20TH CENTURY FOREST-GRASSLAND ECOTONE SHIFT AND EFFECTS OF LIVESTOCK HERBIVORY

by

Temuulen Tsagaan Sankey

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Cliff Montagne

Lisa Graumlich

Approved for the Department of Land Resources and Environmental Sciences

Jon Wraith

Approved for the College of Graduate Studies

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TABLE OF CONTENTS

1. INTRODUCTION TO DISSERTATION 1
References Cited 4

2. FOREST-GRASSLAND ECOTONE SHIFT AND GRAZING EFFECTS IN THE CENTENNIAL VALLEY, MONTANA, USA 5
Introduction 5
Forest-Grassland Ecotone Shift 5
Grazing Effects on Ecotone Shift 7
Grazing Practices in the Centennial Valley 11
Difference in Tree Species Response to Grazing 12
Effects of Abiotic Factors on Ecotone Shift 13
Methods 13
Study Site 13
Field Methods and Airphoto Interpretation 16
Tree-Age Estimate 18
Data Analysis 19
Results 22
Forest-Grassland Ecotone Shift 22
Grazing Effects on Ecotone Shift 28
Current Gradient of Grazing Intensity. 28
Historic Gradient of Grazing Intensity. 29
Gradient Across All Ten Grazing Levels 29
Effects of Abiotic Factors on Ecotone Shift 32
Discussion 33
Forest-Grassland Ecotone Shift 33
Tree Species Response to Grazing 35
Grazing Effects on Ecotone Shift 36
Multiple Interactive Effects 38
Conclusion 40
References Cited 42

3. FOREST-GRASSLAND ECOTONE SHIFT AND EFFECTS OF LIVESTOCK HERBIVORY IN NORTHERN MONGOLIA 46
Introduction 46
Forest-Grassland Ecotone Shift 46
Grazing History in Mongolia 48
Grazing animals in the Darhad Valley 49
Siberian larch (*Larix sibirica*) 51
Methods 52

TABLE OF CONTENTS - CONTINUED

Study Site Description 52
Field Methods 56
Tree-Age Estimate 57
Data Analysis 59
Results 62
Forest-Grassland Ecotone Shift 62
Grazing Impact on Ecotone Shift 68
Discussion 70
Forest-Grassland Ecotone Shift 70
Grazing Effects on Ecotone Shift 73
Conclusion 77
References Cited 80

4. CONCLUSION: UNDERSTANDING FOREST-GRASSLAND ECOTONES, THEIR SHIFTS, AND EFFECTS OF LIVESTOCK HERBIVORY 83
Forest-Grassland Ecotone Dynamics 83
Types of Forest-Grassland Ecotone Shift 87
Future Research on Livestock Herbivory on Ecotone Shift 89
References Cited 90

LIST OF TABLES

Table Page

2.1. Historic and current average of grazing intensity estimated in AUM/ha at our five sites. Current grazing levels provided a gradient of five relatively lower grazing levels (marked with *), while the historic grazing levels provided a gradient of five relatively higher grazing levels. Grazing levels are ranked from low to high within each gradient 15

2.2: Number of trees sampled for age structure analysis 23

2.3. Evidence of ecotone shift at all sites. Number of newly established trees is expressed as the percent of new stems that established since 1942..... 24

2.4: Results of the tree age and distance regression model. Tree age was the response variable and the predictor variables were tree distance and sites..... 26

2.5. Aerial photograph comparison of ecotone tree canopy cover recorded for grid points and rows. (Sites with significant differences between the two dates are marked with *)..... 27

3.1: Number of animals during the three different grazing regimes 54

3.2: Long-term averages of grazing intensity. 54

3.3: Number of trees sampled and stem-age distribution..... 58

3.4: Results of the tree age and distance regression model. Tree age was the response variable and predictor variables included tree distance, sites and interaction terms of tree distance and sites. 64

3.5: Results of the seedling density and quadrat distance regression. Quadrat distance and a quadratic term were the predictor variables. 64

LIST OF FIGURES

Figure Page

2.1: Tree encroachment and grazing effects. Solid lines show trends indicated by previous studies. Some of the previous grazing impact studies indicate facilitation effects of grazing disturbance on tree encroachment, while others indicate inhibition effects on tree encroachment. Dashed lines show my hypothesized trend. Based on the trends in the current literature, I expected that increasing grazing intensity might first facilitate and then inhibit tree encroachment 10

2.2: Comparison of tree regeneration and mortality at the five sites. Mortality rates of the last 60 years were not estimated, but dead stems in our plots were counted as the best estimate of mortality. Number of new stems by far exceeded the number of dead stems. 20

2.3: Tree-age distribution of all sites at a decadal scale. Bins along the X axis are decades. Y axis represents percent of the total trees that established in each decade. Ecotone shift is evidenced by new tree establishment in the last 60 years. Up to 45% of the adult trees established since 1942. 24

2.4: Tree age and tree distance relationship at each site. A single regression model was constructed with a separate indicator variable for each site (Tree age = $ß_0$* Tree distance + $ß_1$*Site 1 + $ß_2$*Site 2 + $ß_3$*Site 3 + $ß_4$*Site 4 + $ß_5$*Site 5). Tree distance was a significant predictor variable and tree age decreased with increasing distance at all sites. Coefficients for Sites 2, 3, and 5 were significantly different (p-value <0.05) compared to Site 1. Site 4 was not significantly different compared to Site 1 (p-value = 0.87).....26

LIST OF FIGURES - CONTINUED

Figure Page

2.5: Grazing impact on aspen and Douglas-fir establishment. Grazing levels across different gradients are on the X axis. Number of new trees established (expressed in percent) under each grazing level is on the Y axis. The ANOVA equations were: Number of new trees = $\beta_0 + \beta_1$*Grazing levels. Figure a and b show aspen and Douglas-fir responses to grazing across the current gradient of lower grazing levels. Figure c and d show aspen and Douglas-fir responses to grazing across the historic gradient of higher grazing levels. Figure e and f show aspen and Douglas-fir responses to grazing across the gradient of ten levels of grazing intensity. Current grazing levels are marked with * in the gradients. Figure g and h show the overall relationship between grazing effects and tree establishment. The regression equations were: Number of new trees = $\beta_0 + \beta_1$* Grazing levels + β_2*(Grazing levels)*2.....30

2.6: A conceptual model in relation to the grazing optimization hypothesis. I propose a single continuous model, indicated by the solid line, of grazing effects on tree encroachment. The dashed line indicates the relationship between herbaceous species productivity and grazing as suggested in the grazing optimization hypothesis. Between lower and medium levels of grazing intensity, tree encroachment decreases with increasing grazing intensity and increasing herbaceous species productivity. At medium levels of grazing intensity, tree encroachment is at its minimum, where herbaceous species productivity is at its optimum. Between medium and higher levels of grazing intensity, tree encroachment increases with increasing grazing intensity and decreasing herbaceous species productivity. 39

3.1: Livestock species distribution during the collective period at the five sites. Site 1-Site 5 are labeled as S1-S5. The first principal component represents a gradient from sheep-dominated to cattle-dominated sites. The second principal component represents a gradient in goat numbers.....56

3.2: Seedling-age distribution. Seedling age ranges from 29 to 80 years. A majority of these stems were established in the decade of 1940 and 1950, and no new seedlings were established after the decade of 1970. These stems were classified as seedlings and were not included in the adult tree-age distribution. 58

LIST OF FIGURES - CONTINUED

Figure Page

3.3: Comparison of new tree establishment and mortality. Mortality rates of the last 80 years were not estimated, but dead stems and stumps in the plots were counted as the best estimate of mortality. Number of new stems by far exceeded the number of dead stems. 60

3.4: A typical lower forest-grassland boundary in the Darhad Valley. Note the trees in the lighter green color in the forefront. They are smaller and shorter than the trees in the background and form a "fairy ring" along the forest boundary. Stems in the "fairy ring" were found at very high density. Although they were mature stems, these stems were classified as seedlings due to their diameter at coring height (<8 cm). The "fairy rings" provided strong indicators of ecotone shift (also note Fig. 3.8).. 62

3.5: Adult tree-age distribution at all sites. Figure a, b, d, c, and e show adult tree-age distribution at a decadal scale at Site 1-Site 5. Up to 95% of the adult trees were new trees that established within the last 80 years. All sites show a pulse of regeneration in the decades of 1930, 1940, and 1950, but no new tree establishment after the decade of 1960. 65

3.6: Tree age and tree distance (expressed in percent) relationship at each site. A single regression model was constructed with a separate indicator variable for each site. Regression equation is: Tree age = 90.6 - (0.2*Tree distance) – (8.3*Site 2) - (5.6*Site 3) – (17.1*Site 4) – (16.6*Site 5) + (0.1*Tree distance*Site 2) + (0.4*Tree distance*Site 3) + (0.2*Tree distance*Site 4) + (0.1*Tree distance*Site 5). Distance was a significant predictor variable and tree age decreased with increasing distance at all sites.....66

3.7: Seedling distribution within the ecotone. Regression equation is: Average seedling density = $ß_0$ + $ß_1$*Quadrat distance + $ß_2$ (Quadrat distance)*2. Distance is measured in meters. Average seedling density increases starting at 5 meters from the grassland end of the plots at 100% herbaceous cover and peaks midway between the grassland and full canopy forest. This peak indicates the "fairy ring". Average seedling density then decreases towards the full canopy forest. 67

LIST OF FIGURES - CONTINUED

Figure Page

3.8: Stem size distribution along lower forest boundary. "Fairy ring" regeneration was often observed along the lower forest boundary (also note Fig. 3.4). This ring consisted of tall, slender stems, at high density, that were classified as seedlings. These stems were too small in size (<8 cm in diameter at coring height) and were not cored. However, my seedling age estimate indicates that a majority of these stems were as old as the stems that were cored and classified as adult trees.....69

3.9: Tree establishment with different grazing regimes. Site 2 had significantly lower tree establishment than Site 5. Sites 2 and 3 also had significantly lower tree establishment than Site 4.....69

3.10: Typical age distribution pattern of multi-aged larch stands (Bondarev, 1997). This was the pattern I expected to see in my tree-age distribution, if no changes were occurring in the ecotones. 71

4.1: Tree encroachment and grazing effects. Solid lines show trends indicated by previous studies. Some of the previous grazing impact studies indicate facilitation effects of grazing on tree encroachment, while others indicate inhibition effects on tree encroachment. Dashed lines show non-linear trends. Based on the trends in the current literature, I expected that increasing grazing intensity might first facilitate and then inhibit tree encroachment. This expected pattern was not observed. Some of the Centennial Valley study results, however, indicated that increasing grazing intensity might first inhibit and then facilitate tree encroachment..... 85

4.2: Commonly proposed factors as causes of tree and shrub encroachment. These factors might have influenced and further enhanced tree encroachment at my study sites. Grazing was the only factor examined in this study 87

4.3: I propose that ecotones might short into the adjacent grassland in three different patterns. These patterns are not mutually exclusive and might occur simultaneously. Type I pattern is a shift in ecotone location over time. Type II pattern is tree density increase within the same forest-grassland boundary location. Type III pattern is fairy ring establishment. Ecotones might also retreat into the adjacent forest, but the possible patterns of retreat are uncertain. 88

ABSTRACT

I studied 20th Century lower forest-grassland ecotone shift in the Centennial Valley in southwestern Montana, USA and the Darhad Valley in northern Mongolia and investigated the effects of livestock herbivory on ecotone dynamics. A total of 525 aspen (*Populus tremuloides*) and 1,703 Douglas-fir (*Pseudotsuga menziesii*) trees were cored and 10,168 seedlings were counted at five sites along the ecotone in the Centennial Valley. A total of 2,968 Siberian larch (*Larix sibirica*) were cored and 4,709 seedlings were counted at five ecotones in the Darhad Valley. Tree-age distribution was constructed to determine 20th Century tree establishment. Tree age and location within the ecotone were correlated to describe the process of ecotone shift into the adjacent grassland. To examine livestock herbivory effects on ecotone shift, the number of new trees was correlated with ten different levels of cattle grazing intensity during the last 60 years in the Centennial Valley and with five different grazing regimes during the last 80 years in the Darhad Valley.

Three different types of ecotone shift into the adjacent grassland were documented: forest boundary shift, densification, and fairy ring establishment. No evidence of ecotone shift upslope towards the forest was found. Grazing intensity had a complex relationship with tree encroachment. Aspen and Douglas-fir tree encroachment was low at medium levels of grazing intensity, but aspen establishment was higher at low and high grazing levels and Douglas-fir establishment was higher at low grazing levels. Siberian larch tree encroachment was higher at low and high grazing intensities by sheep and cattle, but it was lower at low and medium grazing levels by goat-sheep and goat-sheep-cattle mixes. My results implied that grazing can both facilitate and inhibit tree encroachment.

I propose a model of grazing effects on tree encroachment that integrates both inhibition and facilitation effects of grazing disturbance. I also propose a conceptual model of lower forest-grassland ecotone shift and a conceptual model of ecotone shift and livestock herbivory effects. My models suggest that grazing can be used as a tool to maintain the equilibrium between forest and grassland vegetation and to increase or decrease forest expansion.

CHAPTER 1

INTRODUCTION TO DISSERTATION

Forest-grassland ecotone shifts and their proximate causes have been studied in many different parts of the world. Herbivory, known as one of the proximate causes, has received considerable research attention due to its local control over vegetation. Our current understanding of the interaction between forest and grassland vegetation under herbivory effects, however, remains under-developed.

In addition to herbivory, climate change, increased CO_2, nitrogen pollution, drought, and fire suppression have been correlated with ecotone shift (Dando and Hansen, 1990; Archer, 1999; Bachelet et al., 2000; Bartolome et al., 2000; Asner et al., 2004). Forest-grassland ecotone shifts have important implications for carbon sequestration, land surface-atmosphere interactions, biodiversity, primary and secondary productivity, soil development, and populations and carrying capacity of both domestic and wild animals (Archer, 1999).

This project examined 20th Century lower forest-grassland ecotone shift in the Centennial Valley in southwestern Montana, USA and the Darhad Valley in northern Mongolia and studied the effects of livestock herbivory on ecotone shift at a local scale. The objectives of this study were: (1) to determine if lower forest-grassland ecotone shift occurred during the 20th Century at these two study sites and (2) to examine the effects of livestock herbivory on ecotone shift, if ecotone shift had occurred, at a local scale. Two questions were addressed at both study sites: (1) Is the lower forest-grassland ecotone

shifting and is ecotone tree density increasing? (2) If so, do different livestock grazing regimes lead to different rates of ecotone shift? Determining possible causes of lower forest-grassland ecotone shift at a regional scale was not the objective of this study. Potential factors, such as increased CO_2, climate change, and fire suppression, were, therefore, not correlated with ecotone shift.

The results from the two study regions are presented here separately in Chapter 2 and Chapter 3. Chapter 4 is a summary that encompasses the conclusions of the entire dissertation. Chapter 2 reports results and conclusions from the Centennial Valley, where tree species of aspen (*Populus tremuloides*) and Douglas-fir (*Pseudotsuga menziesii*) dominated the lower forest-grassland ecotone and the grazing livestock species included cattle only. This chapter examines ecotone shift, using dendrochronological data and aerial photographs, and compares the effects of different cattle grazing intensities on aspen and Douglas-fir establishment.

Chapter 3 reports results and conclusions from the Darhad Valley, where only one tree species, Siberian larch (*Larix sibirica*), dominated the ecotones and the grazing livestock species included cattle, sheep, and goats. This chapter examines ecotone shift, using dendrochronological data, at five different sites in the Darhad Valley, where grazing regimes differed among sites and changed over time. The grazing regimes differed among sites both in herd composition and herd size. This chapter thus examines the effects of different grazing regimes on ecotone shifts and the effects of changing grazing patterns associated with political, economic, and institutional changes over time.

Chapter 4 is a synthesis that summarizes the findings of this study and our current understanding of shifts in lower forest-grassland ecotones and effects of livestock herbivory on ecotone shift. This chapter summarizes all three types of lower forest-grassland ecotone shift observed in this study. It also synthesizes the effects of livestock herbivory on ecotone shift. In summary, this project describes patterns of ecotone shift and illustrates that livestock herbivory is a complex variable with important consequences for vegetation cover changes across landscapes.

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CHAPTER 2

FOREST-GRASSLAND ECOTONE SHIFT AND GRAZING EFFECTS IN THE CENTENNIAL VALLEY, MONTANA, USA

Introduction

Forest-Grassland Ecotone Shift

As more instances of forest-grassland ecotone shift are observed, it attracts greater attention for its interactions with carbon sequestration and land surface-atmosphere (Archer, 1999; Mather, 2000). Forest-grassland ecotone shift has been correlated with climate change, increased CO_2, fire suppression, herbivory, and snow accumulation (Dando and Hansen, 1990; Kupfer and Cairns, 1996; Bachelet et al., 2000; Bartolome et al., 2000). The effects of these factors are more commonly studied at alpine treeline than at lower forest-grassland ecotones.

I studied a lower forest-grassland ecotone shift in the Centennial Valley in southwestern Montana, USA and investigated two types of ecotone change using dendrochronological data and aerial photographs: a shift in forest-grassland boundary location toward the adjacent grassland and an increase in tree density at the forest-grassland boundary (Arno and Gruell, 1986). I examined the effects of livestock herbivory on ecotone shift using non-experimental observational data of the last 60 years (1) to determine if conclusions from previous grazing studies, some of which had better controlled experiments at shorter time scales, were consistent with patterns observed at decadal time scales; (2) to develop expectations, by using inductive reasoning, regarding

the effects of a broader range of grazing levels on tree encroachment; (3) to determine if the expectations were consistent with patterns observed at decadal time scales; and (4) to propose a unified conceptual model of grazing effects on tree encroachment (Likens, 1989; Pickett et al., 1994). The proposed conceptual model helps us identify further research needs and gaps in our current understanding of the dynamics of ecotone shift and grazing effects.

My objectives were: (1) to determine if lower forest-grassland ecotone shift occurred in the Centennial Valley during the 20th Century; and (2) to examine grazing effects on ecotone shift at a local scale, if ecotone shift had occurred. Three questions were of primary interest: (1) Is the lower forest-grassland ecotone shifting and is ecotone tree density increasing? (2) If so, do different grazing levels lead to different rates and patterns of ecotone shift? (3) Within the same grazing level, do different tree species respond to grazing differently? I also considered effects of topographic variables on ecotone shift and used topographic aspect and slope as covariates.

Determining possible causes of lower forest-grassland ecotone shift at a regional scale was not my objective. I, therefore, did not correlate potential factors such as increased CO_2, climate change, and fire suppression with ecotone shift in the Centennial Valley. Increased CO_2 is expected to provide competitive advantages for woody species over C_4 grasses, which evolved at lower CO_2 levels than the current levels (Bazzaz, 1996). Changes in climate have also been demonstrated to be correlated with forest expansion. Increased temperature, increased and decreased rainfall, periodic droughts and a shift in seasonality and distribution of precipitation events have been suggested as

possible causes of increase in woody vegetation cover (Archer, 1999). Fire suppression is another explanation that has been proposed for forest expansion because fire creates and maintains grasslands (Arno and Gruell, 1986).

Grazing Effects on Ecotone Shift

Woody species encroachment due to grazing has been demonstrated throughout the world, including southern Asia, Australia, Africa, South America, and North America (Archer, 1989). Woody species encroachment due to grazing in North America has been observed in arid and semi-arid regions of western and southwestern USA (Archer, 1999). Studies that compared no grazing with relatively low grazing levels (<0.5 AUM/ha) demonstrate high level of woody species establishment under grazing and suggest that grazing facilitates woody species encroachment (Archer, 1999; Asner et al., 2004). We might, therefore, expect increasing woody species encroachment with increasing grazing intensity at lower grazing levels. The opposite effects of grazing on woody species encroachment have also been demonstrated (Carmel and Kadmon, 1999; Bartolome et al, 2000). Studies that examined higher levels of grazing (0.8-2.5 AUM/ha) suggest that grazing can inhibit tree seedling establishment, survival, and growth. We might, therefore, expect decreasing woody species encroachment into grasslands with increasing grazing intensity at higher grazing levels.

Forest expansion into the adjacent grassland requires a sequence of events: tree seed dispersal into the adjacent grassland, germination of seeds, emergence, growth, survival, and recruitment of seedlings into the tree population (Hill et al., 1995). Each of these processes can be impacted by herbivory, an important local control over vegetation.

Ecological processes of positive net effects of grazing on woody species have been summarized by Archer (1999). They include: (1) Grazing decreases seed production, seedling establishment, biomass, and basal area of palatable herbaceous species and increases their mortality; (2) Reduced herbaceous species ground cover increases sunlight levels on the ground, which increases seed germination and early establishment of woody species seedlings; (3) Reduced herbaceous species biomass decreases fine fuel accumulation and reduces fire frequency, which increases woody species invasion; (4) Invading woody species are less palatable than herbaceous species and are not browsed enough to be eliminated; (5) Grazing makes herbaceous species less able to compete for resources and unable to limit woody species growth and their seedling establishment; and (6) Livestock disperse woody species seeds across the landscape.

Negative effects of grazing on woody species have also been widely documented. They include: (1) Slow growth rate of most woody species allows repeated grazing in their seedling stage when they are most vulnerable to grazing (Alverson et al., 1988; Tilghman, 1989); (2) Intense grazing causes shoot loss, tissue damage, and biomass loss for woody species (Hjalten et al., 1993), which decreases their seedling growth (Alverson et al., 1988; Tilghman, 1989) and increases seedling mortality (Hjalten et al., 1993); (3) Increased seedling mortality reduces recruitment into the tree population (McInnes et al., 1992; Rooney et al., 2002); and (4) Trampling and rubbing against the bark by grazing animals damage woody species and their seedlings (Kay and Bartos, 2000).

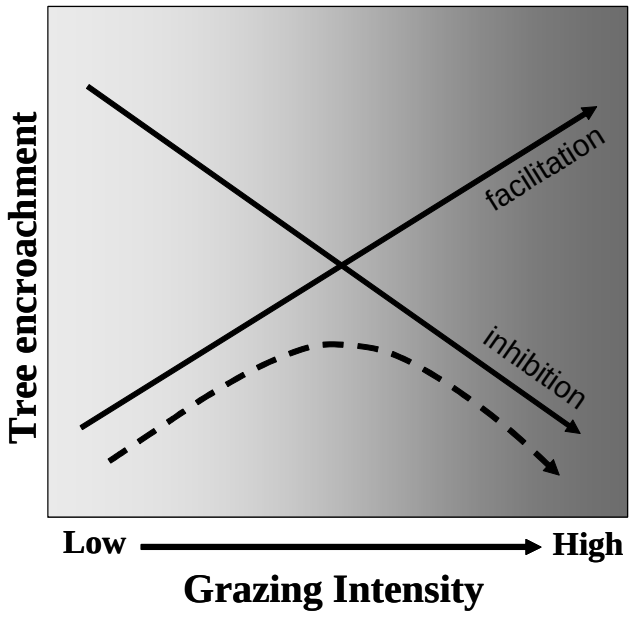
The current literature illustrates two seemingly conflicting grazing impacts on woody species. All grazing impact studies demonstrate one or the other of these two

conflicting impacts, but none demonstrates both. The vast majority of grazing impact studies in the current literature, however, has compared only two or three relatively similar levels of grazing intensity. Such comparisons of limited number of grazing levels might provide only a simple linear relationship between woody species encroachment and grazing disturbance. The potential variability in ecotone shift due to varying levels of grazing intensity needs to be investigated across a wider gradient of multiple levels of grazing intensity.

A wider gradient of multiple grazing levels is difficult to establish and maintain at decadal time scales for purposes of determining long-term grazing effects on tree encroachment. We can, however, rely on scientific methods of inductive reasoning to develop expectations regarding long-term effects of grazing levels across a wider gradient on tree encroachment based on previous studies (Likens, 1989; Pickett et al., 1994). Previous studies of lower grazing levels suggest facilitation effects on woody species expansion and demonstrate positive net effects of grazing disturbance for woody species (Asner et al., 2000, Archer, 1999). Previous studies of higher grazing levels, in contrast, suggest inhibition effects on woody species expansion and demonstrate negative effects of grazing on woody species (Carmel and Kadmon, 1999; Bartolome et al, 2000). We might, therefore, expect a single continuum that integrates both of the locally linear trends of inhibition and facilitation effects across a wider gradient of multiple grazing levels. Based on the trends in the current literature, we might expect that increasing grazing intensity first facilitates and then inhibits woody species expansion (Fig. 2.1). The possibility of such a continuous model needs to be further explored with controlled

experiments, if observational studies such as this can not clearly demonstrate the expectation of a single continuum to be false.

Figure 2.1: Tree encroachment and grazing effects. Solid lines show trends indicated by previous studies. Some of the previous grazing impact studies indicate facilitation effects of grazing disturbance on tree encroachment, while others indicate inhibition effects on tree encroachment. Dashed lines show my hypothesized trend. Based on the trends in the current literature, I expected that increasing grazing intensity might first facilitate and then inhibit tree encroachment.



I studied a 15 km long, single linear stretch of lower forest-grassland ecotone and examined tree regeneration and recruitment patterns as impacted by three different gradients of cattle grazing intensity: (1) a gradient of five relatively lower levels of grazing intensity; (2) a gradient of five relatively higher levels of grazing intensity; and (3) a gradient across all ten levels of grazing intensity. I expected that varying grazing levels would result in both inhibition and facilitation effects of grazing disturbance on tree encroachment (Fig 2.1). My gradients of grazing levels were constructed based on

long-term observational data. I assigned a category to each grazing intensity at each site. The categories do not represent evenly-distributed grazing levels along the gradients (Table 2.1). Further, the third gradient does not combine the two smaller gradients sequentially, and the order of the grazing levels thus changes from the smaller gradients to the broader gradient. I was also unable to control other potential factors that influence tree regeneration and recruitment due to the temporal and spatial extent of our study.

Grazing Practices in the Centennial Valley

The Centennial Valley rangelands are now used for summer grazing by cattle. Cattle are driven into the valley at the beginning of the summer and are driven out at the end of the season. Historically, the valley's rangelands were used for grazing year around and at higher stocking rates until 1960's. Similar to the rest of the western land, grazing pressure in the Centennial Valley was reduced after the Taylor Grazing Act in 1934 (Stoddart and Smith, 1955). Grazing pressure in the valley was further reduced through the decades of 1950 and 1960 as wildlife conservation became a priority and the wildlife refuge reduced its grazing leases to neighboring private ranchers (Red Rock Lakes Wildlife Refuge Annual Reports, 1959-1996). Many of the valley's residents left the Centennial Valley during these decades due to lack of social and economic development in the valley and better employment and access to daily needs outside of the valley (Brenneman, personal communication, 2004; Huntsman, personal communication, 2004). The remaining ranchers, land owners, and land managers started rest-rotation management in 1960's and 1970's (Red Rock Lakes Wildlife Refuge Annual Reports,

1959-1996). These changes resulted in reduced cattle grazing intensity in the Centennial Valley for the rest of the 20th century.

Difference in Tree Species Response to Grazing

Douglas-fir (*Pseudotsuga menziesii*) and aspen (*Populus tremuloides*) are the dominant tree species along the lower forest-grassland ecotone in the Centennial Valley. Aspen is considered to be a seral species in the Centennial Range, while Douglas-fir is a climax species (Mueggler, 1988). Aspen is a deciduous species that regenerates clonally (Debyle and Winokur, 1985). Douglas-fir is a coniferous species that reproduces through seeds (Hermann and Lavender, 1965). Aspen and Douglas-fir are expected to respond to grazing differently due to their differences in palatability and tolerance to grazing. Aspen suckers are preferred by cattle over Douglas-fir seedlings (Smith et al, 1972). Wildlife and domestic cattle grazing decrease aspen green biomass, sucker density and height, and ultimately cause sucker mortality (Smith et al, 1972; Singer et al, 1996).

Douglas-fir is less palatable than aspen, especially in its seedling stage when it is most vulnerable to grazing. Grazing results in a positive net effect for Douglas-fir growth by significantly decreasing herbaceous species, although it causes considerable damage to Douglas-fir through biomass removal and trampling (Hermann and Lavender, 1965). Herbaceous species compete with Douglas-fir seedlings for soil moisture and inhibit seedling establishment (Hermann and Lavender, 1965). I studied the separate response of each tree species to grazing. I explored whether inhibition and facilitation effects of grazing disturbance on tree encroachment differed between aspen and Douglas-fir.

Effects of Abiotic Factors on Ecotone Shift

Topographic slope and aspect are key variables that impact vegetation patterns (Holland and Steyn, 1975). Patterns in aspen growth, for instance, have been shown to be highly correlated with topographic aspect (Brown, 2003). Although such topography-vegetation relationships have been well studied, the interaction of topographic effects and grazing impact has not been adequately studied (Carmel and Kadmon, 1999). Specifically, the effects of such interaction on changes in vegetation patterns need to be addressed to fully understand grazing impacts on ecotone shift. I examined the variability in ecotone shift due to topographic differences and used topographic slope and aspect as covariates with different levels of grazing intensity.

Methods

Study Site

A single, 15 km long lower forest-grassland ecotone was studied in the Centennial Valley in southwestern Montana in the summer of 2003. The Centennial Valley runs east-west at approximately 2100 m elevation and experiences extreme continental climate with cold winters and hot, dry summers. The lower forest-grassland ecotone is on the northerly aspect of the Centennial Mountain Range on the south side of the valley. This ecotone runs through the Red Rock Lakes Wildlife Refuge and adjacent private lands, which are predominantly used for livestock grazing. Two of my sites (lower grazing levels) were on the wildlife refuge, while three sites (higher grazing levels) were privately-owned. The vegetation community type along the ecotone is Douglas-fir-aspen

with structurally simple understory vegetation of 64 % graminoids, 35 % forbs and 1 % shrub. Common graminoids include *Agropyron cristatum*, *Calamagrostis rubescens*, *Elymus glaucus* and *Carex geyeri*. Common forbs are *Fragaria vesca*, *Geranium viscosissimum*, *Thalictrum fendleri*, and *Osmorhiza chilensis*. *Rosa woodsii* and *Berberis repens* are common shrubs (Mueggler, 1988). Fire was suppressed historically in the valley. There has been no fire in the valley over the last 130 years except the late summer of 2003 after my field work was completed. The valley has been grazed by domestic livestock since the mid-1800s.

I selected five contiguous sites along the ecotone to study grazing impact on the lower forest-grassland ecotone shift during the 20th Century. These sites were carefully selected to represent five different grazing regimes and, at the same time, to minimize differences in physiographic and climatic variables. The fives sites provided a gradient of grazing intensity with each site representing one grazing level. The current grazing regime at each site has remained the same over the last 35-40 years. Prior to 1965, however, a majority of the five sites were grazed much more heavily (Brenneman, personal communication, 2004; Huntsman, personal communication, 2004). Grazing intensity at that time also varied among sites such that the historic grazing levels provided another gradient of grazing intensity. Two different gradients of grazing intensity, therefore, were provided, a current gradient of five relatively lower levels of grazing intensity and a historic gradient of five relatively higher levels of grazing intensity. A combination of the two provided a third gradient with a broader range of grazing levels. The historic and current gradients of grazing regimes lasted for 23 years (1942-1965) and

37 years (1965-2002) respectively. The third gradient of grazing intensity included all ten grazing levels from these two different time periods covering 60 years from 1942 to 2002. This third gradient faced the limitations of observational studies in that there were potential temporal differences between the two time periods in factors that influence tree establishment such as climate variability, wildlife population, and changes in vegetation community dynamics.

Table 2.1. Historic and current average of grazing intensity estimated in AUM/ha at our five sites. Current grazing levels provided a gradient of five relatively lower grazing levels (marked with *), while the historic grazing levels provided a gradient of five relatively higher grazing levels. Grazing levels are ranked from low to high within each gradient.

Grazing levels	AUM/ha
Current grazing level 1*	0.00
Current grazing level 2*	0.11
Current grazing level 3*	0.17
Current grazing level 4*	0.79
Current grazing level 5*	1.00
Historic grazing level 1	0.12
Historic grazing level 2	0.28
Historic grazing level 3	0.41
Historic grazing level 4	0.50
Historic grazing level 5	2.00

The grazing intensities were estimated and ranked by calculating the level of use in animal unit months per hectare (AUM/ha). The current gradient of grazing intensity ranged from grazing intensity 1*, the lowest level (AUM/ha = 0), to grazing intensity 5*, the highest level (AUM/ha = 1) (Table 2.1). The historic gradient of grazing intensity was based on grazing history data and interviews of land owners and managers. This gradient also ranged from grazing intensity 1 (AUM/ha = 0.12) to grazing intensity 5 (AUM/ha = 2) (Table 2.1). My estimates indicate long term averages of grazing intensities in AUM/ha, but do not reflect duration, frequency, and timing of the grazing at these sites. Information from interviews with the Centennial Valley residents and land owners indicate no substantial difference in wildlife use among different land ownership throughout the valley (Huntsman, personal communication, 2004), although elk population has increased substantially throughout the valley over the last several decades (Brannon, personal communication, 2005).

Field Methods and Airphoto Interpretation

A total of 106 rectangular plots were established along the ecotone with 20 to 25 plots at each site. Plots were located at fixed intervals within each site (25-150 m depending on the length of ecotone at each site) with their long axis perpendicular to the ecotone. All plots were 10 m wide with varied lengths of 20 m to 366 m depending on the width of the ecotone. The width of the ecotone was determined by the definition of ecotone used in this study: a transition zone between 80% tree canopy cover in the forest and 100% herbaceous cover in the grassland. The forest end of each plot was positioned at 80% tree canopy cover, which was ocularly estimated, to represent full canopy forest

and included mature trees ≥60 years old based on tree size. Each plot extended from the full canopy forest into the adjacent grassland. The grassland end was positioned at 100% herbaceous cover and included the farthest out tree seedling or sucker. All adult trees within each plot were identified to the species level, mapped, and cored at 30 cm above ground with an increment borer to estimate age. Distance of each tree from the forest end of each plot was measured to correlate age estimate and distance of each tree from the forest end of the plots. All seedlings and suckers <2 m in height and/or <8 cm in diameter at coring height were classified as seedlings (we refer to the juvenile of both species herein as "seedlings"). All live seedlings were counted and mapped, by species, in 5m x 5m quadrats within each plot.

To corroborate the dendrochronological data, I used two sets of 1:15,000 scale black and white aerial photographs: one set from 1942 and one set from 1999. The 106 plots observed in the field were located on both sets of aerial photographs as precisely as possible. An additional 43 plots (with no ground truth) were also located randomly along the ecotone on both aerial photographs to increase the sample size to 149 plots (32-34 plots at each site). A point intercept method was used to detect changes in both the tree density along the ecotone and the forest-grassland boundary location (Kadmon and Harari-Kremer, 1999; Brown, 2003). The point intercept method used grids of points on transparent sheets that were placed over the aerial photographs. I used the same definition of lower forest-grassland ecotone in this analysis. The forest end of each grid, therefore, was placed at 80% tree canopy cover. The grassland end of each grid was positioned at 100% herbaceous cover and included the farthest out visible tree. The

number of points within each grid that intercepted a tree canopy was counted to detect changes in tree density. The number of the farthest rows in each grid that intercepted a tree canopy was counted to detect changes in the forest-grassland boundary location.

Additional field data included topographic slope and aspect measurements at each plot and soil profile description at 100 locations. The depth of mollic epipedons was measured in the soils along the ecotone to determine if new trees had established on grassland soils. The depth to which Mollisols meet the mollic epipedon color requirement (10YR 3/2 for moist measurements and 10YR 5/2 for dry measurements) has been known to be an important factor in distinguishing grassland soils from adjacent forest soils (Zelenak, 1995). Mollic epipedon depth was measured in 100 soil profiles located along the longer axis of 20 randomly chosen plots. Starting at the grassland end of the plots, five soil profiles were measured at equal intervals in each of the 20 plots.

Tree-Age Estimate

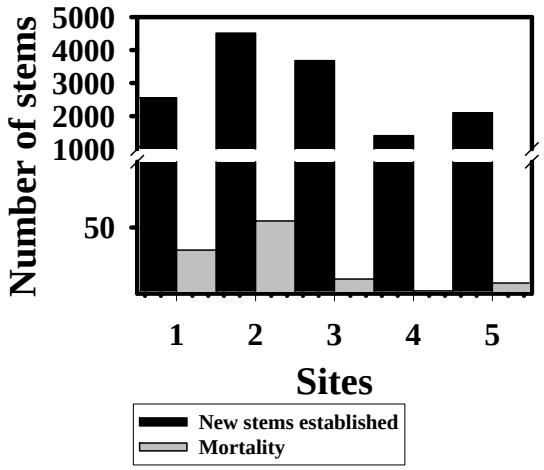
I cored 2,185 trees and processed and dated the core samples using standard dendrochronological methods (Stokes and Smiley, 1968). A total of 331 aspen samples and 1,628 Douglas-fir samples were dated successfully. A total of 194 aspen samples and 85 Douglas-fir samples were eliminated from the analysis because of rotten wood and branch scars. A total of 10,168 seedlings were counted. Seedling-age estimate was based on the age distribution of 30 aspen suckers and 30 Douglas-fir seedlings which were destructively sampled at the base of the stem. Douglas-fir seedlings ranged from 11 to 32 years old and aspen suckers ranged from three to ten years old. I built a regression model using the seedling-age estimate to correlate age and height. Based on this

regression model (R^2 of 0.27 and a *p*-value of 0.002), 29 years were added to the tree ring count of Douglas-fir samples to adjust for the coring height (30 cm above ground). No additional rings were added to the ring count of aspen samples, because the regression model produced a low coefficient of determination (0.02) and a large *p*-value (0.46). DeByle and Winokur (1985) indicate that aspen stems reach 1.5 m in 2-5 years, but some can reach 1.5 m height in the first year. Romme et al. (1995) indicate that unsuppressed and unbrowsed suckers can grow up to 1 m a year making it unnecessary to adjust ages for coring height. All aspen suckers observed at my study sites showed rapid early growth. Suppressed radial growth and lateral stem dominance due to heavy browsing was not observed at any of the sites. I made no estimates of mortality rates over our study period. I counted and mapped standing dead stems as our best available estimate of mortality. This estimate might not include mortality that occurred over the entire study period. It might include only mortality that occurred over the last few years. We would expect dead stems to take at least several decades to fall and decay in the semi-arid southwestern Montana.

Data Analysis

I first determined whether there had been ecotone shift and tree density increase during the study period. I constructed tree-age distribution for each site, by species, at a decadal scale to determine if new trees established during the study period within the ecotone. I also compared regeneration over the study period with the counts of standing dead stems as the best available estimate of mortality (Fig. 2.2).

Figure 2.2: Comparison of tree regeneration and mortality at the five sites. Mortality rates of the last 60 years were not estimated, but dead stems in the plots were counted as the best estimate of mortality. Number of new stems by far exceeded the number of dead stems.



Once it was determined that new trees had established during the study period, I was interested in exploring if a relationship existed between tree age and tree location within the ecotone. Many ecological processes can impact tree regeneration and mortality patterns along the ecotone. Among them, we would expect a process of tree establishment closer to the grassland, which is a necessary mechanism for ecotone shift to occur. A quantitative description of how this process occurs would help describe the pattern that results from this process. I constructed a regression model to describe the process of tree establishment closer to the grassland using adult tree-age estimate with the distance of trees from the forest end of the plots. Tree age was the response variable and tree distance was the predictor variable. The regression model also included our five sites as an indicator variable and interaction terms of tree distance and sites, to reduce the error effects caused by site differences and to test for differences among sites. The

interaction terms were not statistically significant and were, therefore, excluded from the final model. This analysis included the adult trees only. I tested for spatial and temporal autocorrelation in the residuals and found no pattern in the variogram.

To corroborate the dendrochronological data, I analyzed the aerial photograph data using paired T-tests. The number of points and number of farthest rows within the grids that intercepted tree canopy were compared separately through this test between the two dates. Increase in the number of farthest rows that intercepted tree canopy would indicate ecotone shift, whereas increase in the number points (expressed in percent) within the same number of rows would indicate tree density increase. Decrease in the number of rows and points that intercepted tree canopy cover would indicate ecotone retreat.

I then examined grazing effects on ecotone shift. I estimated the number of new trees established each year (expressed in percent) and the number of seedlings established in the last $\leq$32 years (expressed as seedling to adult ratio) under each grazing regime at each site. I performed one-way ANOVA tests to determine grazing effects across each gradient on each tree species. Grazing levels (indicator variable) were the predictor variable and the number of trees and seedlings established was the response variable. I also constructed a regression model of all ten grazing levels (AUM/ha) and tree establishment to describe the overall relationship between grazing and ecotone shift. I built separate regression models for the two tree species. The number of new trees and seedlings established was the response variable and grazing intensity (AUM/ha) and a squared term were the predictor variables. The squared term was not statistically

significant for the Douglas-fir regression. The final model for Douglas-fir thus included only grazing intensity as a predictor variable.

To address the third question, I examined the differential effects of grazing on different tree species through a two-way ANOVA test with grazing levels and tree species as predictor variables. I also performed a four-way ANOVA test to examine the effects of grazing levels, difference in tree species, and topographic aspect and slope on tree establishment. This test simultaneously determined the interaction between grazing levels and difference in tree species, the interaction between grazing levels and aspect, the interaction between grazing levels and slope, the interaction between difference in tree species and aspect, the interaction between difference in tree species and slope, and the interaction between slope and aspect. Tukey's multiple comparison was used for all ANOVA tests with a significant predictor variable. This test used a pair-wise comparison with all pairs and determined where significant differences occurred.

Results

Forest-Grassland Ecotone Shift

A total of 2,185 trees were sampled for tree-age estimate (Table 2.2). Of these, 525 were aspen samples and 1,637 were Douglas-fir samples. The tree-age estimate indicated that a few new Douglas-fir trees established after the decade of 1970. This can be partially explained by our seedling-age estimate. The seedling-age estimate indicated that the age of Douglas-fir seedlings ranged from 11 to 32 years, while the age of aspen suckers ranged from three to ten years. These ranges indicated that Douglas-fir trees that

established since 1970 were classified as seedlings and were not included in the tree-age distribution. Aspen stems that established since 1992 were classified as seedlings and were not included in the tree-age distribution.

Tree-age distribution was constructed at a decadal scale and indicated that new Douglas-fir and aspen trees had successfully established within the ecotone at all five sites in the last 60 years (Fig. 2.3). Up to 45% of the adult Douglas-fir trees were new trees that established since 1942 (Table 2.3).

Table 2.2: Number of trees sampled for age structure analysis

Sites	# Aspen samples	# Douglas-fir samples	Total
1	95	444	539
2	151	489	640
3	82	202	284
4	92	312	404
5	105	190	295
Total	525	1637	2162

An additional 1,244 Douglas-fir stems were counted as seedlings ($\leq$32 years old). These stems provided further evidence of new tree establishment in the last 60 years. New aspen trees $\leq$60 years old made up 1-27% of the adult aspen population (Table 2.3). The additional 8,924 aspen stems counted as suckers were established in the last 10 years and provide additional evidence of successful aspen regeneration.

Table 2.3. Evidence of ecotone shift at all sites. Number of newly established trees is expressed as the percent of new stems that established since 1942.

Sites	Newly established Douglas-fir since 1942	Newly established aspen since 1942	Seedling distance from adult trees (m)	Evidence of ecotone shift (+/-)
1	21	19	64	+
2	45	25	58	+
3	30	11	44	+
4	33	27	43	+
5	42	0.7	112	+

I then analyzed the estimated adult tree age with tree distance from the forest end of the plots to explore if a relationship existed between tree age and tree location in the ecotone and to describe the process of ecotone shift into the adjacent grassland. I constructed a regression model using adult tree age as a response variable and tree distance from the forest end of the plots as a predictor variable with sites as indicator variables (Fig. 2.4). The regression produced significant *p*-values for the model (<0.001) and the predictor variables of distance (<0.001) and site (<0.001) (Table 2.4). Tree age decreased with increasing distance from the forest end of the plots. The coefficients for Sites 2, 3, and 5 were significantly different compared to Site 1 and the coefficient for Site 4 was not significantly different than Site 1 (Table 2.4). The model produced a low R^2 of 0.14.

Figure 2.3: Tree-age distribution of the five sites at a decadal time scale. Bins along the X axis are decades. Y axis represents percent of the total number of trees that established in each decade. Ecotone shift is evidenced by new tree establishment in the last 60 years. Up to 45% of the adult trees established since 1942.

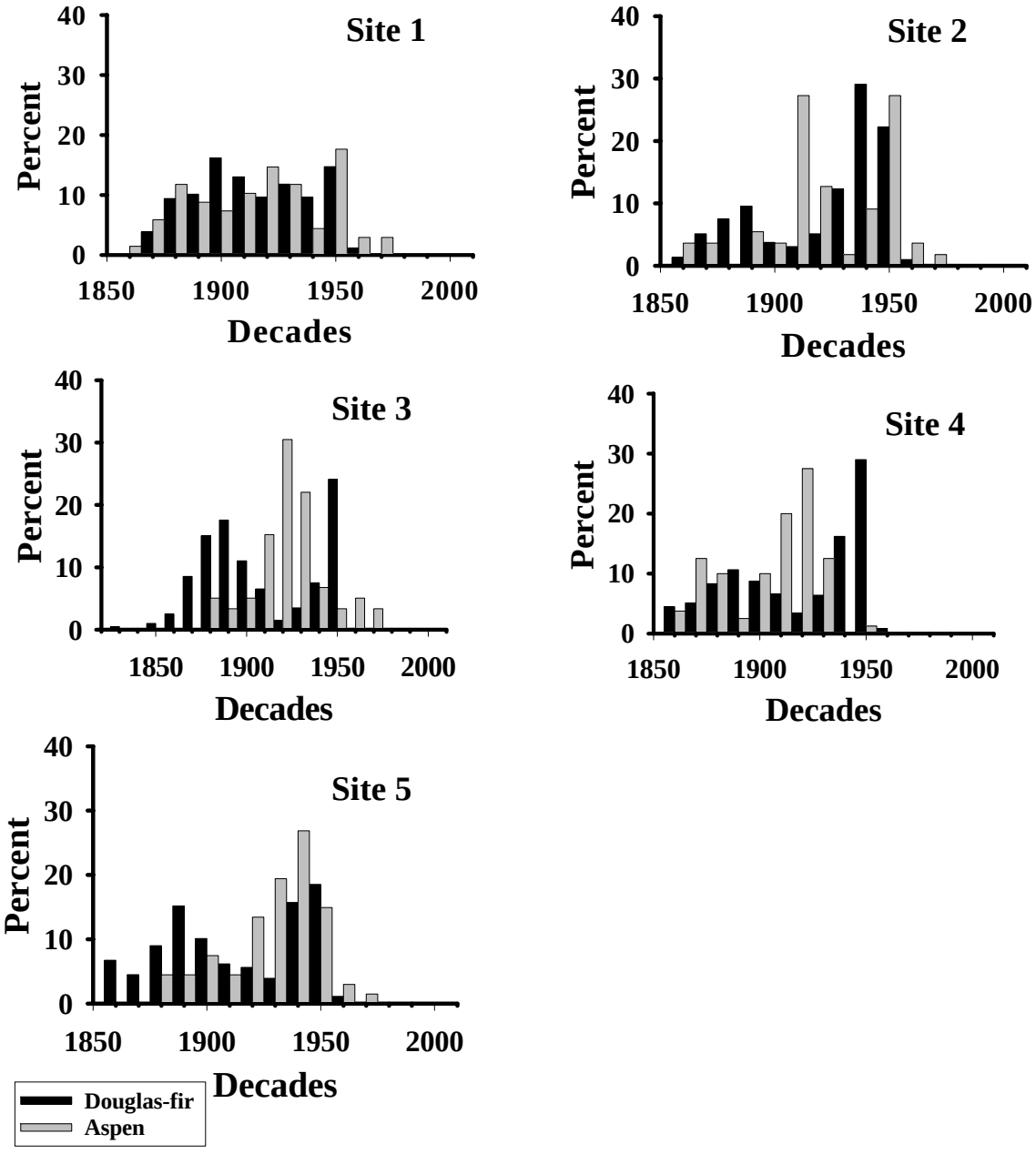
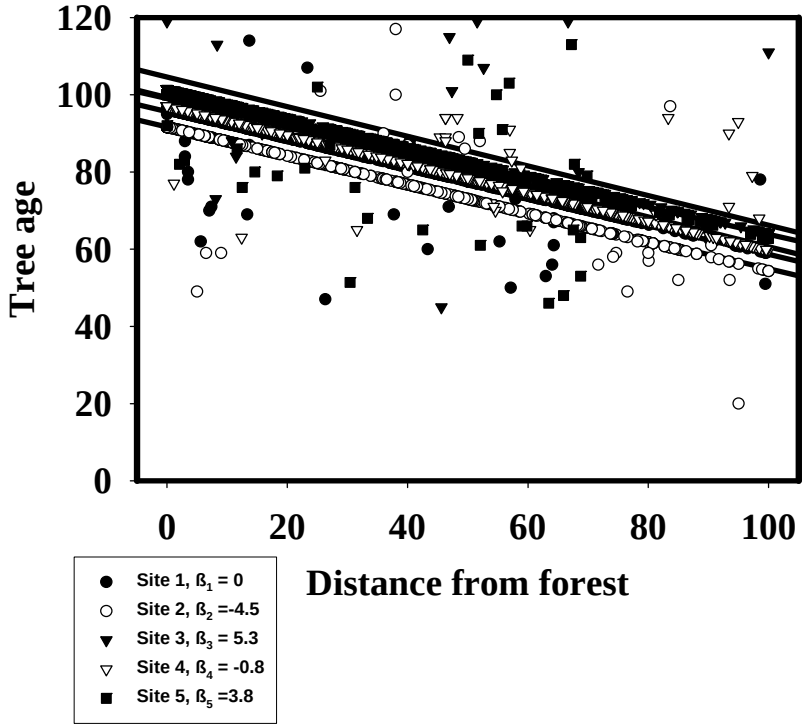


Table 2.4: Results of the tree age and distance regression model. Tree age was the response variable and the predictor variables were tree distance and sites.

Variables	Standard Error	*p*-values
Intercept	0.001	<0.001
Distance	0.007	<0.001
Site	0.45	0.0001

Figure 2.4: Tree age and tree distance relationship at each site. A single regression model was constructed with a separate indicator variable for each site (Tree age = $ß_0$* Tree distance + $ß_1$*Site1 + $ß_2$*Site 2 + $ß_3$*Site 3 + $ß_4$*Site 4 + $ß_5$*Site 5). Tree distance was a significant predictor variable and tree age decreased with increasing distance at all sites. Coefficients for Sites 2, 3, and 5 were significantly different (p-value <0.05) compared to Site 1. Site 4 was not significantly different compared to Site 1 (p-value = 0.87).



To corroborate the dendrochronological data, I compared the aerial photograph data between the two dates (Table 2.5). The aerial photograph comparison showed 15-96% increase in the number of farthest rows in the grids that intercepted tree canopy indicating a shift in the ecotone location towards the grassland. Sites 1, 2, and 3 had a statistically significant increase in the number of farthest rows that intercepted tree canopy. This was consistent with our regression model of tree age and tree distance which showed that tree age tended to decrease with increasing distance from the forest end of our plots (Fig. 2.4). The aerial photograph comparison also showed an increase in the number of farthest out rows that intercepted tree canopy cover at Site 5, but this increase was not statistically significant.

Table 2.5. Aerial photograph comparison of ecotone tree canopy cover recorded for grid points and rows. (Sites with significant differences between the two dates are marked with *).

Sites	Points that intercepted tree canopy 1942	Points that intercepted tree canopy 1990	Rows that intercepted tree canopy 1942	Rows that intercepted tree canopy 1990
1*	59	68	9	13
2*	51	66	7	14
3*	61	65	10	14
4	54	37	9	8
5	53	56	8	10

No evidence of ecotone shift towards the forest was found in the aerial photograph comparison except at Site 4 which had decreased tree cover due to road construction and associated tree cutting. The regression model of tree age and tree distance was consistent with this result and indicated no ecotone retreat, but only ecotone

shift towards the grassland. The aerial photograph point intercept comparison indicated 2-10% increase in tree percent canopy cover along the ecotone. The T-test showed that Sites 1, 2, and 3 had a statistically significant increase in tree cover between the two dates (*p*-value of 0.00001, 0.0001, 0.003) indicating a statistically significant increase in tree density. The tree-age estimate for Sites 2 and 3 is consistent with these results. No decrease in tree canopy cover was observed except at Site 4 where a decrease was observed again due to a road construction and associated tree cutting within the ecotone. An increase in tree cover was also observed at Site 5, but this increase was not statistically significant (p-value of 0.167).

Grazing Effects on Ecotone Shift

I performed a two-way ANOVA test to determine the effects of grazing and the difference in tree species on tree establishment. The tree species and the interaction term of grazing levels and tree species were significant predictor variables (*p*-value 0.001 and 0.003, respectively). This indicated that each tree species responded to different grazing levels differently and, within each species, the response varied due to the grazing levels. I analyzed the separate responses of aspen and Douglas-fir to grazing across all gradients with ANOVA and Tukey's multiple comparison tests.

Current Gradient of Grazing Intensity. I first analyzed the number of aspen trees established in the last 37 years with the current grazing levels. The grazing levels were not a significant predictor variable (p-value = 0.09) and the number of aspen trees established did not differ significantly among different grazing levels (Fig. 2.5 (a)). The current grazing levels were a significant predictor variable for Douglas-fir tree

establishment (p-value <0.001). Grazing intensity 3 had a significantly greater number of Douglas-fir trees established than grazing intensity 2 (Fig. 2.5 (b)). There were no significant differences among Grazing Intensities 1, 2, 4, and 5. There were no detectable patterns in tree establishment across this gradient.

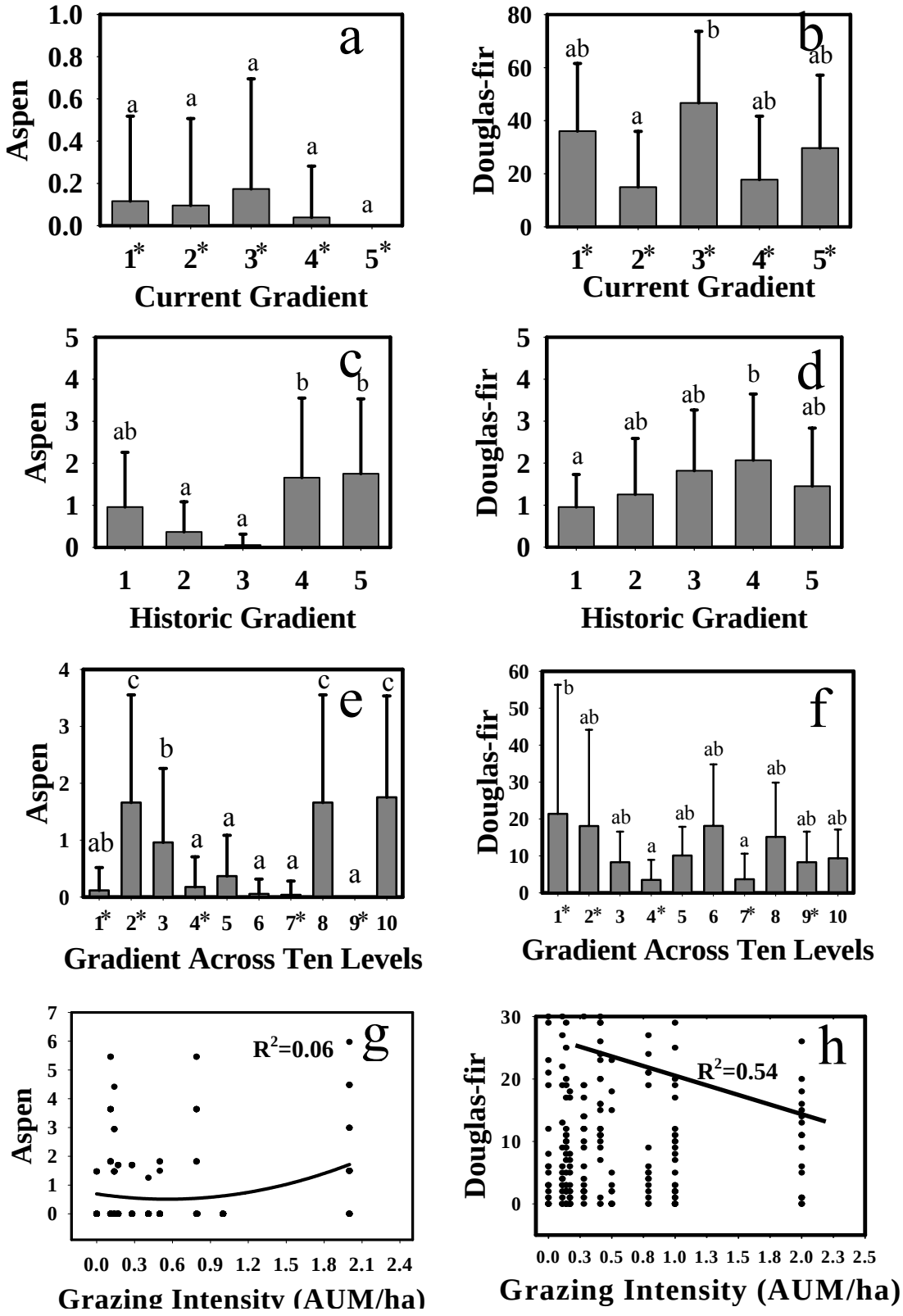
Historic Gradient of Grazing Intensity. The number of aspen trees established between 1942 and 1965 was analyzed with the historic grazing levels through ANOVA test. The historic grazing levels were a significant predictor variable (p-value < 0.001) (Fig. 2.5 (c)). Grazing intensities 4 and 5 resulted in significantly greater numbers of aspen than grazing intensities 2 and 3. Grazing intensity 1 was not significantly different compared to grazing intensities 2, 3, 4, and 5. The historic grazing levels were also a significant predictor variable for Douglas-fir establishment (p-value = 0.03) (Fig. 2.5 (d)). Grazing intensity 4 resulted in significantly greater Douglas-fir establishment compared to grazing intensity 1. Douglas-fir establishment, however, was not significantly different among grazing intensities 2, 3, and 5. There was no consistent and detectable pattern in tree establishment across this gradient.

Gradient Across All Ten Grazing Levels. I first analyzed the number of aspen trees established with all ten grazing levels (Fig. 2.5 (e)). The grazing levels were a significant predictor variable (p-value <0.001) and aspen establishment varied significantly among different grazing levels (Fig. 2.5(e)). Grazing intensities 2*, 8, and 10 had a significantly greater aspen establishment than all other grazing intensities. Grazing intensity 3 had significantly greater aspen establishment than grazing intensities 4*, 5, 6, 7* and 9*. Aspen establishment did not vary significantly among the medium

levels of grazing intensities 4*, 5, 6, and 7*. Aspen establishment was not significantly different at grazing intensities 1* and 9* compared to these medium levels. Overall, aspen establishment appeared greater at low and high grazing levels than at medium grazing levels with notable exceptions for grazing intensities 1* and 9*. The grazing levels were also a significant predictor variable for Douglas-fir establishment (*p*-value = 0.002). Grazing intensity 1 had significantly greater Douglas-fir establishment compared to grazing intensities 4* and 7* (Fig. 2.5 (f)). Douglas-fir establishment, however, did not vary significantly among any of the other grazing intensities. These patterns were not consistent with our expected pattern. Grazing effects did not follow the expected pattern of facilitation effects at low grazing levels and inhibition effects at high grazing levels.

I also constructed a regression model of grazing levels and tree establishment to describe the overall relationship between grazing effects and tree establishment. The regression of all ten grazing levels and aspen establishment produced a significant *p*-value of <0.001 for the model and a low R^2 of 0.06.

Figure 2.5: Grazing impact on aspen and Douglas-fir establishment. Grazing levels across different gradients are on the X axis. Number of new trees established (expressed in percent) under each grazing level is on the Y axis. The ANOVA equations were: Number of new trees = $\beta_0 + \beta_1$*Grazing levels. Figure a and b show aspen and Douglas-fir responses to grazing across the current gradient of lower grazing levels. Figure c and d show aspen and Douglas-fir responses to grazing across the historic gradient of higher grazing levels. Figure e and f show aspen and Douglas-fir responses to grazing across the gradient of ten levels of grazing intensity. Current grazing levels are marked with * in the gradients. Figure g and h show the overall relationship between grazing effects and tree establishment. The regression equations were: Number of new trees = $\beta_0 + \beta_1$* Grazing levels + β_2*(Grazing levels)*2.


a
Aspen
1.0
0.8
0.6
0.4
0.2
0.0
a a a a a
1* 2* 3* 4* 5*
Current Gradient
b
Douglas-fir
80
60
40
20
0
ab a b ab ab
1* 2* 3* 4* 5*
Current Gradient
c
Aspen
5
4
3
2
1
0
ab a a b b
1 2 3 4 5
Historic Gradient
d
Douglas-fir
a ab ab b ab
1 2 3 4 5
Historic Gradient
e
Aspen
ab c b a a a c a c
1* 2* 3 4* 5 6 7* 8 9* 10
Gradient Across Ten Levels
f
Douglas-fir
b ab ab a ab ab a ab ab ab
1* 2* 3 4* 5 6 7* 8 9* 10
Gradient Across Ten Levels
g
Aspen
R2=0.06
0.0 0.3 0.6 0.9 1.2 1.5 1.8 2.1 2.4
Grazing Intensity (AUM/ha)
h
Douglas-fir
R2=0.54
0.0 0.3 0.5 0.8 1.0 1.3 1.5 1.8 2.0 2.3 2.5
Grazing Intensity (AUM/ha)

Grazing intensity and the squared term were significant predictor variables (*p*-value of 0.01 for both). This model showed a slightly curvilinear trend indicating that aspen establishment initially decreased and then increased with increasing grazing intensity, which is consistent with our ANOVA results (Fig. 2.5 (g)), but inconsistent with the expected pattern of facilitation effects at low grazing levels and inhibition effects at high grazing levels.

The regression model of all ten grazing levels and Douglas-fir establishment produced a low R^2 of 0.01. The squared term was not significant as a predictor variable in this model (*p*-value of 0.17 and 0.31 respectively). The final regression model thus included only the grazing intensity as a predictor variable and produced R^2 of 0.54 and a *p*-value of 0.07 for the predictor variable and a *p*-value of <0.0001 for the model. The results of the regression model with the squared term were consistent with our ANOVA results. The ANOVA results showed that Douglas-fir establishment tended to decrease initially between low grazing levels and medium grazing levels. There were no other significant differences found in Douglas-fir establishment among different grazing levels and Douglas-fir did not increase significantly at higher grazing levels. These patterns in both models were consistent with the inhibition effects found in the current literature, but inconsistent with our expected pattern of facilitation effects at low grazing levels and inhibition effects at high grazing levels.

Effects of Abiotic Factors on Ecotone Shift

A four-way ANOVA test was performed to determine the effects of grazing levels, difference in tree species, topographic aspect and slope. Topographic slope and

aspect were not significant predictor variables (*p*-value of 0.12 and 0.62 respectively). None of the interaction terms was significant. At a coarse scale, the entire ecotone occupied a north-facing aspect with little variation in aspect. Aspects in the study sites ranged from 260 degrees (northwest) through north to 40 degrees only (northeast). The slope degrees also varied little between 5 and 20 degrees.

The Centennial Valley lower-forest grassland ecotone was found mostly on grassland soils, Mollisols. The depth to which mollic color requirement was met appeared to decrease towards the forest end of the plots. The thickest mollic epipedons occurred at the grassland end of the plots, where numerous seedlings and newly established younger trees were mapped. The presence of these seedlings and younger trees on grassland soils provided further evidence that the forest-grassland ecotone was shifting into the adjacent grassland. The mollic epipedons, on which these seedlings and younger trees are found, suggested that these soils now support trees, but they have supported grassland vegetation for centuries. Mollic epipedons take up to 1000 years to form. Organic matter in the epipedon decreases when forests encroach on Mollisols. This process of mollic epipedon change and forest soil formation can take 100-1000 years (Birkeland, 1999).

Discussion

Forest-Grassland Ecotone Shift

The results of this study indicated that both types of ecotone change occurred in the Centennial Valley during the study period: a shift in ecotone location towards the

grassland and an increase in tree density within the same boundary location. These changes were evidenced by the combined results from three different sources. First, tree-age estimate indicated that almost half of the adult trees within the ecotone were new trees that established during the study period. The ecotone tree-age distribution showed two interesting patterns. The Douglas-fir tree-age distribution was similar to that of newly established, young Douglas-fir forest stands and was dominated by a much younger range of tree ages compared to typical multi-aged forest stands (Franklin and Hemstrom, 1981). The aspen tree-age distribution showed successful regeneration throughout the 20th Century. This pattern is contrary to aspen tree-age distribution patterns from other studies in the Greater Yellowstone Ecosystem that indicate decreased aspen cover in this region due to lack of 20th Century regeneration (Ripple and Larsen, 2000; Hessl and Graumlich, 2002). Our tree-age distribution patterns suggested that successful tree establishment occurred in both species along the ecotone and the ecotone changed during the 20th Century.

Second, the aerial photograph comparison indicated a statistically significant increase in the number of farthest rows intercepted hit tree canopy at three of the sites. This indicated that new trees had established further in the adjacent grassland over the study period and resulted in a shift in the forest-grassland boundary location. The aerial photograph comparison also indicated that the total number of points that intercepted tree canopy increased during the study period resulting in tree density increase along the ecotone. Other ecotone change studies have also shown that both tree density increase and a shift in ecotone location can occur at the same time (Arno and Gruell, 1986; Dando

and Hansen, 1990). The results of this study are consistent with the conclusions of such studies. The point intercept method has not been commonly used in detecting changes in ecotones. This method, however, has been successfully used to detect changes in tree density in other studies (Kadmon and Harari-Kremer, 1999; Brown, 2003) and was a useful tool in this study.

Third, the regression model of tree age and tree distance indicated that tree age decreased with increasing distance from full canopy forest towards the adjacent grassland. This pattern in the regression model provides a useful description of the process that might be occurring along the ecotone. Although this pattern could result from several different processes that change the ecotone tree population dynamics, it might be likely to result from a particular process of new trees establishing close to the grassland end of the ecotone. This process can result in an overall trend of decrease in tree age from the forest end of the ecotone to the grassland end of the ecotone. The pattern in the regression model of new tree establishment closer to the grassland also supports the trends that we observed in the aerial photograph comparison results and provided further evidence of ecotone shift.

Tree Species Response to Grazing

Three interesting patterns were observed when the responses of aspen and Douglas-fir to grazing were examined. First, the difference in tree species was statistically significant indicating that aspen and Douglas-fir establishment responded to grazing differently. This is consistent with the literature suggesting that aspen and

Douglas-fir are different in their palatability and, therefore, might be impacted by grazing differently. Aspen suckers are preferred by cattle over Douglas-fir seedlings (Smith et al, 1972). Grazing decreases aspen green biomass, sucker density and height, and ultimately causes sucker mortality (Smith et al, 1972; Singer et al, 1996). Douglas-fir is less palatable than aspen, especially in its seedling stage when it is most vulnerable to grazing. Grazing results in a positive net effect for Douglas-fir growth by significantly decreasing herbaceous species, although it causes considerable damage to Douglas-fir through biomass removal and trampling (Hermann and Lavender, 1965).

Second, neither species showed a consistent and detectable pattern of decrease or increase when analyzed with different gradients of grazing intensity. These results showed that tree response to grazing was complex and varied across different grazing gradients. These results might also provide a potential explanation for variable results of tree response to grazing found in the current literature. Third, aspen and Douglas-fir responses to grazing were similar in some aspects across the gradient of all ten grazing levels. Both species showed higher tree establishment at the lower grazing levels than the medium grazing levels. This might indicate that aspen and Douglas-fir can sometimes show a similar response to grazing.

Grazing Effects on Ecotone Shift

First, the results of this study indicated that grazing is a complex variable and can significantly impact both aspen and Douglas-fir establishment in some cases. The patterns observed in this study supported both of the two seemingly conflicting conclusions from previous studies. Some of the results of tree establishment in this study

were consistent with the conclusions of grazing studies that grazing can have inhibition effects on tree establishment (Carmel and Kadmon, 1999; Bartolome et al, 2000). Other results from this study were also consistent with the results of other studies that grazing can have facilitation effects on tree establishment (Dando and Hansen, 1990; Archer, 1999). Furthermore, some of our results did not show significant effects of grazing disturbance on tree establishment. This was consistent with the conclusions of a recent elk browsing study that found no significant effect of different browsing levels on tree establishment (Barnett and Stohlgren, 2001). Taken together, these results showed that grazing was a complex variable. Simple linear trends of inhibition effects and facilitation effects did not appear to hold across varying gradients of grazing intensity at decadal time scales. These results suggested that no consistent conclusions could be made regarding grazing effects on tree establishment across broad ranges of grazing intensity at decadal time scales.

Second, based on the current literature, I expected facilitation effects at low grazing levels and inhibition effects at high grazing levels. The results of this study did not show such a pattern. Instead, the results indicated the opposite pattern compared to the expected trend. The results indicated that grazing might first inhibit and then facilitate tree encroachment. This pattern, where present, was weak and did not hold across our varying gradients. The specific results that do point to the possibility of an interaction between inhibition and facilitation effects were found across the third gradient for aspen. The aspen results across the third gradient, with notable exceptions, suggested that increasing grazing intensity might first inhibit and then facilitate tree establishment.

This pattern might have been weak due to lack of statistical power and the nature of our grazing gradients. The grazing gradients of this study were established based on long-term observational data and lacked experimental control on the nature of the gradient. A better controlled experiment, therefore, might be necessary to provide a conclusive evidence of a consistent trend of tree establishment under grazing effects.

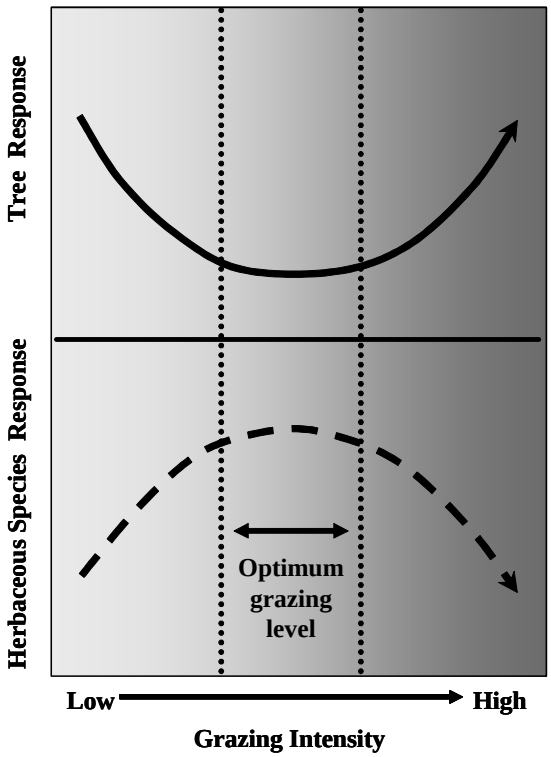
Multiple Interactive Effects

The results of this study and the conclusions in the current literature demonstrate varying effects of grazing on woody species expansion with no consistent trend. These patterns demonstrate the need for future research with process-based experiments to enhance understanding of ecotone dynamics under grazing effects. I suggest that the way forward needs to use a conceptual model such as Figure 2.6 to devise strategies for observing and quantifying multiple interacting processes of inhibition and facilitation effects.

The aspen results in this study, with some exceptions, showed greater tree establishment at low grazing intensities similar to other studies of low grazing intensity (<0.50 AUM/ha) (Archer, 1999; Asner et al., 2004). Aspen establishment, however, then showed a trend of decrease with increasing grazing intensity much like other studies of higher grazing level suggest (0.8-2.5 AUM/ha) (Carmel and Kadmon, 1999). The aspen results then indicated increase in tree establishment at high grazing intensities. This might suggest that multiple conflicting effects can be unified into a single curvilinear trend where inhibition effects dominate from low to medium grazing levels, while

facilitation effects dominate from medium to high grazing levels and the effects are balanced at the medium levels (Fig. 2.6).

Figure 2.6: A conceptual model in relation to the grazing optimization hypothesis. I suggest a single continuous model, indicated by the solid line, of grazing effects on tree encroachment. The dashed line indicates the relationship between herbaceous species productivity and grazing as suggested in the grazing optimization hypothesis. Between lower and medium levels of grazing intensity, tree encroachment decreases with increasing grazing intensity and increasing herbaceous species productivity. At medium levels of grazing intensity, tree encroachment is at its minimum, where herbaceous species productivity is at its optimum. Between medium and higher levels of grazing intensity, tree encroachment increases with increasing grazing intensity and decreasing herbaceous species productivity.



Ecotone shift at lower treelines is limited by many biotic and abiotic factors such as climate, topography, disturbance regime, and plant interactions. Tree competition with herbaceous species, in particular, is an important biotic factor that limits lower ecotone

shift, because newly establishing trees compete for the same resources with herbaceous species (Hermann and Lavender, 1965, Archer, 1994). We expect tree competition with herbaceous species to vary under changing grazing pressure. Grazing optimization hypothesis, developed for herbaceous species, states that herbaceous species productivity increases with increasing grazing intensity at low grazing levels due to overcompensation (McNaughton, 1979). This trend continues up to a point called "the level of optimal grazing" and then declines with increasing grazing intensity at high grazing levels. Between lower and medium grazing levels, therefore, we might expect tree establishment to decrease as herbaceous species productivity increases due to overcompensation. At medium levels of grazing intensity, tree establishment might reach its minimum because herbaceous species productivity is highest at these levels and, thus, tree competition with herbaceous species is greatest. Between medium and higher grazing levels, however, we expect tree establishment to increase because herbaceous species at these levels show a trend of decrease.

Conclusion

This study showed that the lower forest-grassland ecotone in the Centennial Valley is shifting into the adjacent grassland and ecotone tree density is increasing. The effect of grazing on this shift is more complex than previously observed in other studies. The shifting ecotone showed a complex response to grazing effects. I suggested a conceptual model to be tested with process-based experiments to integrate the varying effects of grazing on shifting ecotones. This model, if valid, has important implications

for grazing management and changes in vegetation patterns at a landscape scale. Medium levels of grazing intensity maintain the equilibrium between forest and grassland vegetation and control tree encroachment into productive rangelands, whereas lower grazing levels decrease forest expansion and higher grazing levels increase forest expansion. The proposed model should be tested and validated with other shifting forest-grassland ecotones under grazing effects.

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CHAPTER 3

FOREST-GRASSLAND ECOTONE SHIFT AND EFFECTS OF LIVESTOCK HERBIVORY IN NORTHERN MONGOLIA

Introduction

Forest-Grassland Ecotone Shift

Woody species encroachment into grasslands is increasingly observed and is attracting greater attention because it impacts carbon sequestration and land surface-atmosphere interactions (Archer, 1999; Mather, 2000). Shifts of forest-grassland ecotones have been documented in Asia, Australia, Africa, South America, and North America (Archer, 1989; Mather, 2000). Tree and shrub expansion towards the adjacent grassland has been correlated with climate change, increased CO_2, fire suppression, herbivory, and snow accumulation (Cairns, 1994; Bachelet et al., 2000; Bartolome et al., 2000). In central Asia, woody species expansion into grasslands has been correlated with grazing. This expansion is proposed to be further influenced by climate changes and increased CO_2 (Christensen et al., 2004). Siberian larch (*Larix sibirica*), in particular, has been demonstrated to respond quickly to increased CO_2, increased temperature and precipitation and is expected to broaden its ranges (Mudrik and Vil'chek, 2001).

Siberian larch forest is Mongolia's dominant forest type (Tsogtbaatar, 2004). Distributed throughout the northern and northwestern regions of the country, Mongolia's larch forest is the southern-most fringe of the Siberian taiga and borders the Mongolian grassland steppe. The continuous and patchy larch forest stands at this transition zone have numerous kinds of ecotones and provide an opportunity for studying forest-

grassland ecotones and their shifts. Mongolia, a continental semi-arid country, is known as one of the five most heavily grazed places in the world (Asner et al., 2005). Forest-grassland ecotones of Mongolia, therefore, provide opportunities for studying domestic livestock grazing impact on ecotone shifts.

I studied lower forest-grassland ecotones of five Siberian larch forest stands in the central Darhad Valley in northern Mongolia and investigated two types of ecotone change using dendrochronological data: a shift in forest-grassland boundary location toward the adjacent grassland and an increase in tree density at the forest-grassland boundary (Arno and Gruell, 1986). My objectives were: (1) to determine if lower forest-grassland ecotone shift occurred in the Darhad Valley during the 20^{th} Century; and (2) to examine the effects of different grazing regimes on ecotone shift at a local scale. Two questions were of primary interest: (1) Are lower forest-grassland ecotones shifting and is tree density increasing along the ecotones? (2) If so, do different grazing regimes lead to different rates of ecotone shift? I also considered the effects of abiotic factors of topographic aspect and slope on subsequent variation in ecotone shift within each grazing regime.

Determining possible causes of lower forest-grassland ecotone shift at a regional scale was not our objective. I, therefore, did not correlate potential factors such as increased CO_2 and climate change with ecotone shift in the Darhad Valley. Increased CO_2 is expected to provide competitive advantages for woody species over C_4 grasses, which evolved at lower CO_2 levels than the current level (Archer, 1999; Bazzaz, 1996). Changes in climate have also been demonstrated to be correlated with forest expansion

(Taylor, 1995). Increased temperature, increased and decreased rainfall, periodic droughts, and a shift in seasonality and distribution of precipitation events have been suggested as possible causes of increased woody species cover (Archer, 1999).

Grazing History in Mongolia

Extensive livestock production has been Mongolia's major industry for centuries. Traditional nomadic herding lifestyle and Mongolia's expansive rangelands sustain this industry even in today's market economy. Mongolia's current livestock population is over 30 million and consists of cattle (which includes cows, yaks, and cow-yak hybrid breed), sheep, goats, horses, and camels (Agriteam, 1997). The livestock population reached its peak in the last decade along with increasing number of herders. Mongolia's livestock population was substantially smaller at the beginning of the 20th Century. It continually increased throughout the last century despite the dramatic institutional, political, and economic changes that took place in Mongolia.

A majority of Mongolia's livestock was owned by religious leaders in a few large herds until the early 20th Century. As a result of the 1921 revolution, Mongolia became a socialist country and all of Mongolia's livestock were distributed more evenly in small privately-owned herds. In late 1950s, the Mongolian government established livestock collectives throughout the country and all herders had joined the collectives by 1960 (Fernandez-Gimenez, 2002). All of Mongolia's livestock then became state-owned and herders were paid a regular salary by the government to herd the livestock. The collective administration allocated pastures and regulated pasture use by forming middle-

large sized herds that were moved on a seasonal basis (Fernandez-Gimenez, 2002). In 1992, Mongolia became a democratic country and started the transition to a market economy. The collectives were dismantled and the state-owned livestock were privatized. Currently, all livestock are privately owned and all herders have a constitutional access to all of Mongolia's rangelands, which are publicly owned. All Mongols have a birthright to herding livelihood, which allowed urban dwellers to migrate to the countryside during the economic transition in early 1990s (Fernandez-Gimenez, 2002). This study examined the effects of the changes in grazing patterns and practices, associated with the institutional and economic changes of the past 80 years, on ecotone shift.

Grazing animals in the Darhad Valley

The grazing animals in the Darhad Valley are cattle, horses, sheep, and goats. Forage preferences between these animal species have been known to be substantially different. This difference results from the differences in body size, reticulo-rumen capacity, anatomy of teeth, lips, and mouth structure, grazing ability, agility, and digestive systems of the different species (Vallentine, 2001). Grazing animals can be divided into three groups based on their forage preferences: (1) grazers; (2) intermediate feeders; and (3) browsers. Grazers primarily consume graminoids and strongly avoid woody species. Grazers occasionally consume locally available forbs and woody species when graminoids are not available. Intermediate feeders eat large amounts of graminoids, forbs, and woody species. They are known for their ability to adjust their feeding habits to whatever is locally available. Browsers primarily consume forbs and

woody species and commonly consume green grass during growing seasons, but avoid dry, mature grass (Vallentine, 2001).

Horse and cattle are grazers (Vallentine, 2001). Horses mostly consume graminoids (85% of their diets) and occasionally use forbs and woody species. Cattle also prefer grasses (60-90% of their diets) and use forbs and woody species seasonally. Cattle can switch to woody species or forbs if grasses are not available.

Sheep are intermediate feeders. They are known to be highly selective foragers. Sheep consume large amounts of forbs (3-62 % of their diet) and grasses (36-70% of their diet), and lesser amount of woody species (2-30% of their diet). Sheep can selectively harvest the most palatable and most nutritive portions of grasses, and supplement their diets with forbs and woody species. They consume greater proportion of grasses in their diet than goats do (Gordon and Illius, 1992).

Most studies agree that goats are browsers, although they consume grasses and forbs (Gordon and Illius, 1992). Both their physical characteristics and foraging skills allow goats to selectively graze preferred species, even when grazing conditions are severely deteriorated by other livestock species. Their tongue and mobile upper lip structure enable them to eat short grasses and woody species and forage in areas that offer no other choice (Vallentine, 2001). Goats prefer leaves and tender twigs of woody species and consume young growth of many woody species that are less palatable to other species (Vallentine, 2001). They can consume needle leaves of conifer trees up to 220 cm tall by “riding down” to reach the leaves on higher branches (Child et al., 1985). Goats are recommended to be used to reduce tree and shrub competition in rangelands.

Goat grazing is often prevented in tree plantations where tree seedlings are short or thin enough to be bent over by goats (Child et al., 1985).

Siberian larch (*Larix sibirica*)

The genus *Larix* Miller (Pinaceae family) is distributed in North America, Asia, and Europe. The boreal *Larix* species, including *Larix sibirica*, are deciduous and occupy a wide range of habitats of early successional forests, open-boreal forests, bogs, altitudinal and latitudinal treelines, fluvio-glacial soils, talus slopes, and moraines. Deciduousness, intolerance to shade, efficient nitrogen and carbon use, and the ability to establish on poor soils enable *Larix* species to be dominant at treelines (Lepage and Basinger, 1992). *Larix* is monoecious and bear both pollen and seed cones. Pollen is dispersed by wind. Cone production in *Larix* is periodic before age 25 and abundant after age 45, but filled seeds per cone is low due to low levels of pollination (Owens, 1992).

Siberian larch grows in areas characterized by low humidity and low temperatures. It grows to 40 m or more in height and 45 to 55 cm in diameter. Its wood volume can reach 1000 m^3/ha (Milyutin and Vishnevetskaia, 1992). Siberian larch is commonly used for fire wood and building materials in the Darhad Valley. Larch forests are known to be fire-dependent (DeByle, 1981). The larch forests at our study sites are isolated small stands in the center of the valley. They are less influenced by fire than the expansive, continuous forest stands that surround the valley. I attempted to control for differences in fire history among our sites and limited our sites to those that had not burned for the last several decades. I did not find recent fire scars at our sites during our field work (2004).

Larch germination and seedling establishment are negatively impacted by shading, litter cover, lack of soil moisture, and insolation. Drought and herbivory cause a high rate of seedling mortality (Oswald and Neuenschwander, 1992). The deciduousness makes larch highly palatable to herbivores. In Mongolia, domestic livestock grazing is reported to be one of the three major causes of Siberian larch forest decline (Tsogtbaatar, 2004). Young, dense stands of larch trees have been known to form creating a fringe, known as "fairy ring" in other species such as aspen (DeByle and Winokur, 1985), along the forest edge following a reduction in grazing pressure (Didier, 2001). Further, the 20th Century regeneration pulses of Siberian larches in the Altai Mountains adjacent to our sites have been strongly correlated with decades of warmer temperatures (Moiseev, 2002). I explored the 20th Century larch regeneration patterns at my sites to determine if they coincided with the regionally known warmer periods of the 20th Century. I also used a climate reconstruction from one location in Mongolia closer to my sites than the Altai Mountains. I also explored the 20th Century larch regeneration patterns at my sites to determine if they coincided with the changes in grazing regimes associated with the institutional, political, and economic changes.

Methods

Study Site Description

The Darhad Valley is a remote, undeveloped region in northern Mongolia surrounded by mountains that reach 3000 m of elevation. The valley itself is at 1650 m of elevation and experiences extreme continental climate with cold winters and short, dry

summers. Annual precipitation ranges between 250-350 mm. The main industry in the valley is livestock production. A majority of the valley's residents are nomadic herders, who utilize the valley's public land to graze their cattle, sheep, goats, and horses. The central Darhad Valley is grazed by livestock during the summer season only (Mishig and Buya, personal communication, 2004 and 2005). Information from interviews indicates no substantial differences in wildlife use throughout the valley (Buya, personal communication, 2005). Wild ungulates are rarely seen in the valley (Mishig, personal communication, 2004).

To study livestock grazing impact on lower forest-grassland ecotone shift of the 20th Century, I selected five ecotones at five sites in the central Darhad Valley. My sites were all within a close geographic proximity of 5-15 km to each other. Each site provided an average of a 3 km long ecotone and comprised a forest-grassland ecotone area of approximately 150 ha on small hills away from the major mountain ranges. These sites were carefully selected to represent five different grazing regimes and, at the same time, to minimize differences in physiographic and climatic variables. The five grazing regimes differed both in herd composition and size. The grazing regime at each site, therefore, was determined both in terms of the dominant animal species and the overall grazing intensity. This was based on a detailed survey of the number of animals by species of every household (187 households) that has lived within 5 km of the ecotone during and since the collective period (1959-2004) (Table 3.1), reviews of the local government records, and interviews about the pre-collective grazing history (1921-1959). Both the herd size and composition changed over time at these study sites and have

become more similar among sites over the last decade (Table 3.1), with increased average numbers of cattle and goat per household. Until 1921, the valley's livestock were distributed in few large herds. They were re-distributed into small herds from 1921 to 1959, resulting in locally reduced grazing pressure. In 1959, livestock were re-grouped into few large herds, which were divided into small herds again after 1992.

Table 3.1: Number of animals during the three different grazing regimes

Sites	Pre-collective Period (1922-1959)			Collective Period (1959-1992)			Post-collective Period (1992-2004)		
	Sheep	Goat	Cattle	Sheep	Goat	Cattle	Sheep	Goat	Cattle
Site 1	1500	250	100	3033	528	119	614	318	400
Site 2	840	500	130	1679	1007	266	118	756	731
Site 3	355	260	370	712	528	726	1032	750	850
Site 4	60	40	380	117	81	765	601	402	981
Site 5	1700	150	90	3425	319	178	3114	905	857

Table 3.2: Long-term averages of grazing intensity

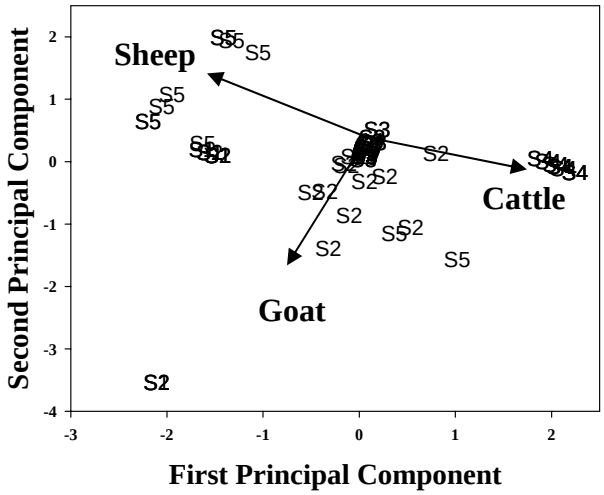
Sites	Overall Grazing Intensity	Overall Grazing Intensity (AUM/ha)	Dominant livestock species	# of households at the site
Site 1	Very low	3.3	Sheep	20
Site 2	Low	4.2	Goat-sheep	32
Site 3	Medium	4.8	Cattle-sheep-goat	56
Site 4	Medium	4.9	Cattle	36
Site 5	High	5.9	Sheep	43

I characterized the collective period herd composition at the five sites through Principal Component Analysis (PCA) to illustrate the differences among the sites in the grazing animal species (Fig. 3.1). Both herd composition and herd size remained stable within each site during this period. This was also a time period with the greatest differences in herd composition and size among sites. The PCA used number of animals by species of this period. The first principal component largely represented a gradient from sheep-dominated to cattle-dominated sites. An inverse relationship between sheep (-0.61) and cattle (+0.60) was observed indicating that high values of cattle were associated with low values of sheep. Sites 1 and 5 were dominated by sheep, while Site 4 was dominated by cattle. The second principal component represented a gradient in goat numbers. Goat numbers were also inversely related with cattle numbers (-0.56) indicating that high values of cattle were associated with low values of goat. Sites 1, 2, and 3 were characterized by greater numbers of goats compared to the rest of the sites. Site 2 had the highest number of goats. Number of horses varied little among the sites and among different time periods. I, therefore, did not include horses in the site characterization by species.

I estimated the overall grazing intensity at each site by calculating the long-term average of the grazing levels in total animal unit months per ha (AUM/ha) (Table 3.2). Different livestock species were weighted differently: cattle equaled 1.0 AUM/ha, horse 1.2 AUM/ha, sheep 0.2 AUM/ha, and goat 0.2 AUM/ha (Lacey et al., 1994). I then ranked the sites Site 1-Site 5 (Table 3.2). Site 1 represented sheep-dominance and very low grazing intensity. Site 2 represented goat-sheep-dominance and low grazing

intensity. Site 3 represented cattle-sheep-goat mix and medium grazing intensity. Site 4 represented cattle-dominance and medium grazing intensity. Site 5 represented sheep-dominance and very high grazing intensity (Table 3.2). I was not able to separately control for differences in herd composition and size due to the spatial and temporal extent of our study.

Figure 3.1: Livestock species distribution during the collective period at the five sites. Site 1-Site 5 are labeled as S1-S5. The first principal component represents a gradient from sheep-dominated to cattle-dominated sites. The second principal component represents a gradient in goat numbers.



Field Methods

A total of 149 rectangular plots were established at the five ecotones with 30 plots at four sites and 29 plots at one site due to a smaller ecotone length. Plots were located at fixed intervals along each ecotone (20-60 m depending on the length of the ecotone) with their long axis perpendicular to the ecotone. All plots were 5 m wide with varied lengths of 11 m to 144 m depending on the width of the ecotone. The width of the ecotone was

determined by the definition of ecotone used in this study: a transition zone between 80% tree canopy cover in the forest and 100% herbaceous cover in the grassland. The forest end of each plot was positioned at 80% mature tree (≥80 years old) canopy cover, which was ocularly estimated and represented full canopy forest. Each plot extended from the forest into the adjacent grassland. The grassland end was positioned at 100% herbaceous cover and included the farthest out tree seedling. Slope and aspect of each plot were measured and recorded. When multiple slope breaks were observed within a plot, the plot was divided into sections of uniform slope and each section was measured separately. All adult trees within each plot were mapped and cored at 30 cm above ground, on the downhill side, with an increment borer to estimate age. Distance of each tree from the forest end of each plot was measured to correlate adult tree-age estimate and distance of each tree from the full canopy forest. All stems ≤8 cm in diameter at coring height were classified as seedlings. All live seedlings were counted and mapped in 5m x 5m quadrats within each plot. Dead stems and stumps were also counted and mapped in each plot to estimate mortality.

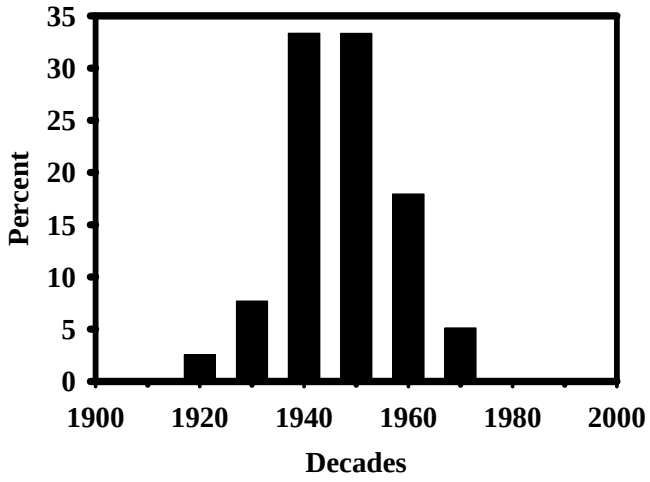
Tree-Age Estimate

I cored 2,968 trees and processed and dated the core samples using standard dendrochronological methods (Stokes and Smiley, 1968). A total of 2,790 samples were dated successfully and 178 samples were eliminated from the analysis because of rotten wood and branch scars in the samples (Table 3.3).

Table 3.3: Number of trees sampled and stem-age distribution.

Sites	# trees cored	# trees successfully dated	% of adult trees established in the last 80 years	# seedlings counted (additional stems ≤80 years old)
Site 1	504	487	74.0	922
Site 2	491	435	69.2	752
Site 3	289	216	55.3	1191
Site 4	869	856	82.8	995
Site 5	815	796	94.7	849

Figure 3.2: Seedling-age distribution. The seedling age ranges from 29 to 80 years. A majority of these stems were established in the decade of 1940 and 1950, and no new seedlings were established after the decade of 1970. These stems were classified as seedlings and were not included in the adult tree-age distribution.



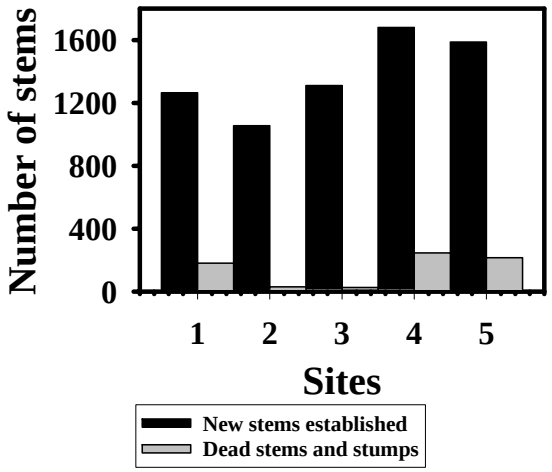
A total of 4,709 seedlings were counted. I destructively sampled 40 seedlings at the base of the stem and built a seedling-age distribution with their age estimate (Fig. 3.2). My seedling age estimate was based on this distribution. My statistical power test indicated that a sample size of 30 seedlings would provide an accurate estimate of seedling age within a standard error of 5 years and 99% confidence interval (*p*-value

0.01). Therefore, I could confidently use the sample size of 40 to build a seedling-age distribution on a decadal scale. The same seedling samples were used to estimate the number of rings lost from ground level to coring height. Eleven years were added to the tree ring count to adjust for the coring height (30 cm above ground).

Data Analysis

I first determined whether there had been ecotone shift and tree density increase during the study period. I constructed tree-age distribution for each site at a decadal scale to determine if new trees established during the study period within the ecotone. I also compared regeneration over the study period with the counts of standing dead stems and stumps as the best available estimate of mortality (Fig. 3.3). Once it was determined that new trees had established during the study period, I was interested in exploring if a relationship existed between tree age and tree location within the ecotone. Many ecological processes can impact tree regeneration and mortality patterns along the ecotone. Among them we would expect a process of tree establishment closer to the grassland, which is a necessary mechanism for ecotone shift to occur. A description of such mechanism would provide an additional evidence of ecotone shift. I examined adult tree-age estimate with the distance of trees from the forest end of the plots and used a regression model to describe the process of ecotone shift. Tree age was the response variable and tree distance was the predictor variable. The regression model also included the five sites as indicator variables and interaction terms of tree distance and sites to reduce the error effects caused by site differences and to test for differences between sites. This analysis included the adult trees only.

Figure 3.3: Comparison of new tree establishment and mortality. We did not estimate mortality rates of the last 80 years, but counted dead stems and stumps in our plots as our best estimate of mortality. Number of new stems by far exceeded the number of dead stems.



I then examined the seedling distribution along the ecotone to further address the first question. The seedlings appeared to have established in the former grassland forming a "fairy ring" along the edge of the forest, because all the stems within the "fairy ring" were small stems of the same size and there were no large stems among them or further in the grassland with a few exceptions (Fig. 3.4). The seedling age estimate indicated that these small stems were successfully established older stems (29-80 years old). I was, therefore, interested in quantitatively describing the seedling distribution within the ecotone. Specifically, I was interested in determining if seedling density varied from the grassland end of the plots to the forest end of the plots at 80% canopy cover, which represented full canopy forest. Given the ecotone definition used in this study, I expected to find few seedlings at the grassland end of the plots because this end of the plots was located at 100% herbaceous species cover and included the farthest out

tree seedlings in the grassland. I expected to find greater numbers of seedlings at the forest end of our plots due to greater seed source and closer distances to the seed source. We, therefore, might expect a decreasing trend in average seedling density from the forest end of our plots towards the grassland end of our plots. Variations in this trend, however, could be observed due to changes in micro-site availability throughout the ecotone and ecological processes that impact regeneration patterns including a dispersal decay function. I expected to find a peak in average seedling density midway between the full canopy forest and 100% herbaceous species cover at the grassland end of the ecotone, if seedlings were regenerating in a pulse forming fringes along the forest-boundary advancing the ecotone. I examined the average seedling density per quadrat with the quadrat distance from the grassland end of the plots using a regression model. Average seedling density was the response variable and quadrat distance was the predictor variable. Sites and interaction terms of sites and quadrat distance were added in the model as predictor variables. However, these variables were statistically insignificant as predictors. They were, therefore, excluded from the final model, which included only quadrat distance and a squared term as predictor variables.

I then performed a one-way ANOVA test to examine grazing effects on ecotone shift. The percentage of stems established in the last 80 years was the response variable and the grazing regime was the predictor variable. Tukey's multiple comparison was used with all pairs to determine where significant differences occurred. I constructed a regression model to determine if topographic aspect and slope explained variation in tree establishment in general. Slope, aspect (cos transformation), and sites (indicator

variable) were the predictor variables in this model. The percentage of new stems was the response variable.

Figure 3.4: A typical lower forest-grassland boundary in the Darhad Valley. Note the trees in the lighter green color in the forefront. They are smaller and shorter than the trees in the background and form a "fairy ring" along the forest boundary. Stems in the "fairy ring" were found at very high density. Although they were mature stems, these stems were classified as seedlings due to their diameter at coring height (≤8 cm). The "fairy rings" provided strong indicators of ecotone shift (also note Fig. 3.8).



Results

Forest-Grassland Ecotone Shift

Adult tree-age distribution was constructed at a decadal scale (Fig. 3.5 (a, b, c, d, and e)). The tree-age distribution indicated that up to 95% of the adult trees were new trees that established within the last 80 years (Table 3.3) in contrast to a typical age distribution pattern of mixed-aged Siberian larch stand (Fig 3.10). An additional 4,709

stems were counted as seedlings. My seedling age estimate indicated that the age of these stems ranged from 29 to 80 years (Fig. 3.2). A majority of these stems were as old as the stems that were cored and classified as adult trees. However, the stems classified as seedlings were too small in size ($\leq$8 cm in diameter at coring height) and were not cored. They were not included in the tree-age distribution, but provided further evidence of new tree establishment in the last 80 years. Both the adult tree-age distribution and seedling-age distribution show high rates of tree establishment during the decades of 1930, 1940, and 1950, indicating a pulse of regeneration during this period. Both the adult tree-age distribution and seedling-age distribution show no new tree establishment after the decade of 1960 and 1970 respectively.

I then analyzed the estimated adult tree age with tree distance from the forest end of the plots to describe the process of ecotone shift. I constructed a regression model (Fig. 3.6) which produced significant *p*-values of <0.001 for the model and all predictor variables of distance, site, and the interaction term (Table 3.4). Site 3 was only marginally significantly different compared to Site 1 (*p*-value = 0.06), but Sites 2, 4, and 5 were significantly different compared to Site 1 (p-values of 0.002, <0.001, and <0.001 respectively). The interaction term of distance and Site 2 was only marginally significant compared to that of distance and Site 1 (*p*-value = 0.06). The interaction terms were significantly different for Sites 3, 4, and 5 compared to the interaction term for Site 1 (p-values of <0.001, <0.001 and 0.001 respectively). Tree age decreased at all sites with increasing distance from the forest end of the plots. The slope of the regression lines

varied significantly among different sites (Table 3.4). The model produced a low R^2 of 0.10. The regression model indicated no ecotone retreat towards the forest.

Table 3.4: Results of the tree age and distance regression model. Tree age was the response variable and predictor variables included tree distance, sites and interaction terms of tree distance and sites.

Variables	Standard Error	*p*-values
Intercept	1.90	<0.001
Distance	0.03	<0.001
Site	0.57	<0.001
Tree distance:Site	0.01	0.001

Next, I analyzed the seedling data to further describe the ecotone shift. Average seedling density was analyzed with quadrat distance from the grassland end of the plots through a regression model to determine if successful seedling establishment varied within the width of the ecotone. This test produced an R^2 of 0.43 and significant *p*-values of <0.001 for both predictor variables and the model (Table 3.5).

Table 3.5: Results of the seedling density and quadrat distance regression. Quadrat distance and a quadratic term were the predictor variables.

Variables	Coefficients	Standard Error	*p*-value
Intercept	-32.87	23.46	0.16
Distance	8.24	1.34	<0.001
Distance*2	-0.11	0.01	<0.001

Figure 3.5: Adult tree-age distribution at all sites. Figure a, b, d, c, and e show adult tree-age distribution at a decadal scale at Site 1-Site 5. Up to 95% of the adult trees were new trees that established within the last 80 years. All sites show a pulse of regeneration in the decades of 1930, 1940, and 1950, but no new tree establishment after the decade of 1960.

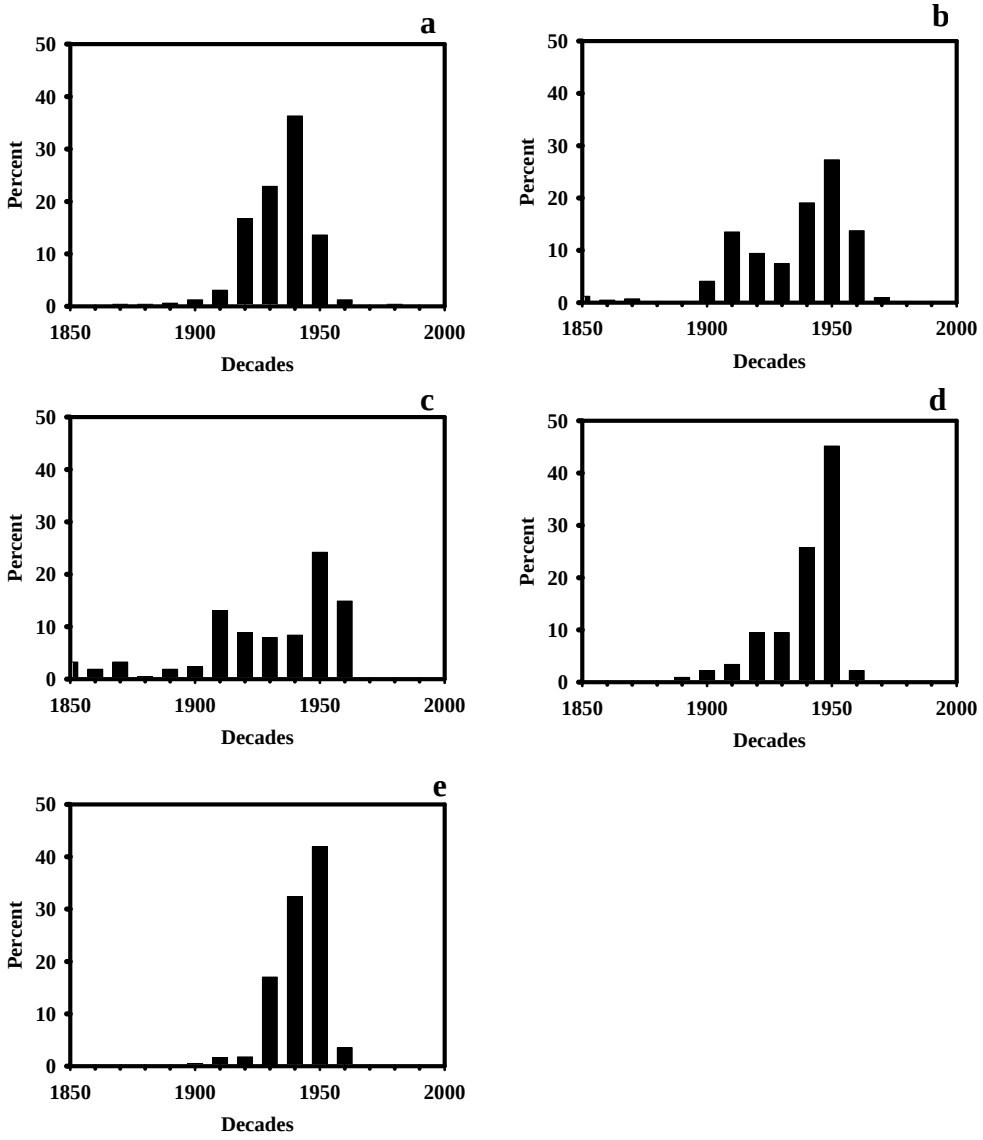
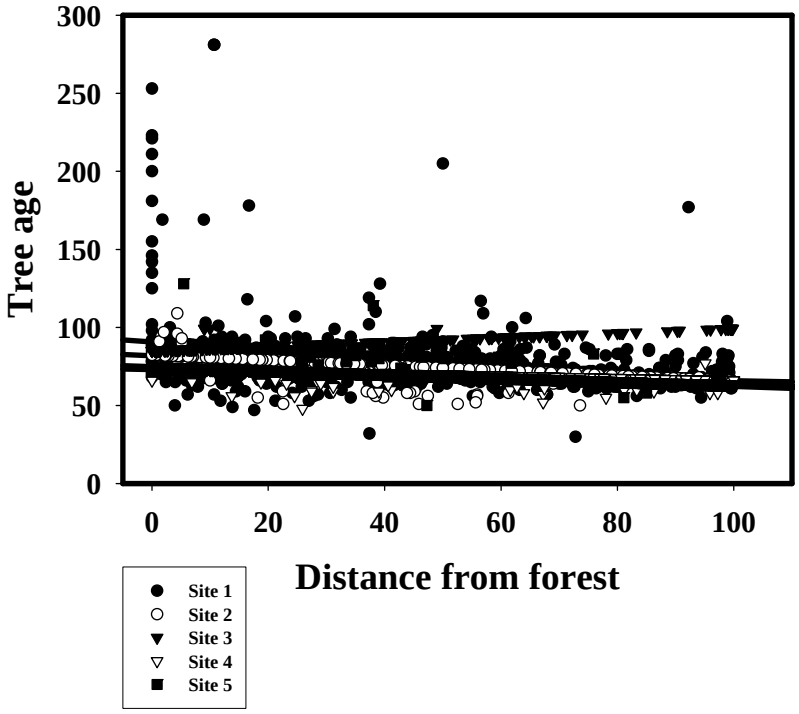


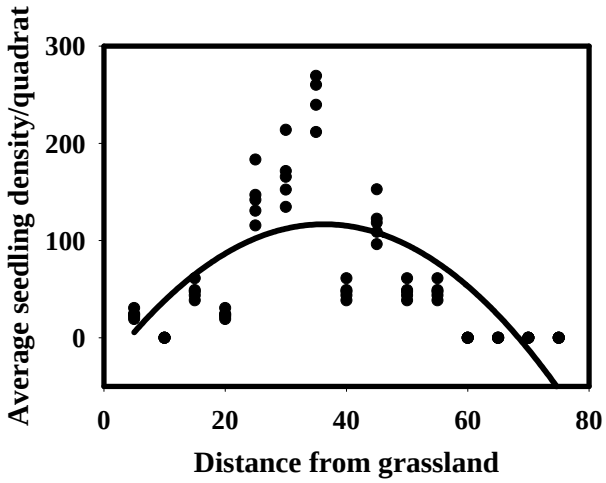
Figure 3.6: Tree age and tree distance (expressed in percent) relationship at each site. A single regression model was constructed with a separate indicator variable for each site. Regression equation is: Tree age = 90.6 - (0.2*Tree distance) – (8.3*Site 2) - (5.6*Site 3) – (17.1*Site 4) – (16.6*Site 5) + (0.1*Tree distance*Site 2) + (0.4*Tree distance*Site 3) + (0.2*Tree distance*Site 4) + (0.1*Tree distance*Site 5). Distance was a significant predictor variable and tree age decreased with increasing distance at all sites.



Average seedling density at the grassland end of the plots appeared to be close to zero, since the grassland end of the plots were located at 100% herbaceous species cover. Starting at approximately 5 m from 100% herbaceous species cover, a few seedlings were found. These smaller distances from the grassland represented distances at which the farthest out seedlings were found outside of the fairy ring. Average seedling density increased from these distances and peaked at approximately 35 m and then decreased with increasing quadrat distance from the grassland end of the plots towards

the full canopy forest (Fig. 3.7). My seedling age estimate indicated that many of these stems have successfully survived up to 80 years and are likely to remain in the tree population. Many stems might have died, but the number of surviving seedlings and new adult trees exceeded our available estimate of mortality, although I did not estimate the mortality rates of the last 80 years (Fig. 3.3). These results provide an evidence of a peak in average seedling density midway between the full canopy forest and 100% herbaceous species cover indicating a pulse of regeneration that formed fairy rings along the forest boundary. These results also provide a description of the distribution of different stem size classes throughout the ecotone observed in the field (Fig. 3.8).

Figure 3.7: Seedling distribution within the ecotone. Regression equation is: Average seedling density = $ß_0 + ß_1$*Quadrat distance + $ß_2$ (Quadrat distance)*2. Distance is measured in meters. Average seedling density increases starting at 5 meters from the grassland end of the plots at 100% herbaceous cover and peaks midway between the grassland and full canopy forest. This peak indicates the "fairy ring". Average seedling density then decreases towards the full canopy forest.



Grazing Impact on Ecotone Shift

I performed a one-way ANOVA to examine effects of grazing regimes on tree establishment. The percentage of new stems established in the last 80 years was the response variable and the grazing regimes were the predictor variable. The grazing regimes were a statistically significant predictor variable (p-value <0.001) (Fig. 3.9). The number of new stems established varied significantly between Site 2 (goat-sheep-dominated and low overall grazing intensity) and Site 4 (cattle-dominated and medium overall grazing intensity) and between Site 2 (goat-sheep-dominated and low overall grazing intensity) and Site 5 (sheep-dominated and high overall grazing intensity) (Fig. 3.9). The number of new stems established also varied between Site 3 (cattle-sheep-goat mix and medium overall grazing intensity) and Site 4 (cattle-dominated and medium overall grazing intensity).

I then constructed a regression model to determine if topographic aspect and slope explained variation in tree establishment. Topographic aspect and slope were not significant predictor variables (p-value of 0.61 and 0.69 respectively). I also used sites in this model as an indicator variable, which was significant (p-value = 0.004). Site 5 was significantly different compared to Site 1 (p-value = 0.03), but all other sites were not statistically significantly different compared to Site 1 (p-values of 0.70, 0.92, and 0.76). A low R^2 of 0.10 and a p-value of 0.01 were produced for the model.

Figure 3.8: Stem size distribution along lower forest boundary. "Fairy ring" regeneration was often observed along the lower forest boundary (also note Fig. 3.4). This ring consisted of tall, slender stems, at high density, that were classified as seedlings. These stems were too small in size (<8 cm in diameter at coring height) and were not cored. However, my seedling age estimate indicates that a majority of these stems were as old as the stems that were cored and classified as adult trees.

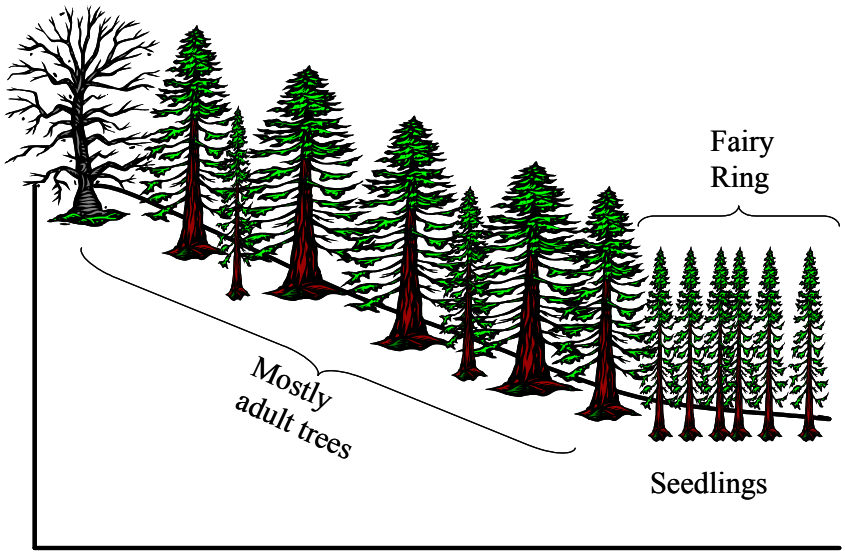
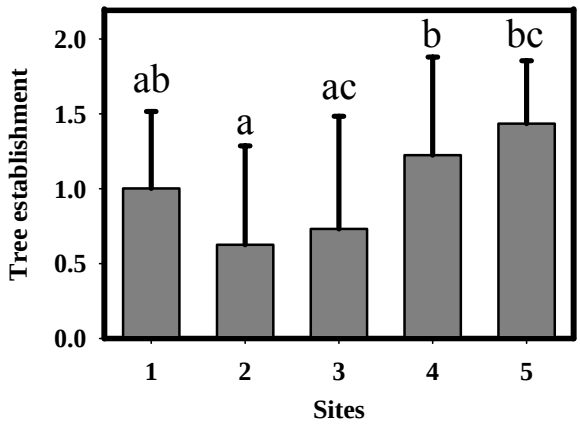


Figure 3.9: Tree establishment with different grazing regimes. Site 2 had significantly lower tree establishment than Site 5. Sites 2 and 3 also had significantly lower tree establishment than Site 4.



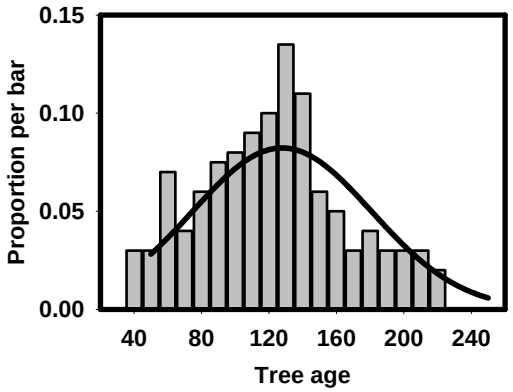
Discussion

Forest-Grassland Ecotone Shift

First, the results of this study indicated that the lower forest-grassland ecotones in the central Darhad Valley changed during the study period. The selected five larch forest stands appeared to be multi-aged stands with diverse tree size classes, although I did not study tree-age distributions of the entire forest stands. I expected the ecotone tree-age distribution to be representative of multi-aged stands, if no changes were occurring in the ecotones and the ecotones were a part of a steady-state system. Multi-aged larch forest stands are expected to show the age distribution pattern in Fig. 3.10, according to Bondarev's (1997) study of larch tree-age distribution patterns in Siberia. This age distribution was suggested to be representative of multi-aged larch stands in this region and was constructed with 1,360 larch tree samples from 40 stands. All stands in this region are indicated to have a multi-aged structure, in which the average stand age is 130 years and the range of tree ages exceeds 400 years (Bondarev, 1997).

The youngest larch forest stands have an age distribution of 40-80 years, whereas age distribution in middle-aged stands is 80-180 years and 180-400 years in old-aged stands (Bondarev, 1997). My tree-age estimate indicated that a majority of the adult trees in the ecotones were new trees that established within the last 80 years. My tree-age distribution, in most cases, was consistent with Bondarev's age distribution of newly established, young forest stands.

Figure 3.10: Typical age distribution pattern of multi-aged larch stands (Bondarev, 1997). This was the pattern I expected to see in my tree-age distribution, if no changes were occurring in the ecotones.



Two of the sites (Sites 2 and 3) showed age distribution patterns, with a few trees >100 years old, which were somewhat similar to Bondarev's distribution of middle-aged stands. A majority of the trees at these two sites, however, were still <80 years old. None of the ecotone tree-age distribution represented the expected age distribution of multi-aged stands in Fig. 3.10. This might suggest that the Darhad Valley ecotones are not representative of the forest stands and the ecotones are changing with new trees that established in the last few decades that currently dominate the age structure. My seedling age estimate (29-80 years) provided further evidence of this changing age distribution pattern. These smaller stems, classified as seedlings, dominated the population within all ecotones. Many of these stems are likely to continue to survive because they might be now large enough not to be killed by livestock herbivory, although some of them will die due to self-thinning and other disturbance factors such as fire. However, Bondarev (1997) states that the northern boreal forest stands preserve their age structure for centuries and age distribution is not so heavily influenced by catastrophic forest fires.

The isolated forest stands I studied are far less impacted by fire than stands in continuous, expansive forests and it might be likely that many of the newly recruited trees at these isolated stands will remain.

Second, the regression results described a process of a shift in the forest-grassland ecotones in the central Darhad Valley. Once new tree establishment was determined to have occurred during the study period, I explored if a relationship existed between tree age and tree location within the ecotone. Tree age decreased with increasing distance from the full canopy forest towards the adjacent grassland at all sites. This indicated that the younger trees were found closer to the grassland end of the ecotone compared to the forest end of the ecotone. This trend provided an evidence of changing forest-grassland ecotones.

Third, the analysis of seedling density and their distribution within the ecotone also suggested a shift in the forest-grassland boundary location. Average seedling density was very low at the grassland end of the plots, which were located at 100% herbaceous species cover, and at the forest end of the plots at 80% tree canopy cover. Seedling density peaked midway between full canopy forest and 100% herbaceous species cover. There were, with a few exceptions, no older mature trees among the high density seedlings. These patterns indicated a pulse of regeneration that resulted in fairy rings along the forest boundary advancing the ecotone into the adjacent grassland. The seedling age estimate showed that these stems were 29-80 years old. This age distribution indicated that these stems were successfully surviving in this environment, facilitating a forest encroachment into the adjacent grassland.

The seedling density analysis also provided a quantitative description for the "fairy ring" pattern of regeneration I observed in the field (Fig. 3.4 & 3.8). Other studies have showed that "fairy ring" regeneration is often associated with a wave regeneration mechanism (DeByle and Winokur, 1985; Bartos, 2001). During this mechanism, new stems establish in pulses creating fringes along the forest boundary in the adjacent grassland. Larch trees are known to regenerate in pulses following reductions in disturbance (Didier, 2001). Furthermore, pulses of Siberian larch regeneration in the Altai Mountain treelines, adjacent to my sites in northern Mongolia, have been correlated with warmer periods of the 1900s, 1920s, 1930s, and 1940s (Moiseev, 2002). Interestingly, a majority of the stems in the "fairy ring" regeneration and a large proportion of the adult trees were established in the decades of 1930, 1940, and 1950. The onset of this pulse regeneration at my sites coincided with the last two decades of the warmer period in the Altai Mountains (Moiseev, 2002). Another climate reconstruction study at a closer location in Mongolia showed that average temperatures increased during the decades of 1930, 1940, and 1950, but decreased during the decade of 1920 (D'Arrigo et al., 2000). This climate pattern also coincides with the pulse regeneration at my study sites and provides a possible explanation for the lesser degree of tree establishment during the decade of 1920.

Grazing Effects on Ecotone Shift

The results of this study indicated that larch tree establishment varied significantly between different grazing regimes at different sites. Some of these differences could be due to the differences among the sites in other biophysical variables,

although we attempted to select sites that were similar in these variables. The grazing regimes differed both in herd size and composition among our sites. I could not separately control for herd size and herd composition due to the temporal and spatial extent of the study. The effects of overall grazing intensities, the effects of different livestock species, and the effects of other biophysical variables are, therefore, correlated in this study and are impossible to separate statistically. I recognize that both the overall grazing intensity and livestock species composition might have contributed to the differences in tree establishment among our sites. The comparisons of the effects of different livestock species and the effects different overall grazing intensities are, therefore, limited to only the cases where either herd size or composition is similar among sites.

Site 3 with cattle-sheep-goat mix had significantly lower tree establishment than Site 4, dominated by cattle, although these two sites had very similar overall grazing intensities of medium level. Seedling density at Site 3 also appeared much lower than seedling density at Site 4. These differences might have been due to the difference in species composition between the two sites. Specifically, these differences might have been associated with the difference between goat grazing and cattle grazing. Cattle, the dominant species at Site 4, are grazers (Vallentine, 2001). Cattle prefer herbaceous species over woody species and are expected to have less impact on trees and tree seedlings. Their negative impact on herbaceous species reduces competition for trees and tree seedlings. Cattle grazing, therefore, might have contributed to the greater tree establishment at Site 4 than at Site 3. Goats, in contrast, are browsers and prefer young

growth on trees and tree seedlings (Vallentine, 2001). Their ability to selectively graze, even in areas severely deteriorated by other animals, and to "ride down" trees out of their reach increases their negative impact on tree establishment. The site with the highest goat number, Site 2, also had the lowest tree establishment compared to all other sites, supporting the same trend of goat impacts. Site 2 also had statistically significantly lower tree establishment compared to Sites 4 and 5, although these two sites had higher overall grazing intensities, and I can not separate the effects of overall grazing intensity from those of livestock species. These results are consistent with the conclusions of other studies that goats have negative effects on tree and tree seedling establishment (Child et al., 1985; Vallentine, 2001).

Two of the sites, Site 1 and Site 5, were dominated by sheep. Site 1 represented the lowest overall grazing intensity, whereas Site 5 represented the highest overall grazing intensity. I found no statistically significant difference in tree establishment between these two sites. This might indicate that low and high overall grazing intensities do not have significantly different impacts on tree establishment, although low and high grazing intensities might have different effects compared to no grazing or medium levels of grazing intensity. This result also might indicate that sheep, in general, do not have substantial negative effects on tree establishment regardless of sheep grazing intensity. Sheep are intermediate feeders and consume large amounts of forbs and grasses, but lesser amount of woody species (Vallentine, 2001). Their effects on tree establishment, therefore, might be hard to detect even at high sheep grazing intensity and might become more pronounced only when sheep are mixed with other livestock species.

The results from all sites indicated that a majority of the new stems were established during the decades of 1930, 1940, and 1950. Interestingly, these decades coincided with the time period when livestock in the Darhad Valley were distributed in small herds. Darhad Valley's livestock were distributed in few large herds before 1920s, when the religious leaders ruled this area. After the 1921 revolution, the large herds were re-distributed into small herds. The collectives were established in the Darhad Valley in 1959 and the livestock were re-grouped into few large herds again. The results of this pulse regeneration during the decades of small herds (1930, 1940 and 1950) were consistent with the conclusions of the other study that documented the establishment of new stands of dense larch trees in "fairy rings" following a reduction in grazing pressure (Didier, 2001). These decades of small herds also coincided with the warmer periods of the 20th Century observed in this region (D'Arrigo, 2000). It is, therefore, difficult to say conclusively that lower grazing pressure caused greater tree establishment during these decades. It might be that the combination of warmer temperatures and lower grazing pressure allowed trees to establish in a pulse during these decades.

My results also indicated that there was an abrupt decline in tree establishment in the decade of 1960. This decline is apparent in both the adult tree-age distribution and seedling age distribution. Furthermore, none of the age distribution patterns showed successful tree establishment following this decade. The decade of 1960 (and the decade of 1970 in the case seedlings) appeared to mark the end of tree establishment of the 20th Century at my sites and coincided with the establishment of the collective. Average temperatures continued to increase throughout the decades of 1960 and 1970 in this

region and remained high with increasing average temperatures in the northern hemisphere throughout the rest of the 20th Century (D'Arrigo, 2000). The abrupt decline in tree establishment, therefore, might be associated with the collective establishment. During the collective period, animals were re-grouped into large herds, increasing the grazing pressure at all sites. The collective operation continued for over three decades and the collective only collapsed in the last decade of the 20th Century. A pulse of larch tree regeneration might occur and a fringe might be observed in the future, since the livestock are now re-distributed in small herds. Such pulse regeneration might be hard to detect currently, because seedlings are still likely to be very small and a fringe is expected to become apparent when seedlings reach the age of over 30 years. I observed a few, very small seedlings, especially at Site 3. However, they were too small to core and I did not estimate their age. These small seedlings were not selected in the cross-section analysis for seedling age estimate, because there were only a small number of such seedlings and they were not representative of the seedling population that dominated most sites. The establishment of these new seedlings and possible pulse regeneration should be continually observed in this area to come to conclusions about the effects of large herds.

Conclusion

This study showed that the lower forest-grassland boundary locations shifted towards the adjacent grassland and tree density along the ecotones increased during the last 80 years until 30-40 years ago in the Darhad Valley. Siberian larch in the Darhad

Valley regenerated in a pulse during the 20th Century, similar to other studies of Siberian larch regeneration in central Asia. The pulse of regeneration occurred in the decades of 1930, 1940, and 1950 and coincided with time periods of small herds at the sites and regionally known periods of warmer temperatures demonstrated in other studies. The combined effects of warmer temperatures and reduced grazing pressure might have contributed to the pulse regeneration. The changes in the grazing practices alone might still have important effects on ecotone change over time. This study showed that there was an abrupt decline in tree establishment later in the 20th Century, despite the continued increase in average temperatures, that coincided with the change in grazing patterns associated with the collective establishment. The observed changes in the ecotones also varied due to the differences in grazing regimes among sites. This study suggested that both overall grazing intensity and livestock species composition might be important in understanding grazing effects on tree encroachment.

These results have important implications for land resource management in the face of global land cover changes. Land managers interested in controlling or promoting forest expansion into adjacent grasslands can utilize combinations of different grazing intensities and different livestock species. The effects of the differences in overall grazing intensity and the differences in species composition need to be more carefully studied in a better controlled experiment to determine which is more important for tree establishment. It is extremely important, although difficult, that the grazing regime controls and experiments continue for a substantial time period to make inferences about long-term changes in ecotone dynamics associated with grazing disturbance. The onset

of a potential pulse regeneration associated with the collapse of the collective system should also be monitored in the future to improve our understanding of the relationship between forest encroachment into grasslands and changes in grazing practices and patterns associated with institutional changes.

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CHAPTER 4

CONCLUSION: UNDERSTANDING FOREST-GRASSLAND ECOTONES, THEIR SHIFTS, AND EFFECTS OF LIVESTOCK HERBIVORY

Forest-Grassland Ecotone Dynamics

I studied 20th Century forest-grassland ecotone shift in the Centennial Valley, MT, USA and the Darhad Valley, Mongolia and examined the effects of livestock herbivory on ecotone shift at a decadal time scale. Two seemingly conflicting trends of grazing effects on tree encroachment are illustrated in the current literature: facilitation effects and inhibition effects. A vast majority of the grazing impact studies demonstrate one or the other of these two conflicting impacts, but none demonstrates both. These two conflicting trends are demonstrated in studies that compared only two or three relatively similar levels of grazing intensity and studies that examined grazing effects at shorter time scales. To understand livestock herbivory effects on tree encroachment at decadal time scales, herbivory effects need to be studied across a broader gradient of grazing intensity. At decadal time scales, drastic changes occur in socio-economic conditions leading to major changes in grazing intensity and grazing management practices. My results indicated that livestock herbivory might have both inhibition and facilitation effects on ecotone shift at decadal time scales as grazing intensity and grazing management practices change over time.

Grazing might show facilitation effects on tree encroachment due to several ecological processes (Archer, 1999): (1) Grazing decreases seed production, seedling establishment, biomass, and basal area of palatable herbaceous species and increases their

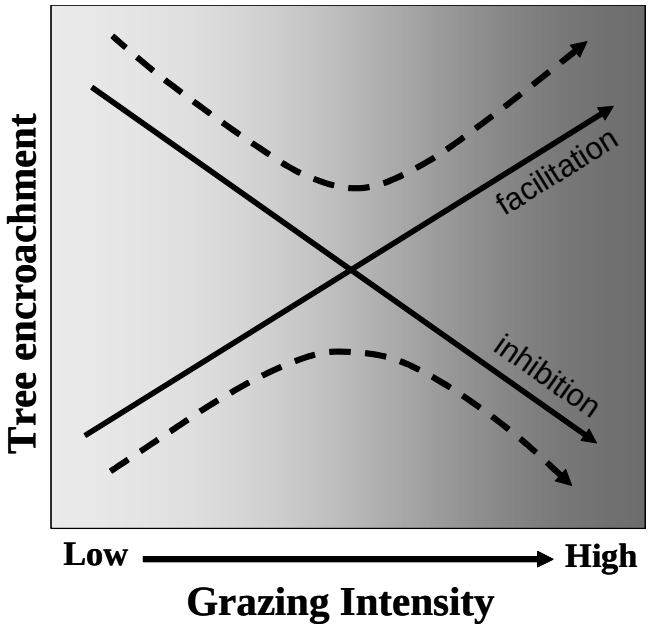
mortality; (2) Reduced herbaceous species ground cover increases sunlight levels on the ground, which increases seed germination and early establishment of woody species seedlings; (3) Reduced herbaceous species biomass decreases fine fuel accumulation and reduces fire frequency, which increases woody species invasion; (4) Invading woody species are less palatable than herbaceous species and are not browsed enough to be eliminated; (5) Grazing makes herbaceous species less able to compete for resources and unable to limit woody species growth and their seedling establishment; and (6) Livestock disperse woody species seeds across the landscape.

Inhibition effects might also be observed due to other processes: (1) Slow growth rate of most woody species allows repeated grazing in their seedling stage, when they are most vulnerable to grazing (Alverson et al., 1988; Tilghman, 1989; McInnes et al., 1992); (2) Intense grazing causes shoot loss, tissue damage and biomass loss for woody species (Hjalten et al., 1993), which decreases their seedling growth (Alverson et al., 1988; Tilghman, 1989) and increases seedling mortality (Hjalten et al., 1993); (3) Increased seedling mortality reduces recruitment into the tree population (McInnes et al., 1992; Rooney et al., 2002); (4) Trampling and rubbing against the bark by grazing animals damage woody species and their seedlings (Kay and Bartos, 2000).

Previous studies of lower grazing levels suggest facilitation effects on woody species expansion (Asner et al., 2000, Archer, 1999). Previous studies of higher grazing levels, in contrast, suggest inhibition effects on woody species expansion (Carmel and Kadmon, 1999; Bartolome et al, 2000). We might, therefore, expect a single continuum that integrates both of the locally linear trends of facilitation and inhibition effects across

a wider gradient of multiple grazing levels. Based on the trends in the current literature, we might expect that increasing grazing intensity first facilitates and then inhibits tree encroachment (Fig. 4.1). My study, however, did not show such a trend. Some of my Centennial Valley results instead indicated that increasing grazing intensity might first inhibit and then facilitate tree encroachment.

Figure 4.1: Tree encroachment and grazing effects. Solid lines show trends indicated by previous studies. Some of the previous grazing impact studies indicate facilitation effects of grazing disturbance on tree encroachment, while others indicate inhibition effects on tree encroachment. Dashed lines show non-linear trends. Based on the trends in the current literature, I expected that increasing grazing intensity might first facilitate and then inhibit tree encroachment. This expected pattern was not observed. Some of the Centennial Valley study results, however, indicated that increasing grazing intensity might first inhibit and then facilitate tree encroachment.



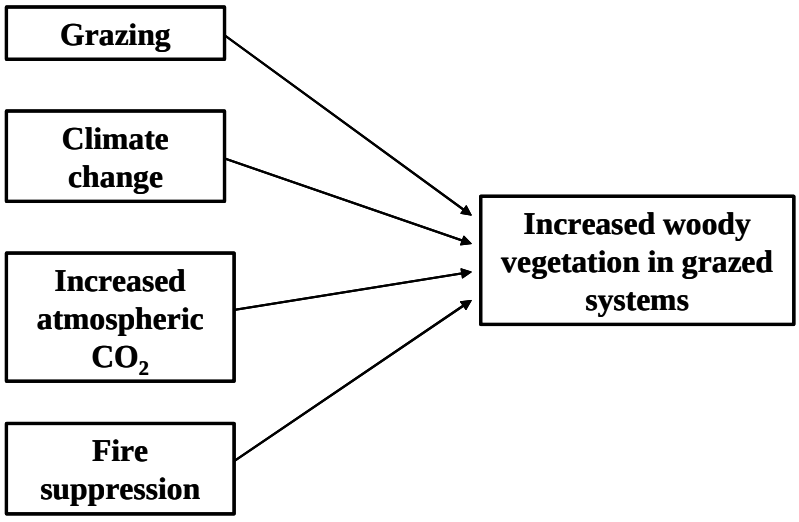
The Centennial Valley study also indicated that herbivory effects on ecotone shift might vary depending on the tree species. Aspen and Douglas-fir showed statistically

significantly different responses to grazing effects. The Darhad Valley study indicated that forest-grassland ecotone response to grazing might vary among different grazing regimes. Tree encroachment was high at the site with cattle grazing at medium overall grazing intensity. Tree encroachment was also high at the site with sheep grazing. In contrast, the sites with high number of goats had lower tree establishment than other sites. These results suggested that different grazing animal species might have important effects on ecotone shift. It is, therefore, important to understand the effects of different grazing animal species in addition to the effects of overall grazing intensity. Furthermore, the Darhad Valley study indicated that changes in grazing management practices had important effects on forest-grassland ecotone shift. Both studies indicated that legacies, especially changes in grazing practices over time, were important to understand. Therefore, the important factors in understanding herbivory effects on ecotone shift include: 1) overall grazing intensity, 2) tree species and their response to grazing, 3) the grazing animal species, and 4) legacies. These factors need to be integrated with types of forest-grassland ecotone shift to understand the dynamics of lower forest-grassland ecotone change.

Ecotone shift at my study sites might have been impacted and further enhanced by combined effects of several factors that are interactive and additive (Fig. 4.2). Possible regional factors that might have contributed to the observed ecotone shift at the study sites include climate change, increased CO_2, and fire suppression. The effects of these factors, however, were likely constant across each study site. Determining possible

causes of lower forest-grassland ecotone shift at a regional scale was not my objective. I, therefore, did not correlate all potential causes with ecotone shift.

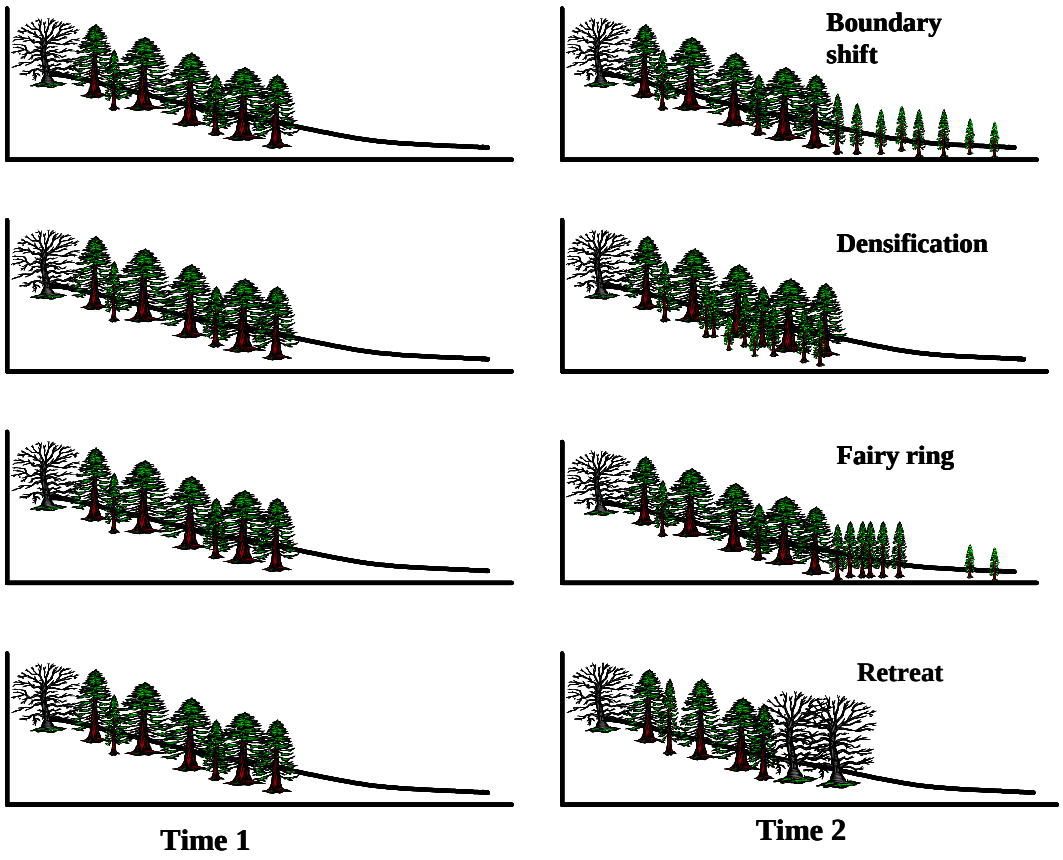
Figure 4.2: Commonly proposed factors as causes of tree and shrub encroachment. These factors might have influenced and further enhanced tree encroachment at my study sites. Grazing was the only factor



Types of Forest-Grassland Ecotone Shift

The patterns of ecotone shift were complex in both the Centennial Valley and Darhad Valley. Three general patterns of forest-grassland ecotone shift towards the adjacent grassland were observed (Fig. 4.3). These patterns were not mutually exclusive and might occur simultaneously. General patterns of ecotone retreat are uncertain, since no evidence of retreats in ecotone location was found in this study. Type I ecotone change is a shift in the forest-grassland boundary location. This type of ecotone change results from a mechanism where new trees establish in the adjacent grassland advancing the ecotone location towards the grassland.

Figure 4.3: Patterns of lower forest-grassland ecotone shift. I propose that ecotones might shift into the adjacent grassland in three different patterns. These patterns are not mutually exclusive and might occur simultaneously. Type I pattern is a shift in the ecotone location over time. Type II pattern is tree density increase within the same forest-grassland boundary location. Type III pattern is fairy ring establishment. Ecotones might also retreat into the adjacent forest, but the possible patterns of retreat are uncertain.



Type II ecotone change is an increase in tree density at the forest-grassland boundary location. During this change, new trees establish within the same boundary location and do not advance the boundary location towards the adjacent grassland. Type II ecotone change occurs in systems where tree establishment sites are available under the forest canopy, but no establishment occurs outside of the forest boundary due to

unfavorable site conditions and disturbance. Type II ecotone change can occur with Type I ecotone change at the same time.

Type III ecotone change is an establishment of a fairy ring in the grassland along the edge of the forest. This change occurs when new trees establish as a fringe in the grassland, adjacent to the forest boundary. Fairy rings consist of new stands of densely distributed new stems of similar age. Fairy ring establishment is often associated with wave regeneration mechanisms. During this mechanism, new regenerations occur as pulses advancing the forest boundary into the adjacent grassland.

Future Research on Livestock Herbivory on Ecotone Shift

The results of this study and patterns in the current literature demonstrate varying effects of livestock herbivory on tree encroachment with no consistent trend. These patterns demonstrate the need for future research with process-based experiments to enhance understanding of ecotone dynamics under grazing effects. I suggest that the way forward needs to use an integrative, conceptual model to devise strategies for observing and quantifying multiple interacting processes of inhibition and facilitation effects.

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