CONIFER COVER INCREASE IN THE GREATER YELLOWSTONE ECOSYSTEM: RATES, EXTENT, AND CONSEQUENCES FOR CARBON

by

Scott Lael Powell

A dissertation submitted in partial fulfillment

of the requirements for the degree

of

Doctor of Philosophy

in

Biological Sciences

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Approved for the Department of Ecology

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ABSTRACT

Increases in the extent and density of woody vegetation have been observed in many locations worldwide. Conifer cover increase in the Greater Yellowstone Ecosystem (GYE) has been documented by historical photos, but the rate and extent remain unquantified. Elevated atmospheric CO_2 levels have focused research attention on carbon budgeting. Carbon sinks associated with conifer cover increase are believed to account for a fraction of the "missing carbon sink," although estimates of the fraction are highly uncertain. I examined changes in conifer cover and aboveground carbon across biophysical gradients in the GYE using a combination of aerial photos, satellite imagery, field data, allometric equations, and statistical techniques. I quantified the percent conifer cover for samples in 1971 and 1999 to determine the frequency and rate of conifer cover increase. I used satellite image change detection to map the extent of conifer cover increase and aerial photo interpretation to quantify the rates of conifer cover increase. I then estimated aboveground carbon stocks for 1985 and 1999 and quantified the source/sink dynamics associated with conifer cover increase and other trajectories of forest change. I determined that the area of conifer forest increased by 7% during the period 1971-1999, at highly variable rates depending upon elevation, aspect, vegetation type, and proximity to conifer forest. Much of the variation in the rates of change was associated with gradients of soil moisture. Conifer cover increased across 685,075 ha between 1985-1999 and was responsible for the aboveground sequestration of 369 Gg C yr^{-1}, offsetting 34% of the carbon source associated with widespread fire and logging during that time period. Climate variability, fire suppression, grazing dynamics, and elevated atmospheric CO_2 levels are the hypothesized determinants of conifer cover increase. Although it is likely that no single factor is singularly responsible, fire frequency has been sufficiently reduced throughout the GYE, and the majority of carbon uptake occurred in forest types adapted to frequent fire. The temporal duration of a carbon sink associated with conifer cover increase therefore remains in question.

CHAPTER 1

INTRODUCTION TO DISSERTATION

Introduction

Changes in climate and land use have potentially significant impacts on ecosystem dynamics. Societal concern over these impacts necessitates research that can explicitly quantify the rates, extent, and consequences of change. Documented increases in the extent and density of woody ecosystems worldwide have been the subject of considerable research attention. This is due in part to the ubiquity of dynamic ecosystems, and in part to the significant consequences that ecosystem dynamics have on a variety of processes, including biogeochemical cycling (Houghton et al. 2000), hydrological cycling (Sahin and Hall 1996), fuel accumulation and fire behavior (Arno and Brown 1989), forage production (Zimmerman and Neuenschwander 1984), and biodiversity (Rosenstock and Van Riper III 2001). In the Greater Yellowstone Ecosystem (GYE), repeat historical photos document that conifer forests have significantly expanded into adjacent grasslands and shrublands, and conifer woodlands have increased in density (Meagher and Houston 1998).

Despite the documentation, knowledge of the extent, rates, determinants, and consequences of conifer cover increase remain under-developed. This dissertation presents a thorough examination of the phenomenon of conifer cover increase in the GYE. I used a variety of methods and data to answer fundamental questions about where conifer cover increase was occurring, how widespread and rapid the changes were, and what the consequences were for carbon storage. The dissertation is organized as three

research chapters that consecutively build on one another, and a final synthesis chapter, that examines this and other research in a broader context.

After this brief introduction, Chapter 2 focuses on an analysis of the frequency and rates of conifer cover increase. The objective in Chapter 2 was to examine both the overall rate of change in the GYE, and the inherent variability in the rates of change as influenced by biophysical setting. I expected that rates of conifer cover increase would be highly variable because of the complexity of vegetation, disturbance regimes, climate, and abiotic gradients in the GYE.

Chapter 3 examines techniques for scaling the findings from Chapter 2 to the entire study area. The objective in Chapter 3 was to accurately quantify the extent of conifer cover increase in the GYE between 1985 and 1999 using satellite imagery and statistical techniques. I present an improved approach for classification of conifer forests in the GYE that enabled a more accurate representation of the often subtle changes associated with conifer cover increase.

Chapter 4 presents an analysis of the consequences of conifer cover increase for carbon source/sink dynamics. The objective in Chapter 4 was to quantify the contribution of conifer cover increase to carbon sequestration in the GYE. In Chapter 4, I developed detailed vegetation maps for two time periods and quantified the land cover change dynamics associated with conifer cover increase, fire, logging, and forest regeneration. Then, based on field samples of forest structure and composition, I analyzed changes in aboveground carbon stocks as a result of these changes.

The final chapter in the dissertation is a synthesis of the current state of knowledge about conifer cover increase in the northern Rocky Mountains. I examined

research from the GYE and across the region to assess the extent and rates of change, the factors contributing to change, and the consequences for carbon storage and fire behavior.

In summary, this dissertation presents a comprehensive assessment of the methods and data required to quantify an important vegetation dynamic over a large, complex region. Previous research on the subject falls short of doing this because of methodological and data constraints. I expect that this research lays the foundation for more detailed studies in other regions, and that collectively these studies will improve our understanding of dynamic ecosystem processes and consequences.

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CHAPTER 2

FREQUENCY, RATES, AND BIOPHYSICAL VARIATION OF CONIFER COVER INCREASE IN THE GREATER YELLOWSTONE ECOSYSTEM

Introduction

In many regions throughout the world, woody vegetation has been distinctly increasing in extent and density. This process is referred to by a variety of names including expansion (Knapp and Soulé 1998), encroachment (Arno and Gruell 1986), invasion (Mast et al. 1997), density increases (Turner and Krannitz 2001), treeline advance (Rupp et al. 2001), afforestation (Soulé et al. 2003), thicketization (Archer et al. 1995), and densification (Kullman and Engelmark 1997). In the Greater Yellowstone Ecosystem (GYE), these changes have been documented by repeat historical photography (Gruell 1983; Meagher and Houston 1998). Some of these changes are attributable to forest regrowth following extensive fires prior to European settlement (Loope and Gruell 1973; Barrett and Arno 1982; Arno and Gruell 1983), but in many locations conifer forests have expanded into grasslands, shrublands, and hardwood ecosystems (Arno and Gruell 1986). Furthermore, many locations that previously supported low density, open-canopy conifer woodlands have increased in density (Arno et al. 1997). In this paper, I collectively refer to both of these processes (conifer expansion into adjacent non-forested areas and the in-filling, or densification of conifer woodlands) as conifer cover increase.

Steep abiotic gradients and static ecotones between conifer forest and non-forest in some locations suggest that edaphic and topographic factors are responsible for the long-term maintenance of vegetation boundaries (Loope and Gruell 1973). Other

research, however, suggests that far from being static, some boundaries between conifer forest and non-forest are dynamic (Jakubos and Romme 1993), driven by changes in climate (Jakubos and Romme 1993), atmospheric composition (Soulé et al. 2003), fire regimes (Arno and Gruell 1986), or grazing regimes (Richardson and Bond 1991). Here, I lay out the results of a systematic study to determine the extent, frequency, rate, and biophysical variation of conifer cover increase in the GYE. Knowledge of these issues is critical to improving our understanding of the potential consequences that conifer cover increase might have for a variety of ecosystem processes, including carbon sequestration and fire behavior.

The intent of this study was to focus solely on the process of conifer cover increase associated with "natural," relatively undisturbed systems. Previous studies have focused on forest regeneration following fire (Turner et al. 1997), logging (Barbour et al. 1998), agricultural abandonment (Brown 2003), and other disturbances such as volcanic eruptions (Lawrence and Ripple 2000). For this reason, I have chosen to exclude from the analysis areas that were recently burned, or that had a strong human footprint, such as agricultural, urban, and logging areas. The GYE is representative in this respect of a much larger region of western North America that is similarly experiencing rapid change in the structure and composition of forests, grasslands, and shrublands.

While several studies have documented the occurrence of conifer cover increase in specific locations around the GYE (Patten 1963; Jakubos and Romme 1993), no previous studies have attempted to quantify the overall extent, frequency, or rate. Simulation modeling of a watershed in the Centennial Mountains showed that the area of conifer forest had increased from 15% to 51% between 1856 and 1996, largely at the

expense of grasslands and shrublands (40% loss), and deciduous forests (75% loss) (Gallant et al. 2003). The results from a single watershed raise questions about the overall rate of conifer cover increase across the entire GYE. How widespread is conifer cover increase and how rapidly is it occurring?

Apart from the overall frequency and rate, it is unknown if conifer cover increase is occurring systematically, or rather only in particular vegetation types or biophysical settings. Some carbon budgeting studies, for example, suggest that woody encroachment into non-forest ecosystems and densification of conifer forests are ubiquitous across vast regions and occurring at constant rates (Houghton et al. 2000; Pacala et al. 2001). To the contrary, I hypothesize that conifer cover increase is occurring only in certain biophysical locations and at highly variable rates. The hypothesized drivers of conifer cover increase (changes in climate, atmospheric composition, fire regimes, and grazing regimes) interact with the demographic processes of reproduction, establishment, growth, and survival, and are mediated by local resources and conditions as determined by the biophysical template. The goal of this study is not to determine which of these factors is likely responsible for conifer cover increase, but rather to quantify the underlying biophysical variability in the distribution of conifer cover increase, and thereby improve understanding of the relative influence of the hypothesized drivers.

A key biophysical factor that potentially regulates the frequency and rate of conifer cover increase is soil moisture. Plant available soil moisture is widely regarded as critical for conifer seedling establishment (Patten 1963). Accurate measures of soil moisture are lacking at broad spatial scales, but elevation and solar aspect are proxies for temperature, precipitation, solar radiation, and evaporative demand, all of which directly

influence patterns of soil moisture. I hypothesize that both elevation and aspect strongly govern the distribution of conifer cover increase. A commonly held notion in the northern Rocky Mountains is that lower elevation forests are moisture limited while higher elevation forests are temperature limited (Daubenmire 1943; Daubenmire 1968). I hypothesize that at lower elevations, conifer cover increase is more widespread and rapid on moister northerly aspects. Conversely, I hypothesize that at higher elevations, conifer cover increase is more widespread and rapid on warmer southerly aspects.

A suite of biological factors based upon the local vegetation also potentially govern the frequency and rate of conifer cover increase. Importantly, proximity to an available seed source has the potential to directly limit the places on the landscape where change can occur. I hypothesize that there are distance thresholds from available seed sources beyond which conifer cover increase is less likely to be observed. Further, I hypothesize that the type of vegetation and the degree of canopy closure strongly influence the frequency and rate of conifer cover increase. Is conifer expansion into grasslands-shrublands as widespread as densification of conifer forests and woodlands? Is densification in lower density conifer woodlands as widespread as in higher density forests?

The 2 specific objectives of this study were as follows:

1) To determine the extent, frequency, and rate of conifer cover increase; and
2) To determine the biophysical variability in the frequency and rate of conifer cover increase.

Methods

Study Area

The 67,156 km^2 study area is located within the GYE, encompassing parts of Montana, Wyoming, and Idaho (Figure 2.1). The boundary of the study area represented the intersection of a Landsat satellite path with the GYE boundary as defined by Parmenter et al. (2003). At the core of the GYE are Yellowstone and Grand Teton National Parks, surrounded by six national forests, the Wind River Indian Reservation, and a matrix of other public and private lands. The biophysical landscape of the GYE is shaped by steep abiotic gradients in elevation, soils, and climate. Elevations range from under 1000 m along lower watershed drainages to over 4,000 m on high mountain ridges. Past volcanic activity is responsible for broad scale patterns in soils across the GYE. The soils of the Yellowstone plateau and other higher elevation locations consist primarily of nutrient poor rhyolites and andesites, whereas lower elevation soils off the plateau consist primarily of nutrient rich glacial outwash and alluvium. The climate of the GYE varies considerably by elevation and latitude, but is generally characterized by short growing seasons and cold winters.

Steep abiotic gradients strongly influence land use and disturbance regimes, and hence shape the distribution of vegetation types (Hansen et al. 2000). Gross vegetation patterns in the GYE have been well documented (Despain 1990), as have land use patterns (Parmenter et al. 2003) and disturbance regimes (Arno and Gruell 1986; Littell 2002). Xeric valley bottoms are dominated by riparian, grassland, and shrubland systems, and are heavily impacted by agriculture, urban, and residential development (Parmenter et al. 2003; Hernandez 2004). Moving upslope, there is a lower treeline

ecotone between non-forest and low density conifer woodlands. Lower elevation forests and woodlands are historically characterized by frequent, low intensity fire regimes (Arno and Gruell 1986) or mixed frequency and intensity fire regimes (Littell 2002), and have been widely impacted by fire suppression, grazing, and logging. Moving upslope, woodlands grade into higher density, mesic conifer forests. These subalpine forests are historically characterized by infrequent, high intensity fire regimes (Romme 1982; Romme and Despain 1989), and have therefore been less impacted by fire suppression (Turner et al. 2003). Higher elevation conifer forests are often patchy towards upper treeline, which is sometimes dominated by krummholtz tree growth forms that give way to tundra and bare, rocky ridges.

Study Design

I analyzed a time series of aerial photos to quantify change in percent conifer cover across the study area between 1971 and 1999. Sample locations were selected with a stratified random design based on vegetation type and biophysical setting. I determined the overall percentage of samples with conifer cover increase and the overall rate and extent of change. I then quantified the variability in the frequency and rate of conifer cover increase by Chi-square analysis and multiple comparisons.

Aerial Photo Interpretation

Data were collected within 2,144 aerial photo reference plots that were arrayed along 20 transects (Figure 2.1). The transects were variable in length and width, but were selected to fully capture gradients of elevation, aspect, and vegetation type. Within each transect, 0.81-ha plots were generated by random sampling, stratified by vegetation type

(as determined from National Forest Service and National Park Service vegetation maps), elevation, and aspect. A plot was sampled if it did not share an edge with another plot, it was not located in a distorted region of the photo, it did not contain obvious rock outcroppings, and it did not contain more than 2 major vegetation types (coniferous forest, grassland-shrubland, and deciduous forest). The majority of aerial photos used for this study were color, at 1:15,840 and 1:24,000. For each transect, I acquired photos for 1971, 1985, and 1999, or as close to these years as possible.

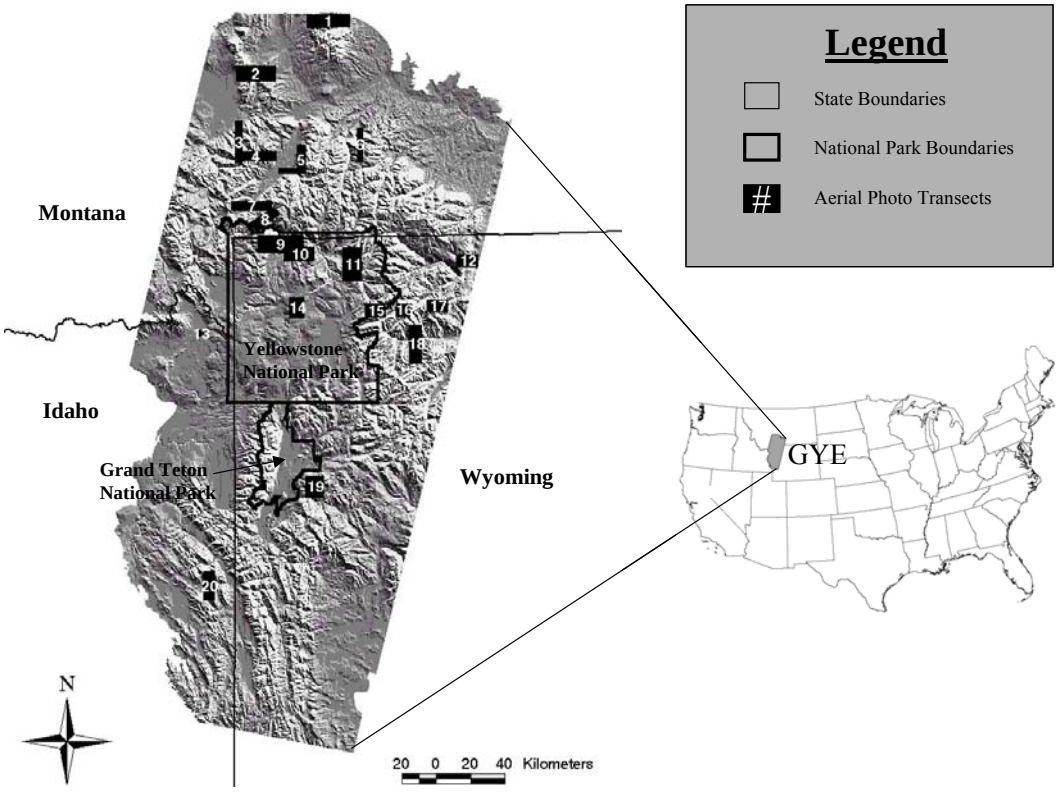

Figure 2.1. 67,156 km^2 study area within the GYE, shown with aerial photo transect locations. Aerial photo transect numbers correspond to transect names in Figure 2.2.

Data derived from the plots followed a hierarchical vegetation classification scheme (Table 2.1). For each time period, I determined the fractional composition of

coniferous forest, deciduous forest, and grassland-shrubland using the point intercept method (Parmenter et al. 2003), whereby I overlayed a 10-dot matrix on a plot and tallied intersections with vegetation components in 10% increments (e.g., 3 dots on conifer and 7 dots on grassland-shrubland was 30% conifer/70% grassland-shrubland). For the purposes of this study, I analyzed the percent composition of conifer (relative to grassland-shrubland) as a key response variable. Positive change in percent composition of conifer was classified as conifer cover increase. I separated conifer cover increase into two categories, depending upon the starting conifer cover. If 1971 conifer cover was zero, I called increase conifer expansion. If 1971 conifer cover was greater than zero, I called increase conifer densification.

Table 2.1. Four level hierarchical vegetation classification scheme for aerial photo interpretation.

<table>
<tr><th>Level 1
Gross Land Cover</th><th>Level 2
Percent Composition</th><th>Level 3
Seral Stage</th><th>Level 4
Species</th></tr>
<tr><td rowspan="6">natural vegetation</td><td rowspan="4">- coniferous</td><td colspan="2">- seedling/sapling stage (0-100% conifer) (~0-40 yrs.)</td></tr>
<tr><td colspan="2">- pole stage (≥ 70% conifer) (~40-150 yrs.)</td></tr>
<tr><td colspan="2">- woodlands (< 70% conifer)</td></tr>
<tr><td>- mature/old-growth stage (≥ 70% conifer) (~150+ yrs.)</td><td>- whitebark pine
- Douglas-fir
- mixed conifer (e.g., Pinus, Abies)</td></tr>
<tr><td colspan="3">- grassland-shrubland (includes grasses, shrubs, forbes, etc…)</td></tr>
<tr><td colspan="2">- deciduous forest</td><td>- aspen
- cottonwood
- willow</td></tr>
<tr><td colspan="4">non-vegetation (snow/ice, cloud, cloud shadow, rock, bare, water, urban, bad scan lines)</td></tr>
<tr><td colspan="4">agriculture</td></tr>
</table>

Objective 1

To determine the extent, frequency, and rate of conifer cover increase in the GYE, I analyzed the change in percent conifer composition between 1971 and 1999. The frequency of conifer cover increase was calculated as the percentage of samples that exhibited an increase in conifer cover between 1971 and 1999. The rate of conifer cover increase was calculated as the total change per sample (e.g., 10% to 30% = 20% change) divided by the number of years between measurements. I calculated the frequency of conifer cover increase across all samples (n = 2,144). I then excluded samples that contained any evidence of prior disturbance from fire or logging, and estimated the percent increase in conifer forest area (n = 1,705). Finally, I excluded samples that were not "eligible" for increase; that is, in 1971 they already had a 100% closed conifer canopy. From this subset, I calculated the frequency and rate of conifer cover increase. Finally, I estimated the percent of eligible area that increased in conifer cover by dividing the area of conifer cover increase by the area eligible for increase.

Objective 2

To determine the variability in frequency and rate of conifer cover increase, I analyzed the results from objective 1 with respect to transect location, biophysical setting, vegetation type, and distance to nearest conifer stand. For vegetation type, I used the 1971 aerial photo vegetation interpretation. The biophysical setting was classified according to the elevation and solar aspect. The distance to nearest conifer variable was computed as the Euclidean distance to the nearest conifer pixel from the land cover map derived by Parmenter et al. (2003). I used Chi-square analysis to compare observed frequencies of conifer cover increase to expected frequencies by biophysical setting and vegetation type. Expected frequencies were calculated according to the proportional

sample size for a given category. I calculated 95% family-wise confidence intervals using the Bonferonni alpha correction for multiple comparisons of both rates and frequencies.

Results

Objective 1

From the complete sample, the frequency of conifer cover increase was 22.4%. This included both conifer expansion into non-forested areas (4.9%) and conifer densification (17.5%). From the subset of samples that were not burned or logged, I estimated that the area of conifer forest increased by 7% between 1971 and 1999. After further reducing the data set only to samples that were eligible for conifer cover increase between 1971 and 1999, I calculated the overall frequency of conifer cover increase across the GYE at 38.3%. The overall rate of conifer cover increase for this subset was 0.22% (+/- 0.03 SE) per year. Over the 28 years of analysis, this rate of change equated to an average conifer cover increase of 6.2%. The percent of eligible area that increased in conifer cover between 1971 and 1999 was 10%.

Objective 2

The frequency and rates of conifer cover increase varied greatly among sampling transects (Figure 2.2). Conifer cover increase was absent or rare in several transects, and widespread in others. Three transects (Eightmile, Tom Miner, and Cinnabar), all from the Paradise Valley region north of Yellowstone National Park (YNP) in Montana, had frequencies of change over 50%. The Eightmile transect also had the highest rate of conifer cover increase, at 0.61% per year. Five other transects (Sunlight, Tom Miner,

Clayton, Clark's Fork, and Brackett) had rates of conifer cover increase of at least 0.30% per year. Two transects (Hayden and Caribou) had rates of conifer cover increase under 0.10% per year, and two other transects (Blacktail and Elkhorn) had no conifer cover increase. Of the six lowest ranked transects in terms of rate of conifer cover increase, 3 were within YNP. Only the Frost Lake transect in YNP exhibited a rate of conifer cover increase above the GYE mean.

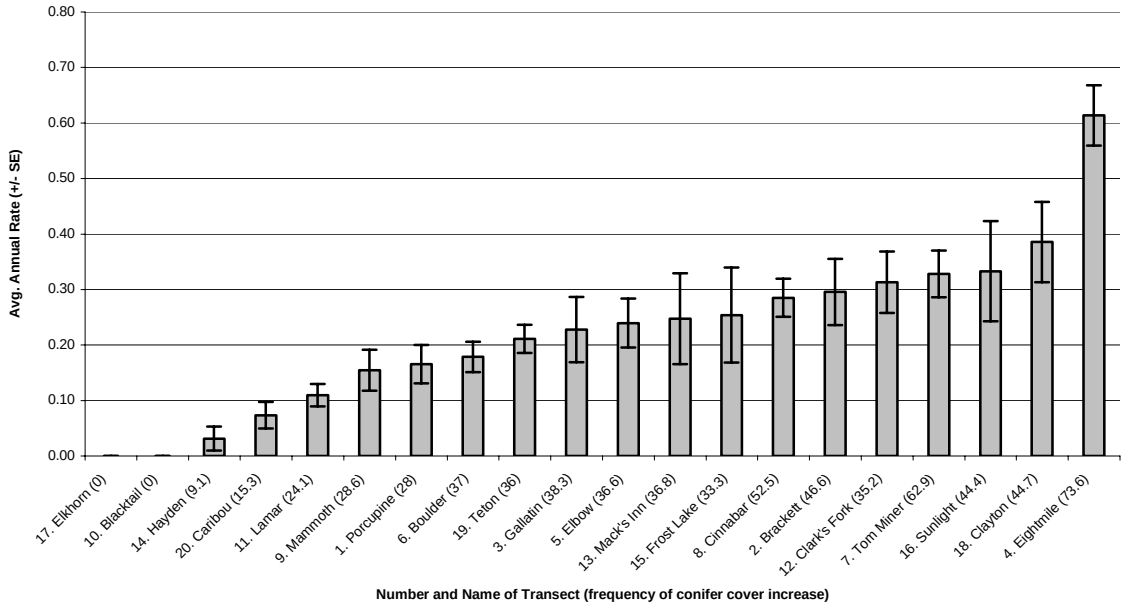

Figure 2.2. Average annual rate of conifer cover increase between 1971 and 1999, by aerial photo transect. Transect number corresponds to Figure 2.1 map. Number in parentheses is the frequency of conifer cover increase for that transect.

The frequency and rate of conifer cover increase varied significantly across the elevation gradient. The rate of conifer cover increase was significantly higher for samples between 1,751-3,000 m than for samples above 3,000 m (Table 2.2). There were significant differences in frequency across the elevation gradient (Figure 2.3). The most notable differences were for samples above 3,000 m, where only 9% exhibited conifer

cover increase, compared to samples between 1,751-2,000 m, where 48% exhibited conifer cover increase.

Table 2.2. Average annual rate and standard error of conifer cover increase by elevation. Rates with the same letter do not differ significantly based on Bonferonni corrected 95% confidence intervals.

	Elevation Class (m)						
	<1,750	1,751-2,000	2,001-2,250	2,251-2,500	2,501-2,750	2,751-3,000	>3,000
Rate (SE)	0.25 (0.05)	0.32 (0.03)	0.25 (0.02)	0.20 (0.02)	0.19 (0.02)	0.25 (0.03)	0.06 (0.04)
Diff	ab	a	a	ab	ab	ab	b

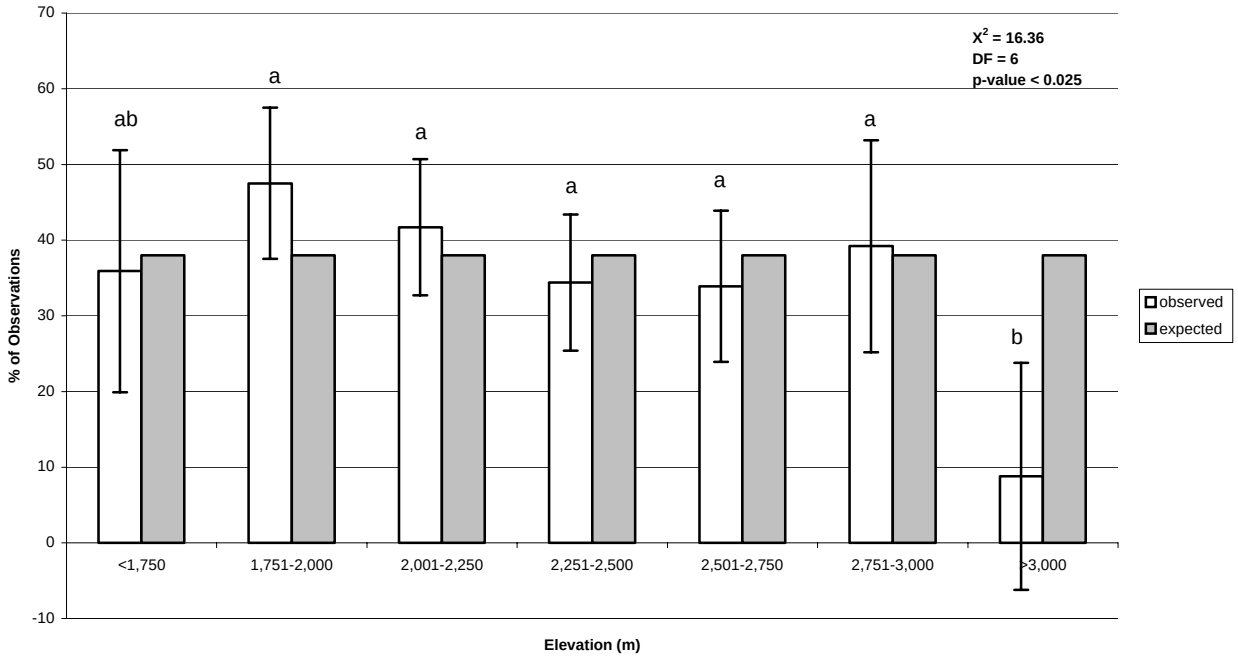

Figure 2.3. Observed vs. expected frequency of conifer cover increase by elevation class. The Chi-square statistic is reported along with its corresponding p-value. Frequencies are shown with Bonferonni corrected 95% confidence intervals. Frequencies with the same letter do not differ significantly.

The frequency and rates of conifer cover increase did not vary significantly by solar aspect. The average annual rate of conifer cover increase was relatively constant across solar aspect classes (Table 2.3). Likewise, there were no significant differences in

observed versus expected frequencies of conifer cover increase by solar aspect class (Figure 2.4).

Table 2.3. Average annual rate and standard error of conifer cover increase by aspect class. Rates with the same letter do not differ significantly based on Bonferonni corrected 95% confidence intervals.

	Aspect Class			
	Northeast	Southeast	Southwest	Northwest
Rate	0.26	0.27	0.24	0.23
(SE)	(0.02)	(0.02)	(0.02)	(0.02)
Diff	a	a	a	a

Note: Northeast = 1-90 degrees; Southeast = 91-180 degrees; Southwest = 181-270 degrees; Northwest = 271-360 degrees.

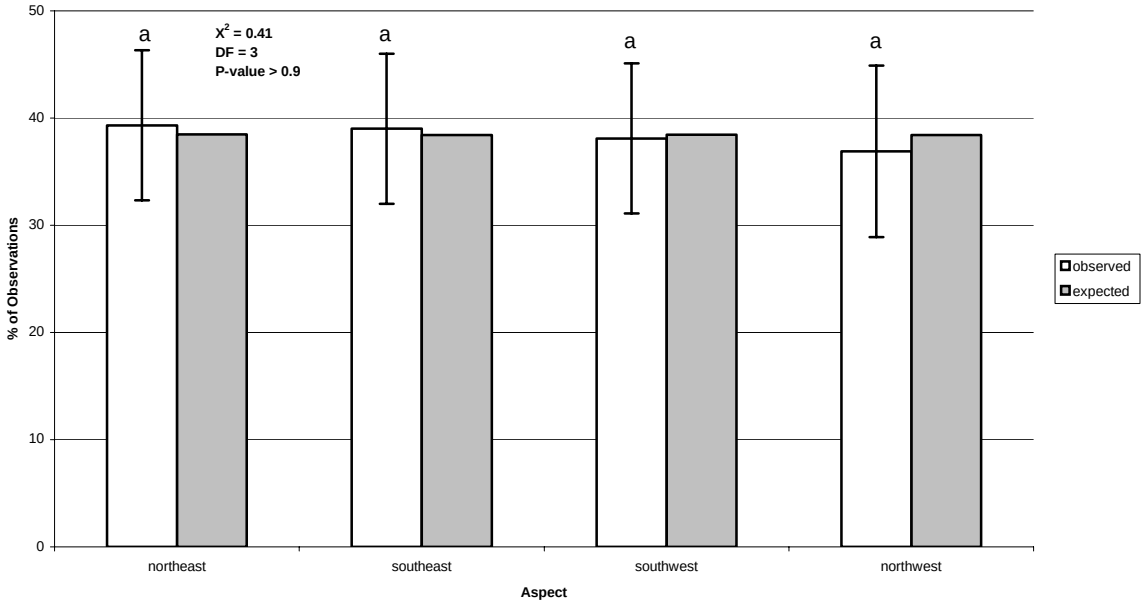

Figure 2.4. Observed vs. expected frequency of conifer cover increase by solar aspect class. The Chi-square statistic is reported along with its corresponding p-value. Frequencies are shown with Bonferonni corrected 95% confidence intervals. Frequencies with the same letter do not differ significantly. Northeast = 1-90 degrees; Southeast = 91-180 degrees; Southwest = 181-270 degrees; Northwest = 271-360 degrees.

Accounting for the interactive effect of elevation and solar aspect revealed a significantly higher rate of conifer cover increase for lower elevation plots on northerly aspects compared to higher elevation plots on northerly aspects (Table 2.4). The

observed frequencies of conifer cover increase were significantly different than expected across the elevation/aspect gradient (Figure 2.5). Lower elevation, northerly aspect samples were the most likely to exhibit conifer cover increase, at 47%, compared to higher elevation, northerly aspect samples which were the least likely, at 31%.

Table 2.4. Average annual rate and standard error of conifer cover increase by elevation, aspect class. Rates with the same letter do not differ significantly based on Bonferonni corrected 95% confidence intervals.

	Elevation, Aspect Class			
	Northerly, Low	Southerly, Low	Northerly, High	Southerly, High
Rate	0.32	0.24	0.20	0.22
(SE)	(0.02)	(0.02)	(0.02)	(0.02)
Diff	a	ab	b	ab

Note: Low elevation < 2,316 m < High elevation; Northerly Aspects = 271-90 degrees; Southerly Aspects = 91-270 degrees.

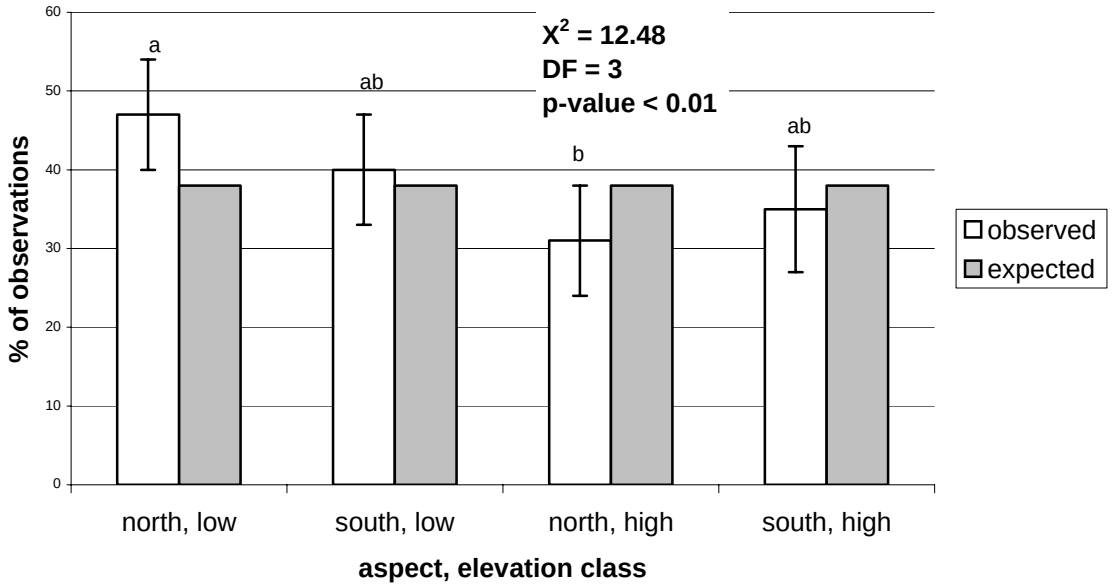

Figure 2.5. Observed vs. expected frequency of conifer cover increase by elevation, aspect class. The Chi-square statistic is reported along with its corresponding p-value. Frequencies are shown with Bonferonni corrected 95% confidence intervals. Frequencies with the same letter do not differ significantly. Low elevation < 2,316 m < High elevation; Northerly Aspects = 271-90 degrees; Southerly Aspects = 91-270 degrees.

The distance to the nearest conifer stand was a strong determinant of the frequency and rate of conifer cover increase. The average annual rate of increase generally declined as the distance to the nearest conifer stand increased. For distances greater than 180 m, the rate of conifer cover increase was significantly lower than for distances less than 60 m (Table 2.5). The frequency of conifer cover increase was generally higher than expected for distances less than 90 m, and lower than expected for distances greater than 90 m (Figure 2.6). At distances between 31 and 60 m, 47% of samples exhibited conifer cover increase, while for distances greater than 180 m, only 11% of samples exhibited conifer cover increase.

Table 2.5. Average annual rate and standard error of conifer cover increase by distance to nearest conifer stand. Rates with the same letter do not differ significantly based on Bonferonni corrected 95% confidence intervals.

	Distance Class (m)							
	0	1-30	31-60	61-90	91-120	121-150	151-180	>180
Rate	0.27	0.24	0.27	0.30	0.08	0.15	0.15	0.05
(SE)	(0.01)	(0.02)	(0.05)	(0.07)	(0.04)	(0.06)	(0.08)	(0.02)
Diff	a	ab	ab	abc	bc	abc	abc	c

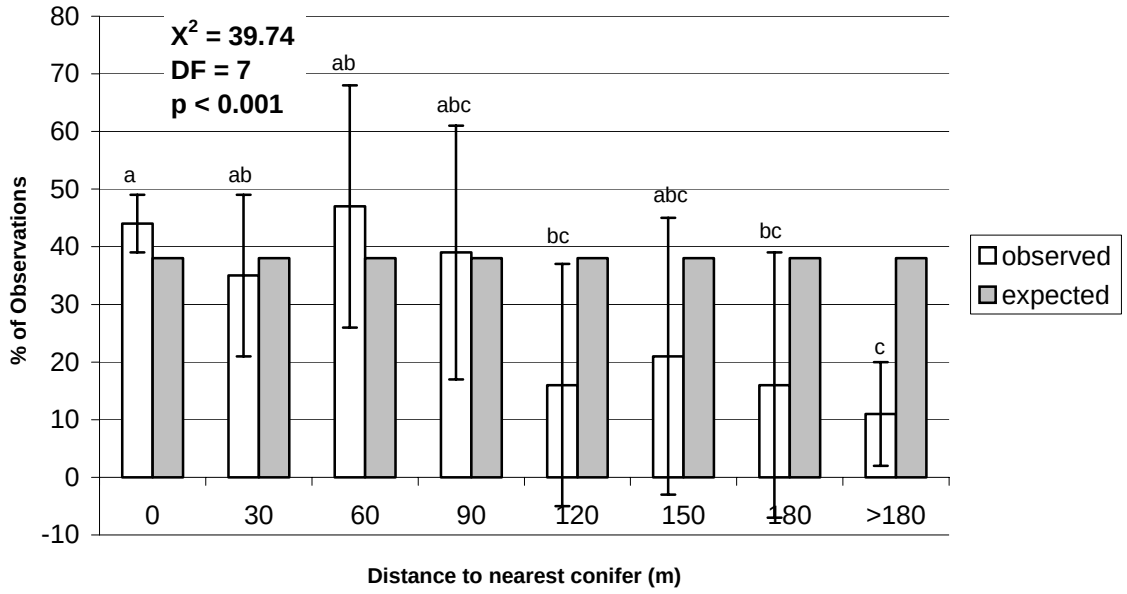

Figure 2.6. Observed vs. expected frequency of conifer cover increase by distance to nearest conifer stand. The Chi-square statistic is reported along with its corresponding

p-value. Frequencies are shown with Bonferonni corrected 95% confidence intervals. Frequencies with the same letter do not differ significantly.

The vegetation type also accounted for significant variability in the frequency and rates of conifer cover increase. Low density conifer woodlands exhibited conifer cover increase at a significantly higher rate than other vegetation types (Table 2.6). Grasslands-shrublands had a significantly lower rate of conifer cover increase than other vegetation types. The observed frequencies of conifer cover increase by vegetation type were significantly different than expected (Figure 2.7). Conifer woodlands exhibited conifer cover increase in 51% of the samples, while conifer cover increase was far less frequent than expected in grasslands-shrublands.

Table 2.6. Average annual rate and standard error of conifer cover increase by vegetation type. Rates with the same letter do not differ significantly based on Bonferonni corrected 95% confidence intervals.

	Vegetation Type		
	Conifer forest	Conifer woodland	Grassland-shrubland
Rate	0.21	0.35	0.10
(SE)	(0.02)	(0.02)	(0.02)
Diff	a	b	c

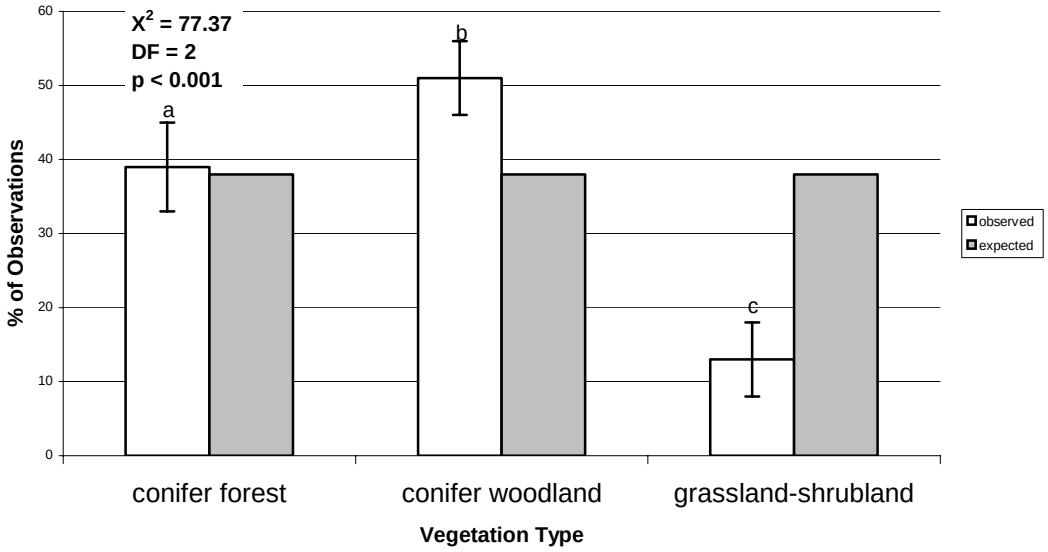

Figure 2.7. Observed vs. expected frequency of conifer cover increase by vegetation type. The Chi-square statistic is reported along with its corresponding p-value. Frequencies are shown with Bonferonni corrected 95% confidence intervals. Frequencies with the same letter do not differ significantly.

Finally, the interaction between vegetation type and biophysical setting accounted for significant variability in the frequency and rate of conifer cover increase. The rate of conifer cover increase was significantly higher for lower elevation, northerly aspect conifer woodlands than for all grassland-shrubland strata (Table 2.7). The observed frequencies of conifer cover increase by vegetation type, elevation, and aspect strata were significantly different than expected (Figure 2.8). Conifer woodlands exhibited conifer cover increase at least as much as expected for all strata, and far more than expected for lower elevations. Grasslands-shrublands exhibited conifer cover increase less than expected across all strata, and far less than expected at higher elevations.

Table 2.7. Average annual rate and standard error of conifer cover increase by vegetation type, elevation, and aspect. Rates with the same letter do not differ significantly based on Bonferonni corrected 95% confidence intervals.

	Conifer woodland				Conifer forest				Grassland-shrubland			
	High		Low		High		Low		High		Low	
	N	S	N	S	N	S	N	S	N	S	N	S
Rate (SE)	0.28 (0.03)	0.26 (0.03)	0.51 (0.04)	0.35 (0.03)	0.17 (0.03)	0.28 (0.05)	0.22 (0.03)	0.18 (0.03)	0.01 (0.01)	0.03 (0.02)	0.17 (0.04)	0.09 (0.03)
Diff	abe	ae	b	ab	ad	abe	ae	ad	c	cd	acd	cde

Note: High = higher elevation (> 2,316 m); Low = lower elevation (<2,316 m); N = northerly aspects (271-90 degrees); S = southerly aspects (91-270 degrees).

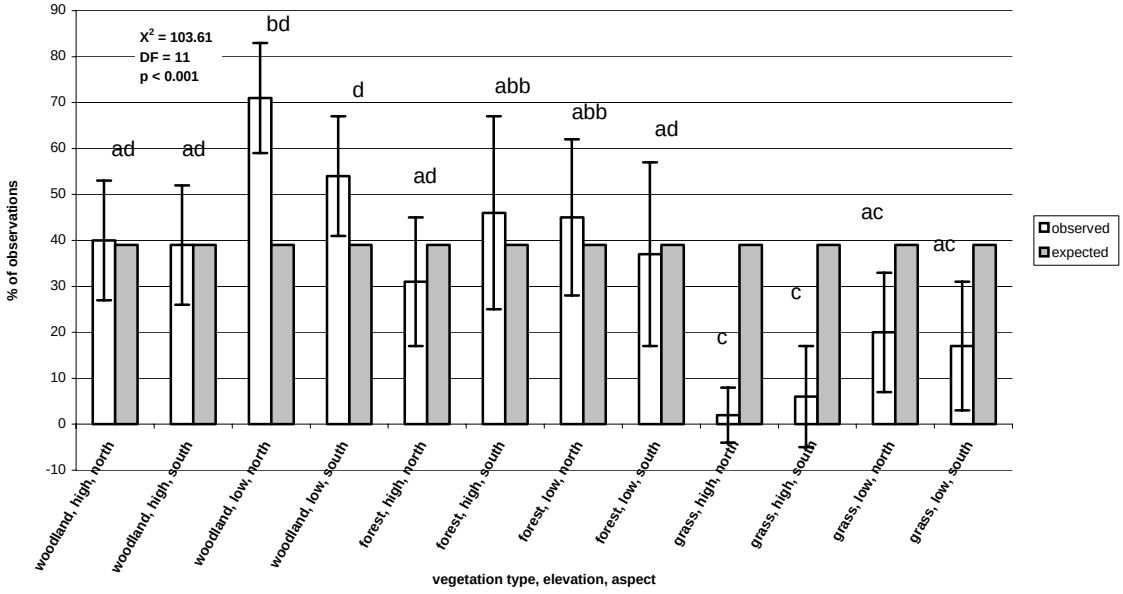

Figure 2.8. Observed vs. expected frequency of conifer cover increase by vegetation type, elevation, and aspect. The Chi-square statistic is reported along with its corresponding p-value. Frequencies are shown with Bonferonni corrected 95% confidence intervals. Frequencies with the same letter do not differ significantly. Woodland = conifer woodland; forest = conifer forest; grass = grassland-shrubland; Low elevation < 2,316 m < High elevation; Northerly Aspects = 271-90 degrees; Southerly Aspects = 91-270 degrees.

Discussion

Conifer cover increase was widespread across the GYE during the period 1971-1999, occurring in nearly one-quarter of all samples. Of that increase, densification of conifer woodlands was more than 3 times as common as expansion of conifer forests into grasslands-shrublands. Apart from fire, logging, and other vectors of forest loss, the area of conifer forest cover increased by approximately 7% over the 28-year time span. Further, nearly 40% of eligible samples increased in percent conifer cover, amounting to approximately 10% of the eligible area. These results strongly suggest that the structure

and composition of conifer forests and conifer-grassland ecotones in the GYE are rapidly changing.

These estimates of conifer cover increase are generally consistent with other studies, but are difficult to compare directly because of methodological differences. The one study that I know of from the GYE that reported the change in extent of conifer forest over time was from a single watershed in the Centennial Mountains west of Yellowstone National Park (Gallant et al. 2003). There, researchers simulated a 36% increase in the area of conifer forest over 140 years, equating to a 0.26% average annual rate of increase. This is consistent with the GYE-wide estimate of a 7% increase over 28 years, equating to a 0.25% average annual rate of increase. This estimate, however, is considerably lower than estimates from studies outside of the GYE. Along the Colorado Front Range, researchers quantified a 0.61% average annual rate of increase in the extent of ponderosa pine forest (Mast et al. 1997), and in central Oregon, researchers quantified a 0.45% average annual rate of increase in juniper cover between 1951 and 1995 (Knapp and Soulé 1998). These latter studies, however, only quantified change across smaller, relatively dynamic areas, rather than across a wide range of biophysical settings. In comparison, the rates of conifer cover increase for the fastest changing settings in this study were over 0.50% per year.

While these measures of overall change across the GYE are noteworthy, they are equally important in revealing the widespread lack of conifer cover increase in most locations. Greater than 60% of all eligible samples did not increase in conifer cover between 1971 and 1999. I noted that the frequency of conifer cover increase varied enormously across sampling transects, from 0% in several transects to nearly 75% in

another. This confirmed my prediction that conifer cover increase was not occurring uniformly across the region, but rather only in certain locations and at highly variable rates. This led me to examine which aspects of the biophysical environment strongly governed the variability of conifer cover increase.

I expected that elevation and aspect, as proxies for temperature, precipitation, solar radiation, and evaporative demand, would strongly influence the frequency and rate of change, but I was surprised that neither variable alone was a strong determinant. While lower elevation samples did increase more rapidly than higher elevation samples, the trend across elevation classes was inconsistent, suggesting that temperature and precipitation alone were not strongly limiting factors for conifer cover increase. I did, however, observe a threshold drop in frequency above 3,000 m, as samples were 5 times less likely to exhibit conifer cover increase than samples between 1,751 and 2,000 m. The extreme temperatures, short growing seasons, and blister rust disease at these higher elevations are likely explanations for this pattern. Conversely, more favorable temperatures and longer growing seasons at lower elevations likely explain the higher rate of conifer cover increase between 1,751 and 2,000 m. Contrary to my expectation, the frequency and rate of conifer cover increase did not vary significantly by solar aspect. Both frequency and rate were nearly equal across solar aspect classes, suggesting that solar radiation alone was not a limiting factor for conifer cover increase. This result is in contrast to research on ponderosa pine expansion along the Colorado Front Range that showed more widespread increase on north facing slopes versus south facing slopes (Mast et al. 1997).

The interaction between elevation and aspect strongly governs plant available moisture conditions. Lower elevations generally have longer growing seasons and higher average temperatures, but they are also associated with drier climates. Conversely, higher elevations typically have shorter growing seasons and lower average temperatures, but moisture is generally adequate, if not excessive in the case of persistent snowpack. Therefore, because of the wide range in elevations and aspects across the study area, elevation and aspect combined were significantly related to the frequency and rate of conifer cover increase in the GYE. I predicted that at lower elevations, conifer cover increase would be more widespread and rapid on moister northerly aspects, while at higher elevations, conifer cover increase would be more widespread and rapid on warmer southerly aspects. My results failed to confirmed these predictions. At lower elevations, conifer cover increase was more frequent and rapid on northerly aspects, but the differences were not significant. At higher elevations, conifer cover increase was more frequent and rapid on southerly aspects, but again, the differences were not significant.

While moisture and temperature gradients are important factors for patterns of conifer cover increase, the proximity to conifer forest is also important to consider. Distance to conifer forest was a strong determinant of the frequency and rate of conifer cover increase. I identified a threshold decrease in the frequency of conifer cover increase for distances greater than 60 m from the nearest conifer stand. Within the 28-year span of observations, conifer cover increase was approximately twice as likely to occur on sites within 60 m from the nearest conifer stand as on sites further than 180 m. There are several likely explanations for this observed trend. Most importantly, nearby conifer forests provide a seed source for conifer seedling establishment and therefore

sites near conifer forest are more likely to exhibit conifer cover increase (Steinauer and Bragg 1987; Lawrence and Ripple 2000). Given adequate conditions for reproduction, seedling establishment, growth, and survival, conifer forests develop biological inertia as the number of individuals increase and seed sources become abundant (Knapp and Soulé 1998).

The type of surrounding vegetation is another factor that influences the frequency and rate of conifer cover increase. The rate of conifer cover increase was significantly higher for conifer woodlands than for either conifer forests or grasslands-shrublands. In fact, densification of conifer woodlands occurred on more than 50% of all eligible sites, while expansion of conifers into grassland-shrubland occurred on only 13% of eligible sites. This result is likely related to the importance of proximity to conifer forest for seed availability and site improvement. Site amelioration improves soil moisture conditions and the probability of seedling survival through shade, buffer from the elements, and protection from browsing and trampling (Sindelar 1971). The significant difference in frequency of increase between conifer woodlands versus conifer forests suggests that as the canopy nears closure, less light, nutrients, and water are available for understory seedlings and saplings. Lower density conifer woodlands are therefore more dynamic and more likely to exhibit conifer cover increase than higher density conifer forests.

Implications for Determinants of Conifer Cover Increase

While this study did not examine the underlying determinants of conifer cover increase in the GYE, it is important to note that the hypothesized determinants are only as important as their influence on conifer reproduction, seedling establishment, growth, and survival. Conifer seedling establishment is strongly governed by soil moisture (Patten

1963). Climate variability, as an hypothesized determinant of conifer cover increase (Jakubos and Romme 1993), can directly influence the physical conditions of a site, rendering soil moisture more or less favorable for conifer seedling establishment. Research indicates that on sites susceptible to drought, conifer cover increase is likely triggered by cooler and wetter conditions, while on mesic sites, conifer cover increase is likely brought on by warmer and drier conditions (Butler 1986; Jakubos and Romme 1993; Miller and Halpern 1998). Atmospheric CO_2 increase has also been hypothesized as a contributor to conifer cover increase (Soulé et al. 2003), largely because of potential improvements in water use efficiency of plants under elevated CO_2 conditions (Romme and Turner 1991). Improved water use efficiency could have the effect of extending the range of a species into warmer and drier locations than where it presently occurs (Graham et al. 1990). Fire suppression (Arno and Gruell 1986) and grazing dynamics (Richardson and Bond 1991) more directly influence the growth and survival aspects of conifer cover increase. Fire suppression removes a direct source of conifer mortality, allowing vegetation succession to proceed unchecked (Sindelar 1971). Grazing, by reducing fine fuels, can also be a de facto form of fire suppression (Butler 1986). At high grazing levels, trampling of conifer seedlings can be a direct source of mortality, while at intermediate levels, grazing can influence the competitive balance between conifers and other species.

Variability in the frequency and rate of conifer cover increase by biophysical setting suggests divergent trajectories of change in forest structure and composition. Human land use impacts and natural disturbance regimes are significantly different in lower elevation forests versus higher elevation forests of GYE. Because of historically

high fire return intervals and more intense grazing, the impact of fire suppression in lower elevation forests has been more pronounced than in higher elevation forests (Houston 1973; Arno and Gruell 1983; Arno and Gruell 1986; Dando and Hansen 1990). Compounded by higher growth rates, lower elevation conifer cover increase is potentially driven by interactions between climate variability, atmospheric change, fire suppression, and grazing regimes, and is occurring most rapidly in cooler, moister locations. Much longer fire return intervals and less intense land use in higher elevation forests of the GYE has rendered a greatly reduced impact of fire suppression and grazing on forest structure and composition. Despite slower growth rates, higher elevation conifer cover increase is potentially driven by climatic variability and atmospheric change, and to a lesser extent by fire suppression and grazing regimes, and is occurring most rapidly in warmer, drier locations.

Limitations and Scope

Few previous studies have attempted to answer fundamental questions about the frequency, rate, and biophysical variation of conifer cover increase across regions as large and complex as the GYE. Most other studies on this subject have dealt with smaller areas, encompassing a narrower range of biophysical conditions. The limitations to studies like this include the difficulty of obtaining accurate spatial datasets for important variables that are hypothesized to drive the process of conifer cover increase. For example, variables such as grazing intensity, duration, and effect, as well as variables dealing with the effects of fire suppression, atmospheric change, and climate variability are difficult to obtain over large areas and long time scales. Despite these caveats, I have presented here a method for quantifying the frequency, rate, and biophysical variation of

conifer cover increase over a large region. While I have not explicitly answered questions about the factors that cause conifer cover increase, I have taken considerable steps towards interpreting the biophysical footprint of the phenomenon. This study, therefore, lays the groundwork for ultimately determining the mechanisms that underlay the patterns.

Research and Management Implications

The ultimate consequences of the widespread and rapid changes brought about by conifer cover increase in the GYE remain unknown and require further research. Potential consequences span from biogeochemical cycling (Houghton et al. 2000) and biodiversity (Rosenstock and Van Riper III 2001), to fire behavior (Arno and Brown 1989), hydrological cycling (Sahin and Hall 1996) and forage availability (Zimmerman and Neuenschwander 1984).

Consequences for biogeochemical cycling include a potential carbon sink in conifer forests of the region, but the magnitude of such a sink remains a question. This study, therefore, lays the foundation for determining the full extent of conifer cover increase across the GYE, and the magnitude of carbon sequestration. Studies from other regions suggest that fire suppression results in conifer cover increase and fuel accumulation that might significantly alter fire behavior (Allen et al. 2002). This alteration has the potential to result in higher intensity fire and the loss of stored carbon to the atmosphere. Future research is required to better understand the relationship between the alteration in the structure and composition of GYE forests and potential fire behavior.

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CHAPTER 3

THE EXTENT AND DISTRIBUTON OF CONIFER COVER INCREASE IN THE GREATER YELLOWSTONE ECOSYSTEM

Introduction

Repeat historical photography of locations throughout the Greater Yellowstone Ecosystem (GYE) documents widespread changes in the structure and composition of conifer forests and adjacent grasslands and shrublands (Gruell 1983; Meagher and Houston 1998). Increases in the extent and density of conifer forest cover are likely associated with changes in climate (Miller and Halpern 1998) and atmospheric composition (Soulé and Knapp 1999), suppression of fires (Arno and Gruell 1986), and dynamic grazing regimes (Butler 1986). This process is pervasive across many regions of the world and is referred to by a variety of names including expansion (Knapp and Soulé 1998), encroachment (Arno and Gruell 1986), invasion (Mast et al. 1997), density increases (Turner and Krannitz 2001), treeline advance (Rupp et al. 2001), afforestation (Soulé et al. 2003), thicketization (Archer et al. 1995), and densification (Kullman and Engelmark 1997).

In many locations across the GYE, conifer forests have expanded into grasslands, shrublands, and hardwood ecosystems (Arno and Gruell 1986). Furthermore, many locations that previously supported low density, open-canopy conifer woodlands have increased in density (Arno et al. 1997). In this paper, I collectively refer to both of these processes (conifer expansion into adjacent non-forested areas and the in-filling, or densification of conifer woodlands) as conifer cover increase.

Accurate quantification of the extent and rate of this phenomenon is critical for assessment of ecological consequences, including biogeochemical cycling (Houghton et al 2000), fire behavior, and risk to human communities (Arno and Brown 1989). Carbon sinks attributed to conifer cover increase, for example, are hypothesized to account for some fraction of the "missing sink" in global carbon budgets (Houghton et al. 1999; Schimel 2002). This study lays the groundwork for an assessment of the contribution that conifer cover increase makes towards carbon sequestration by quantifying accurately the extent of the phenomenon across a large region.

In Chapter 2, I quantified the rates of conifer cover increase for a large sample of sites using a time series of aerial photos. While the rates of change for these locations were accurately determined from aerial photo interpretation, spectral detection of conifer cover increase across large landscapes presents a greater challenge for two inter-connected reasons. First, only a relatively short interval (~20 years) of moderate resolution (30 m) Landsat imagery is available for analysis. Second, harsh climate, poor soils, and short growing season result in slow conifer growth rates in the GYE, rendering change associated with conifer cover increase relatively subtle over a short time period. This study builds upon Chapter 2 by addressing this challenge. I present methods for the classification of conifer cover and the quantification of change in conifer cover between 1985 and 1999 across a large portion of the GYE. I relied on remote sensing techniques to detect the extent of conifer cover change and aerial photo interpretation to quantify the rates of change. Conifer cover increase was classified with the aid of a spectral transformation that was correlated with forest disturbance and forest regrowth.

The intent of this study was to focus solely on the process of conifer cover change associated with "natural,", relatively undisturbed systems. Many remote sensing studies have focused on changes associated with forest harvest (Cohen et al. 2002), forest regeneration (Fiorella and Ripple 1993), wildfire (Hudak and Brockett 2004), urbanization (Qi et al. 2004), agricultural expansion (Guild et al. 2004), and agricultural abandonment (Brown 2003), among other trajectories of forest change. No remote sensing studies that I know of have attempted to quantify the extent of conifer cover increase across such a large area. For this reason, I have chosen to exclude from the analysis areas that have recently burned, or that have a strong human footprint, such as agricultural, urban, and logging areas. The GYE is representative in this respect of a much larger region of western North America that is similarly experiencing rapid change in the structure and composition of forests, grasslands, and shrublands.

Traditional land cover classifications derived from satellite remote sensing often rely on categorical classifications that depict fixed edges between discrete classes. Subtle changes associated with conifer cover increase, however, are not easily addressed in a categorical context. GYE vegetation change has previously been classified categorically, with some classes representing mixtures, such as conifer and herbaceous (Parmenter et al. 2003). These mixed classes, however, contained high biophysical variability, and therefore were unable to depict compositional and structural changes that did not involve transitions between discrete classes. Subtle increases in conifer cover were often undetected as a result.

One goal of this study was to improve upon the classification of conifer forests in the GYE by using a continuous classification approach. For this, I measured conifer

cover along a gradient between pure conifer and pure grassland-shrubland. Continuous classifications of vegetation and biophysical variables more accurately represent the natural gradient between classes (Atkinson 1999) and are increasingly common (White et al. 1997; Cohen et al. 2003), because often they are necessary for ecosystem and biogeochemical modeling (Running et al. 1999). A variety of techniques have been used to classify continuous variables including mixture modeling (Defries et al. 1999; Sabol et al. 2002) and classification trees analysis (Hansen et al. 1996), yet multiple regression analysis (Cohen and Spies 1992; Jakubauskas and Price 1997; Lawrence and Ripple 1998) is the most widely used approach.

Traditional multiple regression approaches for continuous variable classification, however, overlook an important assumption about ordinary least squares (OLS) regression methods, namely that the independent variables (usually the spectral variables) are measured without error. When error is present in the independent variable, the violation of this assumption results in attenuation of variance in the predictions relative to the observed data (Cohen et al. 2003). There are a number of potential sources of error in remotely sensed data (Curran and Hay 1986), many of which can be minimized by conversion of spectral digital numbers (DN) to reflectance values. However, if sources of error remain and are not adequately measured, traditional OLS regression approaches might not be appropriate.

A solution to this problem is to use a form of regression termed reduced major axis (RMA) regression, or orthogonal regression, which makes no assumptions about measurement errors in either the independent or dependent variable (Larsson 1993). RMA regression minimizes error in both the X and Y direction, instead of minimizing

error in a single direction like OLS (Curran and Hay 1986). As a result, RMA regression tends to reduce the attenuation of predictions above the mean and the amplification of predictions below the mean (Cohen et al. 2003). For this study, I sought a regression technique that better maintained the variance structure of the sample data set, especially at the tails of the distribution of percent conifer cover, where I expected to see significant conifer cover increase. Other studies have found RMA regression to be an improvement over OLS regression for continuous classification of canopy cover because it better preserved the relative variance structure of the sample dataset and therefore minimized attenuation of predictions (Larsson 1993; Cohen et al. 2003).

The specific objectives for this study were to:

1) Classify conifer cover across the GYE for 1985 and 1999; and
2) Quantify the extent and distribution of conifer cover increase between 1985 and 1999.

Methods

Study Area

The 67,156 km^2 study area was located across the GYE, encompassing parts of Montana, Wyoming, and Idaho (Figure 3.1). The boundary of the study area represented the intersection of a Landsat satellite path with the GYE boundary as defined by Parmenter et al. (2003). At the core of the GYE are Yellowstone and Grand Teton National Parks, surrounded by six National Forests, the Wind River Indian Reservation, and a matrix of other public and private lands. The biophysical landscape of the GYE is shaped by steep abiotic gradients in elevation and soils (Hansen et al. 2002). Elevations

range from 969 m along lower watershed drainages to 4198 m on high mountain ridges. Past volcanic activity is responsible for broad scale patterns in soils across the GYE. The soils of the Yellowstone plateau and other high elevation locations consist primarily of nutrient poor rhyolites and andesites, whereas low elevation soils off the plateau consist primarily of nutrient rich glacial outwash and alluvium. The climate of the GYE varies considerably by elevation and latitude, but is generally characterized by short growing seasons and cold winters.

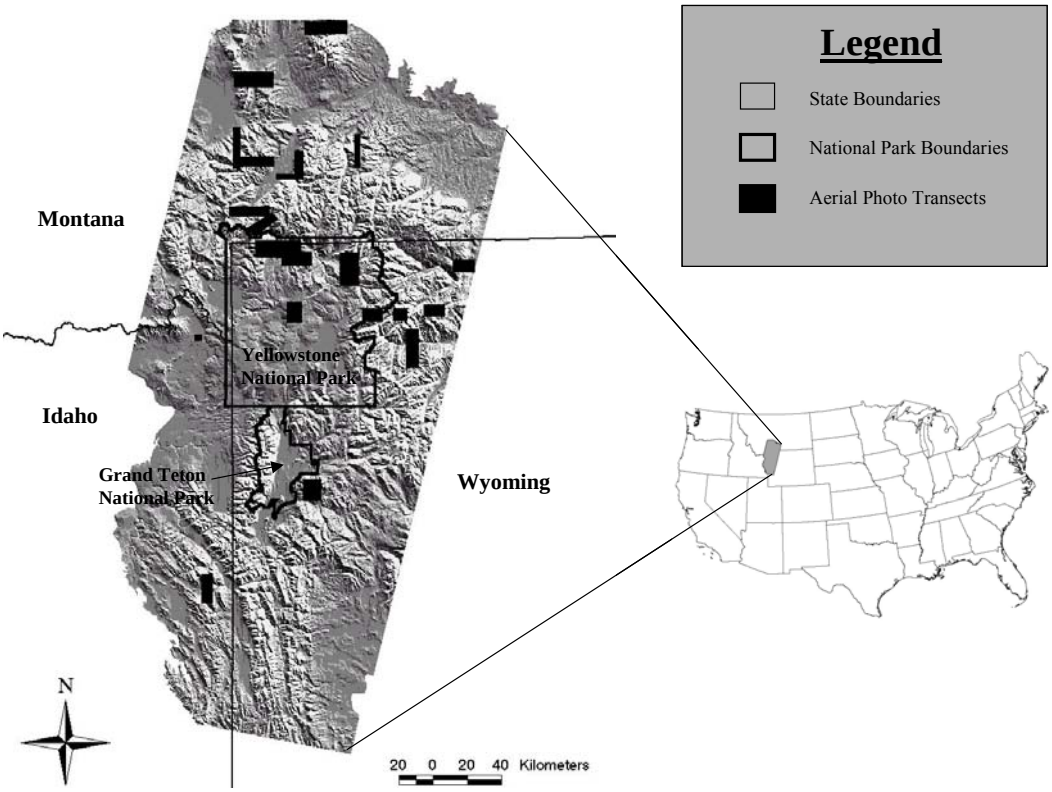

Figure 3.1. 67,156 km^2 study area within the GYE, shown with aerial photo transects.

Vegetation of the GYE is a mosaic of conifer dominated forest interspersed with grasslands, shrublands, and hardwood forests (Parmenter et al. 2002). Lower elevation conifer forests are composed primarily of Douglas-fir (*Pseudotsuga menzeisii*), juniper (*Juniperus scopulorum*), lodgepole pine (*Pinus contorta*), ponderosa pine (*Pinus*

ponderosa), and limber pine (*Pinus flexilis*). Middle to high elevation conifer forests are composed primarily of lodgepole pine, engelmann spruce (*Picea engelmanni*), subalpine fir (*Abies lasiocarpa*), and whitebark pine (*Pinus albicaulus*). Low elevation grasslands dominated by fescue (*Festuca idahoensis*) and wheatgrass (*Agropyron cristatum*) form a mosaic with conifer and hardwood forests and predominate below the lower elevation tree line. Shrublands, characteristically sagebrush (*Artemesia spp.*), occur on dry, fine textured soils at lower to middle elevations. At higher elevations, mesic alpine meadows are common among conifer forests. Upper treeline often contains krummholtz tree growth forms that give way to tundra and bare, rocky ridges.

Study Design

I used a combination of aerial photos, satellite imagery, and statistical methods to quantify conifer cover across the study area for 1985 and 1999 (Figure 3.2).
I developed reference data from a time series of aerial photos, including percent conifer cover, to determine the rates of conifer cover increase (see Chapter 2 for detailed aerial photo methods). Based on these reference data, I used satellite imagery to map conifer cover across the study area for 1985. From satellite image change detection, I determined the extent of conifer cover increase between 1985 and 1999, and then estimated 1999 conifer cover based upon the rates of change.

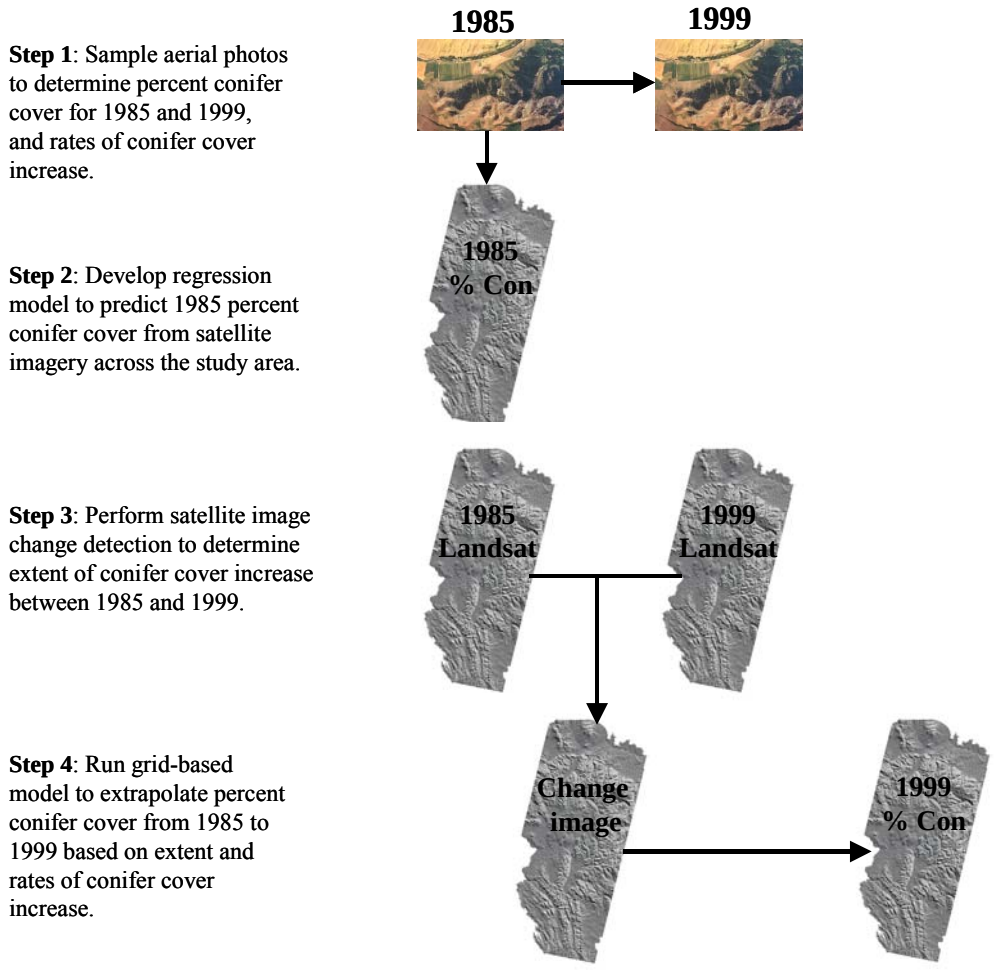

Figure 3.2. General overview of study design.

Satellite Image Processing

I acquired 2 dates of 1985 Landsat TM and 3 dates of 1999 Landsat ETM+ imagery for each of 3 scenes (Table 3.1). The 1999 Landsat ETM+ images were acquired with Level-1G radiometric and geometric correction. I selected the summer dates as reference images to which all other images were geometrically corrected. Image to image geometric correction using ground control points resulted in root mean square errors less than 0.5 pixels. I radiometrically and atmospherically corrected all images to at-sensor-reflectance values using the COST radiometric normalization routine (Chavez

1996), including haze correction. I then computed the Tasseled Cap transformation for each image (Kauth and Thomas 1976), using coefficients from Crist (1985) applied to at-sensor-reflectance values. I mosaiced each of the three scene assemblages to create single season images. After mosaicing, I masked out unwanted pixels, such as clouds, cloud shadows, water, rock, ice, snow, urban areas, agricultural areas, and bad scan lines.

Table 3.1. Landsat satellite imagery used in this study.

Sensor	Path/Row	Date
Landsat TM	38/28	June 14, 1985
Landsat TM	38/29	June 14, 1985
Landsat TM	38/30	June 14, 1985
Landsat TM	38/28	September 16, 1985
Landsat TM	38/29	September 16, 1985
Landsat TM	38/30	September 16, 1985
Landsat ETM+	38/28	July 13, 1999
Landsat ETM+	38/29	July 13, 1999
Landsat ETM+	38/30	June 29, 2000
Landsat ETM+	38/28	September 15, 1999
Landsat ETM+	38/29	September 15, 1999
Landsat ETM+	38/30	September 15, 1999
Landsat ETM+	38/28	December 4, 1999
Landsat ETM+	38/29	December 4, 1999
Landsat ETM+	38/30	December 4, 1999

1985 Vegetation Classification

In order to classify 1985 conifer cover as a continuous variable along a conifer to grassland-shrubland gradient, I first masked out pixels that contained deciduous forest. To do this, I carried out a level 2 categorical land cover classification with classification tree analysis (CTA) in S-PLUS ("tree" function). To build the classification tree model, I used the vegetation type (conifer forest, grassland-shrubland, and deciduous forest) as the response variable. For predictor variables, I used 1985 summer and fall Landsat TM bands 1-5 and 7, Tasseled Cap brightness, greenness, and wetness, Tasseled Cap

difference images between summer and fall, and elevation, slope, and aspect. I randomly selected two-thirds of the aerial photo reference data to build the classification tree model and the remaining one-third to independently validate the classification accuracy. The final classification tree rules were mapped out across the study area, and the conifer and grassland-shrubland pixels were isolated for further analyses.

Regression Modeling of 1985 Conifer Cover

I integrated the spectral reflectance data into a single index using canonical correlation analysis (CCA), in order to maximize the correlation between spectral reflectance and conifer cover reference data. To develop the CCA index, I used Landsat TM 1985 summer and fall bands 1-5, and band 7, as well as the three Tasseled Cap bands (brightness, greenness, and wetness). I then used RMA regression to develop a linear relationship ($y = a + \beta x + \varepsilon$) between the CCA index (x) and percent conifer cover (y) by calculating the slope (β) and intercept (a) as follows (after Curran and Hay 1986):

slope:
$\beta = \sigma y / \sigma x$ (1)

intercept:
$a = \overline{y} - \beta \overline{x}$ (2)

(term definitions: σ = sample standard deviation; $\overline{y}$ and $\overline{x}$ = sample means)

From the regression equation, I mapped 1985 percent conifer cover across the study area.

Model Evaluation and Validation

To evaluate the RMA regression model, I calculated the coefficient of determination (R^2). To independently validate the model, I used the remaining one-third

of the reference data to compare observed values to model predictions. For this, I carried out an OLS regression between observed and predicted percent conifer cover values and analyzed the coefficient of determination (R^2), the root mean square error (RMSE), and the model variance ratio (standard deviation of predicted values divided by the standard deviation of observed values).

Change Detection and 1999 Conifer Cover

In order to quantify the extent of conifer cover increase, I first derived a spectral index called the "Disturbance Index" (Healey et al. in review) for both 1985 and 1999 imagery, using the following formula:

> Disturbance Index = (Tasseled Cap brightness – (Tasseled Cap greenness + Tasseled Cap wetness))

I then differenced the two images by subtracting the 1985 image from the 1999 one. The differenced image clearly depicted trajectories of forest change between 1985 and 1999. I analyzed a boxplot of spectral value distributions from this image for known locations of conifer gain (e.g., conifer cover increase), conifer loss (e.g., logging), and no-change, to determine the locations of spectral thresholds for change classification (Figure 3.3). For conifer cover increase, I subsetted all pixels with values less than the maximum conifer gain value (-13). For conifer cover decrease, I subsetted all pixels with values greater than the minimum conifer loss value (54). I classified the remainder of the pixels, with values greater than –13 and less than 54 as no-change.

In order to minimize errors of commission, I masked out locations where I knew conifer cover increase was unlikely to occur. In Chapter 2, I identified a threshold distance of 60 m from the nearest conifer stand beyond which conifer cover increase was

less common over a 28-year time period. For this study, I re-analyzed these data for a 14-year time period (1985-1999), and determined that over 90% of conifer cover increase occurred within 30 m of the nearest conifer stand. Therefore, I restricted the extent of conifer cover increase to within 30 m of the nearest conifer stand. Additionally, in order to focus the analysis solely on conifer cover increase not associated with forest regeneration following logging or recent fire, I masked out the locations of logging and fire prior to 1985 by compiling GIS data layers for each of the national forests and national parks within the study area. I validated the accuracy of the conifer cover increase map with independent data derived from aerial photo interpretation.

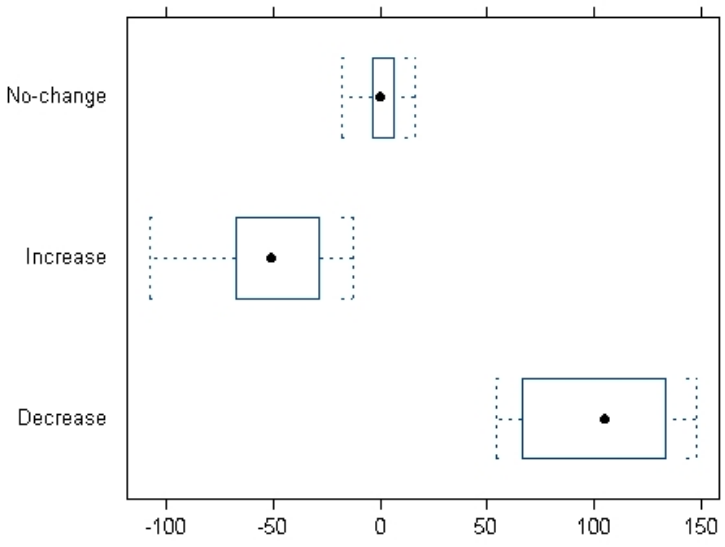

Figure 3.3. Boxplot of spectral value distributions for known locations of conifer change.

To estimate 1999 percent conifer cover for pixels classified as conifer cover increase, I extrapolated percent conifer cover from 1985 with a grid-based model. For

pixels not classified as conifer cover increase locations, the 1999 conifer cover value remained the same as 1985. I calculated the 14-year change from 1985 to 1999 based on the rates of conifer cover increase derived from aerial photo interpretation, stratified by vegetation type (grassland-shrubland; conifer woodland; conifer forest). Rates of conifer cover increase were calculated only from samples that exhibited conifer cover increase.

Finally, I analyzed the spatial distribution of conifer cover increase. To distinguish between conifer expansion and conifer densification, I analyzed the changes with respect to 1985 starting conditions. Changes that occurred in locations with no conifer cover were classified as conifer expansion, while changes that occurred in locations with an existing conifer cover were classified as conifer densification. I then investigated the spatial distribution of change with respect to biophysical setting, by calculating the percent of conifer cover increase pixels within elevation and aspect categories.

Results

1985 Percent Conifer Cover

The overall accuracy of the 1985 level 2 categorical vegetation classification (Figure 3.4) was 84% (Table 3.2).

Table 3.2. Error matrix for 1985 categorical vegetation classification.

Classified Data	Reference Data			Row total	Producer's accuracy (%)	User's accuracy (%)
	Conifer	Deciduous	Grass-Shrub			
Conifer	320	11	21	352	89	91
Deciduous	3	36	1	40	75	90
Grass-Shrub	36	1	39	76	64	51
Column total	359	48	61	468		
Overall accuracy = 395/468 = 84%						

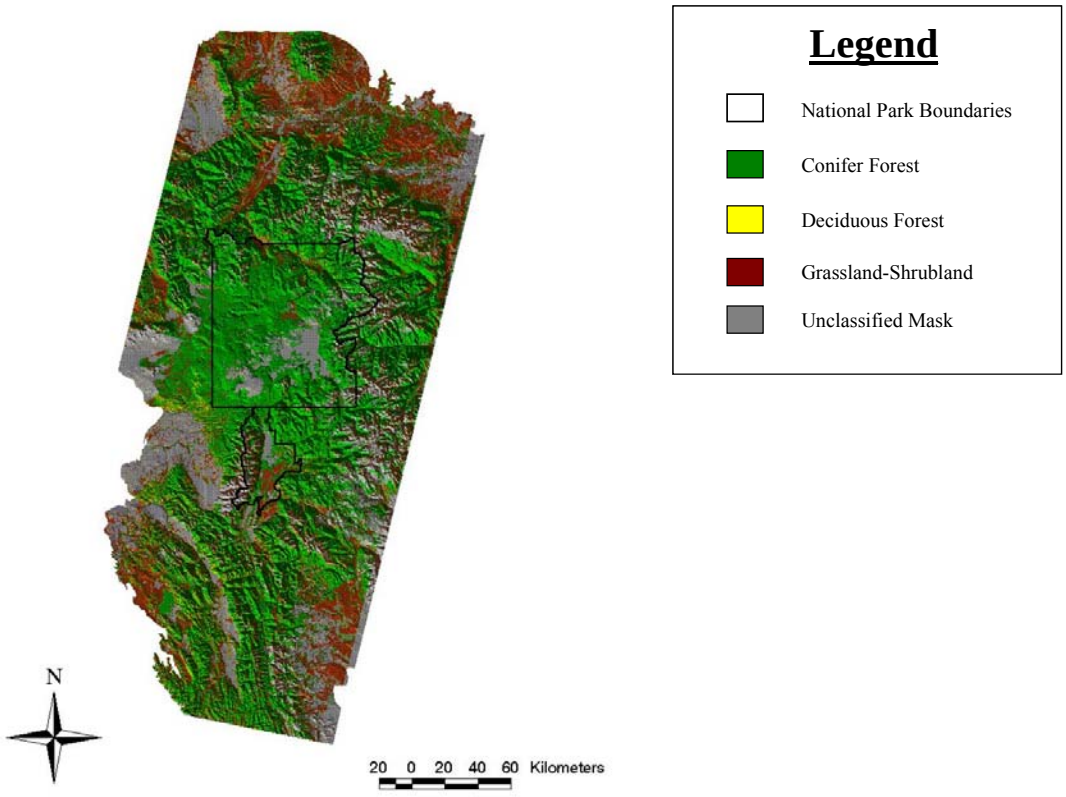

Figure 3.4. 1985 level 2 categorical vegetation classification.

Deciduous forest comprised a mere 5% of the natural vegetation of the GYE in 1985. The remaining 95% of the pixels were subset to develop a map of percent conifer cover. The spectral index (U1) derived from CCA was highly correlated with the percent conifer cover response variable (r = 0.86). The RMA regression equation between U1 and percent conifer cover was:

1985 percent conifer cover = 130.53 + (1112.38*U1)

The RMA regression model explained a large amount of the variation in percent conifer cover, with an R^2 of 0.73. The validation of the regression model against

withheld data, by OLS regression between observed and predicted values, yielded an R^2 of 0.72 (Figure 3.5). The RMSE between observed and predicted values was 13.5 and the model variance ratio was 0.98.

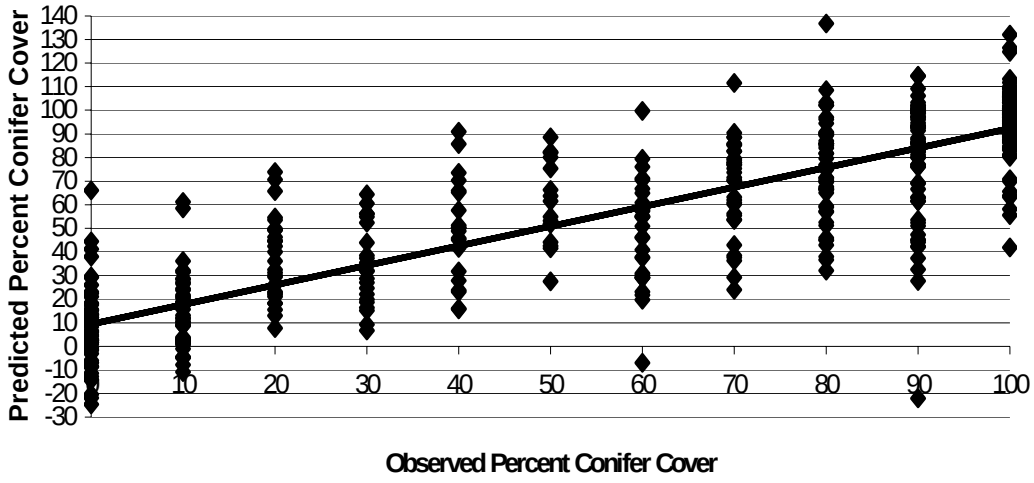

Figure 3.5. Validation of 1985 percent conifer cover by OLS regression between observed and predicted values.

The map of 1985 percent conifer cover (Figure 3.6) revealed that grassland-shrubland dominated the lower elevation valleys to the north and south of Yellowstone National Park. Higher conifer cover forest predominated within Yellowstone National Park and the surrounding higher elevation mountain ranges, while lower conifer cover forest predominated in the lower elevation forests outside Yellowstone National Park and adjacent to the grassland-shrubland valleys.

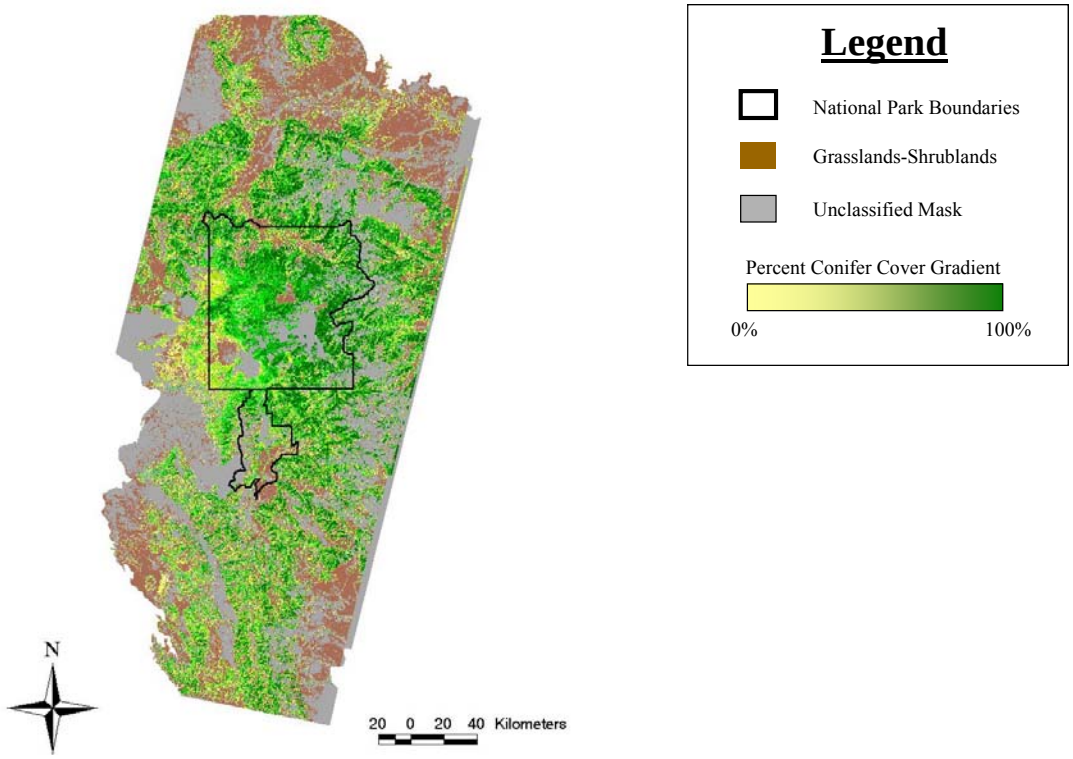

Figure 3.6. 1985 continuous classification of percent conifer cover.

1985-1999 Percent Conifer Cover Change

The area of conifer cover increase in the GYE between 1985 and 1999 was 685,075 ha (Figure 3.7). Conifer expansion resulted in the conversion of 90,323 ha of grassland-shrubland to conifer woodland. The majority of conifer expansion (63%) occurred at lower elevations (< 2,316 m), where it was slightly more common on northerly aspects (51%). Conversely, at higher elevations, expansion was more common on southerly aspects (57%). Conifer densification resulted in the cover increase of existing conifer forest on 594,752 ha. The spatial distribution of conifer densification was skewed towards lower elevations (54%) and northerly aspects (54%). At lower elevations, densification was more common on northerly aspects (58%), while at higher

elevations, it was more common on southerly aspects (51%). Cumulatively, the area of conifer cover increase between 1985 and 1999 represented 16% of the entire classified study area, and was especially evident in the lower elevation conifer forests outside of Yellowstone National Park.

For the map of conifer cover increase, conifer cover decrease, and no-change, the overall accuracy was 68% (Table 3.3). For the conifer cover increase class, the producer's accuracy was 67% and the user's accuracy was 66%.

Table 3.3. Error matrix for 1985 – 1999 conifer cover change image.

Classified Data	Reference Data			Row total	Producer's accuracy (%)	User's accuracy (%)
	Increase	Decrease	No-change			
Increase	58	3	27	88	67	66
Decrease	0	60	0	60	69	100
No-change	29	24	60	113	69	53
Column total	87	87	87	261		
Overall accuracy = 178/261 = 68%						

Note: Abbreviations are as follows: Increase = conifer cover increase; Decrease = conifer cover decrease; no-change = no-change in conifer cover.

1999 Percent Conifer Cover

In Chapter 2, aerial photo interpretation of more than 2,000 plots across the GYE revealed that nearly 40% of samples increased in percent conifer cover between 1971 and 1999. Depending upon vegetation class, average rates of conifer cover increase varied between 0.55% and 0.72% per year (Table 3.4). These rates of change equate to average 14-year increases in conifer cover of between 7.71% for conifer forest to 10.14% for grassland-shrubland. The validation of the 1999 percent conifer cover map against withheld data, by OLS regression between observed and predicted values, yielded an R^2 of 0.72.

Table 3.4. Average annual rate of conifer cover increase (+/-standard error) and 14-year change by vegetation class.

Vegetation Class (percent conifer cover)	Average annual rate (%) of conifer cover increase (+/- SE)	Average 14-year increase (%)
grassland-shrubland (0% conifer)	0.72 (+/-0.08)	10.14
conifer woodland (1-69% conifer)	0.68 (+/-0.02)	9.51
conifer forest (70-100% conifer)	0.55 (+/-0.03)	7.71

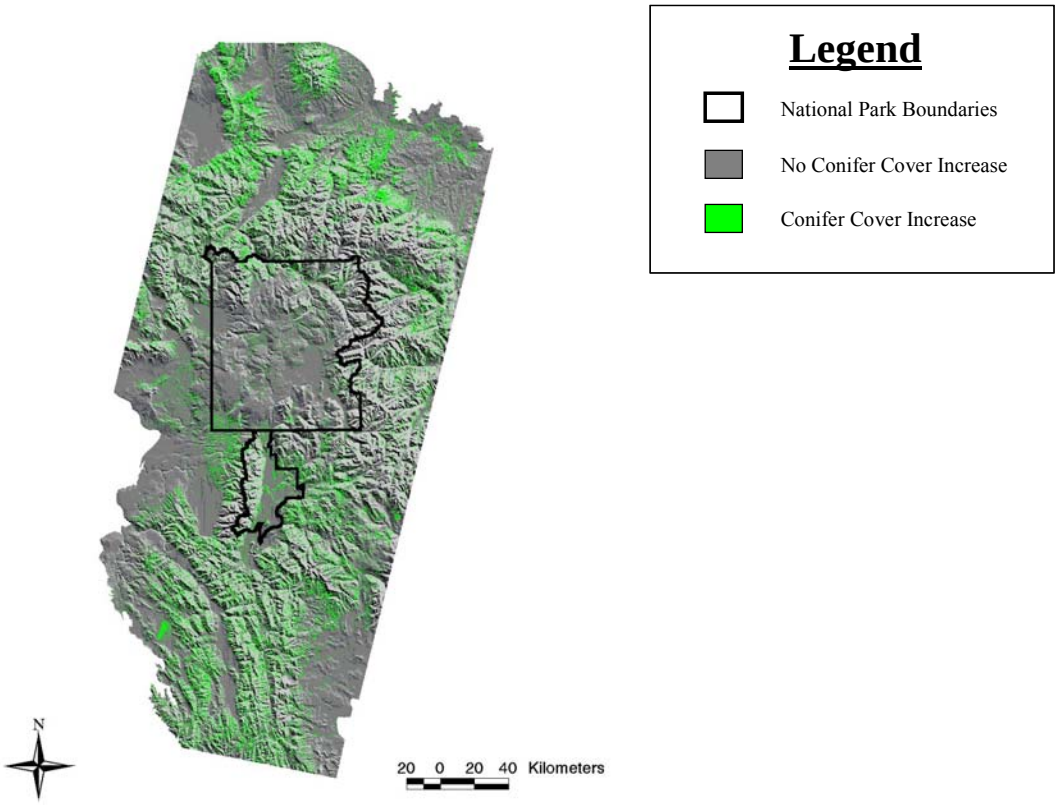

Figure 3.7. Distribution of conifer cover increase between 1985 and 1999.

Discussion

The use of a continuous classification approach for mapping conifer forests across a large, complex region like the GYE is a substantial improvement over the use of a categorical classification approach. Previously, Parmenter et al. (2003) categorically classified conifer woodlands in the GYE with low accuracy due to the high biophysical variability represented by this class. In contrast, by isolating the 95% of the study area that fell along the gradient between pure coniferous and pure grassland-shrubland, and then developing a continuous classification, I was able to depict more accurately the inherent variability of this mixed class.

RMA regression proved to be an accurate and appropriate technique for continuous classification of percent conifer cover. The technique effectively maintained the observed variance in the predictions, as evidenced by the variance ratio of 0.98 between observations and predictions. This was significant because of the importance of accurately mapping percent conifer cover at the lower end of the distribution, where conifer cover increase was more likely to occur. I compared predictions from OLS regression to predictions from RMA regression and found that for values below the mean, RMA regression reduced amplification of the predictions.

By determining the extent of conifer cover increase from satellite image change detection, and the rate of conifer cover increase from aerial photo interpretation, I was able to quantify subtle changes that would otherwise be difficult or impossible to detect over a region as large as the GYE. The results of this study provide us with a more complete picture of the extent and distribution of conifer cover increase in the GYE. This is the first study that I know of to quantify conifer cover increase with remote sensing

across a region as large and complex as the GYE. Assuming that rates of change over the last several decades are indicative of future change, I would expect significant future changes in the structure and composition of forests, grasslands, and shrublands of the GYE. Projected over 100 years, for example, the rates of change that I observed translate into 55% to 72% increases in conifer cover in some locations.

Conifer expansion between 1985 and 1999 occurred on approximately 2% of the study area, primarily at or near lower elevation forest-grassland ecotones. This is due in part to lower elevations having longer growing seasons and more favorable conditions, and in part to lower elevation forests of the GYE being more heavily impacted by fire suppression and grazing. Conifer expansion has been well documented at many other lower elevation ecotones in the GYE and elsewhere (Arno and Gruell 1986 in southwestern Montana; Mast et al. 1998 on the Colorado Front Range; Meagher and Houston 1998 in Yellowstone National Park; Bachelet et al. 2000 in the Black Hills of South Dakota).

The remainder of conifer expansion between 1985 and 1999 occurred at or near higher elevation forest-grassland ecotones. While conifer expansion was not as widespread in higher elevation forests, my results are consistent with other research documenting conifer expansion into sub-alpine meadows and grasslands of the GYE and elsewhere (Dunwiddie 1977 in the Wind River Range in Wyoming; Butler 1986 in the Lemhi Mountains of Idaho; Jakubos and Romme 1993 in Yellowstone National Park; Miller and Halpern 1998 in the Oregon Cascade Range).

Conifer density increased between 1985 and 1999 on approximately 13% of the study area. Conifer densification accounted for the vast majority of the total area of

conifer cover increase. Unlike conifer expansion, there was not a strong elevation trend in the distribution of conifer densification, with only a slight majority of the change occurring in lower elevation forests. My quantification of widespread conifer densification is consistent with other studies that have documented conifer densification across western conifer forests (Covington and Moore 1994 in northern Arizona; Arno et al. 1997 in western Montana; Soulé and Knapp 1999 in central Oregon).

The results from this study were consistent with the results from Chapter 2, underscoring the importance of soil moisture and temperature conditions for conifer seedling reproduction, establishment, and growth. At lower elevations, where soil moisture is more likely a limiting factor (Daubenmire 1968), conifer cover increase was more common on moister northerly aspects. Conversely, at higher elevations, where temperature is more likely a limiting factor (Richardson and Bond 1991) and soil moisture is often adequate or even excessive, conifer cover increase was more common on warmer southerly aspects.

Limitations and Scope

Overall, the area that increased in conifer cover represented only a small fraction of the total area that was eligible for conifer cover increase. This is likely a function of several factors. First, conifer growth rates in the GYE are relatively slow given harsh climatic and abiotic conditions. Therefore, change over a 14-year time period can be rather subtle. Second, given this subtlety, spectrally discriminating change at a spatial resolution of 30 m is challenging. As the accuracy assessment of conifer cover increase between 1985 and 1999 demonstrates, my approach likely underestimates the extent of conifer cover increase (omission error = 1 – producer's accuracy = 33%). Conifer cover

increase reference data were classified as no-change in 33% of cases (but never as conifer cover decrease). It is likely that for some samples, conifer cover measurably increased according to aerial photo interpretation, but was not sufficient to register a measurable spectral change.

The method presented here for continuous classification of conifer cover and quantification of change in conifer cover offers excellent potential for use at larger spatial extents and in other regions experiencing similar forest dynamics. Conifer cover increase is a widespread phenomenon, yet we lack information on its rates and extent. Thus there is a pressing need for easily implementable approaches such as this one. I have demonstrated the utility of this approach for the GYE, despite the limited 14-year span of satellite imagery and slow conifer growth rates. With a longer time series of satellite imagery in warmer and/or wetter regions with higher rates of change, this method could be expected to yield even more accurate results.

Research and Management Implications

The results of this study lay the groundwork for further analysis of the contribution that conifer cover increase makes towards carbon sequestration in the GYE. Between 1985 and 1999, conifer cover increase added significantly to the stock of aboveground carbon. However, the loss of aboveground carbon due to fire and logging were likely significant during this time period. I am currently undertaking further analyses to quantify the carbon source/sink dynamics in the GYE associated with these land cover change trajectories.

Despite the ability to quantify historical and current conifer cover, future prognostication of conifer dynamics remains extremely difficult. This is largely due to

uncertainty associated with the temporal duration of aboveground carbon stocks in conifer forests (Sampson and Clark 1996). As a result of "missed" fire return intervals in some forest types, the increased conifer cover and potential fuels accumulation have created conditions that depart from their historical range. The significance of this with respect to carbon storage is that some forest types, which historically were adapted to frequent, low intensity fire, might have a fundamentally altered fire regime, thereby jeopardizing stored carbon. While there is mounting evidence to support these facts in some western coniferous forests (Allen et al. 2002), research is lacking in the GYE. Overall, this is a subject deserving increased research attention.

Acknowledgements

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CHAPTER 4

THE CONTRIBUTIONS OF CONIFER COVER INCREASE AND DECREASE TO CARBON DYNAMICS IN THE GREATER YELLOWSTONE ECOSYSTEM

Introduction

Forests, grasslands, and shrublands of the Greater Yellowstone Ecosystem (GYE) have undergone widespread changes in structure and composition over the past century (Meagher and Houston 1998). On the one hand, logging and extensive stand replacement fires, like those that occurred in 1988 in and around Yellowstone National Park (Turner et al. 1997), have converted large tracts of mature coniferous forest to early seral stage conditions. On the other hand, in many locations conifer forests have expanded into adjacent grasslands and shrublands, and increased significantly in density and cover (Gruell 1983; Meagher and Houston 1998). These latter changes are likely due to a variety of interacting factors including fire exclusion (Arno and Gruell 1986), dynamic grazing regimes (Butler 1986), climate change and variability (Jakubos and Romme 1993), and atmospheric change (Soulé and Knapp 1999).

Despite pervasive changes, there are few accurate estimates regarding the extent of conifer cover decrease due to fire and logging, the rates and extent of conifer cover increase due to expansion, or the consequences these changes have on carbon stocks. Similar conifer dynamics are occurring across vast regions of the Rocky Mountains and the western United States (Schimel et al. 2002), and thus quantifying the carbon dynamics in the GYE provides valuable insight to a much larger region. In Chapter 3, I quantified the extent of conifer cover increase in the GYE between 1985 and 1999 at

685,075 ha. The objective in this chapter was to additionally quantify the extent of conifer cover decrease in the GYE, and estimate the changes in live aboveground carbon stocks as a result of these contrasting dynamics. I did not attempt to quantify the changes in belowground carbon stocks because quantification with remote sensing is highly uncertain, and research indicates that belowground carbon pools are relatively constant in spite of conifer cover increase (Smith and Johnson 2003). I also did not examine changes in other aboveground carbon components, such as coarse woody debris or snags, because they were not presumed to change significantly as a result of conifer cover increase over a 14-year time period. I used a combination of aerial photos, satellite imagery, field data, allometric equations, and statistical methods to quantify the reservoirs and fluxes of aboveground carbon in the GYE between 1985 and 1999.

Carbon budgets have received increased attention because of documented increases in atmospheric carbon dioxide and hypothesized linkages to climate warming. Since the start of the industrial revolution, the atmospheric concentration of carbon dioxide has increased by approximately 31 +/- 4%, and the global mean surface temperature has risen by 0.6 +/- 0.2^{o}C during the 20th century (IPCC 2001). Quantified emissions, or sources, of carbon dioxide remain larger than quantified reservoirs, or sinks, of carbon dioxide, resulting in an undiagnosed "missing sink." Current estimates of the size of the conterminous U.S. terrestrial sink range from 300,000 – 580,000 Gg C yr^{-1}, but the temporal and spatial dimensions, as well as the drivers of the sink, remain uncertain (Pacala et al. 2001).

Carbon dynamics in the GYE have been historically driven by disturbances such as fire and more recently logging. Historical fire regimes, in terms of their frequency and

intensity, are highly variable, and directly relate to the temporal duration and release of carbon stocks. Higher elevation forests in the GYE, composed of lodgepole pine (*Pinus contorta*), subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmanni*), and whitebark pine (*Pinus albicaulus*), are historically characterized by infrequent, high intensity fire regimes (Arno 1980). The widespread fires of 1988 in and around Yellowstone National Park occurred mostly at higher elevations, and affected an estimated 250,000 ha (Turner et al. 1997). In contrast, lower elevation forests in the GYE, composed primarily of Douglas-fir (*Pseudotsuga menzeisii*), juniper (*Juniperus scopulorum*), and lodgepole pine are historically characterized by frequent, low intensity fire regimes (Arno and Gruell 1986) or mixed frequency and intensity fire regimes (Littell 2002). However, in comparison to historical measures fire has been less common in some forests of the GYE during the past century (Arno and Gruell 1986; Littell 2002; Schmidt et al. 2002), especially at lower elevations. This has potentially contributed to an increased conifer cover, and hence storage of carbon.

Conifer forests store more aboveground carbon than their former grassland or shrubland counterparts (Hansen et al. 2000), and conifer density increases also result in greater storage of aboveground carbon. Therefore, carbon sinks attributed to conifer cover increase are hypothesized to account for some fraction of the "missing sink" in global carbon budgets (Houghton 1999; Schimel 2002). Current carbon accounting systems remain imprecise with regard to the influence of conifer cover increase on carbon uptake (Houghton et al. 1999). At the national level, few carbon budgeting studies have attempted to account for conifer cover increase, and to date, only inventory-based approaches have produced reliable estimates (Houghton et al. 1999; Houghton et

al. 2000; Pacala et al. 2001). Acknowledging substantial uncertainty, Pacala et al. (2001) estimated that woody encroachment into non-forest ecosystems accounted for approximately 120,000 – 130,000 Gg C yr^{-1} in the conterminous U.S., a substantial portion of the estimated 300,000 – 580,000 Gg C yr^{-1} total conterminous U.S. carbon sink (Pacala et al. 2001). Higher accuracy quantification of the contribution of woody encroachment to carbon uptake has generally been confined to small, local scale analyses (Asner et al. 2003).

The temporal duration of a forest carbon sink in the GYE remains in question, however, as a result of high fuel accumulation and potentially increased risk of high intensity wildfire. This is particularly the case in lower elevation forests where the historical fire return interval was high, and the rate of conifer cover increase is high. In the absence of fire, the accumulation of both dead and live biomass has potentially resulted in a higher likelihood of crown fire, and thus the potential loss of stored carbon (Sampson and Clark 1996). Many such locations are well outside their historical range of variability with respect to fire frequency, intensity, size, severity, and landscape pattern (Schmidt et al. 2002). In high frequency, low intensity fire regimes that are rapidly accumulating carbon, the release of carbon associated with high intensity fire could potentially offset the gains associated with carbon sequestration (Sampson and Clark 1996).

Because of these uncertainties, it is critical for land managers to understand where the most rapidly changing places are on the landscape, and what the implications of these changes are for carbon storage. Where in the landscape are carbon uptake and carbon loss occurring? The results of this study can help guide management of fuels and

potential carbon sinks in rapidly changing conifer forests of the GYE. By providing a case study of carbon flux in the GYE, this study can aid in our understanding of the relative roles played by conifer cover increase and decrease in carbon source/sink dynamics. How much does conifer cover increase contribute to carbon sequestration, relative to carbon loss from conifer cover decrease? What are the implications of changes in the GYE for the carbon budget and the "missing sink"?

Specifically, the objectives for this study were to:

1) Map GYE vegetation cover for 1985 and 1999, according to dominant type, seral stage, and percent conifer cover, and quantify key land cover changes over that time period; and
2) Quantify changes in aboveground carbon stocks in the GYE between 1985 and 1999 as a result of conifer cover increase and decrease, and assess their relative contributions to carbon source/sink dynamics.

Methods

Study Area

The 67,156 km^2 study area was located within the GYE, encompassing parts of Montana, Wyoming, and Idaho (Figure 4.1). The boundary of the study area represented the intersection of a Landsat satellite path with the GYE boundary as defined by Parmenter et al. (2003). At the core of the GYE are Yellowstone and Grand Teton National Parks, surrounded by six National Forests, the Wind River Indian Reservation, and a matrix of other public and private lands. The biophysical landscape of the GYE is shaped by steep abiotic gradients in elevation and soils. Elevations range from 969 m

along lower watershed drainages to 4,198 m on high mountain ridges. Past volcanic activity is responsible for broad scale patterns in soils across the GYE. The soils of the Yellowstone plateau and other high elevation locations consist primarily of nutrient poor rhyolites and andesites, whereas low elevation soils off the plateau consist primarily of nutrient rich glacial outwash and alluvium. The climate of the GYE varies considerably by elevation and latitude, but generally is characterized by short growing seasons and cold winters.

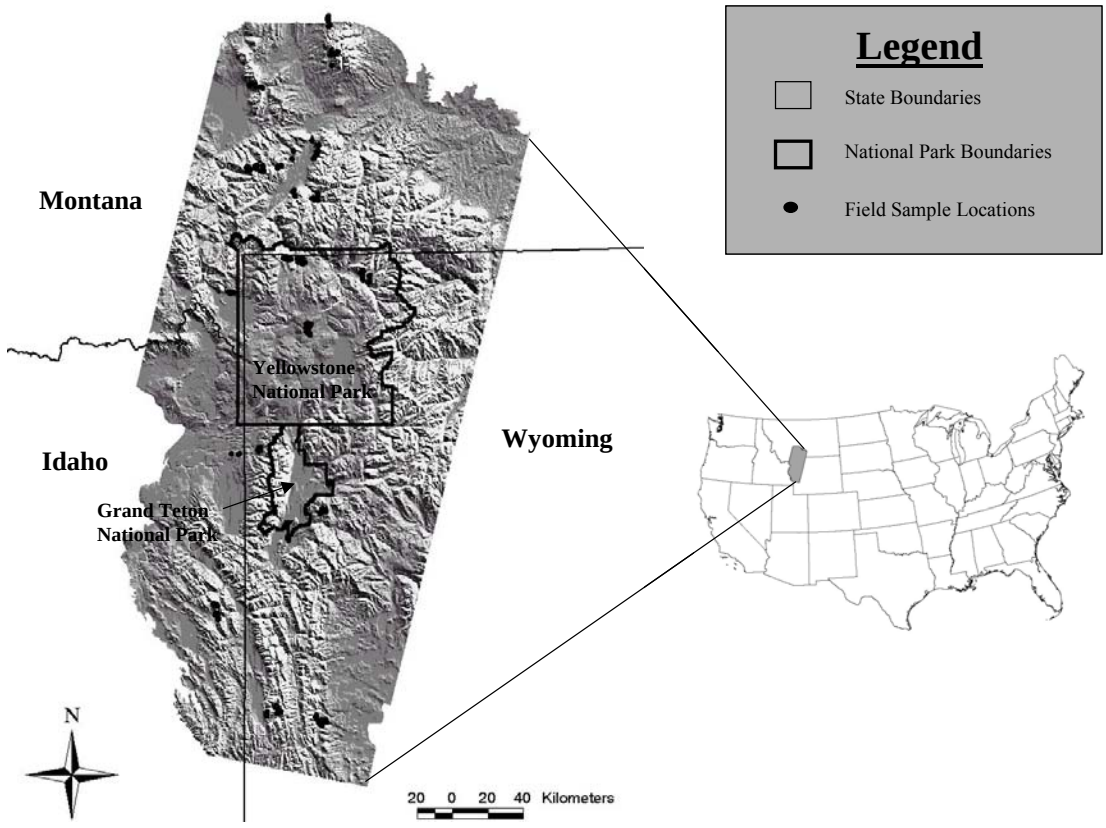

Figure 4.1. 67,156 km^2 study area within the GYE, shown with field sample locations.

Vegetation of the GYE is a mosaic of conifer dominated forest interspersed with grasslands, shrublands, and hardwood forests. Lower elevation conifer forests are composed primarily of Douglas-fir, juniper, lodgepole pine, ponderosa pine (*Pinus*

ponderosa), and limber pine (*Pinus flexilis*). Middle to high elevation conifer forests are composed primarily of lodgepole pine, Engelmann spruce, subalpine fir, and whitebark pine. Low elevation grasslands dominated by fescue (*Festuca idahoensis*) and wheatgrass (*Agropyron cristatum*) form a mosaic with conifer and hardwood forests and predominate below the lower elevation tree line. Shrublands, characteristically sagebrush (*Artemesia spp*.), occur on dry, fine textured soils at lower to middle elevations. At higher elevations, mesic alpine meadows are common amongst conifer forests. Upper treeline often contains krummholtz tree growth forms that give way to tundra and bare, rocky ridges.

Study Design

I used a combination of aerial photos, satellite imagery, field data, allometric equations, and statistical methods to map GYE vegetation cover and quantify the reservoirs and fluxes of aboveground carbon between 1985 and 1999 (Figure 4.2). I developed training data from aerial photos, including dominant vegetation type, seral stage, and percent composition of conifer for 1971, 1985, and 1999 and used these to quantify the rates of conifer cover increase (see Chapter 2 for detailed methods on aerial photo interpretation and calculation of the rates of change). The spectral and biophysical characteristics of these training sites were analyzed with classification tree analysis (CTA), and used to generate categorical maps of vegetation type and seral stage for both 1985 and 1999 (see Chapter 3 for detailed methods on satellite image processing). The structural and compositional characteristics of forest stands were quantified from field data, and I drew on published allometric equations to estimate aboveground biomass. I then developed statistical functions to relate aboveground biomass to vegetation type,

seral stage, and percent conifer cover. I converted aboveground biomass estimates to carbon content, extrapolated aboveground carbon content across the study area for 1985 and 1999, and quantified the net change between 1985 and 1999.

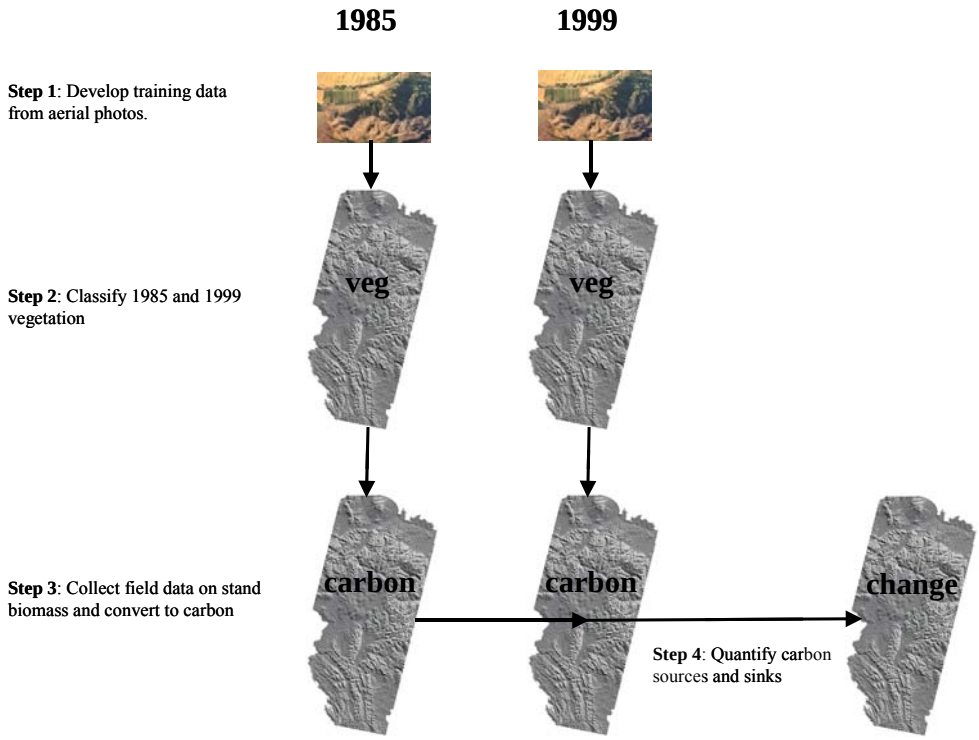

Figure 4.2. General overview of study design.

1985 Vegetation Classification

I derived level 2, 3, and 4 vegetation maps (Table 4.1) for 1985 using classification tree analysis (CTA) as implemented by S-PLUS statistical software ("tree" function). Predictor data layers for each classification year consisted of the reflective Landsat bands, the Tasseled Cap indices for each date, Tasseled Cap seasonal difference images, and topographic data derived from a digital elevation model (DEM) (Table 4.2). I cumulatively built each vegetation level by subsetting appropriate pixels for further, more specific classification. The level 2 classification consisted of only three classes:

coniferous, deciduous, and grassland-shrubland. For the level 3 classification, I further classified coniferous pixels into conifer woodlands, seedling/sapling seral stage, pole seral stage, and mature/old-growth seral stage. For the level 4 classification, I further classified mature/old-growth conifer (≥ 70% conifer) into Douglas-fir, whitebark pine, and mixed conifer species. For each separate classification, I divided the reference data into two sets, one for model building and one for model validation. From the model building set, a full classification tree was fitted using the class probability splitting rule to partition the data. From the full tree, a cross-validation procedure was implemented to identify a smaller, more optimal tree for pruning purposes. Once reduced, the splitting rules were used to guide classification of a thematic image. Standard measures of accuracy were calculated for each image using the withheld validation data.

Table 4.1. Four level hierarchical vegetation classification scheme for aerial photo interpretation and satellite classification.

<table>
<tr><th>Level 1
Gross Land Cover</th><th>Level 2
Percent Composition</th><th>Level 3
Seral Stage</th><th>Level 4
Species</th></tr>
<tr><td rowspan="5">natural vegetation</td><td rowspan="4">- coniferous</td><td colspan="2">- seedling/sapling stage (0-100% conifer)
(~0-40 yrs.)</td></tr>
<tr><td colspan="2">- pole stage (≥ 70% conifer)
(~40-150 yrs.)</td></tr>
<tr><td colspan="2">- woodlands (< 70% conifer)</td></tr>
<tr><td>- mature/old-growth stage (≥ 70% conifer)
(~150+ yrs.)</td><td>- whitebark pine
- Douglas-fir
- mixed conifer
(e.g., Pinus, Abies)</td></tr>
<tr><td colspan="3">- grassland-shrubland (includes grasses, shrubs, forbes, etc…)</td></tr>
<tr><td colspan="2">- deciduous forest</td><td>- aspen
- cottonwood
- willow</td></tr>
<tr><td colspan="4">non-vegetation (snow/ice, cloud, cloud shadow, rock, bare, water, urban, bad scan lines)</td></tr>
<tr><td colspan="4">agriculture</td></tr>
</table>

Table 4.2. Predictor data layers for classification tree analysis.

Year	Predictor Data Layers
1999	Summer Landsat bands 1,2,3,4,5,7
	Fall Landsat bands 1,2,3,4,5,7
	Winter Landsat bands 1,2,3,4,5,7
	Summer Tasseled Cap brightness, greenness, wetness
	Fall Tasseled Cap brightness, greenness, wetness
	Winter Tasseled Cap brightness, greenness, wetness
	Tasseled Cap brightness difference (fall-summer)
	Tasseled Cap greenness difference (fall-summer)
	Tasseled Cap wetness difference (fall-summer)
	Tasseled Cap brightness difference (summer-winter)
	Tasseled Cap greenness difference (summer-winter)
	Tasseled Cap wetness difference (summer-winter)
	Elevation, aspect, slope
1985	Summer Landsat bands 1,2,3,4,5,7
	Fall Landsat bands 1,2,3,4,5,7
	Summer Tasseled Cap brightness, greenness, wetness
	Fall Tasseled Cap brightness, greenness, wetness
	Tasseled Cap brightness difference (fall-summer)
	Tasseled Cap greenness difference (fall-summer)
	Tasseled Cap wetness difference (fall-summer)
	Elevation, aspect, slope

1999 Vegetation Classification

For the 1999 vegetation classification, I reclassified only pixels that had changed from 1985, thereby minimizing mis-classification errors. In Chapter 3, I derived a spectral change image that I used to classify trajectories of conifer cover gain and conifer cover loss. Gain or loss of conifer cover was attributable to either seral stage changes (from disturbance or succession) or percent conifer cover changes (from expansion or densification). Based upon the spectral change thresholds that I identified for conifer cover gain and conifer cover loss, and the 1985 thematic classification, I partitioned change between 1985 and 1999 into four categories:

Seral stage changes

1) Seral stage advancement, where I identified conifer cover gain and the 1985 cover type was seedling/sapling or pole seral stage conifer.

2) Seral stage regression, where I identified conifer cover loss and the 1985 cover type contained conifer.

Percent conifer cover changes

3) Conifer expansion, where I identified conifer cover gain and the 1985 cover type was grassland-shrubland.

4) Conifer densification, where I identified conifer cover gain and the 1985 cover type contained conifer.

I reclassified the seral stage change pixels with the same methods as the 1985 classification. For seral stage advancement locations that were seedling/sapling in 1985, I reclassified the 1999 vegetation as either seedling/sapling, pole stage, or conifer woodland. For seral stage advancement locations that were pole stage in 1985, I reclassified the 1999 vegetation as either pole stage or mature/old growth. Conversely, for seral stage regression locations that in 1985 were either pole stage, mature/old growth, or conifer woodland, I reclassified the 1999 vegetation as either seedling/sapling or grassland-shrubland. As with the 1985 classification, standard measures of accuracy were calculated for each image using the withheld validation data.

In order to quantify changes in percent conifer cover between 1985 and 1999, I calculated the rates of increase from aerial photos, stratified by vegetation type, seral stage, and species. Like in Chapter 3, I calculated the change in percent conifer cover for aerial photo samples that exhibited conifer increase. This analysis builds upon that study

by further considering the effect of seral stage and species on the rates of change. In a grid-based model, I added the 14-year increase in conifer cover to the 1985 value to derive the 1999 value (Figure 4.3). For example, for pole stage stands, I calculated a 0.45% (+/- 0.04 SE) average annual rate of conifer cover increase from aerial photo interpretation. Extrapolated to 14 years (1985 – 1999), this equated to a 6.3% increase in conifer cover. For a 50% conifer cover pixel in 1985, the projected conifer cover in 1999 was 56.3%.

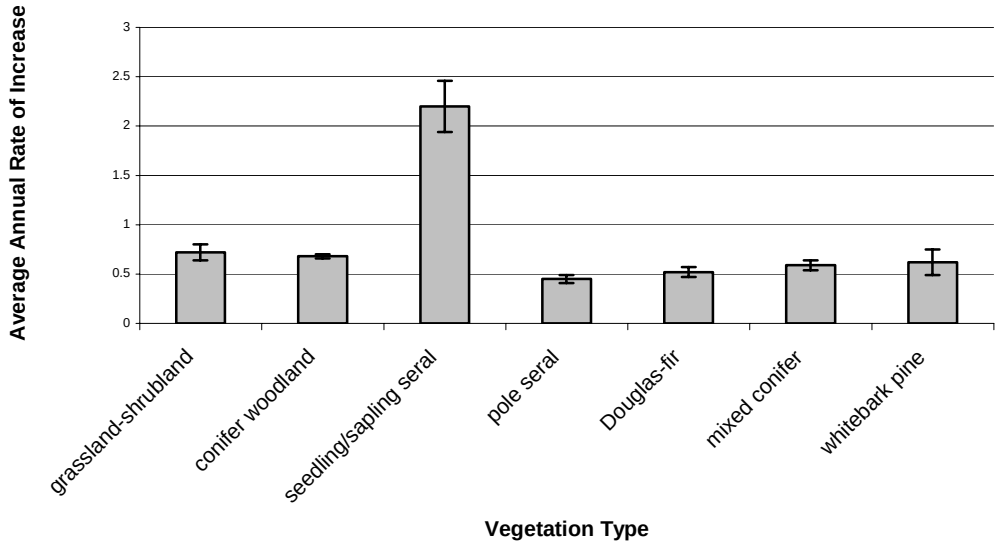

Figure 4.3. Average annual rate and standard error of conifer cover increase by vegetation type.

Finally, I analyzed the trajectories of vegetation change with respect to biophysical setting and fire regime. In order to do this, I overlayed the maps of vegetation change with elevation and aspect grids, and maps of historical natural fire regime and current fire regime condition derived by the U.S. Forest Service Fire Modeling Institute (Schmidt et al. 2002).

Field Sampling of Stand Biomass, Structure, and Composition

In order to estimate the biomass of each stand type, I collected field data from 241 plots. These field plots were within fourteen transects, positioned across gradients of elevation, aspect, and cover type, and were selected to maximize spatial distribution and capture the full range of variability in forest structure and composition across the GYE (Figure 4.1). I selected the locations of field plots within sampling transects according to a stratified random sampling design using vegetation class, aspect, and elevation as strata criteria. I also sampled across gradients of percent conifer cover, seral stage, and stand origin (e.g., fire and logging). I located the field plots using GPS, and measured a suite of structural, compositional, and topographical attributes using a nested plot design (Hansen et al. 2000) (Figure 4.4). In addition, using aerial photos I estimated the percent conifer cover for each field plot.

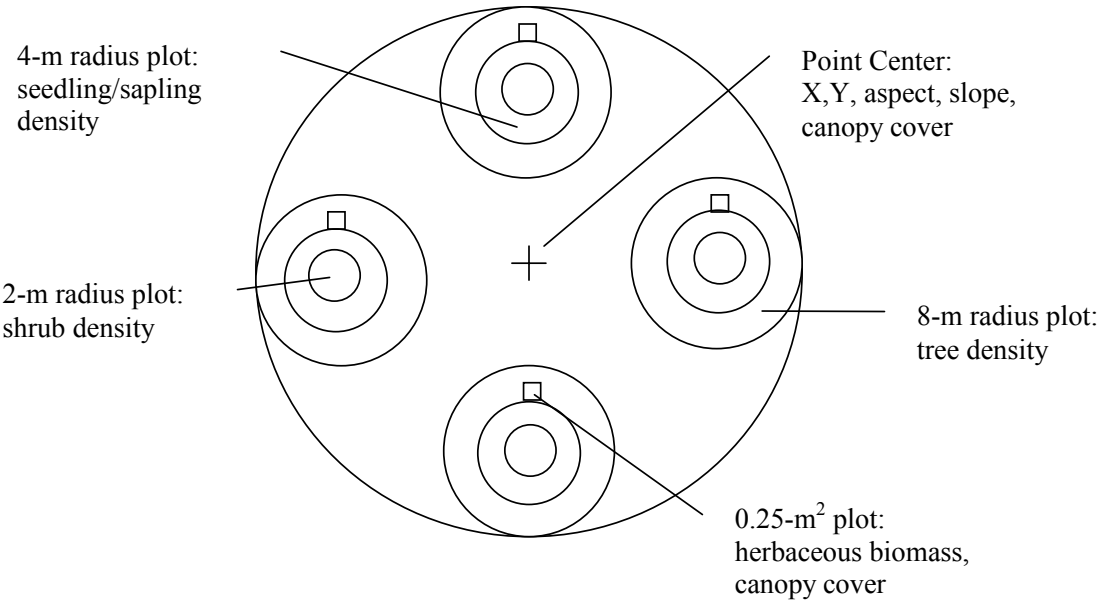

Figure 4.4. Nested plot design for field sampling and attributes measured at each scale.

In the nested plot design each individual plot was comprised of four subplots, each of which were themselves comprised of four smaller, nested subplots. I recorded the general aspect, average slope, and canopy cover at the center X,Y location. I located four subplots at 20 m distance in each of the four cardinal directions. Each subplot center was itself the center of an 8 m, 4 m, and 2 m radius plot. Within the 8 m radius plots, I recorded tree density by species. Within the 4 m radius plots, I recorded seedling/sapling density by height class. Within the 2 m radius plots, I recorded shrub density by species. Finally, I established 0.25 m^2 plots 5 m north of each of the four plot centers, and recorded canopy cover at these locations. Within these plots, I clipped all seasonal herbaceous growth and brought it back to the laboratory for dry weighing.

Estimation of Aboveground Biomass and Carbon Stocks

I calculated live aboveground biomass and carbon content for each field plot using allometric scaling equations provided by the software BIOPAK (Means et al. 1994). The components of live aboveground biomass that I measured in the field were trees, shrubs, seedlings/saplings, and herbaceous cover. I summarized field data as the mean of the four subplots per plot.

Tree and shrub density were scaled to stems per hectare by species. Species specific allometric equations from BIOPAK were used to convert the number of stems to aboveground biomass. If the equation for a species was not available in BIOPAK, the most appropriate substitution was made based upon structural and physiognomic considerations. Seedling/sapling density was measured according to height class, which was converted to diameter-at-base in order to calculate aboveground biomass.

Herbaceous biomass was measured directly by weighing the dried herbaceous clippings from each of the four 0.25 m^2 subplots per plot, and taking the mean value from all subplots.

Live aboveground biomass was then calculated for each plot as the sum of component parts: trees, shrubs, seedlings/saplings, and herbaceous cover. From the estimates of biomass, I calculated the carbon content as 51.2% of biomass (Koch 1989), the general estimate derived for western softwoods, including Douglas-fir, lodgepole pine, spruce, and fir.

Extrapolation of Biomass and Change Across Study Area

I calculated the mean live aboveground biomass for each vegetation type. In addition, I used ordinary least squares (OLS) regression to develop relationships between live aboveground biomass and percent conifer cover by vegetation type and seral stage. I used square root transformations on each variable in order to linearize the relationship between response and predictor variables. I evaluated the regression models by calculating the coefficient of determination (R^2). For both 1985 and 1999 vegetation, I extrapolated estimates of live aboveground biomass across the study area using statistical functions derived for Douglas-fir, mixed conifer, whitebark pine, conifer woodland, pole stage, and seedling/sapling stage. For the grassland-shrubland and burn classes, I simply extrapolated the mean live aboveground biomass estimates across the study area. I converted the estimates of live aboveground biomass to carbon and analyzed changes in live aboveground carbon stocks between the two dates.

Results

1985 and 1999 Vegetation Classifications and Change

The vegetation map for 1985 revealed that 3 vegetation classes comprised 82% of the study area (Figure 4.5): grassland-shrubland (34%), conifer woodland (30%), and mature/old-growth mixed conifer (18%). The remaining 18% of the study area consisted of smaller fractions of mature/old-growth Douglas-fir (5%), hardwood forest (5%), mature/old-growth whitebark pine (3%), seedling/sapling seral stage (3%), and pole seral stage (2%) (Table 4.3).

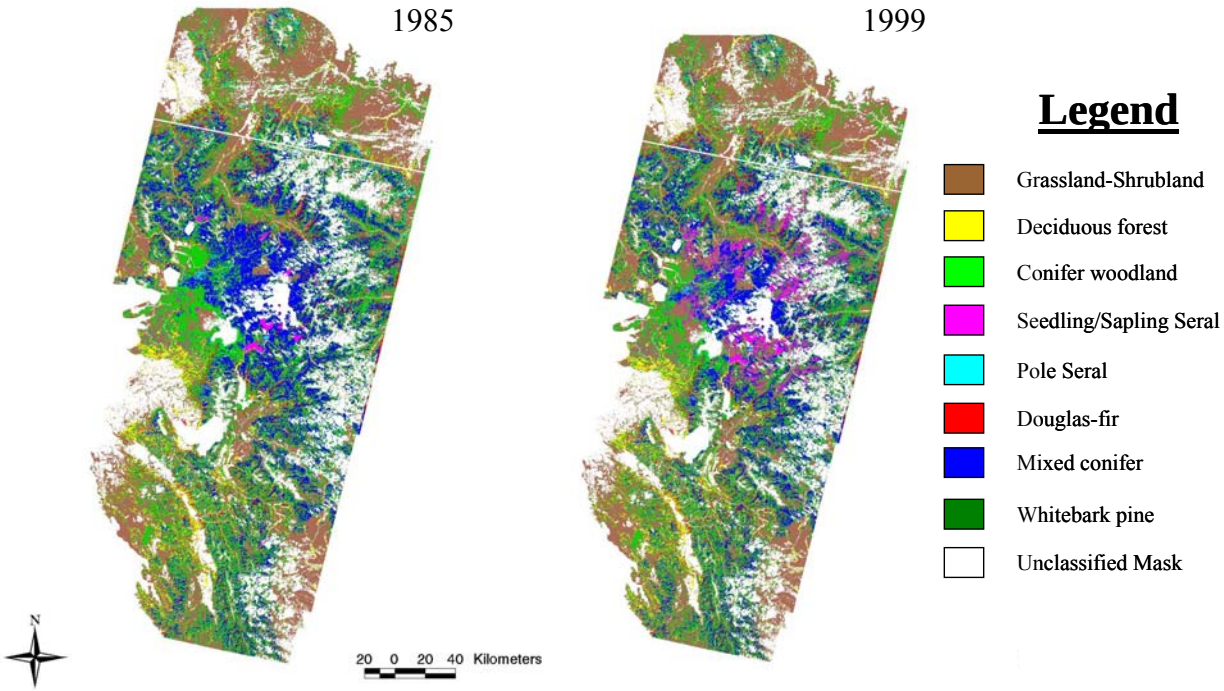

Figure 4.5. 1985 and 1999 classified vegetation of the GYE.

Table 4.3. Results of 1985 and 1999 vegetation classifications and change analysis.

Vegetation Class	1985 area (ha)	% total area 1985	1999 area (ha)	% total area 1999	85-99 change (ha)	Relative change (%)
Grassland-Shrubland	1,654,319	34	1,742,662	36	+88,342	+5
Deciduous	244,531	5	240,450	5	-4,081	-2
Conifer Woodland	1,467,984	30	1,377,404	28	-90,581	-6
Seedling/Sapling	131,189	3	280,106	6	+148,917	+114
Pole seral	117,699	2	111,204	2	-6,495	-6
Douglas-fir	258,716	5	247,740	5	-10,976	-4
Mixed conifer	887,772	18	761,859	15	-125,913	-14
Whitebark pine	130,924	3	131,711	3	+787	+1

While the majority of the study area did not change between 1985 and 1999, there were some important vegetation changes. Seral stage regressed on 337,394 ha of forest land due primarily to fire and logging (Figure 4.6). These changes were mostly distributed at higher elevations (75%) across all aspects (53% on northerly aspects). Meanwhile, seral stage advanced on 59,833 ha of forested areas that were disturbed (e.g., by fire or logging) before 1985, primarily at lower elevations (84%) and northerly aspects (60%).

In addition to these changes, I determined in Chapter 3 that conifer expansion between 1985 and 1999 resulted in the conversion of 90,323 ha of grassland-shrubland to conifer woodland, and conifer densification resulted in the density increase of existing conifer forest on 594,752 ha (Figure 4.6). Combined, 89% of the conifer cover increase between 1985 and 1999 occurred within areas characterized by 0-100+ year historical fire frequency with mixed severity. Additionally, 44% of the conifer cover increase occurred within areas that were classified as having either moderately or significantly departed from their historical fire regime.

The net result of all of these vegetation dynamics was that by 1999, the dominance of the 3 primary vegetation classes dropped by about 3 percent (Figure 4.5

and Table 4.3). Conifer cover decrease, largely attributable to fire and logging, contributed to a 5% increase in grassland-shrubland, a 114% increase in seedling/sapling, a 6% decrease in conifer woodland, a 6% decrease in pole stage, and an 11% decrease in mature/old-growth conifer (Figure 4.7).

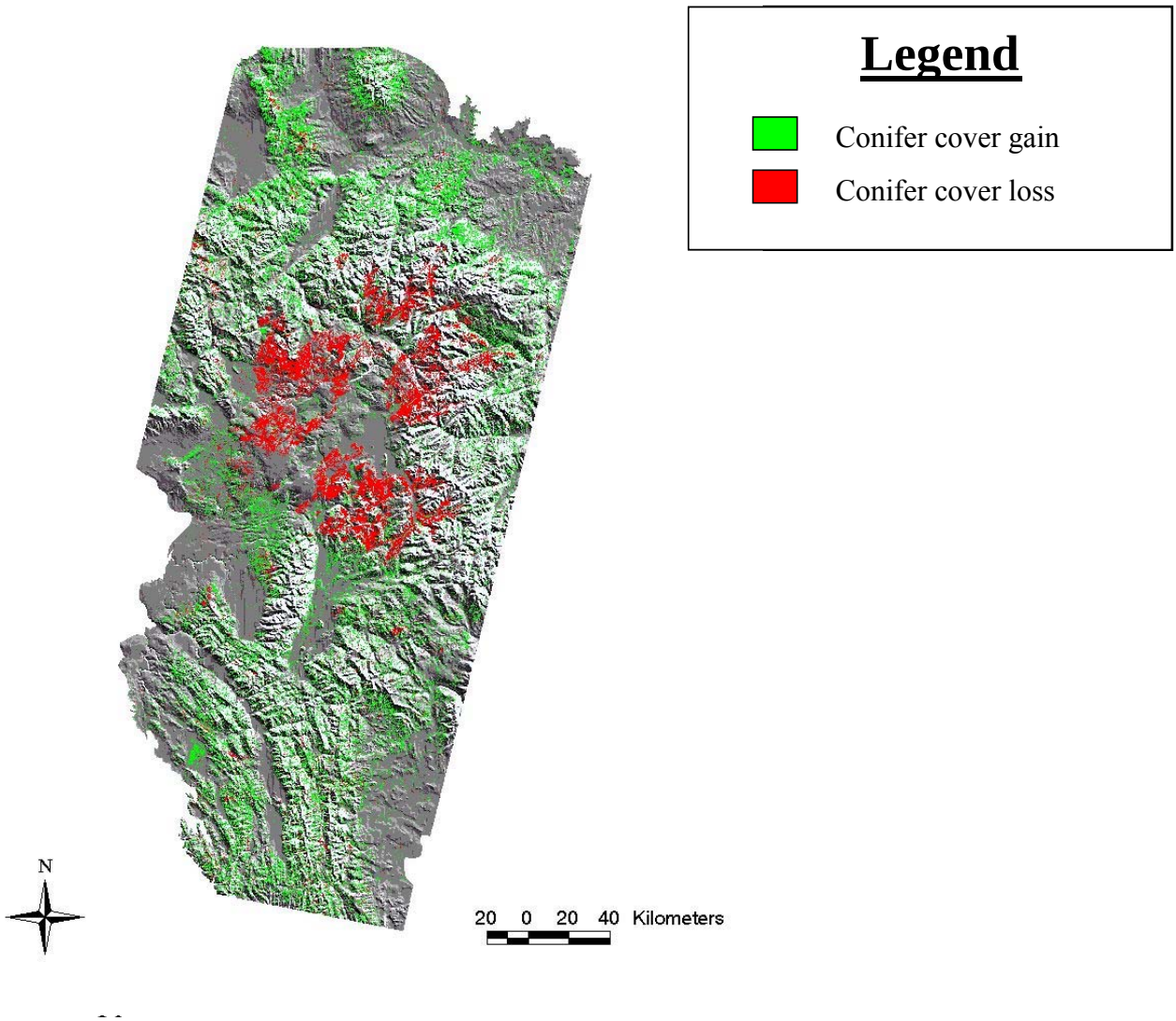

Figure 4.6. Conifer cover gain and loss 1985 – 1999.

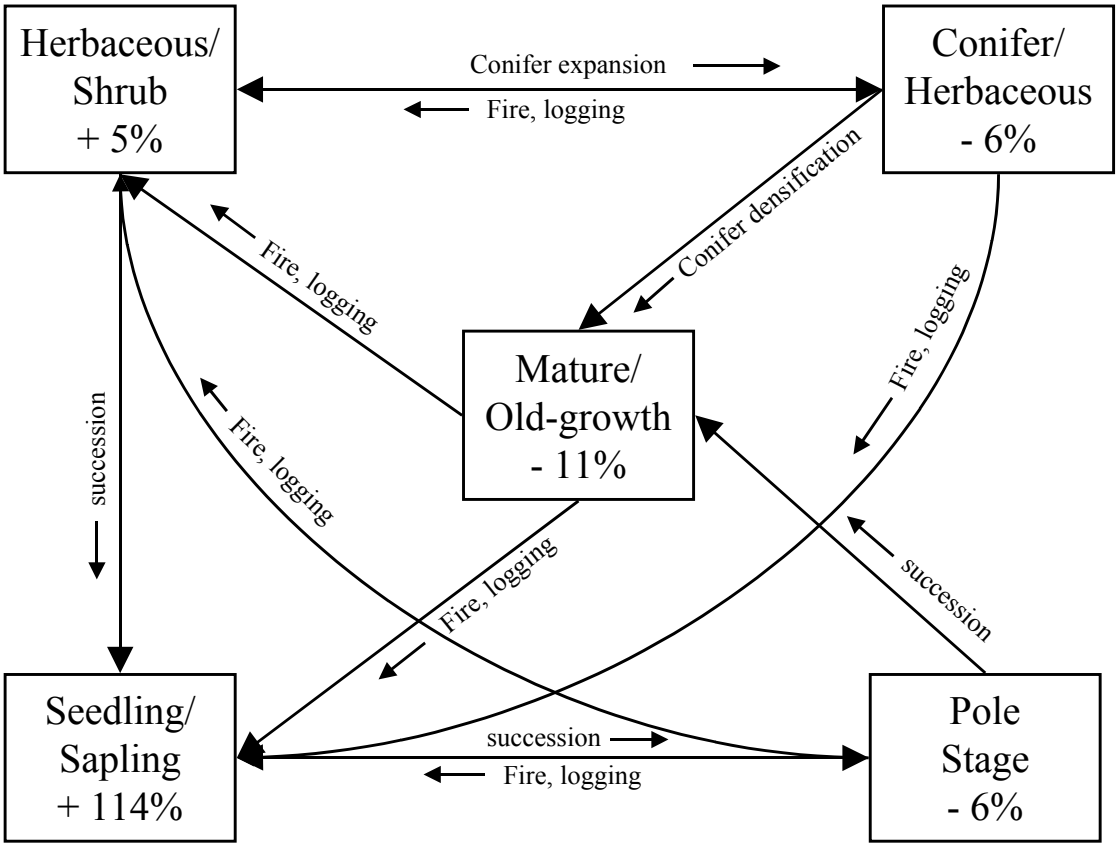

Figure 4.7. Vegetation changes and trajectories 1985 – 1999.

Classification Accuracy Assessment

For 1985 vegetation, the overall accuracy for level 2 was 84%, for level 3 seral stage it was 69%, and for level 4 species it was 68%. For 1999 vegetation, the overall accuracy for level 2 was 88%, for level 3 seral stage it was 73%, and for level 4 species it was 68%. For complete accuracy assessment results, including producer's and user's accuracy for each class, please refer to Appendix B.

Aboveground Biomass and Carbon Content

Estimates of live aboveground biomass ranged from 2,916 kg/ha for grassland-shrubland plots to 154,241 kg/ha for mature/old-growth Douglas-fir plots (Figure 4.8).

Live aboveground biomass was strongly related to percent conifer cover, with R^2 values ranging between 0.66 and 0.86 (Table 4.4). Because such a large percentage of the variation in live aboveground biomass was explained by percent conifer cover, I was able to extrapolate predictions of live aboveground biomass across the landscape for two time periods.

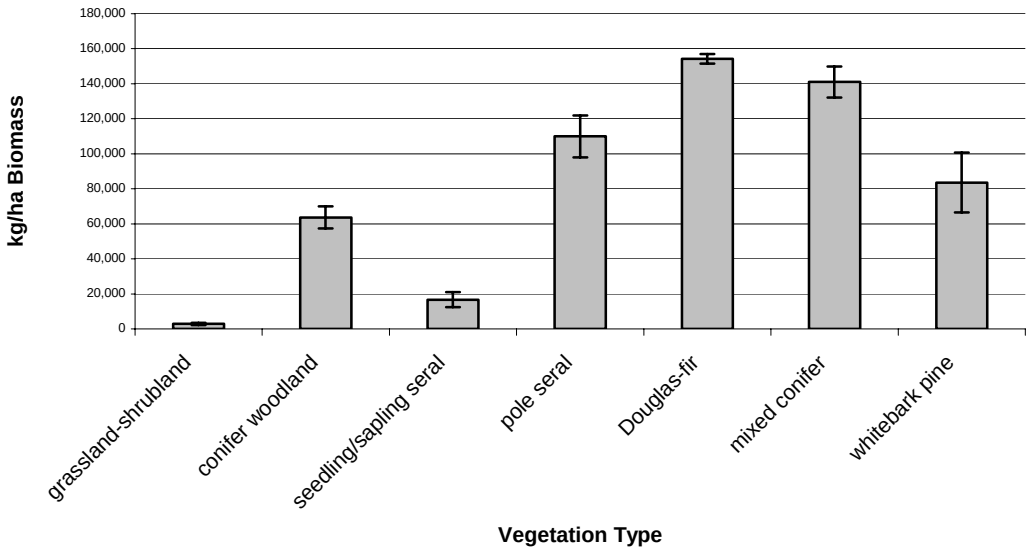

Figure 4.8. Average aboveground live biomass and standard error by vegetation type.

Table 4.4. Regression results for prediction of live biomass from percent conifer cover.

Vegetation Type	Regression Equation	p-value	R^2
Douglas-fir	Live bio=1.53(% con)^2 + 21.65(% con) + 43.91	0	0.73
Mixed conifer	Live bio=0.80(% con)^2 + 26.38(% con) + 44.70	0	0.77
Whitebark pine	Live bio=29.92(% con) + 45.72	5.55e-16	0.80
Conifer woodland	Live bio=4.22(% con)^2 + 4.15(% con) + 46.22	0	0.66
Pole seral	Live bio=28.85(% con) + 46.63	0	0.79
Seedling/sapling seral	Live bio=0.92(% con)^2 + 8.48(% con) + 45.70	1.53e-08	0.66

Note: Live bio = sqrt(live biomass); % con = sqrt(percent conifer cover)

Aboveground Biomass and
Carbon Change 1985 – 1999

Changes in the extent and density of conifer forest resulted in substantial aboveground live carbon gains between 1985 and 1999. Conifer expansion across 90,323 ha increased aboveground live carbon by 274 kg C ha^{-1} yr^{-1}, resulting in net carbon sequestration of 25 Gg C yr^{-1}. Conifer densification across 594,752 ha increased aboveground live carbon by 579 kg C ha^{-1} yr^{-1}, resulting in net carbon sequestration of 344 Gg C yr^{-1}.

Meanwhile, changes in seral stage between 1985 and 1999 resulted in even greater changes in aboveground live carbon on a per hectare basis. Seral stage advancement on 59,833 ha increased aboveground live carbon by 699 kg C ha^{-1} yr^{-1}, resulting in net carbon sequestration of 42 Gg C yr^{-1} over the entire study area. Seral stage regression on 337,394 ha decreased aboveground live carbon by 3,180 kg C ha^{-1} yr^{-1}, resulting in a net carbon loss of 1,073 Gg C yr^{-1} over the entire study area.

Overall, as a result of all vegetation cover change between 1985 and 1999, live carbon stocks decreased by 143 kg C ha^{-1} yr^{-1}. The net loss of live carbon as a result of these changes was 662 Gg C yr^{-1}. Despite the live carbon gain of 369 Gg C yr^{-1} provided by conifer expansion and densification, as well as seral stage advancement, the GYE was a net source of carbon during the period 1985-1999.

Discussion

Fourteen years of vegetation dynamics in the GYE resulted in substantial changes in conifer forest structure and composition, and consequent changes in aboveground carbon stocks. I quantified the dynamics associated with both seral stage changes and

conifer cover increase. The most pronounced changes between 1985 and 1999 were those associated with seral stage regression, largely as a result of fire and logging, that resulted in significant loss of aboveground carbon stocks. Conifer cover increase was also pervasive and accounted for significant aboveground carbon sequestration. Overall, however, a carbon sink associated with conifer cover increase accounted for only a fraction of the total carbon source associated with fire and logging, and thus between 1985 and 1999 the GYE was a net carbon source.

Land Cover Dynamics 1985 – 1999

The widespread fires of 1988 in and around Yellowstone National Park, coupled with other fires between 1985 and 1999 and logging activity during that same time period, combined to regress approximately 7% of the study area from later successional forest types back to early successional cover types. The majority (75%) of these changes occurred in higher elevation forests that are typically characterized by multi-centennial fire return intervals (Romme 1982; Romme and Despain 1989), suggesting that 20th century fire suppression had little to do with these events. The remaining 25% of these changes, however, occurred in lower elevation forests that are historically characterized by frequent, low intensity fire regimes (Arno and Gruell 1986) or mixed frequency and intensity fire regimes (Littell 2002). Other research suggests that these lower elevation forests have been greatly impacted by fire suppression, potentially resulting in a shift towards higher intensity fire (Allen et al. 2002). It is important to note that other processes such as wind throw, forest pests, and pathogens could potentially result in seral stage regression. While I did not attempt to classify the individual contributions of these forest dynamics, I did estimate that the area logged or harvested between 1985 and 1999

on national forests surrounding Yellowstone National Park was between 13,000 – 37,000 ha (S. Powell, *unpublished data*).

Changes in seral stages associated with fire and logging have previously been accurately monitored with remote sensing techniques (Cohen et al. 2002 for logging; Hudak and Brockett 2004 for fire). More subtle vegetation dynamics associated with conifer cover increase, however, have not been previously quantified for large area assessments with remote sensing techniques. Therefore, in addition to quantifying seral stage changes I developed a technique to quantify the extent of conifer cover increase from Landsat imagery, and the rate of conifer cover increase from aerial photos.

As a cumulative result of seral stage and percent conifer cover changes between 1985 and 1999, mature/old-growth conifer forest decreased in area by 11%, conifer woodland decreased by 6%, and pole seral stage conifer forest decreased by 6%. Correspondingly, the area of conifer seedling/sapling regeneration increased by 114%, and the area of grassland-shrubland increased by 5%. The magnitude of seral stage regression between 1985 and 1999 masks the changes associated with conifer cover increase, namely the increase in conifer woodland and the decrease in grassland-shrubland. My results are consistent with the GYE land cover change analysis of Parmenter et al. (2003), who quantified a 17.5% decrease in the area of conifer forest (all mature/old-growth conifer, and pole stage conifer in this study) between 1975 and 1995.

Carbon Dynamics 1985 – 1999

Apart from quantifying the overall vegetation dynamics in the GYE between 1985 and 1999, the second objective of this study was to quantify the changes in live aboveground biomass and carbon associated with these vegetation dynamics. Most

significantly, other researchers have speculated that dynamics such as conifer cover increase could account for some portion of the "missing carbon sink" (Houghton 1999; Schimel 2002). A critical challenge for carbon modeling is the dearth of information on changes in forest biomass stocks across landscapes (Baccini et al. 2004). While some remote sensing research has documented methods of direct estimation of biomass from spectral reflectance (e.g., Jakubauskas and Price 1997), these have often been limited to smaller, more homogenous regions. In Chapter 3 I quantified percent conifer cover across the GYE for multiple time periods. I was therefore able to exploit the positive correlation between percent conifer cover and live aboveground biomass and quantify the extent of carbon uptake attributable to conifer cover increase.

Conifer cover increase between 1985 and 1999 resulted in substantial aboveground carbon gain. Overall, total live aboveground carbon increased by 369 Gg C yr^{-1} between 1985 and 1999 as a result of conifer cover increase. On a per hectare basis, conifer expansion accumulated 274 kg C ha^{-1} yr^{-1}, while conifer densification accumulated 579 kg C ha^{-1} yr^{-1}. These estimates of carbon sequestration are generally consistent with other published estimates. Houghton et al. (2000) estimated the rates of carbon accumulation from woody encroachment across 224 million ha in several regions of the U.S. For the Pacific region (including juniper, ponderosa pine, and sagebrush encroachment), they estimated accumulation of 650 kg C ha^{-1} yr^{-1}, and for the Rocky Mountain region (including juniper and ponderosa pine encroachment), they estimated accumulation of 900 kg C ha^{-1} yr^{-1}. For accumulation of carbon in 5.3 million ha of northern Rocky Mountain ponderosa pine forests as a result of fire exclusion (akin to

conifer densification), Houghton et al. (2000) estimated accumulation of 2,500 kg C ha^{-1} yr^{-1}, including an additional 20% for belowground carbon.

The above estimates, however, are all highly uncertain, as the actual extent of conifer cover increase was unknown and likely overestimated (Houghton et al. 2000; Pacala et al. 2001). To calculate the magnitude of overestimation, I calculated the amount of carbon uptake in the study area under the assumption of Houghton et al. (2000) that woody encroachment had occurred across the entire area of non-forest ecosystems. Using their estimate of 900 kg C ha^{-1} yr^{-1} for carbon accumulation by woody encroachment in the Rocky Mountain region, I calculated carbon uptake estimates that were 60 times higher than my results. Using my more conservative estimate of 274 kg C ha^{-1} yr^{-1} for carbon accumulation by conifer encroachment, I still calculated carbon uptake estimates that were 18 times higher than my results. The results from chapters 2 and 3 demonstrated that while conifer cover increase was widespread, it was not occurring uniformly across all biophysical settings. Between 1985 and 1999, conifer expansion into non-forest ecosystems occurred on only 2% of the study area. For all conifer cover increase, I determined that approximately 40% of eligible samples did show an increase between 1971 and 1999, at highly variable rates. Given these facts, it is likely that previous studies significantly overestimated the amount of carbon sequestered by conifer cover increase and the contribution to the "missing sink."

Apart from the carbon dynamics associated with conifer cover increase, the significant loss of aboveground carbon as a result of seral stage regression greatly overshadowed carbon sequestration from conifer cover increase. Seral stage regression primarily from fire and logging between 1985 and 1999 resulted in substantial biomass

loss. Total live aboveground carbon decreased by 1,073 Gg C yr^{-1} between 1985 and 1999 as a result of seral stage regression. On a per hectare basis, seral stage regression resulted in the loss of 3,180 kg C ha^{-1} yr^{-1}. Slightly offsetting the carbon loss associated with seral stage regression was the carbon gain associated with seral stage advancement, resulting in live biomass accumulation of 42 Gg C yr^{-1}, or 699 kg C ha^{-1} yr^{-1} on a per hectare basis.

Overall, during the period 1985 – 1999, the GYE was a net carbon source of 662 Gg C yr^{-1}. On a per hectare basis across the entire study area, this was equivalent to the loss of 143 kg C ha^{-1} yr^{-1}. Conifer cover increase between 1985 and 1999 did offset 34% of the carbon released by fire and logging, but harsh abiotic and climatic conditions in the GYE limit the extent and rates of increase. Therefore, despite a carbon sink provided by conifer cover increase and seral stage advancement, the widespread occurrence of stand replacement fires between 1985 and 1999 provided a greater source of aboveground carbon.

Limitations and Scope

The results from the GYE suggest that detailed analyses from other regions might cast light on important carbon source/sink dynamics. Given widespread woody encroachment in a variety of ecosystems worldwide, it is critical to accurately quantify the rates, extent, and consequences for carbon in these systems.

There are, however, several limitations to this study that are important to recognize. For one, my method of carbon accounting was designed to broadly quantify changes in live aboveground carbon stocks. Therefore, I did not directly factor net primary productivity into my calculations. Instead, by classifying vegetation types into

seral stages and measuring changes in percent conifer cover, I integrated changes in age classes, stem densities, and tree growth. It is therefore likely that across the study area I underestimated the aboveground carbon sink in vegetation by not accounting for primary productivity in forest stands that did not register a seral stage or percent conifer cover change.

A second important limitation to this study involved my focus solely on aboveground carbon dynamics. Although some research suggests that belowground carbon response to woody encroachment is dependent upon soil moisture gradients (Jackson et al. 2002), other research indicates that belowground carbon stocks are relatively stable in response to conifer cover increase (Smith and Johnson 2003). Belowground carbon stocks are likely less stable in response to fire and logging, and it is likely that carbon loss associated with these processes would further contribute to a net carbon source (Sampson and Clark 1996). Belowground carbon loss has been shown to increase with increasing fire severity (Johnson 1992). Belowground carbon dynamics is an important subject that warrants further research and has important consequences for carbon budgeting. Ultimately, over an area as large as the GYE, changes in aboveground carbon stocks were more readily and accurately measured with remote sensing tools, and I expect that the results of this study will provide a basis for further research.

Further, by focusing solely on live carbon stocks, it is likely that I overestimated the actual carbon source associated with fire and logging. Both fire and logging are associated with large spatial and temporal variability (Turner et al. 1997; Sampson and Clark 1996) in the amount of carbon released to the atmosphere or other sinks. I made the simplified assumption that fire was stand-replacing and that logging was clear-

cutting, and that both processes effectively eliminated the aboveground live carbon stocks.

A fourth limitation to this study was my interpretation of carbon source/sink dynamics from the perspective of two temporal snapshots. By focusing solely on carbon stocks, and not the actual processes of vegetation growth and decomposition, my snapshot of forest dynamics in the GYE was potentially representative only of a narrow window of large scale carbon release. Only a fraction of ecosystem carbon is released at the time of fire, and subsequent rates of decomposition and regrowth significantly govern the carbon balance (Sampson and Clark 1996). For the GYE, it is likely that after net ecosystem production recovers following the 1988 fires, the system will shift to being a carbon sink until the next widespread stand replacement disturbance.

Finally, it is critical to discuss the problem of compounding error in my estimates. A number of known sources of error are present throughout the study, from vegetation classification, to change detection, to biomass estimation, and carbon extrapolation. At most levels of analysis, I have attempted to address error by presenting validation results. Quantification of the extent and rates of conifer cover increase are more adequately validated than quantification of the rates of carbon uptake. Comparison to previous studies of carbon uptake is based largely upon the extent of conifer cover increase. Despite these important limitations, this study does provide significant insight into the rates, extent, and aboveground carbon consequences of conifer cover increase over a large area.

Research and Management Implications

The spatial distribution of carbon source/sink dynamics in the GYE, with respect to the biophysical environment, can aid in interpretation of the consequences of these dynamics for research and management purposes. My results show that the majority of carbon release from seral stage regression occurred in higher elevation forests. The historical frequency and intensity of fire events such as the 1988 fires in and around Yellowstone National Park suggest a multi-centennial fire return interval (Romme 1982; Romme and Despain 1989).

In contrast, however, my results also show that the majority of carbon sequestration from conifer cover increase occurred in lower elevation forests. Approximately 89% of the observed conifer cover increase between 1985 and 1999 occurred in forest types with historically high fire frequency and mixed intensities. As a result of "missed" fire return intervals in some forest types, the increased conifer cover and build-up of fuels have created conditions that depart from their historical range. The U.S. Forest Service Fire Modeling Institute classifies 43% of the GYE as having either moderately or significantly departed from its historical fire regime. I determined that 44% of the conifer cover increase between 1985 and 1999 occurred within these areas. The implication of this finding with respect to carbon storage is that some forest types that historically were adapted to frequent, low intensity fire, might now respond differently to fire given significant conifer cover increase. The changing structure and composition of some forest types could potentially result in changes to fire frequency and intensity. Therefore, the temporal duration of carbon gains remains a major uncertainty. It remains to be seen if the changes in GYE forests will result in changes to fire

frequency and intensity, but mounting evidence from other western coniferous systems suggest that this might be the case (Allen et al. 2002). If so, then the contribution of conifer cover increase to a carbon sink might be even further reduced.

Further research into the dynamics between conifer cover increase and fire is necessary to guide potential fuels management and carbon sink maintenance. This study lays the groundwork for providing land managers with explicit information about the biophysical nature and dynamics of forest carbon. With this information, land managers are likely to better understand the implications of their management actions relative to the location, extent, and rates of change of carbon sources and sinks.

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CHAPTER 5

CONIFER COVER INCREASE IN THE NORTHERN ROCKY MOUNTAINS: RATES, DETERMINANTS, AND CONSEQUENCES FOR CARBON STORAGE AND FIRE

Introduction

The dynamics between non-woody and woody vegetation have received considerable attention in the scientific literature because of the importance these dynamics have for ecosystem functions. Changes in the extent, structure, and composition of woody ecosystems have been described for many systems worldwide, from the arctic (Suarez et al. 1999; Rupp et al. 2001; Silapaswan et al. 2001) to the southwestern United States (Buffington and Herbel 1965; Savage and Swetnam 1990; Allen and Breshears 1998). These dynamics have also been referred to by a wide variety of names, including expansion (Knapp and Soulé 1998), encroachment (Arno and Gruell 1986), invasion (Mast et al. 1997), density increases (Turner and Krannitz 2001), treeline advance (Rupp et al. 2001), afforestation (Soulé et al. 2003), thicketization (Archer et al. 1995), and densification (Kullman and Engelmark 1997). Despite the global scale of this phenomenon, there remains critical uncertainty about the extent, rate, and determinants of change. Furthermore, the consequences of change for carbon storage and fire behavior are poorly understood.

Since European settlement of the western United States, conifer forests have increased in extent and density across large portions of the northern Rocky Mountains. These changes have been well documented by repeat photography (Gruell 1983; Meagher

and Houston 1998). Some are attributable to forest regrowth following extensive fires prior to European settlement (Loope and Gruell 1973; Barrett and Arno 1982; Arno and Gruell 1983), but in many locations conifer forests have expanded into grasslands, shrublands, and hardwood ecosystems (Arno and Gruell 1986). Furthermore, low density, open-canopy conifer woodlands have increased in density in many regions (Arno et al. 1997). In this paper, I collectively refer to both of these processes (the expansion of conifer forests into adjacent non-forested areas, and the in-filling of conifer woodlands) as conifer cover increase.

Conifer dynamics in the northern Rocky Mountains must first be considered in the context of longer temporal scales. Conifer-grassland ecotones have shifted continuously for at least thousands of years. Paleoecological studies of pollen records from Yellowstone National Park, for example, indicate extensive and frequent fluctuations in conifer forest distribution since the last deglaciation (Millspaugh et al. 2000). A cooler, wetter climate following the retreat of glaciers (~17,000 to 12,800 years before present) fostered a widespread grass (*Poaceae*) and sagebrush (*Artemesia*) community across Yellowstone and much of the northern Rocky Mountains. A warming trend followed this period between ~14,000 to 11,000 years before present that enabled the establishment of *Picea, Abies*, and *Pinus* forests on the central plateau of Yellowstone. Upper and lower timberlines then shifted upward and downward periodically over the next 10,000 years in response to intensification of summer insolation, which effectively juxtaposed summer-wet and summer-dry regimes (Romme and Turner 1991; Millspaugh et al. 2000). Despite these frequent changes, evidence from the western U.S. suggests that vegetation

dynamics in the past 120 years have occurred at rates not previously witnessed during the Holocene, potentially as a result of anthropogenic factors (Miller and Wigand 1994).

The goal of this paper is to synthesize the current state of knowledge about conifer cover increase in the northern Rocky Mountains. I chose to focus on the northern Rocky Mountain region for a number of reasons. The rates of change and extent of area impacted by conifer cover increase across the region are poorly understood. A number of studies have attempted to quantify these figures for specific sites or small areas, yet no synthesis has been done for the entire region. The northern Rocky Mountains are also compelling for other reasons. Because of the complexity in the region's vegetation, climate, and topography, there is likely high variability in the rates of conifer cover increase. As a result, there is especially high uncertainty about the role of conifer cover increase in the carbon cycle. A carbon sink attributed to conifer cover increase in the western United States is hypothesized to account for some fraction of the "missing sink" in carbon budgets (Houghton 1999; Schimel 2002).

In this paper, I synthesized research on the following three topics:

1) The rates and extent of conifer cover increase;
2) The factors contributing to conifer cover increase; and
3) The consequences of conifer cover increase for carbon storage and fire behavior.

I suggest that the rates of conifer cover increase in the northern Rocky Mountains are highly variable, governed by forest type, biophysical setting, and disturbance. Four factors are widely cited as determinants of conifer cover increase: climate variability, elevated atmospheric CO_2 levels, changes in fire regimes, and changes in grazing

regimes. I suggest that these hypothesized determinants are not uniformly distributed across landscapes and are mediated by the biophysical setting. Therefore, I expect variable influence on demographic processes that constrain the rates and extent of conifer cover increase. Finally, I suggest that because of the inherent variability in the rates of conifer cover increase, carbon gains are not uniformly distributed. If in fact carbon sequestration is concentrated in forest types that are historically adapted to frequent fire, we might expect a concomitant response in fire behavior.

I begin by briefly describing the northern Rocky Mountains. I then examine each of the above topics by reviewing literature, and close by drawing major conclusions.

Description of Region

The northern Rocky Mountain region is split by the continental divide into west-side mountains (northern Idaho, northwestern Montana, northeastern Washington, and southeastern British Columbia) and east-side mountains (eastern Idaho, northwestern Wyoming, central Montana, and southwestern Alberta) (Arno 1980). The northern Rocky Mountains are characterized by steep abiotic (e.g., climate, soils, and topography) gradients that interact with disturbance and land use to shape the distribution of vegetation. While the west-side mountains are generally wetter and warmer than the east-side mountains, the entire region is characterized by a significant reduction in precipitation in summer months that often desiccates fuels. This results in forest ecosystems that are largely fire driven (Habeck and Mutch 1973).

Valley bottoms across the northern Rocky Mountains are generally dominated by riparian, grassland, and shrubland systems, and are widely impacted by agriculture,

urban, and residential development (Hansen et al. 2002; Parmenter et al. 2003; Hernandez 2004). Moving upslope, there is often a lower treeline ecotone between non-forest and conifer woodlands (e.g., *Pinus, Juniperus, Pseudotsuga*). Lower elevation forests and woodlands are historically characterized by frequent, low intensity fire regimes (Arno and Gruell 1986; Arno et al. 1997) or mixed frequency and intensity fire regimes (Littell 2002), and have been widely impacted by fire suppression, grazing, and logging. Continuing upslope, woodlands grade into higher density, mesic conifer forests (e.g., *Abies, Picea, Pinus*). Subalpine forests are historically characterized by infrequent, high intensity fire regimes (Romme 1982; Romme and Despain 1989).

Extent and Rates of Change

Knowledge of the rates and extent of conifer cover increase is under-developed in the northern Rocky Mountains. Several studies have examined change at specific locations or across small areas, but due to methodological differences it is difficult to compare results among studies for a regional perspective.

Much of the research in the northern Rocky Mountains has focused on rates of change in lower elevation forest types. In ponderosa pine (*Pinus ponderosa*) forests, for example, fire frequency has been effectively reduced, and in many locations understory species such as Douglas-fir (*Pseudotsuga menziesii*) have increased in density (Arno et al. 1995; Arno et al. 1997). Research from old-growth ponderosa pine/Douglas-fir and ponderosa pine/western larch (*Larix occidentalis*) stands in western Montana documented average basal area increases of over 70% during the 20th century (Arno et al. 1995; Arno et al. 1997).

In another lower elevation forest type, the expansion of Douglas-fir forests into adjacent grasslands and shrublands has been widely documented in Montana and Wyoming (Arno and Gruell 1986; Meagher and Houston 1998). Near Butte, Montana, Dando and Hansen (1990) used a time series of aerial photos between 1954 and 1979 to quantify the extent of conifer cover increase. Their analysis revealed a 35% relative increase in the area of Douglas-fir and Rocky Mountain juniper (*Juniperus scopulorum*) forest, equating to a 1.4% increase per year.

Conifer cover increase has also been documented in a number of higher elevation subalpine forest locations across the northern Rocky Mountains. Whitebark pine (*Pinus albicaulis*) forests in the Big Hole Range of Idaho and Montana, for example, have increased in stem area since at least 1753 (Murray et al. 2000). Simulation modeling showed that the stem area of all species increased by 85% over that time period. In another study in the Wind River Mountains of Wyoming, conifer expansion into subalpine meadows began in 1890 and continued until 1963 at an average tree establishment rate of 2.6% per year (Dunwiddie 1977). Similarly, in subalpine forests of the Lemhi Mountains in east-central Idaho, researchers documented significant conifer expansion into meadows starting in the late 1800's and continuing until 1950 (Butler 1986). Dendrochronological evidence from three sites revealed an average tree establishment rate between 0.27% and 0.73% per year over the 84 years of analysis.

The few studies that have examined larger spatial extents indicate that the rates of conifer cover increase are not uniform, but rather vary considerably by forest type. A study in the Centennial Mountains of southwestern Montana, for example, quantified long-term forest dynamics at the scale of a small watershed (Gallant et al. 2003).

Researchers used simulation modeling in conjunction with dendrochronological and chronosequential data to backdate forest composition and seral stage to 1856. The results revealed a 36% absolute increase in the area of conifer forest over 140 years, equating to a 0.26% increase per year. Conifer forest increase was especially rapid on previously sagebrush/grassland sites, exhibiting an 8-fold increase in the number of conifer patches. Alternatively, higher elevation subapline forests did not change greatly over the 140 years, likely as a result of slow growth rates (Gallant et al. 2003).

Another study quantified rates and extent of conifer cover increase between 1985 and 1999 across a large portion of the Greater Yellowstone Ecosystem (GYE) (Chapters 2 and 3). Using satellite imagery to quantify the extent of increase and aerial photos to quantify the rates of increase, researchers estimated that 685,075 ha increased in conifer cover during that time period. Conifer cover increase was more rapid on conifer woodland sites (<70% cover) than on either conifer forest sites (>70% cover) or adjacent grassland-shrubland sites.

By examining large, complex landscapes, these studies also demonstrate that rates of change vary considerably by biophysical setting, even within a forest type. In western Montana ponderosa pine forests, for example, rates of total basal area increase were nearly twice as high on moist sites than on dry sites (Arno et al. 1995; Arno et al. 1997). In the GYE, rates of conifer cover increase in lower elevation conifer woodlands were 46% higher on moist northerly aspects than on dry southerly aspects. Similarly, in lower elevation grasslands-shrublands, rates of conifer expansion were nearly twice as high on moist northerly aspects than on dry southerly aspects.

While forest type or biophysical setting are by themselves insufficient explanations for why conifer cover increase has occurred in the northern Rocky Mountains, they are important factors governing variable rates of change across the region. Consideration of this variation sets the stage for examination of the determinants of change.

Determinants of Change

Widespread conifer cover increase across the northern Rocky Mountains prompts the compelling question of what factors are responsible for these changes. Four factors are widely cited as determinants of conifer cover increase: climate variability, elevated atmospheric CO_2 levels, changes in fire regimes, and changes in grazing regimes. But how do these factors specifically influence the dynamics between woody and non-woody vegetation?

Because of the complexity in the northern Rocky Mountains, the determinants of conifer cover increase likely operate at local to regional scales. The underlying complexity in the physical template of the region limits to some extent where conifer forests occur and where they are likely to expand their range. A key element of this physical template is soil moisture, which is influenced by climate, geology, and vegetation. In the GYE, I determined that much of the biophysical variation in the frequency and rates of conifer cover increase was associated with gradients in soil moisture (Chapter 2). However, while soil moisture is an important factor governing the rates of change, conifer cover increase in the northern Rocky Mountains is likely

triggered and fostered by disturbance, or lack of disturbance, that directly or indirectly influences conifer demographic processes (Richardson and Bond 1991).

Conifer demographic processes associated with conifer cover increase include reproduction, seedling establishment, growth, and survival. The hypothesized determinants of conifer cover increase are only as important as their influence on demographic processes. The determinants have both direct and indirect influence on these processes. By a direct influence, I imply that there is an immediate response in the process. For example, fire is a direct source of conifer seedling mortality. An indirect influence, on the other hand, is one that affects a demographic process through changes in biological interactions, namely interspecific competition. For example, reduced interspecific competition following heavy grazing is an indirect influence on the growth of conifer seedlings. As illustrated by the above examples, each of the hypothesized determinants likely has both positive and negative influences, as well as both direct and indirect influences. Finally, the hypothesized determinants likely operate either independently or jointly to drive conifer forest dynamics. The conceptual diagram below (Figure 5.1) illustrates the linkages between conifer demographic processes and the hypothesized determinants of change.

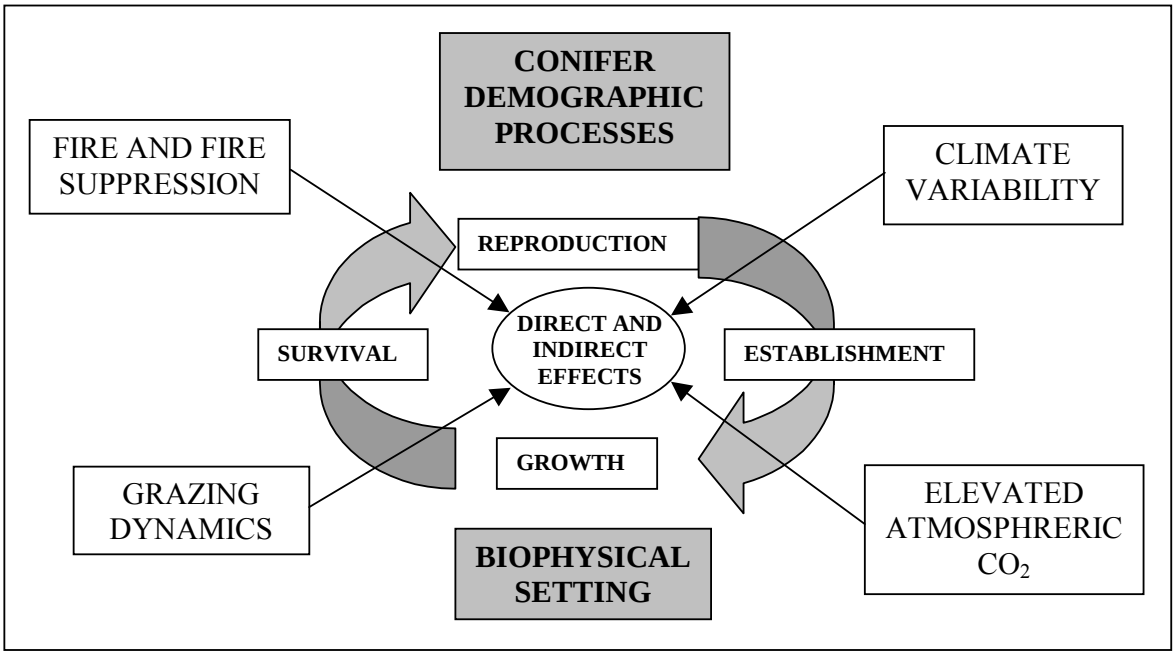

Figure 5.1. Conceptual diagram of the demographic processes and determinants of conifer cover increase.

Climate Variability

Climate variability and its influence on temperature and soil moisture is widely recognized as an important factor governing conifer cover increase (Richardson and Bond 1991). Because of the range of conditions in the northern Rocky Mountains, in many locations species occur at or near their climatic limits. Therefore, climate variability can have both direct positive and negative influence on conifer reproduction, seedling establishment, growth, and survival. It can also indirectly drive competitive interactions between species, thus promoting or inhibiting conifer cover increase (McMinn 1952). The success of conifer cover increase hinges upon seedling establishment, which is largely governed by adequate soil moisture (Daubenmire 1968). Tree seedlings begin their growth later in the season compared to grasses and often are not able to descend their tap roots deep enough to escape or endure soil drought

(Daubenmire 1968). In a study of rooting depth in northern Idaho, for example, Daubenmire (1968) observed that by early summer, the maximum conifer root length was 140 mm with no lateral roots compared to 270 mm for grasses with abundant adventitious roots and tillers. These findings are consistent with those of McMinn (1952), who concluded that the physiological limitations of species in northern Idaho and eastern Washington prevented their spread into areas where soil drought was more extensive than they could tolerate.

Periods of favorable climate, therefore, are often associated with pulses of conifer reproduction and seedling establishment. Because of the topographic complexity and range of forest types in the northern Rocky Mountains, favorable climate conditions can take many forms. For sites where soil moisture is limiting, favorable climate is often expressed as wetter conditions. For warmer, xeric lower elevation forests in the northern Rocky Mountains, cooling trends tend to favor seedling establishment, while for cooler, xeric higher elevation forests, warming trends tend to favor seedling establishment. Patten (1963) documented the importance of favorable climatic conditions in the Madison Range of southwestern Montana, observing that after years with heavy snows and rains, conifer seedlings were more likely to establish and survive into the following winter. In cold, dry meadows in Yellowstone National Park, warm and wet climatic trends that coincided with episodic lodgepole pine (*Pinus contorta*) seed production were favorable for tree seedling establishment (Jakubos and Romme 1993). Indirectly, the timing of drought and precipitation can also significantly influence the competitive interactions between trees and grasses. In southwestern Montana, a drought that

significantly reduced herbaceous growth, followed by high levels of precipitation, resulted in reduced interspecific competition with conifers (Dando and Hansen 1990).

For sites that are not limited by moisture, favorable climates are often expressed as drier, warming trends. In higher elevation, subalpine forests in the northern Rocky Mountains, temperature, not moisture, is often the limiting factor for tree seedling establishment and survival (Richardson and Bond 1991). Climatic warming trends that reduce winter severity and increase the length of the growing season can be beneficial for conifer seedling survival (Gallant 2003). In moist meadow locations in the Lemhi Mountains of Idaho, for example, tree seedling establishment was directly aided by warm and dry climatic trends that resulted in snowpack reductions and subsequent meadow soil drying (Butler 1986).

Changes in Fire Regimes

The European settlement of the northern Rocky Mountains ushered in widespread livestock grazing (Wyckoff and Hansen 1991), which had the effect of reducing herbaceous fuels. Along with the valuation of timber as an economic commodity, direct and indirect fire suppression became a common phenomenon throughout forests and grasslands of the northern Rocky Mountains. Due to the ecological importance of fire in northern Rocky Mountain ecosystems (Habeck and Mutch 1973), the reduction in the extent and frequency of fire over the last century, especially in lower elevation forests, has likely fostered significant changes in forest structure, composition, and pattern (Gallant et al. 2003).

Fire suppression alone, however, is generally not viewed as a causative factor of conifer cover increase. Rather, fire suppression in disturbance-dependent ecosystems

permits vegetation succession to proceed unchecked (Sindelar 1971). Biological inertia then develops as the number of individuals continue to increase and seed sources become abundant (Soulé et al. 2003). In the absence of fire, conifer seedlings and saplings are able to attain a critical height that reduces their probability of mortality from fire (Arno and Gruell 1983). As forest succession proceeds, microhabitat improvements continue to benefit the establishment of later successional species.

The lower elevation forest-grassland ecotones in the northern Rocky Mountains have received a great deal of attention with regard to fire suppression and conifer cover increase. Conifer cover increase has been widely reported in lower elevation ponderosa pine, Douglas-fir, and Rocky Mountain juniper forests. A number of studies have pointed to fire suppression as the primary factor in conifer cover increase (Houston 1973; Arno and Gruell 1982; Arno and Gruell 1986; Dando and Hansen 1990). Douglas-fir forests in southwestern Montana have received particular attention because of the large extent and high rate of conifer cover increase throughout the last century (Gruell 1983). Historic fire return intervals in these forests were estimated to be between 25-40 years (Arno and Gruell 1983; Arno and Gruell 1986), partially attributable to frequent Native American burning (Barrett and Arno 1982). Frequent, low-intensity fires that swept through the understory of open Douglas-fir stands maintained lower densities of trees by killing young conifer seedlings and saplings. With a significant reduction in fire frequency and extent in the 20th century, the probability of conifer survival increased and forests expanded their range and increased in density.

A similar set of circumstances has been well documented in the lower elevation ponderosa pine forests of the northern Rocky Mountains. Thick-barked ponderosa pine is

especially adapted to surviving frequent, low-intensity surface fires that historically maintained open, low density forest structure (Arno et al. 1997). In the absence of fire, many ponderosa pine forests have increased significantly in overall basal area and density (Arno et al. 1995; Arno et al. 1997; Turner and Krannitz 2001). In addition, much of the basal area increase is attributed to understory development of less fire resistant species (Arno et al. 1995).

In higher elevation subalpine forests, dendrochronology has revealed a much longer fire return interval, upwards of several centuries (Arno 1980; Romme 1982; Romme and Despain 1989). However, in many subalpine forests fire has been effectively reduced in overall extent during the 20th century (Arno 1993). Several higher elevation studies have shown that conifer forests have expanded into alpine meadows throughout the northern Rocky Mountains (Dunwiddie 1977; Butler 1986; Jakubos and Romme 1993) and increased dramatically in stem area (Murray 2000). Many subalpine forests have also dramatically changed in species composition over the past century, and key species, such as whitebark and lodgepole pine, that depend upon fire for reproduction have been significantly reduced in some locations (Arno et al. 1993; Murray 2000).

Changes in Grazing Regimes

Grazing regimes have profoundly shaped the dynamics between woody and non-woody vegetation in the northern Rocky Mountains. In addition to large numbers of native ungulates in the northern Rocky Mountains, European settlement in the mid-1800's brought extensive sheep and cattle grazing of grasslands and lower elevation forests (Wyckoff and Hansen 1991). In many instances, grazing was a de facto form of fire suppression. High frequency, low intensity fires were historically fueled by

herbaceous vegetation, but grazers removed these fine fuels, reducing the probability of fire spread.

Grazing animals both directly and indirectly influence the establishment, growth, and survival of conifer forests. From the direct stand point, trampling (Dunwiddie 1977) and browsing (Patten 1963) of conifer seedlings is a source of mortality and high grazing levels often limit the expansion of conifer forests into adjacent grasslands and shrublands. The cessation or reduction of grazing in some systems can reduce this source of mortality and in some instances lead to extensive conifer cover increase (Butler 1986), as was the case in a subalpine meadow in the Wind River Mountains of Wyoming (Dunwiddie 1977). Conversely, in some cases the hooves of grazing animals break up the soil surface and thick herbaceous sod layers and thereby provide seed bed opportunities for conifer establishment (Dunwiddie 1977; Richardson and Bond 1991).

Competition between conifer seedlings and herbaceous vegetation is a key controlling factor of ecotonal dynamics. By preferentially eating herbaceous plants, grazing animals indirectly influence the competition between grasses and trees (Richardson and Bond 1991). As grazing pressures mount, woody shrubs and trees are often the competitive victors and increase in abundance and density. Intermediate grazing levels are most closely associated with extensive conifer cover increase, as higher levels can be destructive to conifer seedlings and lower levels foster competitive growth of herbaceous vegetation (Butler 1986). As succession proceeds from grasslands to shrublands to forests, significant physical changes can occur that benefit the continued establishment of conifer seedlings. These microsite ameliorations brought on by shading include reduced soil surface temperatures, increased soil moisture, physical protection

from trampling and wind, and increased soil organic matter from litter accumulation (Patten 1963; Sindelar 1971). In Douglas-fir forests of southwestern Montana, for example, sagebrush expansion typically precedes Douglas-fir expansion, and sagebrush act as "nurse plants" in improving the microsite environment for continued forest succession (Sindelar 1971). The shade provided by sagebrush has been observed to reduce the soil surface temperatures by 45%-57% (Burkhardt and Tisdale 1976).

Atmospheric Change

Although it has received considerably less attention in the northern Rocky Mountains, elevated atmospheric CO_2 concentration has been hypothesized to be a contributor to conifer cover increase (Soulé et al. 2003). Since the start of the industrial revolution, the atmospheric concentration of CO_2 has increased by approximately 31 +/- 4% (IPCC 2001). The C_3 photosynthetic pathway of plants (including northern Rocky Mountain conifer species) is not saturated at current atmospheric CO_2 levels (Graham et al. 1990). Therefore, elevated CO_2 levels could theoretically result in more frequent stomatal closure and reduced loss of water, conferring an advantage to conifers growing near their moisture limits (Norby et al. 2001). Increased water use efficiency could, in theory extend the range of a species into drier locations where it does not presently occur (Graham et al. 1990). Elevated CO_2 levels could also result in increased rates of photosynthesis that promote increased tree growth rates. This was observed in subalpine conifers in California (LaMarche et al. 1984), where increased tree growth rates exceeded expectations from climate trends alone and were more consistent with the elevated CO_2 hypothesis.

While a direct link between conifer cover increase and atmospheric change has not yet been demonstrated, there are examples from other western U.S. regions where such a relationship is a distinct possibility. At a site in central Oregon, for example, juniper cover doubled between 1961 and 1994 (Knapp and Soulé 1996). The researchers at this site effectively ruled out connections to the other frequently cited determinants of conifer cover increase, and concluded that the juniper increase was consistent with the elevated CO_2 hypothesis. Climate variability was insignificant, grazing had never occurred on the site, and fire was not a significant component of the historical vegetation dynamics. Moreover, they concluded that the juniper increase had occurred under more arid conditions, suggesting that only increased water use efficiency by juniper could explain the phenomenon. In another study, the same authors (Soulé et al. 2003) documented rates of radial growth in juniper forest and concluded that the greatest increase in radial growth occurred in the second half of the study, a period coincident with rapid CO_2 increase. Other studies from the western U.S. have also documented increased levels of water use efficiency in Douglas-fir and Monterey pine (*Pinus radiata*) under elevated CO_2 levels (Hollinger 1987).

Consequences for Carbon Storage and Fire Behavior

Documented increases in atmospheric CO_2 and hypothesized linkages to climate warming have resulted in an increase of research attention to carbon dynamics. Quantified emissions, or sources of CO_2, remain larger than quantified reservoirs, or sinks of CO_2, resulting in an undiagnosed "missing sink." Current estimates of the size of the conterminous U.S. terrestrial sink range between 300,000 – 580,000 Gg C yr^{-1}, but

the temporal and spatial dimensions, as well as the drivers of the sink, remain uncertain (Pacala et al. 2001).

Carbon sinks attributed to conifer cover increase are hypothesized to account for some fraction of the "missing sink" in carbon budgets (Houghton 1999; Schimel 2002). Conifer forests store more aboveground carbon than their former grassland or shrubland counterparts, and increases in conifer density result in greater storage of aboveground carbon (Hansen et al. 2000; Chapter 4). Current carbon accounting systems, however, retain high uncertainty with regard to the influence of conifer cover increase on carbon uptake (Houghton et al. 1999).

At the national level, few carbon budgeting studies have attempted to account for conifer cover increase, and to date only inventory-based approaches have produced reliable estimates (Houghton et al. 1999; Houghton et al. 2000; Pacala et al. 2001). Acknowledging substantial uncertainty, Pacala et al. (2001) estimated that woody encroachment into non-forest ecosystems accounted for approximately 120,000 – 130,000 Gg C yr^{-1} in the conterminous U.S., a substantial portion of the estimated 300,000 – 580,000 Gg C yr^{-1} total conterminous U.S. carbon sink (Pacala et al. 2001). However, the actual extent of woody encroachment in this study was unknown and likely overestimated (Houghton et al. 2000; Pacala et al. 2001).

The results of research in the GYE (Chapters 2 and 3) demonstrated that while conifer cover increase was widespread, it was not occurring uniformly across all biophysical settings. Between 1985 and 1999, conifer expansion into non-forest ecosystems occurred on only 5% of the eligible study area. Moreover, while conifer cover increase in the GYE between 1985 and 1999 did result in substantial aboveground

carbon gain (Chapter 4), the estimates of carbon uptake were lower than other published estimates (Houghton et al. 2000). Conifer expansion into non-forested areas accumulated an average of 274 kg C ha^{-1} yr^{-1}, while conifer densification accumulated an average of 579 kg C ha^{-1} yr^{-1}. In comparison, for woody encroachment across 153 million ha in the Rocky Mountain region (including juniper and ponderosa pine encroachment), Houghton et al. (2000) estimated accumulation of 900 kg C ha^{-1} yr^{-1}. For accumulation of carbon in 5.3 million ha of northern Rocky Mountain ponderosa pine forests as a result of fire exclusion (akin to conifer densification), Houghton et al. (2000) estimated accumulation of 2,500 kg C ha^{-1} yr^{-1}, including an additional 20% for belowground carbon. Because of uncertainties in the extent of conifer cover increase and the amount of carbon uptake, it is likely that previously published estimates of contributions to the "missing sink" are significant overestimates. Rates and extent of conifer cover increase are highly variable across the northern Rocky Mountains, and generalized estimates of carbon uptake do not take this into account.

Conifer cover increase across the northern Rocky Mountains has potentially significant consequences for fuel loads and fire behavior. In many locations, forest structural and compositional changes are associated with increased occurrence of insect epidemics and diseases, resulting in heavy fuel accumulations (Arno and Brown 1989). Fuel accumulations in turn serve as catalysts for intense fires (Arno and Brown 1989). This is particularly the case in lower elevation forests throughout the northern Rocky Mountains, where historical fire return intervals are high and the rate of conifer cover increase is high (Chapter 2). Many locations are well outside their historical range of variability with respect to fire frequency, intensity, size, severity, and landscape pattern

(Schmidt et al. 2002). The potential release of carbon associated with high intensity fire could offset the gains associated with carbon sequestration (Sampson and Clark 1996).

Historically, as much as 80% of the northern Rocky Mountains experienced low or mixed severity fire regimes (Barrett 1999). After a 90% reduction in wildfires in the 20th century, only about 40% of northern Rocky Mountain forests remain under a low or mixed severity fire regime, the remaining 60% now considered intense severity (Barrett 1999). According to the U.S.F.S. Fire Modeling Institute's classification of historical natural fire regimes (Schmidt et al. 2002), up to 85% of the GYE is historically characterized by 0-100+ year fire frequency with mixed severity. The results of research in the GYE indicated that 90% of the observed conifer cover increase between 1985 and 1999 occurred within these areas (Chapter 4). Furthermore, the U.S.F.S. Fire Modeling Institute classifies 43% of the GYE as having moderately or significantly departed from its historical fire regime. The results of the GYE research determined that 44% of the conifer cover increase between 1985 and 1999 occurred within these areas (Chapter 4). The implication of these findings with respect to carbon storage is that forest types that were historically adapted to frequent, low intensity fire might now respond differently to fire. In many locations, these forests have a higher canopy coverage and more ladder-fuel. If and when fire is returned to these systems, it might result in higher severity fire and greater loss of stored carbon. Mounting evidence from many western coniferous systems suggests that this might be the case (Allen et al. 2002). In a comparison of fire behavior between dense, encroached ponderosa pine stands and lower density ponderosa pine stands, for example, researchers found that fire behavior was significantly less intense in the lower density stands (Fulé et al 2001).

Conclusions

Conifer cover increase in the northern Rocky Mountains bears a strong resemblance to changes elsewhere in the western United States. Changes in ponderosa pine forests in particular have been well studied across their range, from Arizona (Covington and Moore 1994), to Colorado (Mast et al. 1997), to Utah (Madany and West 1983), to Wyoming (Fisher et al. 1987), and South Dakota (Bachelet et al. 2000). Like in the northern Rocky Mountains, these changes have been attributed to reductions in fire frequency, the effects of grazing animals, and climate variability. Changes in juniper forests have also received considerable attention across the western U.S., from southeastern Idaho (Burkhardt and Tisdale 1976), to southeastern Oregon (Soulé et al. 2003), to the prairies of Kansas (Briggs et al. 2002). Like in ponderosa pine, the increase in area and density of juniper forests has been attributed to a reduction in the frequency and extent of fire, grazing regimes, and climate variability. In a few studies, the authors suggest that elevated atmospheric CO_2 levels might also be a factor (Knapp and Soulé 1996; Soulé et al. 2003).

In many locations across the western U.S., we see evidence of rapid conifer cover increase, exceeding rates of change observed in the northern Rocky Mountains. In eastern Kansas, researchers documented red cedar (*Juniperus virginiana*) expansion into prairie at an average rate of 2.3% per year (Briggs et al. 2002). Along the Colorado Front Range, the extent of ponderosa pine increased at a rate of 0.61% per year (Mast et al. 1997), and in central Oregon, the extent of juniper cover increased at a rate of 0.45% per year (Knapp and Soulé 1998). What these results suggest is that the rates of conifer

cover increase are governed by biophysical setting but that the probability of conifer cover increase is governed by climate variability, fire suppression, grazing regimes, and response to elevated CO_2. While these determinants are generally similar across regions, harsh climate conditions in the northern Rocky Mountains likely render the rates of change low relative to other locations in the western U.S.

Overall, conifer cover increase in the northern Rocky Mountains is well documented, but information about the extent, rates, determinants, and consequences is lacking. The northern Rocky Mountains are a highly complex region in terms of climate, soils, topography, vegetation types, and disturbance regimes. Because of this complexity, the hypothesized determinants of conifer cover increase do not have uniform effects across the landscape. Fire suppression and grazing have not evenly affected all forest types in the region, and climate variability and elevated CO_2 levels have variable effects depending upon biophysical location. As a result, there is extremely high variability in the process of conifer cover increase. Rates of conifer cover increase are likely highest where the biophysical setting is favorable, and a confluence of factors interacts in such a way as to positively influence conifer reproduction, seedling establishment, growth, and survival.

Although no single determinant of conifer cover increase is universally viewed as causative in the northern Rocky Mountains, there is substantial agreement in the literature that climate variability, fire suppression, grazing dynamics, and elevated CO_2 levels all have a potential impact. Interactions between climate variability, fire suppression, and grazing dynamics have significantly reduced the frequency and extent of fire in many conifer ecosystems that were historically adapted to a high frequency, low intensity fire

regime. In the absence of frequent fire, conifer seedlings have been able to escape a direct source of mortality. By reducing the amount of fine fuel in fire dependent systems, grazing animals have contributed to fire suppression, and also reduced interspecific competition between conifer seedlings and other competitive species. While disturbance or a lack of disturbance are critical factors in conifer cover increase, the process is also highly dependent upon favorable climate conditions that facilitate conifer demographic processes. In the absence of favorable climate conditions for conifer reproduction or seedling establishment, fire suppression or grazing alone are unlikely to promote an increase in conifer cover. Plant response to elevated CO_2 presents a potential exception to this notion, because by increasing water use efficiency in marginal locations, it is possible that conifers will expand their range into locations previously unsuitable for their existence.

Regardless of the factors promoting conifer cover increase across the northern Rocky Mountains, the consequences of these changes are significant for carbon uptake, fuel loads, and fire behavior. While the extent of conifer cover increase in the northern Rocky Mountains is likely less than has been previously reported in some carbon budgeting studies (Houghton et al. 2000), conifer cover increase is associated with a significant carbon sink (Chapter 4). However, because some of the carbon gain is a result of "missed" fire return intervals, heavy fuel loads and the potential risk of intense wildfire jeopardize the longevity of a carbon sink.

More detailed research on variability in the rates of conifer cover increase across the northern Rocky Mountains is necessary. An improved understanding will enable better forecasting of the contribution of conifer cover increase to carbon dynamics and

fire behavior. Apart from the importance of improving carbon budgets for regional, national, and global carbon budgeting efforts, it is imperative that land managers in the northern Rocky Mountains have accurate information about the location of carbon sinks, their rate of accumulation, and their effect on fire behavior. With accurate information, managers are more likely to understand the implications of their management actions relative to carbon sinks and fire, and improve prioritization of management activities.

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APPENDICES

APPENDIX A

DATA DOCUMENTATION

Aerial Photos

The majority of aerial photos used for this research were acquired from the U.S.D.A. Aerial Photography Field Office, in Salt Lake City, Utah. I acquired 1971 and 1999 color photos at a scale of 1:15,840, and 1981 color photos at a scale of 1:24,000. In addition, I used a series of aerial photos from the Yellowstone National Park archives: 1969 color photos were at a scale of 1:15,840; 1990 color photos were at a scale of 1:24,000; and 1998 color infrared photos were at a scale of 1:30,000. Finally, in a few instances, I used aerial photos that were acquired from the U.S.G.S. National Aerial Photography Program: 1989 and 1999 color infrared photos were at a scale of 1:15,850.

Satellite Imagery

Six Landsat TM images from 1985 and 9 Landsat ETM+ images from 1999/2000 were acquired from the U.S.G.S. EROS Data Center in Sioux Falls, South Dakota. The Landsat 5 TM images were obtained for Path 38, Rows 28-30, on 7/14/85 and 9/16/85, and delivered in NLAPS data format, in UTM projection. The Landsat 7 ETM+ images were obtained for Path 38, Rows 28-30, on 7/13/99, 9/15/99, 6/29/00, and 12/4/99. For Landsat 5 TM imagery, visible, near-IR, and mid-IR bands were resampled to 30 m resolution, and the thermal band was resampled to 120 m resolution (but not used for this study). For Landsat 7 ETM+ imagery, visible, near-IR, and mid-IR bands were resampled to 30 m, and the thermal band was resampled to 60 m resolution (but not used for this study). In addition, for the ETM+ imagery, a panchromatic band was resampled to 15 m resolution but not used for this study.

Vegetation and Fire Data

I acquired vegetation and fire data for each of the National Forests and National Parks of the Greater Yellowstone Ecosystem. A listing of the data sets and contacts follows:

Bridger-Teton National Forest
Jackson, Wyoming
Stand Data Set: fwvgtim;
Contact: GIS Coordinator, J. Katzer
Fire Data Sets: r420yrfirehis; firehis_pl
Contact: D. Prevedel

Gallatin National Forest
Bozeman, Montana
Stand Data Set: gnf_std_plus;
Contact: GIS Coordinator, S. Swain
Fire Data Set: gnf_fire poly
Contact: S. Swain

Custer National Forest
Billings, Montana
Stand Data Set: cnf_tsmrs
Contact: GIS Coordinator, D. Arzy

Beaverhead-Deerlodge National Forest
Dillon, Montana
Stand Data Set: Tmb_stands_sz
Contact: GIS Coordinator, T. O'Neil

Caribou-Targhee National Forest
St. Anthony, Idaho
Stand Data Set: tnf_veg
Contact: GIS Coordinator, J. Warrick
Fire Data Set: r420yrfirehis
Contact: D. Prevedel

Shoshone National Forest
Cody, Wyoming
Fire Data Set: shoshone_fires
Contact: GIS and GPS Coordinator, K. Ostrom

Grand Teton National Park
Moose, Wyoming

Data Set: Combined habitat and cover types for Grand Teton National Park
Contact: GIS Specialist, Grand Teton National Park

Yellowstone National Park
Spatial Analysis Center, YNP
Vegetation Data Set: Pre 1988 cover types of Yellowstone National Park; Post 1988 cover types of Yellowstone National Park
Fire Data Sets: Fire history perimeters of Yellowstone National Park; 1988 fire perimeter map of Yellowstone National Park
Contact: GIS Specialist, Spatial Analysis Center, A. Rodman

Ancillary Data

Data Set: Current condition class, version 2000
Originator: Fire Sciences Laboratory, Rocky Mountain Research Station
Missoula, Montana

Data Set: Historical natural fire regimes, version 2000
Originator: Fire Sciences Laboratory, Rocky Mountain Research Station
Missoula, Montana

Data Set: Digital Elevation Model (DEM) (also for derivation of aspect and slope)
Originator: U.S.G.S. EROS Data Center
Sioux Falls, South Dakota

APPENDIX B

VEGETATION CLASSIFICATION ACCURACY

1985 AND 1999 LEVEL 2,3,4 VEGETATION

For chapters 2 and 3, 1985 and 1999 vegetation were classified with classification tree analysis (CTA) at each of 3 hierarchical levels of classification. The error matrix for each classification accuracy assessment follows:

Table B.1. Error matrix for 1985 level 2 categorical vegetation classification.

Classified Data	Reference Data			Row total	Producer's accuracy (%)	User's accuracy (%)
	Conifer	Deciduous	Grass-Shrub			
Conifer	320	11	21	352	89	91
Deciduous	3	36	1	40	75	90
Grass-Shrub	36	1	39	76	64	51
Column total	359	48	61	468		
Overall accuracy = 395/468 = 84%						

Table B.2. Error matrix for 1985 level 3 categorical vegetation classification.

Classified Data	Reference Data				Row total	Producer's accuracy (%)	User's accuracy (%)
	MOG	Pole	Seed/sap	Woodland			
MOG	66	28	2	5	101	81	65
Pole	8	22	0	0	30	44	73
Seed/sap	0	0	30	4	34	61	88
Woodland	7	0	17	40	64	82	63
Column total	81	50	49	49	229		
Overall accuracy = 158/229 = 69%							
Note: abbreviations are as follows: MOG = mature/old-growth conifer; Pole = pole seral conifer; Seed/sap = seedling/sapling seral conifer; Woodland = conifer woodland							

Table B.3. Error matrix for 1985 level 4 categorical vegetation classification.

Classified Data	Reference Data			Row total	Producer's accuracy (%)	User's accuracy (%)
	Doug-fir	Mixed con	Whitebark			
Doug-fir	43	24	2	69	70	62
Mixed con	16	91	22	129	73	71
whitebark	2	10	26	38	52	68
Column total	61	125	50	236		
Overall accuracy = 160/236 = 68%						

Table B.4. Error matrix for 1999 level 2 categorical vegetation classification.

Classified Data	Reference Data			Row total	Producer's accuracy (%)	User's accuracy (%)
	Conifer	Deciduous	Grass-Shrub			
Conifer	397	11	14	422	90	94
Deciduous	7	31	1	39	69	79
Grass-Shrub	36	3	77	116	84	66
Column total	440	45	92	577		
Overall accuracy = 505/577 = 88%						

Table B.5. Error matrix for 1999 level 3 categorical vegetation classification.

Classified Data	Reference Data				Row total	Producer's accuracy (%)	User's accuracy (%)
	MOG	Pole	Seed/sap	Woodland			
MOG	80	23	10	8	121	86	66
Pole	9	28	0	1	38	52	74
Seed/sap	0	1	30	2	33	67	91
Woodland	4	2	5	38	49	78	78
Column total	93	54	45	49	241		
Overall accuracy = 176/241 = 73%							
Note: abbreviations are as follows: MOG = mature/old-growth conifer; Pole = pole seral conifer; Seed/sap = seedling/sapling seral conifer; Woodland = conifer woodland							

Table B.6. Error matrix for 1999 level 4 categorical vegetation classification.

Classified Data	Reference Data			Row total	Producer's accuracy (%)	User's accuracy (%)
	Doug-fir	Mixed con	Whitebark			
Doug-fir	44	23	0	67	69	66
Mixed con	18	90	24	132	73	68
Whitebark	2	10	26	38	52	68
Column total	64	123	50	237		
Overall accuracy = 160/237 = 68%						