meadow scale.

As a result of the low species variance explained by the first CCA, a second analysis, CCA-2, was used to test for an influence of sample location (one of six meadows) on species variation between prairies. The cumulative percent species variance explained increased in CCA-2 to 5.8% and 7.3% on the first and second axes respectively. This slight increase in species variance explained, suggests that there might be only small differences in species composition between the six sampled meadows that is not accounted for in CCA-1. Differences in community composition between the six meadows that are not a result of the burn regime could confound the results and interpretation of the ordination. Vegetation within the Hook Lake area meadows is not homogeneous and the meadows sampled vary in size, shape, and relative distance to one another. The disturbance history of the meadows may also differ. Without pre-burn data, the plant communities described in this study can not be considered a direct result of the fire regime alone. However the CCA-2, which included the meadow as an environmental variable, does not suggest substantial differences in species composition based on the meadow sampled alone. Despite the small amount of species variance explained in CCA-1, the use of CCA remains an appropriate technique for describing species response to particular sets of environmental variables (e.g. management activities, or more specifically in this case, prescribed burning) (McCune, 1997) and the ordination diagrams (Figures 2.3 & 2.4) suggest important plant species responses to prescribed burning in the Hook Lake area.

The main environmental gradient of the sampled meadow communities, as identified by the CCA, is plant litter biomass (LIT). LIT has an intra-set correlation value of 0.80 with the first ordination axis (Table 2.3). The intra-set correlations represent the correlation between environmental variables and the ordination axes (ter Braak, 1986). In Figure 2.3, plant species on the right side of the diagram are associated with high plant litter biomass while species on the left side of the diagram are associated with low litter biomass. Species present at the high LIT end of the ordination plot such as *Petasites sagittatus* and *Carex atherodes* are plants that are characteristic of wet meadows in the SRL (Raup, 1935; Reynolds, 1987). This suggests that dead plant litter build-up may be greater in the wetter meadows where poor drainage leads to anaerobic conditions which might inhibit decomposition. Timoney (1996), determined that out of six dominant herbaceous species in the Peace-Athabasca delta, *Carex atherodes* was most strongly correlated with graminoid litter cover. Considering that litter build-up may be greatest in wet meadow areas and that wet meadows generally do not burn well (C. Gates, pers. comm.), spring burning in the SRL is probably less effective at rejuvenating herbaceous growth in wet meadow patches.

The meadow areas sampled were at the moderately dry to dry end of the moisture gradient, which was determined in the field by the dominant plant species and the height of the vegetation. Plant litter biomass was expected to decrease in burned meadows. The frequency of the fires depends partly on fuel loads *i.e.* litter and living biomass, and this relationship is revealed in the placement of the B-3 (burned three times) variable and the LIT (plant litter) variable on the ordination plot (Figure 2.3). The mean values for LIT, based on 300 samples (25 cm x 25 cm) decreased from 50.8 g $\pm$ 18.0 s.d. on unburned meadows, to 40.0 g $\pm$ 18.2 s.d. on B-1 (burned once) meadows, and to 30.5 g $\pm$ 17.6 s.d. on B-3 (burned three times) meadows. The reduced plant litter biomass remained detectable three years following burning. Removal of plant litter by fire may lead to increased soil temperatures and reduced soil moisture (Whelan, 1995). These changes in microsite conditions could have an important effect on plant community composition.

The second major gradient revealed by the CCA is burning frequency which is represented by the second axis. B-0 has the strongest intra-set correlation with the 2nd

axis (0.96), followed by B-3 (– 0.64) (Table 2.3). The relatively long distance of the B-3 centroid from the plot origin is indicative of its relatively high importance on the 2nd ordination axis (ter Braak, 1994). The placement of a species on the plot is the centroid of the samples in which that species occurs. Thus, plant species that are located near the top of the ordination plot along the second axis, (*e.g., Erysimum cheranthoides, Senecio eremophilus* (Figure 2.3)), occur most frequently in samples from unburned meadows, while plant species located near the bottom half of the plot, that lie close to the B-3 centroid when a perpendicular line is drawn to the B-3 vector, (*e.g., Polygonum amphibium, Vicia americana, Carex aeana, Juncus balticus*), occur most frequently in samples taken from meadows burned three times.

Differences in species composition between meadows in each of the three different treatments are further supported by the results of a discriminant function analysis. The results of the DFA clearly indicate three groups representing samples from the three burn regimes, B-0, B-1, and B-3 (p <0.001) . There is some overlap between the groups, which is visible on the DFA plot (Figure 2.5). This overlap is not unexpected since the stratified sampling scheme was restricted to moderately dry meadows that are characterized by the dominance of only a few species in combination with a relatively small pool of frequently occurring species.

Two species, *Juncus balticus* (baltic rush) and *Carex aeana* (hay sedge), are both important in the ordination (*i.e.* high weight) and appear strongly related to the B-3 regime on the ordination plot (Fig. 2.3). Qualitative comparisons of pre- and post-fire herbaceous biomass on NP meadow, suggest that rushes are favored by a multi-year burn treatment (C. Gates, pers. comm.). Both *Carex* spp. and *Juncus* spp. are known to have long-term persistent seed-banks (Thompson, 1992). The size of a species seed bank can play an important role in post-disturbance population dynamics (Whelan, 1995). Whelan (1995), speculates that since a plant community's seed-bank fluctuates according to the season, a spring fire that burns much of the annual seed-bank before plants have a chance to produce seeds that season, might have a greater impact on species with fewer, short-lived, seeds in the seed bank (Whelan, 1995). Archibold *et al.* (1998), found that the temperature during spring burns in northern mixed prairie plantings, usually remained unchanged at a depth of 5 cm. Thus, plant species that have longer-lived seeds that accumulate in the soil might have an advantage over seeds nearer the soil surface that are more likely to be destroyed by a ground fire.

2.4.2 Relationship between plant communities and burn regime

An ordination diagram of the 300 sample sites reveals several distinct plant groups associated with the two gradients, plant litter biomass on the 1st axis and burn regime on the 2nd axis (Fig. 2.4). Plant groups C (*Carex aeana, Calamagrostis* spp.) and D (*Calamagrostis* spp., *Carex aeana, Juncus balticus*) are tightly clustered and appear strongly associated with the B-3 regime (meadows burned three times since 1992). Plant groups A (*Calamagrostis* spp.), F (*Calamagrostis* spp., *Carex atherodes*), and H (*Carex atherodes*), were also relatively tightly clustered and appeared to be most strongly associated with unburned meadows (B-0) and single-burn meadows (B-1). Plant groups B (*Agropyron trachycaulum, Achillea millefolium*) and G (*Poa* spp., *Carex atherodes*), were more diffuse than the other groups but still showed general tendency toward low litter biomass (group B), and medium-high litter biomass along the burn regime gradient (group G). Plant group E (*Epilobium angustifolium, Calamagrostis* spp., *Carex atherodes*) does not appear from the ordination diagram to be strongly influenced by either plant litter biomass or burn regime.

The strong association of *Carex aeana* and *Juncus balticus* with meadows burned three times is also revealed in the ordination plot of sample sites, labeled according to community type (Figure 2.4). Plant community groups C (*Carex aeana, Calamagrostis* spp.) and D (*Calamagrostis* spp., *Carex aeana, Juncus balticus*) occur most frequently on meadows burned three times. Together, these two groups account for approximately one third of the 300 samples. While *Carex atherodes* is a frequently-occurring species in Group C, its mean percent cover is relatively low (2.7) compared to those communities in which it is an indicator species (refer to Table 2.1). *Achillea millefolium*, a fairly common species in dry meadows, is an associate species of Group C. While *Carex aeana* and *Juncus balticus* are only associate species in Group D, which is dominated by *Calamagrostis* spp., these two species are characteristic of this group which is generally very low in total herbaceous cover (personal observation).

The frequency of community types C (*Carex aeana, Calamagrostis* spp.) and D (*Calamagrostis* spp., *Carex aeana, Juncus balticus*) in meadows that were burned three times is important with respect to improving bison habitat. *Juncus balticus*, the second most common plant on dry meadows and *Carex aeana*, one of the three most common sedges on dry meadows, comprise only 1 - 4% and *ca.* 2% respectively, of bison's diet (Reynolds *et al.*, 1978), suggesting low palatability of these species to bison. Bison tend to prefer food from wet meadow areas (Reynolds *et al.*, 1978). *Calamagrostis* spp. and *Carex atherodes* together comprise the main component of the diet of bison in the SRL (92% spring diet, 70% summer diet, 79% fall diet, and 77% winter diet) (Reynolds *et al.*, 1978). Plant Groups A, F, and H are dominated by one or both of these two species and are all generally located above the 1^{st} axis on the ordination plot (Figure 2.4). The location of the samples belonging to plant groups A, F, and H, suggests that communities dominated by the main bison forage species *Calamagrostis* spp. and *Carex atherodes*, are inhibited by the B-3 regime.

Moss (1953) similarly reported a decline in wet meadow plant species from a severely burned marsh in northern Alberta, where a *Scholocloa festucacea*-dominated marsh containing patches of *Calamagrostis* spp. and *Carex atherodes* was apparently replaced by various pioneer species, many of them weedy, including: *Atriplex patula, Artemisia biennis, Chenopodium rubrum, *Lactuca pulchella, *Urtica gracilis, Chenopodium album, Equisetem arvense, *Epilobium angustifolium, Erigeron canadensis, *Stachys palustris, *Populus tremuloides,* and among other less frequent species: **Taraxacum* sp., **Senecio eremophilous, *Potentilla norvegica, *Hordeum jubatum, *Achillea millefolium*, and **Agropyron trachycaulum* (*species also recorded in present study).

Fire frequency and season of burn may interact with other environmental conditions to favor particular species (Biondini *et al.*, 1989). In general, results of the present study indicate that dry meadow plant associations and poorer bison forage species were more abundant in areas that were burned three times between 1992 and 1995 compared to unburned meadows or meadows burned once. Drier conditions within the meadows may be related to climate patterns, burning regime or a combination of the two. The SRL area has experienced a drying trend in the past several decades (Timoney *et al.*, 1996). The summer of 1998 was particularly dry and hot in the SRL. Climate records for the Mackenzie Region, which includes the SRL, show that the spring of 1998 was the warmest spring on record between 1948 and 1999. During the same time period, 1998 ranks as the 9th driest spring in the Mackenzie Region (Environment Canada, 1999). Seasonal variation in weather has been shown to have as strong an influence on plant communities as the fire season (Biondini *et al.*, 1989). Long-term monitoring of plant communities, edaphic factors, and climate patterns in the SRL meadows might reveal more about a potentially complex relationship between management regime, climate variation, and plant community composition.

2.4.3 How does burning affect shrub vigor and survivorship?

Spring burning in the SRL negatively affected willow shrub vigor within the time-frame of this study. In terms of shrub survivorship, a logistic regression shows plant litter biomass as having a weakly positive effect on willow survivorship while depth of the OH horizon had a weakly negative effect on survivorship ($p = 0.02$ and $p < 0.01$). The contribution of plant litter and OH soil horizon thickness to the logistic regression model was small relative to the burn variables. A positive association between plant litter and willow survivorship may reflect less severe burns; *i.e.*, if the litter remained high after a burn then the burn was probably not very intense and therefore would not cause as much harm to the shrub compared to a more intense burn. One would expect the OH soil horizon thickness to be positively correlated with plant litter and thus have a similar relationship to shrub survivorship as plant litter. However, while the burn intensity might be inferred from the amount of plant litter removed, low to moderately high burn intensities would probably have less influence on the OH soil horizon thickness. The small negative effect of OH soil horizon thickness on shrub survivorship may suggest that where the OH soil horizon was thick, the high plant litter that one would expect to be associated with a thick OH horizon might have provided more fuel for an intense fire, therefore negatively impacting shrub survival. Determining the nature of the relationship between plant litter, OH horizon depth, and shrub survival post-fire, requires further study that includes pre- and post-fire measurement of these variables.

Far more standing dead shrubs (Class I) were found on meadows burned three times (24%) compared to meadows burned once (12%) or not at all (0.03%). I cannot account for any shrubs which may have burnt completely to the ground, leaving little or no evidence of their former presence since all sampling was conducted post-fire and shrubs were not tagged prior to burning. However, the full area of the 1000 m^2 plots in which shrubs were sampled was thoroughly examined at the ground level in search of herbaceous species and a small (ground-level) charred remnant of a shrub was encountered only once.

Chowns *et al.* (1997) reported a *ca.* 20% reduction in live willow volume from a single plot on the North Prairie that was in the B-3 regime. Whether a 20-25% reduction in individual willows is sufficient to maintain the semi-open condition of meadows in the Hook Lake area requires further research. Moody and Mack (1988) modeled plant invasions in a grassland and concluded that the success of controlling an invasion was greatly increased when at least 30% of satellite plants were destroyed. Furthermore, the temporal dynamics of pulses in willow establishment in the nearby Peace-Athabasca delta (Timoney, 1996) suggest that control measures would be more effective if they were timed with periods of high shrub establishment.

More information is revealed about the variability in response of the shrubs to the three burn regimes when the effect of the three burn regimes on *Salix* spp. shrubs is separated into the four shrub vigor classes. The results of a G-statistic test of independence between shrub vigor class and burn regime indicate significant differences in the frequency of shrubs among the four vigor classes and three burn regimes ($p < 0.01$). However the largest differences occur between unburned meadows and those burned once or three times. The majority of willow shrubs on unburned meadows were very healthy Class IV shrubs, with the exception of a small proportion (7.9%) in Class III, indicating that factors other than fire affect shrub vigor. In contrast, willow shrubs on meadows burned either once or three times were more evenly distributed among the four vigor classes (Figure 2.6).

A comparison of shrub vigor between meadows burned once or three times reveals relatively slight differences. There was only a small difference in the proportion of Class II re-sprouting shrubs between meadows burned once (10.1%) and those burned three times (13.4%). Similarly, the proportion of shrubs in vigor Class III was almost exactly the same on meadows burned once (34.9%) or three time (34.1%), indicating little difference in the effect of single and multiple burns on moderate reductions in shrub vigor

Visually healthy and flourishing shrubs in class IV account for 49% of the willow shrubs sampled. Approximately 92% of sampled willow shrubs on unburned meadows occur in class IV, indicating an overall robust willow community on unburned meadows. A much smaller proportion of Class IV shrubs on meadows burned once (43%), suggests that while the mortality rates are relatively low in single-burned meadows (12%), shrub vigor appears to have been significantly affected by this regime. The proportion of Class IV shrubs on meadows burned three times was also quite low (29%). Taken together, the proportion of shrubs in each of the four classes for all three burn regimes indicate that while shrub mortality may be relatively low as a result of the fires, shrub vigor appears to be substantially reduced by both single and multiple burn regimes.

The difference between the single and three burn regimes was most apparent when comparing dead vs. living shrubs. However, a comparison of shrub vigor between these two burn regimes indicated relatively little difference in fire effect. Differences in fire intensity between fires might have played an important role in plant responses. Litter that was removed in the first burn might have resulted in a reduction in the intensity and severity of subsequent burns. Burn reports for the SRL fires documented overall lower intensity fires in 1993 compared to 1992 (refer to GNWT internal reports, Ft. Smith). Other studies in grassland systems have shown significantly higher biomass consumption of woody plants in the first year of burning compared to the second year of burning (Pendergrass *et al.*, 1998). Recovery of plant litter may take longer periods between burns than was practiced in the Hook Lake area meadows. The B-3 regime does appear to move relatively more shrubs from Class IV into lower vigor classes than the B-1 regime. This may contribute to the doubling of the total proportion of shrubs killed in the B-3 regime when compared to the B-1 regime (Figure 2.6).

2.5 Conclusion

Vascular plant communities differed between unburned, single-burn meadows, and meadows burned three times. Plant communities associated with the three-burn regime were characterized by the dominant or frequent species *Carex aeana*, *Calamagrostis* spp., and *Juncus balticus*, at the 1 m^2 scale. *Salix* spp. mortality increased from less than 1% on unburned meadows to *ca.* 12% on meadows burned once, and *ca.* 24% on meadows burned three times. Differences in shrub vigor were larger between unburned meadows (B-0) and meadows burned once (B-1) or three times (B-3), than between B-1 and B-3 meadows. Differences in shrub vigor between B-1 and B-3 meadows appear only at the extreme classes of standing dead (Class I) and flourishing (Class IV). Further research with permanent plots and tagged shrubs that compares pre-fire and post-fire vegetation would add to our understanding of the long-term changes in plant community composition in response to different burn regimes.

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CHAPTER 3

Changes in shrub and tree cover in the Hook Lake area meadows between 1973 and 1997

3.1 Introduction

Evidence suggests that open meadows in the Hook Lake area of the Slave River Lowlands (SRL) are becoming increasingly fragmented by shrub and tree encroachment. This evidence is based on aerial photography, local knowledge of the meadows, and historic use of the area for muskrat trapping. It has been suggested that if this trend of shrub and tree expansion within meadows continues, the open meadows will soon be converted to shrubland and closed forest. Evidence of succession on levees in the SRL delta, and of dry grasslands succeeding to closed forest in the nearby Peace-Athabasca delta, suggest a similar process may be underway in the Hook Lake area (English *et al.*, 1995; Jacques, 1990). The sedge and grass meadows of the SRL are primary habitat for the resident Hook Lake bison population. Resource managers and community leaders are concerned about the possible loss and reduced quality of bison habitat (Hook Lake Prescribed Burn Project, GNWT). Effective habitat management for the area requires a better understanding of the spatial and temporal dynamics of shrub and tree establishment in the meadows.

Historical accounts by early travelers support the hypothesis that woody plant cover has increased in the SRL meadows. A very early account by Peter Fiddler of travelling up the Slave River to Slave Lake with members of the Chipewyan tribe in 1792, describes the site where a bison cow was killed as "the edge of a very extensive plain, not a single tree to be seen…it extends probably very near the vicinity of the Slave Lake.." (Crutchfield, 1997). A little more than a century later, in a report from George A. Mulloy to the Department of the Interior in 1911, Mulloy states "At Grand Detour (*immediately south of Hook Lake*), the sloughs become immense hay meadows, ½-2 miles in width and stretching Northwest as far as the eye can see. This immense hay-slough or meadow, as it is falsely called by some people here, is said to run all the way to Resolution, broken only occasionally by clumps of alders and small spruce thickets." (Crutchfield, 1997). Additional reports to the Department of the Interior in 1914, describe the area south of Little Buffalo River as "boggy and flooded deep with water" during the spring (Crutchfield, 1997), suggesting that water levels may have previously acted as a constraint on shrub or tree growth within the meadows. In more recent times, with the gradual drying out of sloughs, willow (*Salix* spp.) dominated shrub communities have increased in extent within the meadows (Hook Lake Prescribed Burn Project, GNWT).

A general drying trend in the SRL area may be linked to long-term climate patterns or down-river changes in the water flow regime resulting from the W.A.C. Bennet Dam in British Columbia. Timoney *et al.* (1997) suggest that climate change or oscillation, as inferred from muskrat returns and fire and flooding cycles, underlies the decades long drying trend observed in the nearby Peace-Athabasca Delta. The Slave River flows north from the delta with the main proportion of its flow originating from Lake Athabasca. Spring runoff in the Peace River has a strong influence on the hydrology of the Slave River (NRBS, 1997). Although the W.A.C. Bennet Dam is approximately 500km upstream from the Slave River Delta, the mean annual peak flows in the Slave River have decreased since the filling of the reservoir (English *et al.*, 1995). Although the degree of change in mean annual peak flow diminishes further down-river, reduced flows are believed to have altered Slave River delta development (English *et al.*, 1995). Little is known about how the drying trend and reduced flows in the SRL might be related to overland flooding and control of woody plant establishment in the meadows.

The pattern of vegetation succession may also reveal information about the mechanism of vegetation change. Nucleation, the phenomenon of individual plant species serving as a focus that facilitates the establishment of other species, can be detected by changes in the spatial pattern of vegetation during succession (Yarranton and Morrison, 1974). When nucleation occurs, the initial establishment of a particular species may be either critical, or beneficial but not necessary for the establishment of subsequent colonizers (Blundon *et al.*, 1993). The frontal advance of a large patch, *e.g.* forest edge, is another spatial pattern of succession. However, the establishment and growth of many small "satellite" plants has been shown in simulation models to occupy space faster, collectively, than a single large expanding focus (Moody and Mack, 1988). Many small, well distributed invasive plants would be expected to coalesce and cover more area in less time than a single patch that is initially larger and grows faster than the satellites (Moody and Mack, 1988). Controlling a shrub invasion of the satellite type can be more effective by directing efforts at the many satellite plants (Cook *et al.*, 1996). Many shrubs will also tend to establish along riparian areas which may offer favorable conditions. Disturbance and seed dispersal by animals concentrating near riparian areas has also been shown to facilitate shrub invasion (Brown and Carter, 1998).

In this study I assess large-scale shrub and tree establishment over a 24 year period in the Hook Lake meadows using remote sensing change detection techniques. I used digitized aerial photographs from 1973 and 1997 to quantify changes in shrub and tree cover within meadows and to interpret qualitatively shrub establishment patterns. Change detection techniques are most commonly used with satellite image data, but some studies have applied these methods to aerial photographs (Mast *et al.*, 1997). Assessing the accuracy of change detection can be difficult and challenging, and to date most studies have refrained from presenting quantitative results, which does not always advance the science for future work (Congalton and Green, 1999). In this project I used a color composite technique that permits both numeric estimates of the area converted from open meadow to shrubs or trees as well as qualitative interpretation of the patterns of shrub and tree establishment in the landscape.

3.2 Objectives

My research objective was to assess large scale shrub and tree establishment and expansion in the Hook Lake area meadows between 1973 and 1997, by determining the relative area occupied by new woody vegetation cover and the main patterns of shrub and tree establishment.

3.3 Methods

3.3.1 Overlaying digital aerial photographs

Corresponding pairs of black and white aerial photographs of the Hook Lake area taken in late June 1973 (1:24,000) and September 1997 (1:20,000) were used to detect landscape-level changes in vegetation cover in meadows. Five meadows were selected for the change detection analysis based on photograph quality and because they were part of the field-based portion of this project (see Chapter 2). The quality of the 1973 photographs was generally very poor, possibly due to several factors such as the time of day or season when the photograph was taken, the angle at which the photograph was taken, or the developing process. This resulted in either poor contrast between vegetation types or bright sunlight reflection spots and dark shadow effects on many of the photographs. The best photographs were selected for analysis and the contrast was improved when necessary by manually enhancing the digital images. The poor photograph quality meant that the emphasis was placed on qualitative rather than quantitative interpretation of the change maps.

Aerial photographs that captured most of the meadow of interest were scanned using a flatbed reflective scanner at 300dpi (1:20,000 photographs) or 375dpi (1:24,000 photographs) for a resulting pixel size of 1.7 meters. A mosaic of two photographs was created to capture the entire area of Al's meadow (Figure 3.1 c). With the exception of Al's meadow, image mosaics were avoided due to variability of reflectance values between single-date images, which had the potential to interfere with change detection threshold values. The digital photographs were saved as bitmaps and imported into PCI (PCI Inc., Richmond Hill, Ontario) as ".pix" format files.

In some cases where the brightness value for a known feature differed between the 1973 and 1997 paired images (*e.g.* water bodies that are black in one set and white in the second set), the feature was manually altered using Adobe Photoshop software. The contrast between herbaceous and woody vegetation types was also slightly modified in most of the images (HK, NP, AN, DN), by selecting problem areas of known vegetation types, *e.g.* wet meadows that were displayed as dark areas or trees that reflected the sunlight, and lightening or darkening as necessary before importing the digital images into PCI. A problem area was defined as an area that had a high potential to be misclassified based on its brightness values. Problem areas were traced and selected on screen and brightened or darkened as necessary, an attempt was made to keep all photograph-manipulation to a minimum.

Within the GCP Works component of PCI, matching images from 1973 and 1997 were registered to each other by collecting uncontrolled ground control points (GCP) on both images. The 1973 photograph was considered the georeferenced image and the 1997 photograph was the uncorrected image. The two images were displayed on the screen beside each other and individual shrubs or small shrub clumps that were visible in both images were manually selected as ground control points. A minimum of 10 GCP's were identified for each pair of images. The 1997 image was registered to the 1973 image using a second order cubic re-sampling model. Cubic convolution resampling provides a sharper image than the nearest neighbor method (Lillesand and Kiefer, 1994).

Detection of changes in vegetation cover was achieved by registering the 1973 image in the red plane to the 1997 image in the green plane, to create a red-green composite (see Heeramen *et al.*, 1993). Within GCPWorks, this is achieved by selecting the first channel on the earlier 1973 image which is automatically assigned the red color gun, and selecting the second channel on the 1997 image, which is automatically assigned the green color gun. The combination of the red and green in the final change image (map), results in varying shades of red, green, yellow, and black. Pixels with a high intensity red color have a high digital numeric value (0 – 255 levels) and indicate a change from herbaceous cover in 1973 to woody cover in 1997.

3.3.2 Determining threshold values

A digital numeric value threshold representing areas changed from herbaceous meadow (bright red) in the 1973 image to shrubs or trees (dark green) in the 1997 image, was determined by sampling the "change pixels" in Imageworks (PCI). The range of digital numeric values representing a change from herbaceous to woody cover, was determined as follows: 1) locating red areas within meadows on the change maps, 2) verifying a herbaceous to woody cover change by referring to the original photographs, 3) plotting the digital numeric values of "true change" pixels as (x, y) coordinates (x = red channel, y = green channel), and 4) identifying the upper and lower limits of the digital numeric values on the plots, at sample sizes of $\underline{N}$ = 30, 60, and 120. A threshold range was determined separately for each of the five meadow samples because the spectral quality of each photograph could differ in response to several factors: the time the photograph was taken, the direction of the flight path, and film processing.

3.3.3 Calculating changes in herbaceous to woody vegetation cover

The multi-layer modeling command in XPACE (PCI) was used to create a separate binary image of each of the five meadows, containing only those pixels with digital numeric values within the threshold range. Since the five meadow images all contained a portion of the surrounding forest matrix, a separate classification report was calculated for eight smaller samples, $2.25 km^2$ in area, that were extracted from areas within the meadow images and did not include forest matrix. A 1.5 km x 1.5 km square was selected because it was large enough to contain the smallest meadow (AL) while also excluding most of the surrounding forest. By excluding the forest matrix, the samples were more comparable by having a similar proportion of the image that had the potential to change from herbaceous to woody cover. The area of change within each of the binary images was then calculated using the Multispectral-MLR Classifier Report option in XPACE. The number of pixels, area in square meters, and percent of the total image, that changed from herbaceous meadow to woody cover between 1973 and 1997 was calculated. A mode filter was passed over the image using a 5 x 5 pixel size window. The mode filter calculates the mode of the grey digital numeric values surrounding the pixel and adjusts the numeric value of the center pixel to be more similar to its neighbors, thereby replacing small "island" themes by the larger surrounding theme. The area of change was calculated on the filtered maps as it was with the unfiltered maps. Both the change maps and binary images were studied for patterns in woody vegetation establishment.

3.4 Results

3.4.1 Accuracy of image registration

As noted above a minimum of ten ground control points (GCP's) were used to register the 1997 image to the 1973 image. The Root Mean Square error (RMSE) terms were generated from the GCP residual errors in GCPWorks after the images were registered (Table 3.1). The average RMS error was 2.09 for the X coordinate and 2.37 for the Y coordinate. The RMS error ranged from 0.98 to 3.27 for the X coordinate and 1.11 to 5.25 for the Y coordinate. An RMS error term of less than 1 pixel is recommended for remotely sensed data (Bernstein *et al.*, 1983; Jensen, 1986). An effort was made to reduce the RMSE error in each of the five pairs of images by removing and re-selecting GCP's. However, because shrubs and trees were used as the GCP's, and there was 24 years between the images, there was a limited number of potential GCP's. Jensen et al. (1987) had similar difficulties reducing the RMSE in their image-to-image registration using aircraft Multispectral Scanner data. Eventually they were able to reduce the RMSE from 5.0 with 97 GCP's, to 2.26 using 87 GCP's after dividing the image into four separate sections. RMSE terms greater than 1 pixel are not uncommon when aerial photographs are co-registered but they must be taken into consideration when interpreting the results (Brown and Arbogast, 1999; Kitzberger and Veblen, 1994).

3.4.2 Interpretation and classification of change maps

Interpretation was based on a visual comparison of the color-composite change maps (Figures 3.1 a – e) with the original air photographs. The goal was to identify areas that had herbaceous meadow cover in 1973 and woody vegetation in 1997. Changes from meadow (bright, light red) to woody cover (dull, dark green), appear in the change map as red to burgundy pixels (Figures 3.1 a-e). Meadow areas in both time periods appear as yellow-orange in the resulting change maps, and areas that have woody vegetation cover in both images appear dark grey to black in the change maps. Green areas on the final change maps represent a change from a darker green in 1973 to lighter red in 1997, suggesting "new meadow", but the original aerial photographs show little to no conversion of wood cover to herbaceous cover between the two dates, which would be seen in the color change maps as bright green (low red value in 1973 image and high green value in 1997 image). The green areas on the change maps represent differences in brightness intensity within a vegetation cover type between the two dates. Bright green areas within meadows on the change maps often indicate a change from a very wet meadow, with standing water, in 1973 to a drier meadow in 1997. For the purpose of assessing shrub establishment, I focussed interpretation and analysis on the red component of the color change maps that represented new shrub or tree cover since 1973. Any further reference to vegetation change applies to meadow to woody cover change only.

3.4.3 Threshold range

The threshold of digital numeric values representing a change from herbaceous to woody cover was determined independently for each of the five meadow images. The threshold ranges (see Table 3.1) differed only slightly between each of the five change images. Figures 3.2 a-o, illustrate the distribution of digital number values on the red and green channels for those pixels representing a herbaceous to wood cover change. The threshold range was estimated at three sample sizes, based on the digital number value plots, to ensure an adequate sample size. The threshold range changed only slightly for three of the five meadows when the sample size increased from 60 to 120. The threshold on channel 2 of Al's meadow (AL) increased from 0-90 to 0-100, channel 2 of North meadow (NP) increased from 0-80 to 0-90, and on Ann's meadow (AN), channel 1 increased from 160-255 to 115-255 and channel 2 increased in range from 25-125 to 15-130. The slight increase with increasing sample size suggests a representative sample at $\underline{N}$ = 120. The final threshold range was estimated from the change value plots with $\underline{N}$ = 120, where the upper and lower limits of the digital numeric values, excluding outliers, became the threshold values (Table 3.1).

3.4.4 Quantitative changes in shrub cover

The area representing a change from herbaceous cover to woody cover was calculated for each of the five meadows. The Hook meadow image (HK) had the largest proportion of herbaceous to shrub change pixels of all five meadows, 21%, followed by Ann's meadow (AN) 11%, Al's meadow (AL) 10%, North meadow (NP) 10%, and Dan's meadow (DN) 4%. The total area (m^2) representing a change from herbaceous meadow to woody cover for all five change images is summarized in Table 3.1. Figures 3.3 a-e are threshold maps that show only those areas from the change maps that are within the threshold range; *i.e.*, represent a change from meadow to woody cover. It is apparent from the threshold maps that a large number of pixels within the surrounding forest areas were within the threshold range for pixels classified as shrub establishment pixels.

The total area (m^2) of change and proportion of the area that changed in each of the eight 2.25 km^2 samples within the five meadows was calculated (Table 3.2). The threshold maps of the eight sample areas reveal patterns of woody vegetation growth across the meadow landscape (Figures 3.4 a-h). The approximate proportion of change pixels within the whole meadow sample is similar to that of the corresponding 2.25 km^2 sample (Tables 3.1 and 3.2). The eight samples do indicate some variability in the proportion of change pixels within different areas of the same meadow. For example 21% of the Hook meadow map was classified as change, while the two sub-samples Shk1 and Shk2, taken from within it, show 20% and 13% of the image as change pixels. Samples for Ann's meadow, San1 and San2, were calculated to contain 8% and 17% change pixels, while the meadow image AN had 11% change pixels. Samples from the remainder of the meadows, Sal1 (AL), Snp1 (NP), Snp2 (NP), and Sdn1 (DN), contained 6%, 11%, 7%, and 4% change pixels, respectively.

The 5 x 5 pixel mode filter did not have a strong influence on the area of change that was detected. The filter eliminated much of the noise from the images that was likely due to the high registration error but the proportion of change area calculated in the filtered images differed only by 1 - 3 % from that of the unfiltered images (Tables 3.1 and 3.2).

Stow *et al.* (1990) found that applying a "majority" moving window filter increased change detection accuracy and reduced commission errors.

3.4.5 Trends in shrub establishment

The change maps and threshold maps reveal patterns of shrub/tree establishment in each of the five meadows. Observation of the color-composite change maps (Figure 3.1 a-e), show that a large proportion of new woody vegetation established within the meadows, not just along the forest-meadow edge. Both large and small patches of new shrubs and trees occur within the meadows. Certain areas within meadows (*e.g.*, along creeks or the edges of sloughs) appear to have been more prone to shrub establishment than others. The relevance of these different patterns in shrub establishment will be discussed.

Table 3.1 Summary of change detection results of five meadows in the Hook Lake region of the SRL

	HK	*AN*	*AL*	*NP*	*DN*
Area (km)	4.1 x 4.0	3.4 x 3.6	4.6 x 3.6	3.8 x 4.2	3.3 x 2.5
Total m^2	17029615	12303684	16674486	16092180	8269735
Change m^2	3558694	1402690	1698361	1669241	365539
% image	**21%**	**11%**	**10%**	**10%**	**4%**
% filtered image	**19%**	**10%**	**7%**	**9%**	**3%**
Threshold -Red	125-255	115-255	150-225	140-245	150-240
-Green	<100	<125	<100	<90	<105
RMS error (pixel)	2.3, 5.3	3.3, 2.9	2.4, 1.2	1.0, 1.4	1.5, 1.1
RMS error (m)	3.9, 8.9	5.6, 4.9	4.2, 2.0	1.2, 2.5	2.5, 1.9

Table 3.2 Summary of change detection results in eight 2.25 km^2 samples within five meadows in the Hook Lake region. Threshold ranges and RMS error terms are given in Table 3.1 under respective meadow samples. "Change" means herbaceous to woody vegetation cover.

	Shk1	*Shk2*	*San1*	*San2*	*Sal1*	*Snp1*	*Snp2*	*Sdn1*
Meadow	Hook	Hook	Ann	Ann	Al	North	North	Dan
Change m^2	458501	301901	174345	389586	138879	245378	160213	99344
% image	**20%**	**13%**	**8%**	**17%**	**6%**	**11%**	**7%**	**4%**
% filtered image	**20%**	**12%**	**7%**	**14%**	**4%**	**10%**	**6%**	**3%**

Figure 3.1 a (Facing page) Color composite change map of co-registered 1973 and 1997 aerial photographs of Hook Meadow (HK) in the Slave River Lowlands, Northwest Territories.

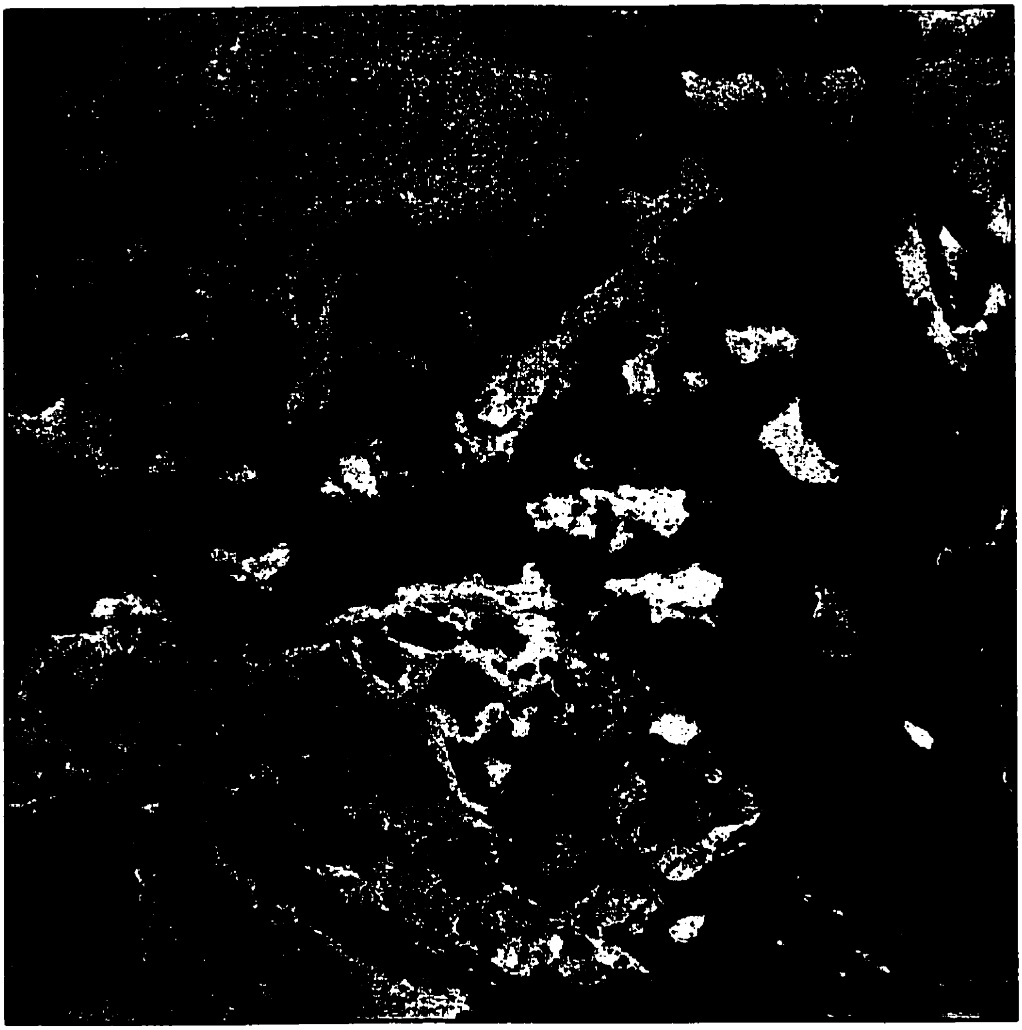


Figure 3.1 b (Facing page) Color composite change map of co-registered 1973 and 1997 aerial photographs of Ann's Meadow (AN) in the Slave River Lowlands, Northwest Territories.

Figure 3.1 c (Facing page) Color composite change map of co-registered 1973 and 1997 aerial photographs of Al's Meadow (AL) in the Slave River Lowlands, Northwest Territories.

Figure 3.1 d (Facing page) Color composite change map of co-registered 1973 and 1997 aerial photographs of North Meadow (NP) in the Slave River Lowlands, Northwest Territories.

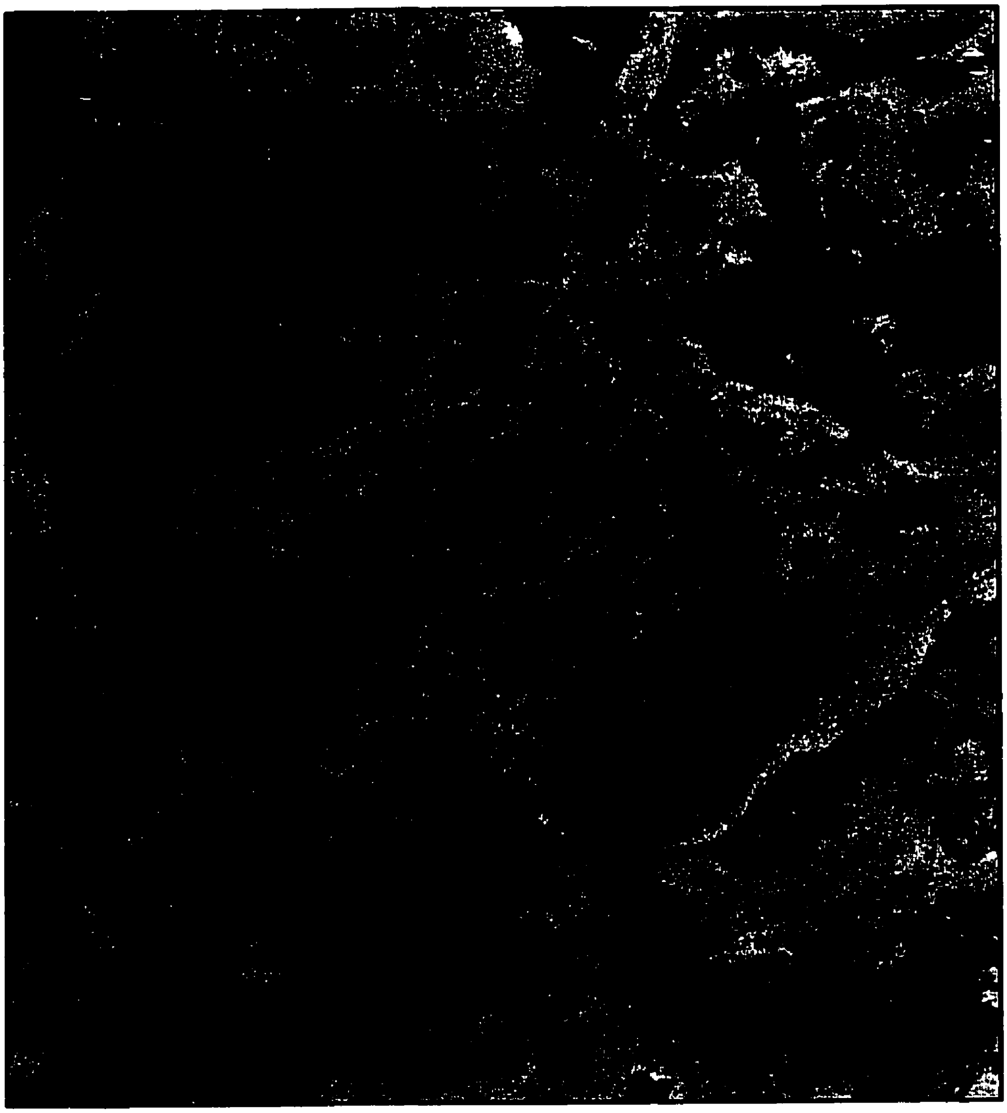


Figure 3.1 e (Facing page) Color composite change map of co-registered 1973 and 1997 aerial photographs of Dan's Meadow (DN) in the Slave River Lowlands, Northwest Territories.

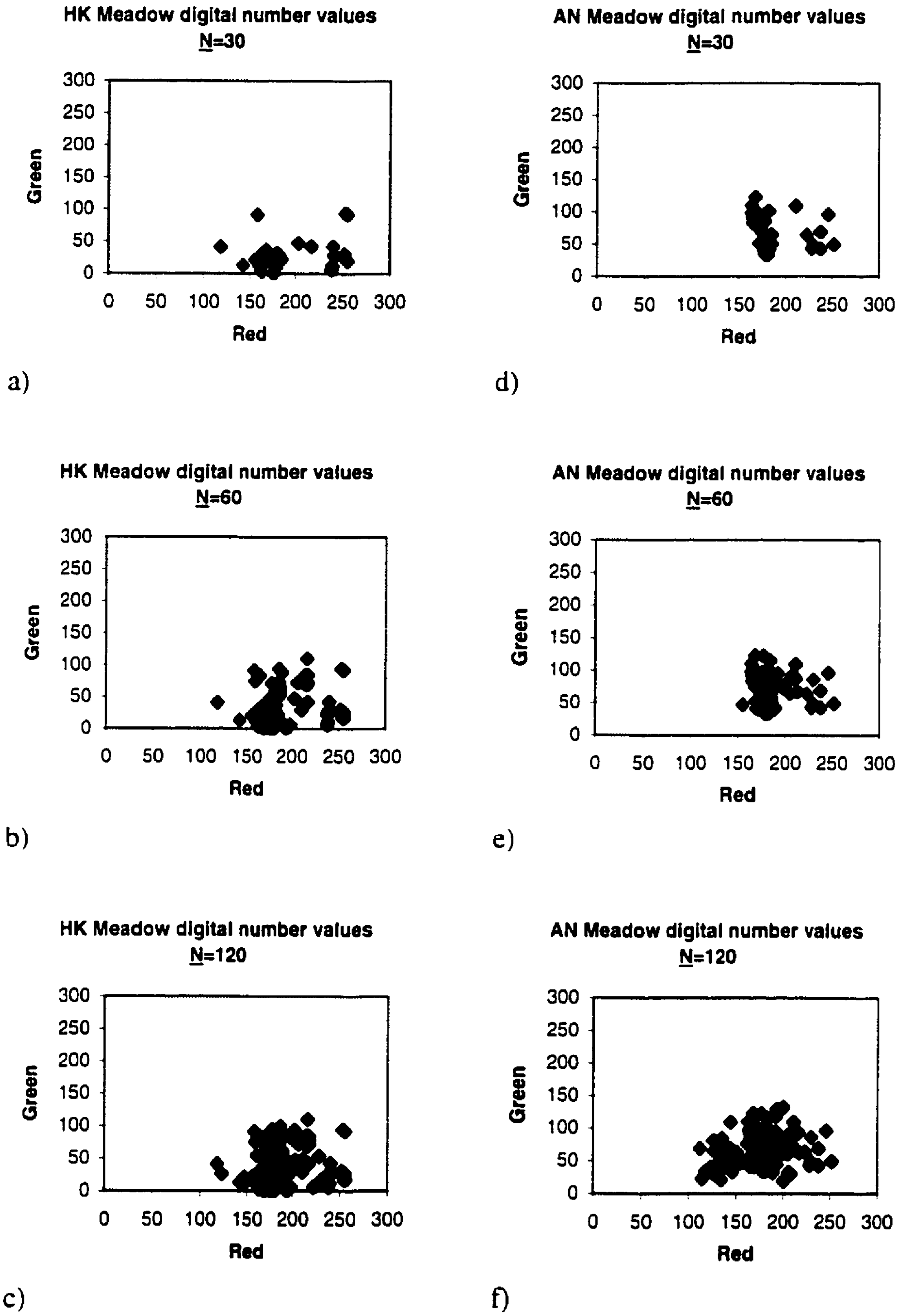
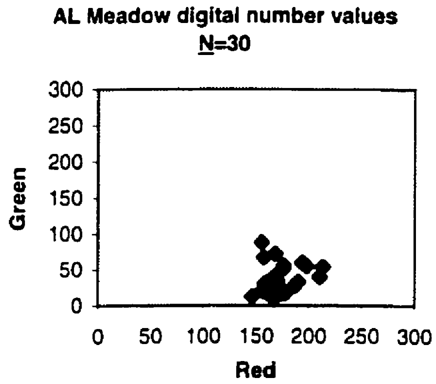
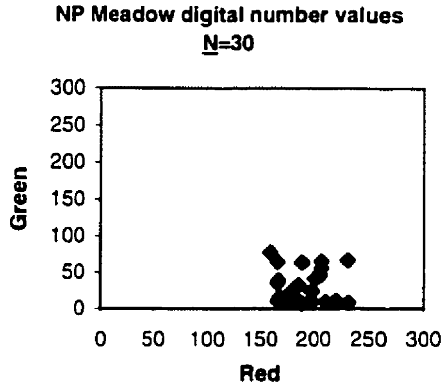


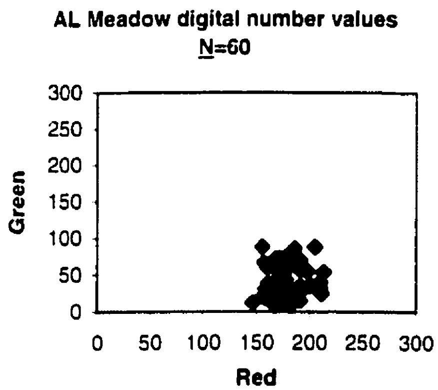
Figure 3.2 (a - p) Threshold plots of digital numeric values for pixels representing areas that changed from herbaceous cover to shrub or tree cover. Sample size refers to the number of pixels (N = 30, 60, and 120).


AL Meadow digital number values
N=30
Green
Red
0
50
100
150
200
250
300

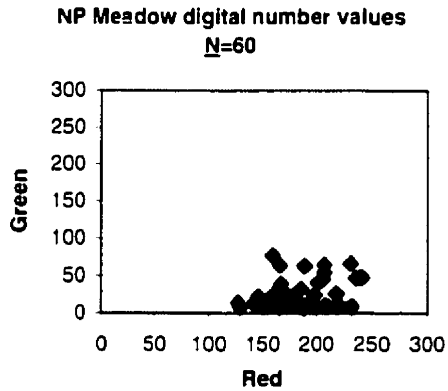
g)


NP Meadow digital number values
N=30
Green
Red
0
50
100
150
200
250
300

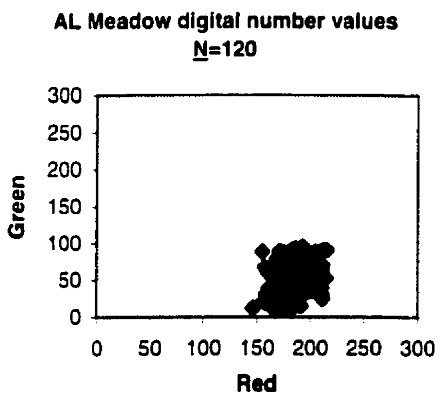
j)


AL Meadow digital number values
N=60
Green
Red
0
50
100
150
200
250
300

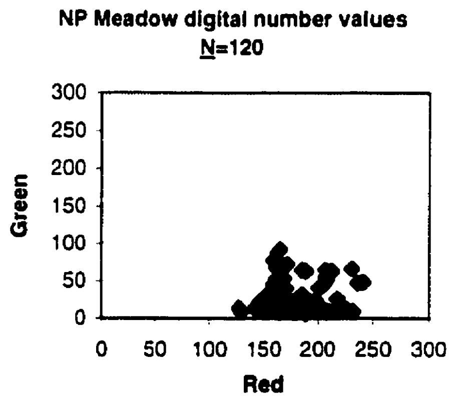
h)


NP Meadow digital number values
N=60
Green
Red
0
50
100
150
200
250
300

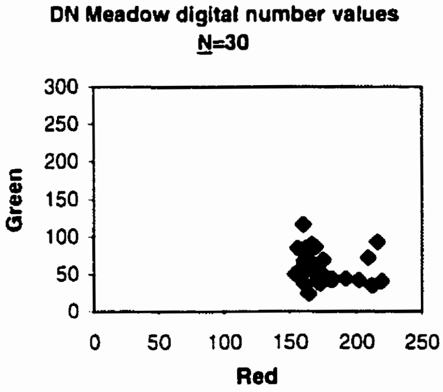
k)


AL Meadow digital number values
N=120
Green
Red
0
50
100
150
200
250
300

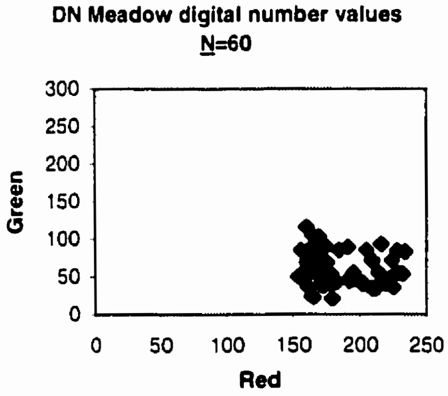
i)


NP Meadow digital number values
N=120
Green
Red
0
50
100
150
200
250
300

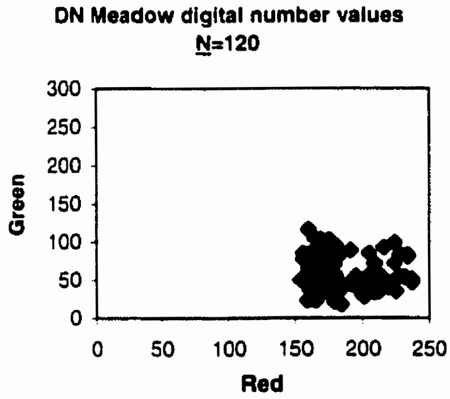
l)


DN Meadow digital number values
N=30
300
250
200
150
100
50
0
Green
0
50
100
150
200
250
Red

m)


DN Meadow digital number values
N=60
300
250
200
150
100
50
0
Green
0
50
100
150
200
250
Red

n)


DN Meadow digital number values
N=120
300
250
200
150
100
50
0
Green
0
50
100
150
200
250
Red

o)

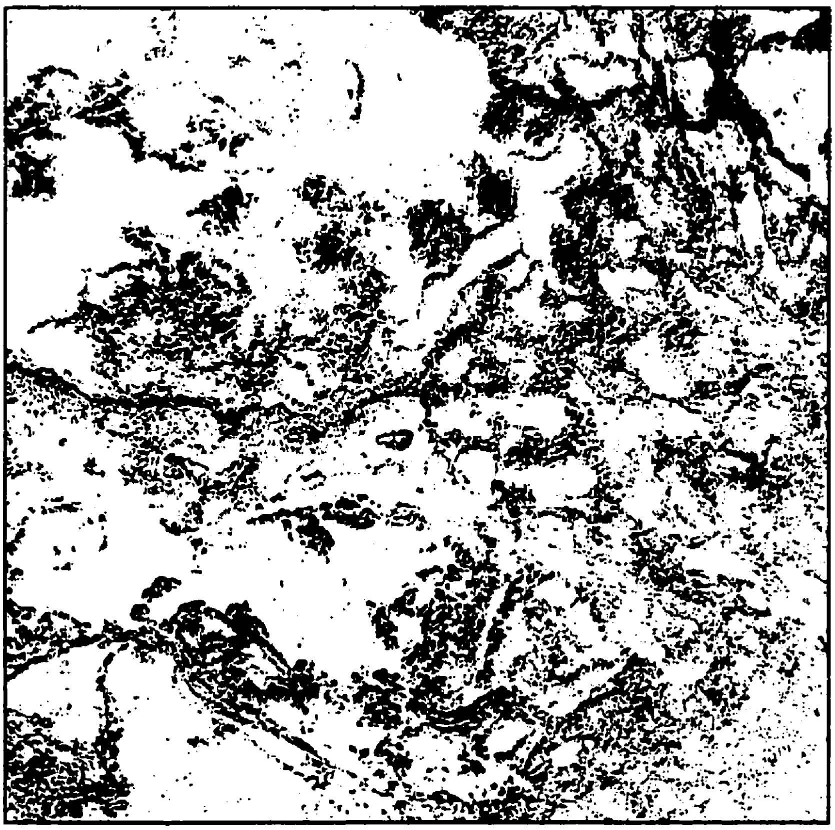


Figure 3.3 (a) Threshold map of Hook meadow (HK) displaying area classified as new shrub and tree cover since 1973.

Figure 3.3 (b) Threshold map of North Meadow (NP) displaying areas classified as new shrub and tree cover since 1973.

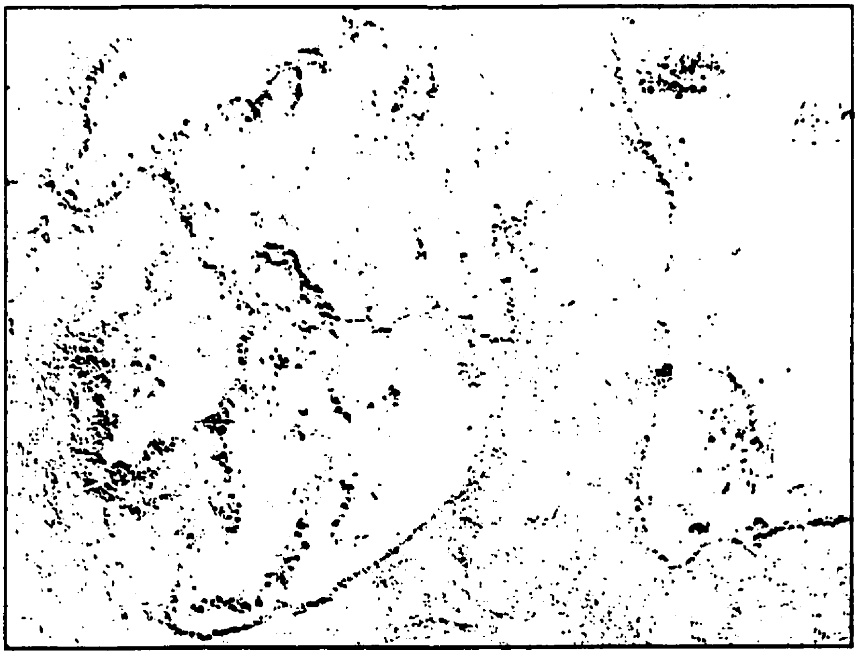


Figure 3.3 (c) Threshold map of Dan's Meadow (DN) displaying areas classified as new shrub and tree cover since 1973.

Figure 3.3 (d) Threshold map of Ann's Meadow (AN) displaying areas classified as new shrub and tree cover since 1973.

Figure 3.3 (e) Threshold map of Al's Meadow (AL) displaying areas classified as new shrub and tree cover since 1973.

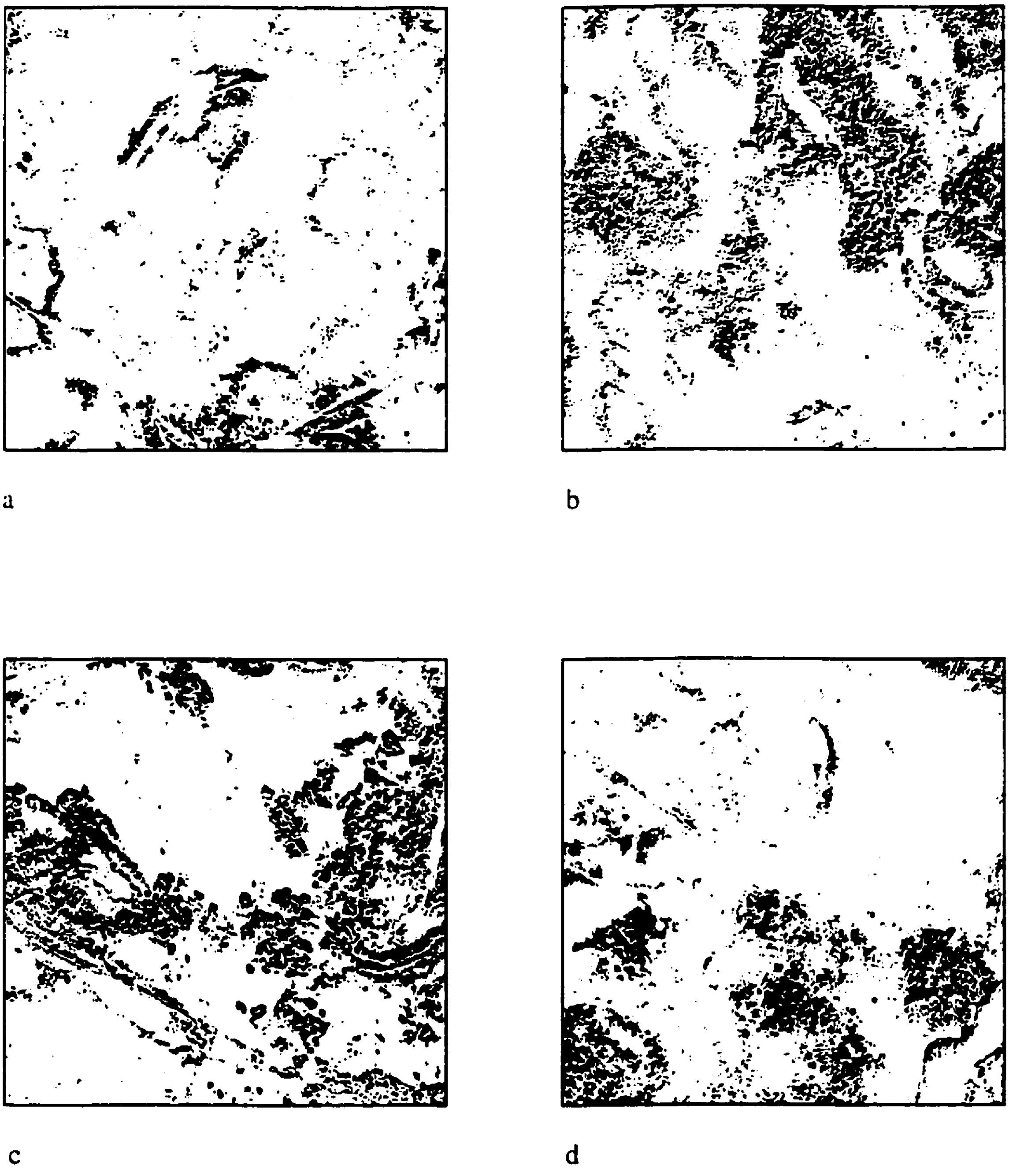
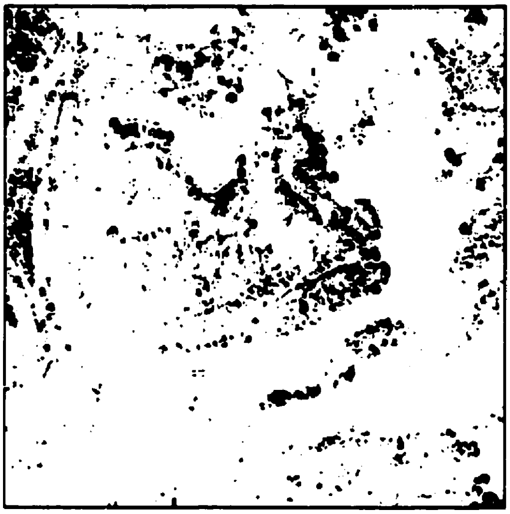
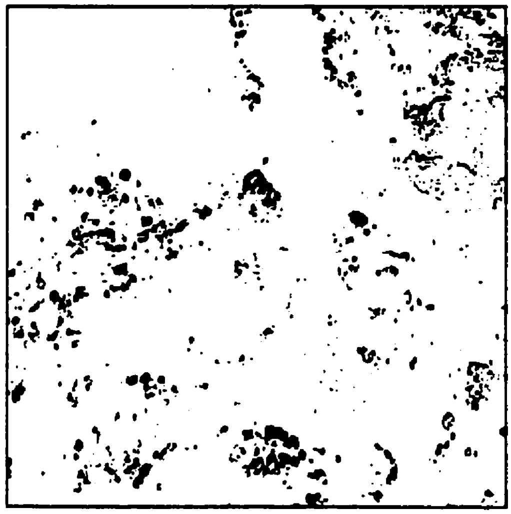


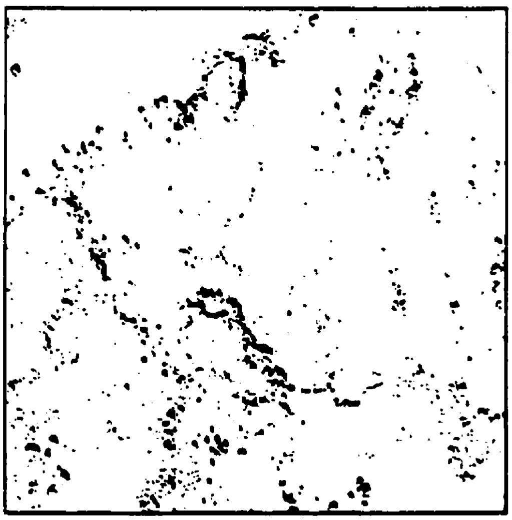
Figure 3.4 (a – d) Threshold maps of 2.25 km^2 samples from within five meadows in the Hook Lake area, displaying areas classified as new shrub of tree cover since 1973. a) Ann's Meadow – San1, b) Ann's Meadow – San2, c) Hook Meadow – Shk1, d) Hook Meadow – Shk2



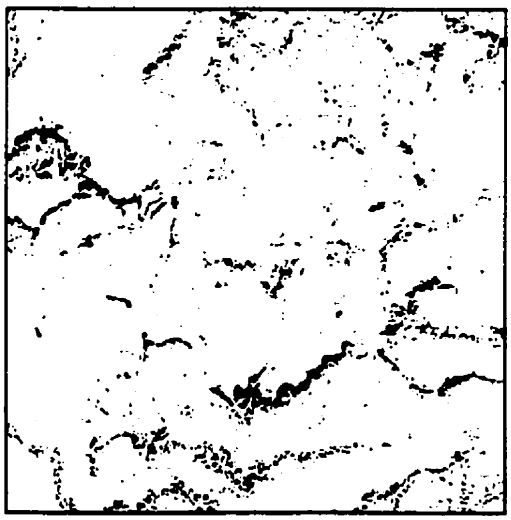
e



f



g



h

Figure 3.4 (e - h) Threshold maps of 2.25 km^2 samples from within five meadows in the Hook Lake area, displaying areas classified as new shrub of tree cover since 1973. e) North Meadow – Snp1, f) North Meadow – Snp2, g) Dan's Meadow – Sdn1, h) Al's Meadow – Sal1.

3.5 Discussion

3.5.1 Change detection accuracy

The poor quality of the 1973 aerial photographs reduced both the accuracy of co-registration of the time sequence images and the post-registration classification of herbaceous to shrub change pixels. Change detection with digital images requires that radiance differences due to actual differences in the object scene be large relative to radiance differences due to other factors for good signal to noise ratios (Singh, 1989). However, many of the 1973 photographs did not have distinct digital numeric values associated with the vegetation types. There was a fairly large overlap in the digital numeric values (intensity of grey) between the herbaceous and woody vegetation types, some of this overlap may be attributed to shadow effects or the film developing process. In general, herbaceous vegetation was light grey and woody vegetation was dark grey to black in all photographs, but in certain areas of the 1973 photographs, forest edges and interior forest areas have bright spots that have high grey digital numeric values in the images. For this reason, some of the superficially bright areas were manually darkened using Adobe Photoshop (version 5.0) software.

Shadow effects in both sets of aerial photographs also interfered with the robustness of change detection but the nature of the problem did not lend itself to manual correction. The shadows cast by taller trees and shrubs in both the 1973 and 1997 aerial photographs tended to vary in size and direction, both within the 1973 photograph-set and between the 1973 and 1997 photograph-sets, possibly a result of the photographs being taken during different seasons (spring and early autumn) or different times of the day, or different flight paths. The opposing shadows introduce further error into the change detection process because a dark shadow over a light meadow would produce similar digital numeric values as a shrub in 1997 over meadow in 1973, both would seem to represent a change from herbaceous to woody cover.

A crucial step in change detection with digital images is accurate registration (Lillesand and Kiefer, 1994). The cubic convolution re-sampling model that was used in this project is the most accurate model currently available. However, the lack of fixed reference points in the SRL landscape left only large shrubs, trees or shrub/tree clusters that were present in both 1973 and 1997 to be used as ground control points (GCP's) in the registration process. Differences in the size of the GCP's resulting from tree growth over the 24 year time period and slight differences in scale between the two sets of photographs made precise selection of the central pixel of the shrubs/trees difficult. Aircraft imagery may also have more inherent distortion that is less easily corrected for than that in satellite imagery. Jensen *et al.* (1987) list important differences between aircraft and satellite remote imagery that can have a strong influence on registration accuracy. They describe how images from relatively stable satellite platforms tend to have only small systematic distortions that are easily corrected compared to distortions in images taken from a plane in which minor turbulence and variations in speed and altitude tend to create less systematic distortions over smaller areas. Furthermore when two aircraft images are co-registered both contribute distortion to the registered image. Despite the problems presented above, aerial photographs may be the most appropriate source of data depending on the object being studied, for example when a high resolution, historical perspective is required (Brown and Arbogast, 1999).

Image-to-image registration of aerial photographs in this project resulted in a high residual mean square error (RMSE) (see Table 3.1). Even with high-quality time sequence photographs taken in the same season and at the same altitude, accurate registration may not be possible, but the general trends of changes may still be quite informative. In a change detection study using aerial photographs that were taken at approximately the same time of day, in the same season, at the same altitude and similar airplane position, Kitzberger and Veblen (1999), still had significant co-registration errors. The high RMS errors tempered the interpretation of their results but did not prevent them from detecting major structural changes in the landscape that contributed to their understanding of the spatio-temporal vegetation dynamics at a forest-grassland ecotone. As a result of the high RMS error in the present study, only general trends in the change maps are interpreted.

A 5 x 5 pixel moving window mode-filter was applied to each of the output change images to minimize small rectification errors however the filter did not substantially alter the estimates of area changed. The filter may have reduced both omission and commission errors but it also has the effect of removing smaller, isolated areas of change. Additionally, small individual shrubs or trees less than 1.7 m in diameter (the resolution of the digital images) would have been eliminated from the change detection analysis from the beginning. A large proportion (76 %) of the willow (*Salix* spp.) shrubs sampled in the field study component of this project (N = 1198, see Chapter 2) had a width less than 1.7 m. The scale at which the change detection analysis was performed may have resulted in a significant proportion of new shrubs and trees that went undetected. The spatial distribution pattern of smaller shrubs and trees that escaped this analysis may identify areas of more recent shrub and tree establishment with a high potential for expansion.

3.5.2 Increases in shrub and tree cover

Calculations of the change area at both the meadow (mean 14 km^2) scale and 2.25 km^2 sample scale, indicate an increase in shrub/tree area on each of the five meadows. These results confirm earlier speculation of shrub expansion in the SRL meadows. Field studies in 1997 confirm that shrubs of the genus *Salix* are dominant in the Hook Lake area (see Chapter 2). One of the characteristics of *Salix* is to thrive in changing environments. Argus (1973), provides a detailed comparison of *Salix* characteristics with Erendorfer's type 1 colonizer, which occurs in "labile successional stages or open facies of otherwise more or less closed associations". The ecological, reproductive, and evolutionary characteristics of *Salix* interact to create a highly successful colonizer (Argus, 1973). *Salix* are most successful on "unstable" landscapes; the SRL is a dynamic landscape, subject to overland flooding and large herbivore interactions.

Climate patterns may influence the establishment of woody vegetation in grasslands. In a study of tree invasion in a pine/grassland ecotone, Mast *et al.* (1997) determined that periods of favorable climate conditions for seedling establishment corresponded with increased rates of tree invasion. Williams and Hobbs (1989) found that the invasion of *Baccharis pilularis* shrubs in grasslands in San Francisco Bay area was strongly influenced by temporal precipitation patterns. Survival of *Baccharis pilularis* seedlings was highest when spring rainfall continued into warmer spring months, sustaining the seedling while the roots grew deep before the hot and dry summer months. In western North America, oscillations in the climatic regime appears to support the episodic establishment of different plant life forms over time (Neilson, 1987) and climate trends may play an important role in willow establishment in the SRL.

Timoney *et al.* (1997) provide evidence that the nearby Peace-Athabasca delta is currently experiencing a decades-long drying trend that likely results from climate change or oscillation. Gradual drying of wet or moderately wet meadows over a long time period may improve soil drainage and facilitate the establishment of willows. On perched basins in the Peace-Athabasca delta, Dirschl *et al.* (1974) reported that *Calamagrostis* meadows were replaced over time by *Salix planifolia* willow communities and that as soil drainage improved, *Salix bebbiana* began to dominate. In a summer field study in 1998, I found *Salix bebbiana* to be the most dominant species of willow in the moderately dry Hook Lake area meadows of the SRL (see Chapter 2). If the drying trend continues, shrub and tree cover would be expected to increase in the SRL meadows.

Reduced frequency of overland flooding in the meadows may also contribute to improved drainage and willow establishment. Overland flooding of perched basins in the Peace-Athabasca delta has been shown to occur less frequently since the construction of the

W.A.C. Bennet Dam in 1967, while willow shrublands were shown to increase from 10.4% to 25.5% between 1976 and 1989 (Jacques, 1990). The spring runoff of Peace River is a major influence on the hydrology of the Slave River (NRBS, 1997). In the Slave River Delta there has been a general shift to increased cover of *Salix* spp. and *Alnus* spp. assemblages, indicative of drying in a normally wet environment (NRBS, 1997).

Anecdotal evidence suggests that overland flooding has also decreased in the SRL. North meadow (NP), which saw an increase in shrub cover in this study, is called "Rat Lake" by many of the elders in Ft. Resolution (Pete King, pers. comm.). A smaller meadow located immediately north of this one is called Big Rat Lake. The names refer to the size of muskrats that were trapped there during the 1930's and 1940's (T. Unka, pers. comm.). Drying out of sloughs and ponds is believed to have begun sometime in the 1940's. People used to camp at a site called 'Spruce Island' when they trapped muskrats on North Prairie (NP, also called Little Rat Lake) during the 1940's (T. Unka, pers. comm.). Flooding records for the Hook Lake area meadows were not available. There is no record of overland flooding of the Hook Lake meadows since the 1950's.

The fire history of the SRL may also influence vegetation dynamics. Fire is known to reduce shrub cover in many grassland systems. Aboriginal burning practices in northern Alberta and possibly further north were common until the 1940's (Lewis and Ferguson, 1988) and summer fires caused by lightening are a relatively common occurrence in the boreal forest. Evidence of a fire more than ten years old was observed on Dan's meadow (DN) during the 1998 field season and natural ignition resulted in most of North meadow

(NP) burning in August 1998. Fire may play an important role in structuring vegetation in the SRL meadows, but in the absence of major changes to the burning regime, it is unlikely that fire alone is the major constraint on shrub establishment in this system.

Fewer bison in the Hook Lake population has also been suggested as a contributing factor of increased willow cover (Hook Lake Prescribed Burn Project, GNWT). The population of bison in the Hook Lake area has declined from approximately 1900 in 1971 (Van Camp and Calef, 1987) to about 180 in 1987 (GNWT files). During the 1990's the population has varied in size between 200 and 450 (C. Gates pers. comm.). While willow has been shown to be an important component of wood bison's diet in the Mackenzie Bison Sanctuary (Larter and Gates, 1991), it is not a major dietary component for the Slave River Lowland bison population (Reynolds et al., 1978). In a survey of willow shrubs in the Hook Lake area, conducted in 1998, I observed very little evidence of browsed willows.

3.5.3 Patterns of shrub establishment

Results of this study include differences in the amount and patterns of shrub establishment among the five meadows. A range from 4% to 21% of changed area was calculated from the change maps. These differences could be attributed to a variety of interacting factors. In a study examining forest expansion into grassland, spatial variation in establishment was attributed to geomorphology, topography and also management practices (Knight *et al.*, 1994). Landscape elements may influence shrub and tree establishment patterns in the SRL.

In the Hook Lake area meadows, it is possible that soil moisture heterogeneity across the landscape may influence shrub establishment patterns. Fewer shrubs occur on very wet or very dry meadows (personal observation). Disturbance or grazing by bison might also affect shrub establishment patterns. In the lower-right corner of the HK meadow change map (Fig. 3.3.2 a), the remnants of an old circular corral are visible. Shrub establishment is particularly high within the corral area, possibly as a result of the high levels of disturbance or nutrients associated with the bison. Sample Shk1 (Fig. 3.4 c), which includes a portion of the corral, had the highest proportion of change, 20% among the eight sample areas.

The change maps and threshold maps highlight the patterns of shrub and tree establishment on the meadows. On HK meadow (Fig. 3.1 a), several shrub establishment patterns are apparent, including along forest edges, along abandoned stream channels, and in large clumps within the meadows. On NP the general pattern of establishment is somewhat different, with smaller shrub clusters and individual shrubs relatively evenly distributed within the meadow. In the smaller, AL meadow, Fig. 3.1 c shows the majority of new shrubs establishing along the meadow-forest edge. DN meadow, which is located just west of NP, shows a pattern of shrub establishment similar to NP, with many smaller shrub clusters and individual shrubs establishing within the meadow. The southwest corner of DN shows a relatively high level of establishment (Fig. 3.1 e). On AN, there appears to be a small proportion of shrubs establishing along the forest edge and in both small and large clusters within the meadow. A large patch of new shrubs appears in the top right corner of Fig 3.1 b and there also appears to be new shrub growth along several creeks.

Figures 3.4 a-h, show just the change pixels occurring within the eight 2.25 km^2 samples from within meadow areas and illustrate the high degree of variability in both the patterns presented above and the total amount of shrub and tree establishment within the different meadows. Smaller, more evenly distributed patches of new shrubs and trees can be seen on each of the five meadows, but are most apparent on three of the five, NP, DN and AN. The presence of many small isolated shrubs and trees may lead to a future increase in the rate of expansion of shrubs and trees in the landscape.

The predominant pattern of shrub establishment on a meadow may be an important factor influencing the rate of spread of shrubs within the meadow. If a large patch of shrubs initially has the same area as the collective area of many small isolated shrubs, and they all grow at the same rate, then the isolated shrubs can be expected to occupy more area faster than the single large patch (Mack, 1985). In an area of the Konza Prairie Research Natural Area in Kansas, where forest was shown to increase from 157 ha to 241 ha in area between 1939 and 1985, there was both an increase in the total number of patches and a decrease in the mean size of forest patches (Knight *et al.*, 1994).

Knowledge of the predominant pattern of shrub and tree establishment could aid in understanding the mechanisms involved and improve control efforts. In a simulation model of plant invasions that spread from both large focal patches and satellite plants, Moody and Mack (1988) found that control measures were greatly improved by destroying even 30% of the satellites. Their model suggests that control efforts must also be directed at smaller nascent foci within the landscape matrix. In the Hook Lake area meadows, small isolated patches of new shrubs and trees are visible in the change maps. Also, a large number of shrubs with diameters less than 2 m went undetected in the change detection analysis. Further studies with higher resolution data might identify areas of more recent and extensive establishment of shrubs in the Hook Lake area meadows that might be important target areas for effective control.

3.6 Conclusions and further research

On average 11% of the sampled meadow areas had newly established shrubs or trees since 1973. Both the amount of shrub and tree establishment and the dominant pattern of establishment varied among the five meadows studied. Much remains to be understood about the vegetation dynamics of shrub and tree expansion in the SRL meadows. A more traditional approach to change detection that involves post-classification change detection of digitized polygons representing the different vegetation types might improve change detection accuracy. This approach would be quite time consuming if one wanted to detect changes at a small scale that included small shrub clusters and individual shrubs, but may result in a more robust spatial database that could be added to and readily analyzed to test the influence of other factors, such as soil moisture, slope, proximity to water bodies, proximity to forest edge, etc., on shrub establishment rates. Ongoing monitoring of large-scale vegetation changes with high resolution remote imagery to measure the rates of change over discrete time periods could reveal important temporal patterns in shrub and tree establishment (see Yool *et al.*, 1997).

3.7 References

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CHAPTER 4

General conclusions and further research

The vegetation dynamics of the SRL meadows are complex and require further research. The combined results of the field-based study and historic aerial photograph image analysis indicate that some of the Hook Lake area meadows have experienced extensive woody plant establishment in recent years and that spring-lit fires alone may not be effective at maintaining the high-quality, meadow habitat preferred by bison. Specific conclusions that are drawn from this study are presented below and their implications for management follow.

4.1 Changes in woody vegetation cover

Change detection analysis of black and white aerial photographs of the Hook Lake area in 1973 and 1997 reveals large areas that have changed from herbaceous to woody cover during that time period. Succession of the meadows to shrubland and forest appears to be occurring. High error terms associated with the registration of the time-sequence images prevents conclusive statements about the absolute amounts of change and therefore, the following numbers are presented as approximate estimates. An average of at least 11% of the sampled meadow area in 1997 had woody vegetation cover new since 1973. The amount of new woody vegetation cover in eight 2.25 km^2 samples, varied from a low of 4% to a high of 20%. The differences in the amount of change between these meadows may reflect differences in large-scale environmental conditions between the meadows.

Variation in new woody vegetation cover was also apparent within meadows. Several patterns of shrub and tree establishment within meadows were revealed by the time-sequence images. While forest advance appears to be operating to a small degree in all five of the meadows, three of the five meadows had many small patches and individual shrubs in a random to clumped distribution within the meadows. "Satellite" patches of shrubs and isolated individual shrubs have the potential to contribute more to the collective replacement of herbaceous cover than forest advancement, through the process of nucleation (Mack, 1985). Woody plant establishment along abandoned stream channels and along the edge of drying sloughs within meadows was also apparent in the images.

4.2 Effects of prescribed fire on meadow vegetation

Canonical Correspondence Analysis (CCA) identified plant litter biomass as strongly correlated with the first ordination axis and burn regime as strongly correlated with the second ordination axis. Using cluster analysis eight plant community groups were distinguished within the dry meadow habitat type. Plant communities C (*Carex aeana* and *Calamagrostis* spp.) and D (*Carex aeana*, *Calamagrostis* spp. and *Juncus balticus*) were both highly associated with the three burn regime. The CCA explained only a small portion of the species variance and the additional species variance may be accounted for by other more important environmental variables that were not measured in this study and by species variation between the six meadows sampled. However, a low proportion of variance explained by species abundance data is typical of CCA (ter Braak, 1990) and the ordination diagrams reveal strong trends in the plant species responses to prescribed burning.

The frequency of community types with the dominant species, *Carex aeana* and *Juncus balticus*, in meadows burned three times is important with respect to bison forage. These two plants represent only a very small proportion of bison's diet. Conversely, the plant community types dominated by the key bison forage plants, *Calamagrostis* spp. and *Carex atherodes*, were much less associated with the three-burn regime. However, *C. atherodes* is characteristic of wet meadows (Reynolds, 1987), and one might expect a moisture gradient within the coarse grouping of dry meadows. The very dry conditions characteristic of the meadows burned three times suggest that these meadows may have become more dry as a result of the fires, possibly through higher ground surface temperatures following fire.

Both single and multiple spring burns had a significant effect on willow shrub survivorship. While *ca.* 12% of shrubs on meadows burned once were standing dead shrubs, the number doubled to 24% of standing dead shrubs on meadows burned three times. Shrub vigor also decreased significantly in burned meadows, however, there were only small differences in the middle classes of shrub vigor between meadows burned once or three times.

4.3 Management implications and further research

The results of the image analysis of aerial photographs is corroborated by other studies which indicate that northern meadows in the SRL and surrounding area appear to be shifting toward more shrub- and tree-dominated communities (Jeffrey, 1961; Jaques, 1990). Many variables may be interacting to bring about this shift in vegetation (*e.g.* climate change, isostatic rebound, hydrology changes in response to WAC Bennet dam) and trying to override these variables may be futile. Maintaining a landscape in a particular state indefinitely may not be possible or desirable. However, improving our understanding of the ecology of northern meadows and using this knowledge within an adaptive management framework may provide the best option for setting and achieving long-term, ecologically sound management goals. This concept is described by Johnson (1999): "The overall goal of adaptive management is not to maintain an optimal condition of the resource, but to develop an optimal management capacity." The research recommendations that follow are based on the results of this study and are intended to further the practice of adaptive management of the SRL meadows.

1. Long-term monitoring of vegetation change. Remotely sensed imagery is readily available and change detection techniques using high quality, high resolution images would provide an effective tool for monitoring spatial and temporal vegetation changes in the SRL. The use of multi-date imagery would aid in determining the rates of changes and the influence of yearly climatic variability on shrub and tree establishment.

2. Investigate processes behind the patterns of shrub and tree establishment. An understanding of the process and environmental conditions influencing the patterns of shrub and tree establishment in meadows would help to identify areas with greater

potential for shrub and tree invasions. This could be accomplished through spatial analyses of new shrub and tree establishment patterns and their relationship to large scale environmental variables, for example: topography, fire history, flooding history, dominant vegetation, soil moisture availability, and grazing.

3. Design future management actions as experiments. Since continued prescribed burning is planned for the SRL meadows, a detailed study of the vegetation, before and after burning, should be an integral component of each project. Plans for burning new meadow areas provide an ideal situation for testing the state-and-transition model (Westoby *et al.*, 1989) by comparing pre-fire and post-fire vegetation structure, at the same point in space for a variety of meadow types and fire regimes.

4. Consider the role of landscape heterogeneity. The open meadows of the Hook Lake area are not homogeneous in their vegetation structure. The mosaic of wet and dry meadow communities occurs along a moisture and possibly salinity gradient. Various landscape features such as sloughs, stream channels, bison wallows, aspen (*Populus tremuloides*) colonies, etc., also contribute to the heterogeneous character of the meadow landscape. Knowledge of how these landscape features influence the severity of prescribed fire is essential to understanding how fire affects vegetation dynamics across the landscape as a whole.

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Appendix 1a. List of plant species recorded from 300 1 m^2 quadrats and included in the Canonical Correspondence analysis, cluster analysis, and discriminant function analysis.

Sedges and Rushes

Carex atherodes Spreng.
Carex aeana Fern.
Juncus balticus L.

Grasses

Agropyron trachycaulum (Link) Malte
Agrostis scabra Willd.
Calamagrostis spp.
Hierochloe odorata (L.) Beauv.
Hordeum jubatum L.
Poa spp.

Forbs

Achillea millefolium L.
Antennaria mycrophylla Rydb.
Arnica lonchophylla Greene
Aster ciliolatus Lindl.
Aster pauciflorus Nutt.
Cirsium drummondii T. & G.
Cirsium foliosum (Hook.) DC.
Epilobium angustifolium L., *s.lat.*
Erigeron elatus (Hook.) Greene
Erysimum cheiranthoides L.
Fragaria virginiana Duchesne
Galium boreale L.
Galium trifidum L.
Gentiana acuta Michx.
Geum aleppicum Jacq.
Geum macrophyllum Willd.
Lactuca pulchella (Pursh) DC.
Lathyrus ochroleucus Hook.
Petasites sagittatus (Banks) A.Gray
Polygonum amphibium L.
Potentilla arguta Pursh *s. lat.*
Potentilla norvegica L.
Potentilla pennsylvanica L.
Ranunculus cardiophyllus Hook.
Rumex occidentalis S. Wats.
Senecio eremophilus Richards.

Senecio indecorus Greene
Senecio paupercaulus Michx.
Solidago canadensis L.
Stachys palustris L. *s. lat.*
Stellaria calycantha (Ledeb.) Bong. *S. lat.*
Stellaria longifolia Muhl.
Taraxacum officinale Weber
Thalictrum venulosum Trel.
Vicia americana Muhl.
Viola adunca J. E. Smith

Shrubs
Ribes oxycanthoides L.
Rosa acicularis Lindl. *S. lat.*
Rubus acaulis Michx.

Appendix 1b. Additional plant species recorded from within thirty 20m x 50m plots.

Grasses
Glyceria pulchella (Nash) K. Schum.

Forbs
Antennaria rosea (Eat.) Greene
Artemesia biennis Willd.
Aster falcatus Lindl.
Cicuta mackenzieana Raup
Descurainia sophioides (Fisch.) O.E. Schulz
Epilobium ciliatum Raf.
Lepidium densiflorum Schrad.
Potentilla anserina L. *s. lat.*
Primula incana M. E. Jones
Ranunculus macounii Britt.
Silene menziesii Hook.
Sisyrinchium montanum Greene
Solidago multiradiata Ait.
Urtica gracilis Ait.

Shrubs
Ribes lacustre (Pers.) Poir.
Rubus ideus L.
Vaccinium vitis-idaea L.

Appendix 1c. *Salix* spp. shrubs recorded within thirty 20m x 50m plots.

Salix bebbiana Sarg.
Salix glauca L. *s. lat.*
Salix macCalliana Rowlee
Salix petiolaris of auth. Not Sm.
Salix planifolia Pursh
Salix pseudomonticola Ball.
Salix serrisima (Bailey) Fern.