Ecosystems (2007)
DOI: 10.1007/s10021-007-9023-1

ECOSYSTEMS

Conifer Cover Increase in the Greater Yellowstone Ecosystem: Frequency, Rates, and Spatial Variation

Scott L. Powell,[1,2,*] and Andrew J. Hansen[1]

[1]*Department of Ecology, Montana State University, Bozeman, Montana 59717-3460, USA;* [2]*Pacific Northwest Research Station, Corvallis Forestry Sciences Laboratory, USDA Forest Service, Corvallis, Oregon 97331, USA*

ABSTRACT

Extensive fires in recent decades in the Greater Yellowstone Ecosystem (GYE) garnered much attention for causing a significant decrease in the extent of conifer forest cover. Meanwhile, conifer forests in unburned parts of the GYE have continued to increase in extent and density. Conifer cover increase has been well documented by repeat historical photography, but the average rate of increase and the spatial variation remain unquantified. We examined changes in conifer cover across biophysical gradients in the GYE based on stratified random samples from aerial photographs. The percent conifer cover for samples in 1971 and 1999 was quantified to determine the frequency and rate of conifer cover change. A slight majority of samples (56%) showed no change, whereas increases (22%) were balanced by decreases (22%). However, among samples that were not recently burned or logged, or already closed-canopy, nearly 40% increased in conifer cover, at an average annual rate of 0.22%. We quantified significant variability in the frequency and rate of conifer cover increase across gradients of elevation, aspect, vegetation type, and proximity to nearby conifer forest. The most dynamic locations were low density conifer woodlands on northerly aspects at lower elevations, with average annual rates of increase up to 0.51%. This study is significant because it demonstrates that rates of conifer cover increase vary across biophysical gradients, an important consideration for management of dynamic forest ecosystems. Improved understanding of this variability helps us to better understand what factors ultimately cause conifer cover increase. It is also a critical step towards accurate quantification of the magnitude of carbon uptake by conifer cover increase.

Key words: Yellowstone; conifer expansion; biophysical factors; forest dynamics; conifer cover; aerial photos.

INTRODUCTION

Conifer forest dynamics in the Greater Yellowstone Ecosystem (GYE) have been well documented, especially in the wake of the widespread fires of 1988 (Romme and Despain 1989). Conspicuous forest disturbances, like fires and logging, have quantifiable effects on the extent of forest cover (Parmenter and others 2003). In contrast to these dynamics, more subtle changes in forest cover associated with succession are occurring across vast areas, but present a greater challenge for regional quantification. Critical uncertainties remain, therefore, in our knowledge of how widespread these changes are relative to forest disturbance, and to what biophysical factors these changes are related.

Received 31 May 2005; accepted 23 August 2006

**Corresponding author; e-mail:* scottpowell@fs.fed.us

As in the GYE, in many other regions throughout the world, woody vegetation is increasing in extent and density. This process has been referred to by a variety of names including expansion (Knapp and Soulé 1998), encroachment (Arno and Gruell 1986), invasion (Mast and others 1997), density increases (Turner and Krannitz 2001), treeline advance (Rupp and others 2001), afforestation (Soulé and others 2003), thicketization (Archer and others 1995), and densification (Kullman and Engelmark 1997). In the GYE, these changes have been widely 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 and others 1997). In this paper, we collectively refer to both these processes (conifer expansion into adjacent non-forested areas and the in-filling, or densification of conifer woodlands) as conifer cover increase.

In some locations, steep abiotic gradients and stable ecotones between conifer forest and non-forest suggest that edaphic and topographic factors are responsible for the long-term maintenance of vegetation boundaries (Loope and Gruell 1973). In many other locations, however, boundaries between conifer forest and non-forest are dynamic, and research suggests that ecotones are governed by changes in climate (Jakubos and Romme 1993), atmospheric composition (Soulé and others 2003), fire regimes (Arno and Gruell 1986), or grazing regimes (Richardson and Bond 1991). Here, we lay out the results of a systematic study to determine the frequency, rate, and spatial variation of conifer cover increase across biophysical gradients 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.

For a broader context, we analyze both conifer cover increase as well as decrease, to cast light on their relative importance across the GYE. The ultimate goal of this study, however, is to specifically quantify the dynamics of conifer cover increase not associated with regeneration following fire, logging, or other stand replacement disturbance. Previous studies have focused on forest regeneration following fire (Turner and others 1997), logging (Barbour and others 1998), agricultural abandonment (Brown 2003), and other disturbances such as volcanic eruptions (Lawrence and Ripple 2000). For this reason, we have chosen to exclude from some of our analyses 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 large portion of North America that is experiencing rapid change in the structure and composition of forests, grasslands, and shrublands.

Although 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 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 and others 2003). These results from a single watershed raise questions about the overall frequency and rate of conifer cover increase across the 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 and others 2000; Pacala and others 2001). To the contrary, we hypothesize that conifer cover increase is occurring at highly variable rates across biophysical gradients. Biophysical gradients potentially govern the spatial variability of conifer cover increase by influencing important demographic processes such as reproduction, seedling establishment, growth, and survival. Where conditions are most favorable for these processes, we predict widespread and rapid conifer cover increase.

A key biophysical factor that potentially regulates the frequency and rate of conifer cover increase is soil moisture. Plant available soil moisture is 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.

We hypothesize, therefore, that elevation and aspect are strongly correlated to the distribution of conifer cover increase. A commonly held notion in the northern Rocky Mountains is that lower elevation forests are moisture limited whereas higher elevation forests are temperature limited (Daubenmire 1943, 1968). We hypothesize, therefore, that at lower elevations, conifer cover increase is more widespread and rapid on moister northerly aspects. Conversely, we hypothesize that at higher elevations, conifer cover increase is more widespread and rapid on warmer southerly aspects.

The surrounding vegetation also potentially governs the frequency and rate of conifer cover increase. Apart from influencing soil moisture conditions, the surrounding vegetation also governs competition. Furthermore, the proximity to a seed source has the potential to directly limit the places on the landscape where cover increase can occur. We hypothesize, therefore, that conifer cover increase is more widespread and rapid in conifer woodlands, than in grasslands–shrublands, or higher density conifer forest. We further hypothesize that the frequency and rate of conifer cover increase decline with increasing distance from conifer forest.

The specific objectives of this study, therefore, were first to determine the overall frequency of conifer cover changes across the GYE, second to determine the rate of conifer cover increase, and third to determine the spatial variability in the frequency and rate of conifer cover increase across biophysical gradients. By quantifying this underlying spatial variability, we hope to improve understanding of the drivers of conifer cover increase. Changes in climate, atmospheric composition, fire regimes, and grazing regimes are hypothesized influences over conifer cover increase. These mechanisms are themselves influenced by biophysical gradients, therefore, characterizing variability in the frequency and rate of conifer cover increase casts light on their relative importance.

METHODS

Study Area

The 67,156 km^2 study area is located within the GYE, encompassing parts of Montana, Wyoming, and Idaho (Figure 1). The boundary of the study area represents the intersection of a Landsat satellite path with the GYE boundary as defined by Parmenter and others (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 more nutrient-rich andesites. Lower elevation soils off the plateau consist primarily of nutrient-rich glacial outwash and alluvium. The climate of the GYE varies considerably by elevation, latitude, and longitude, but is generally characterized by short growing seasons and cold winters. Climate severity generally increases with elevation across the study area. Mean annual temperature on the Yellowstone plateau at Old Faithful, WY (elevation ~2,225 m) varies between −7.6 and 9.6°C. Annual precipitation at Old Faithful averages 61.7 cm, with 548.4 cm of snowfall. In comparison, in a low-elevation valley at Bozeman, MT (elevation ~1,463 m), mean annual temperature varies between −0.5 and 12.8°C. Annual precipitation at Bozeman averages 46.4 cm, with 216.7 cm of snowfall.

Steep abiotic gradients strongly influence land use and disturbance regimes, and hence shape the distribution of vegetation types (Hansen and others 2000). Gross vegetation patterns in the GYE have been well documented (Despain 1990), as have land use patterns (Parmenter and others 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 and others 2003; Hernandez 2004). Upslope, there is an ecotone between non-forest and low-density conifer woodlands. Lower elevation conifer woodlands are composed primarily of Douglas-fir (*Pseudotsuga menziesii*), Rocky Mountain juniper (*Juniperus scopulorum*), and lodgepole pine (*Pinus contorta*), but ponderosa pine (*Pinus ponderosa*) and limber pine (*Pinus flexilis*) are also found in some locations. 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. Further upslope, woodlands grade into higher density, mesic conifer forests, composed primarily of Douglas-fir, lodgepole pine,

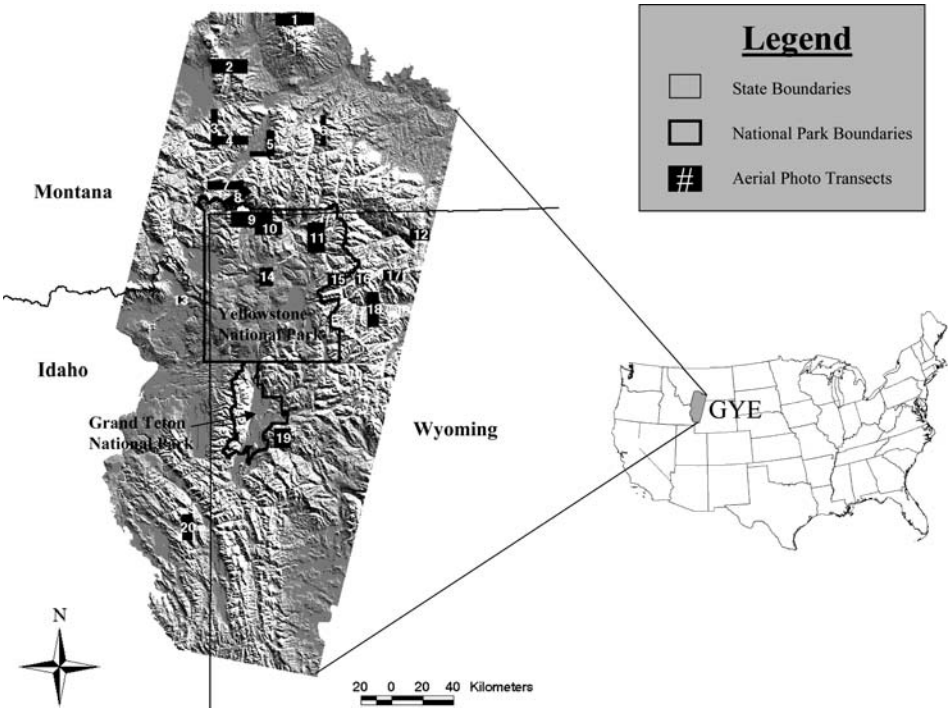

Figure 1. The 67,156 km^2 study area within the GYE is shown with aerial photo transect locations. Numbers correspond to transect names in Figure 3.

engelmann spruce *(Picea engelmannii)*, and subalpine fir (*Abies lasiocarpa*). These subalpine forests are historically characterized by infrequent, high-intensity fire regimes (Romme 1982; Romme and Despain 1989), and have likely been less impacted by fire suppression (Turner and others 2003). Higher elevation conifer forests, composed primarily of lodgepole pine, engelmann spruce, subalpine fir, and whitebark pine (*Pinus albicaulis*), 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

We 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. We determined the overall percentage of samples with conifer cover change and the overall rate of change for samples with cover increase. We then characterized the variability in the frequency and rate of conifer cover increase using 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 1). The transects were variable in length and width, but each one was 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 (coniferous, hardwood, and herbaceous as determined from National Forest Service and National Park Service vegetation maps), elevation (above and below 2,316 m), and aspect (northerly and southerly). The 2,316 m elevation break corresponds roughly to the level of Yellowstone‘s central plateau, which is distinctive from its surroundings. This elevation break also corresponds to the upper elevation limit of Douglas-fir communities and the lower elevation limit of whitebark pine communities. A plot was sampled if it did not share an edge with another plot and it did not contain obvious rock outcroppings. We only sampled plots that were located away from the edges of an aerial photo, to minimize the effects of distortion. The aerial photos used for this study were color, or color infrared, at 1:15,840, 1:24,000, or 1:30,000 scales. Sample plots were appropriately scaled to match photo scales. For each transect, we acquired photos as closely as possible to the years 1971 and 1999, to match previously acquired satellite imagery for a related study, and to capture the availability of high-quality color aerial photos.

Sample plots were accurately located using Landsat imagery as an initial guide, and then matching the identical location in subsequent photo years. For each time period, we determined the fractional composition of coniferous forest and grassland–shrubland using the point intercept method (Parmenter and others 2003), whereby we overlayed a 10-dot matrix on a plot and tallied intersections with vegetation components in 10% increments (for example, 3 dots on conifer and 7 dots on grassland-shrubland was 30% conifer/70% grassland–shrubland). For the purposes of this study, we analyzed the percent composition of conifer (relative to grassland–shrubland) as the key response variable. Positive change in percent composition of conifer was classified as conifer cover increase. We separated conifer cover increase into two categories, depending upon the starting conifer cover. If 1971 conifer cover was zero, we called the increase conifer expansion. If 1971 conifer cover was greater than zero, we called the increase conifer densification. Negative change in percent composition of conifer was classified as conifer cover decrease. We separated conifer cover decrease into three categories (burn, harvest, and other decrease) based upon photo interpretation.

To determine the frequency of conifer cover change in the GYE, we analyzed the change in percent conifer composition between 1971 and 1999. The frequency of conifer cover change for each category was calculated as the percentage of samples that exhibited a change in conifer cover between 1971 and 1999. To calculate the frequency of conifer cover increase in recently undisturbed samples, we excluded from our calculations samples that contained any evidence of prior disturbance from fire or logging. Further, to focus our analysis on samples where cover increase was even a possibility, we excluded samples that were not ‘‘eligible‘‘ for increase; that is, in 1971 they already had a 100% closed conifer canopy. The rate of conifer cover increase was calculated as the total change per sample (for example, 10–30% = 20% change) divided by the number of years between measurements.

To determine the variability in frequency and rate of conifer cover increase, we analyzed transect location, biophysical setting, vegetation type, and distance to nearest conifer. For vegetation type, we used the 1971 aerial photo vegetation interpretation, reclassified as either conifer forest (>70% conifer cover), conifer woodland (10–70% conifer cover), or grassland–shrubland (<10% conifer cover). The biophysical setting was partitioned into classes of elevation and solar aspect corresponding to topographic and vegetative gradients. The distance to nearest conifer was computed as the Euclidean distance to the nearest pixel containing at least 30% conifer cover according to the 1985 land cover map derived by Parmenter and others (2003). We used Chi-square analysis to compare observed frequencies of conifer cover increase to expected frequencies by biophysical setting, vegetation type, and distance to nearest conifer. Expected frequencies were calculated according to the proportional sample size for a given category. We also calculated 95% family-wise confidence intervals using the Bonferonni alpha correction for multiple comparisons of both rates and frequencies.

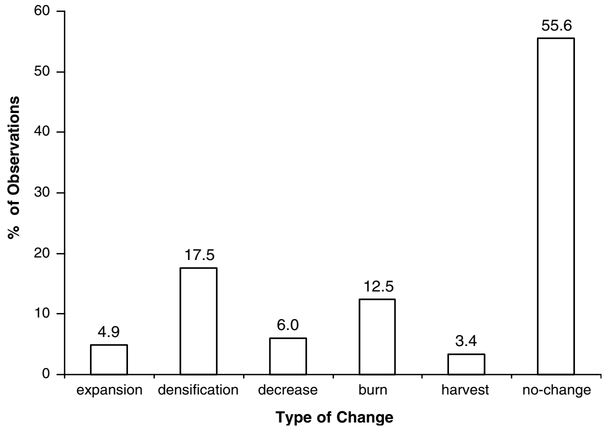

Figure 2. Frequency of conifer cover change by change category.

Results

From our entire sample of 2,144 locations across the GYE, conifer cover change between 1971 and 1999 was observed in nearly half of the samples (Figure 2). Samples with conifer cover increase (22.4%) occurred with nearly equal frequency to samples with conifer cover decrease (21.9%). Conifer densification (17.5%) was the most frequent change, followed by fire (12.5%).

In samples that were not recently burned or logged, and were eligible for cover increase, the frequency of conifer cover increase between 1971 and 1999 was 38.3%. The rate of conifer cover increase over this time period 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 frequency and rate of conifer cover increase varied among sampling transects (Figure 3). 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

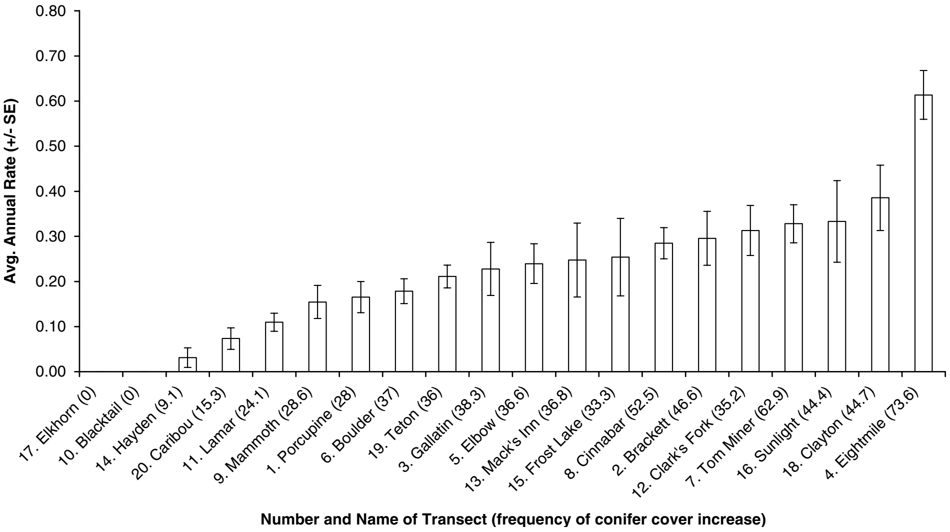

Figure 3. Average annual rate of conifer cover increase between 1971 and 1999, by aerial photo transect. Preceding numbers correspond to transect locations in Figure 1. Numbers in parentheses are the frequencies of conifer cover increase.

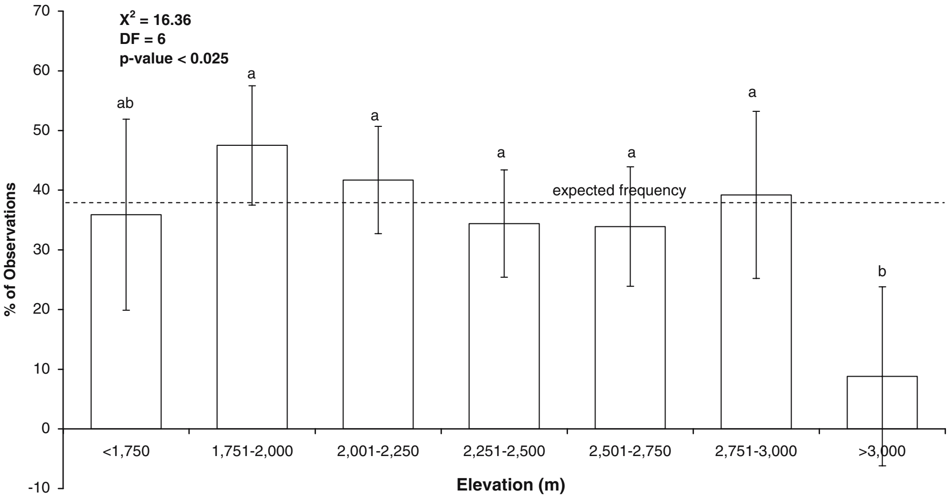

Figure 4. Frequency of conifer cover increase by elevation class. *Dashed line* represents the expected frequency. The Chi-square statistic is reported at the *top left* along with its corresponding *p*-value. Frequencies are shown with Bonferonni corrected 95% confidence intervals. Frequencies with the same letter do not differ significantly.

cover increase over 50%. Of the six lowest ranked transects in terms of rate of conifer cover increase, three were within YNP. Only the Frost Lake transect in YNP exhibited a rate of conifer cover increase above the GYE mean.

The frequency and rate of conifer cover increase varied significantly across the elevation gradient. The frequency of conifer cover increase was significantly lower for samples above 3,000 m than for samples between 1,751 and 3,000 m (Figure 4). Above 3,000 m only 9% of samples exhibited conifer cover increase, compared to 48% of samples between 1,751 and 2,000 m. The rate of conifer cover increase was also significantly lower for samples above 3,000 m than for samples between 1,751 and 2,250 m (Table 1).

There were no significant differences in observed versus expected frequencies of conifer cover increase by solar aspect class (Figure 5). Likewise, the average annual rate of conifer cover increase was relatively constant across solar aspect classes (Table 1).

Accounting for the interactive effect of elevation and solar aspect revealed a significantly higher frequency of conifer cover increase for lower elevation plots on northerly aspects compared to higher elevation plots on northerly aspects (Figure 6). 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%. The rates of conifer cover increase were also significantly higher for lower elevation, northerly aspect samples than for higher elevation, northerly aspect samples (Table 1).

The surrounding vegetation also accounted for significant variability in the frequency and rate of conifer cover increase. The observed frequencies of conifer cover increase by vegetation type were

Table 1. Average Annual Rate of Conifer Cover Increase by Biophysical Factor

Variable	Category	Rate	SE	Diff
Elevation (m)	<1,750	0.25	0.05	ab
	1,751–2,000	0.32	0.03	a
	2,001–2,250	0.25	0.02	a
	2,251–2,500	0.20	0.02	ab
	2,501–2,750	0.19	0.02	ab
	2,751–3,000	0.25	0.03	ab
	>3,000	0.06	0.04	b
Aspect	Northeast	0.26	0.02	a
	Southeast	0.27	0.02	a
	Southwest	0.24	0.02	a
	Northwest	0.23	0.02	a
Aspect/Elevation	North, low	0.32	0.02	a
	South, low	0.24	0.02	ab
	North, high	0.20	0.02	b
	South, high	0.22	0.02	ab
Vegetation Type	Conifer forest	0.21	0.02	a
	Conifer woodland	0.35	0.02	b
	Grassland–shrubland	0.10	0.02	c
Conifer Distance (m)	0	0.27	0.01	a
	1–30	0.24	0.02	ab
	31–60	0.27	0.05	ab
	61–90	0.30	0.07	abc
	91–120	0.08	0.04	bc
	121–150	0.15	0.06	abc
	151–180	0.15	0.08	abc
	>180	0.05	0.02	c
Vegetation, Elevation, Aspect	Woodland, high, north	0.28	0.03	abe
	Woodland, high, south	0.26	0.03	ae
	Woodland, low, north	0.51	0.04	b
	Woodland, low, south	0.35	0.03	ab
	Forest, high, north	0.17	0.03	ad
	Forest, high, south	0.28	0.05	abe
	Forest, low, north	0.22	0.03	ae
	Forest, low, south	0.18	0.03	ad
	Grass–shrub, high, north	0.01	0.01	c
	Grass–shrub, high, south	0.03	0.02	cd
	Grass–shrub, low, north	0.17	0.04	acd
	Grass–shrub, low, south	0.09	0.03	cde

Significant differences are calculated based on Bonferonni corrected 95% confidence intervals. Rates with the same letter do not differ significantly.

significantly different than expected (Figure 7). Conifer woodlands exhibited conifer cover increase in 51% of the samples, compared to only 13% in grasslands–shrublands. Low-density conifer woodlands also exhibited conifer cover increase at a significantly higher rate than other vegetation types, whereas grasslands–shrublands had a significantly lower rate of conifer cover increase than other vegetation types (Table 1).

The proximity to the nearest conifer stand strongly influenced the frequency and rate of conifer cover increase. 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 8). At distances between 31 and 60 m, 47% of samples exhibited conifer cover increase, whereas for distances greater than 180 m, only 11% of samples exhibited conifer cover increase. The average annual rate of increase generally declined as the distance to the nearest conifer stand increased (Table 1). For distances greater than 180 m, the rate of conifer cover increase was significantly lower than for distances less than 60 m.

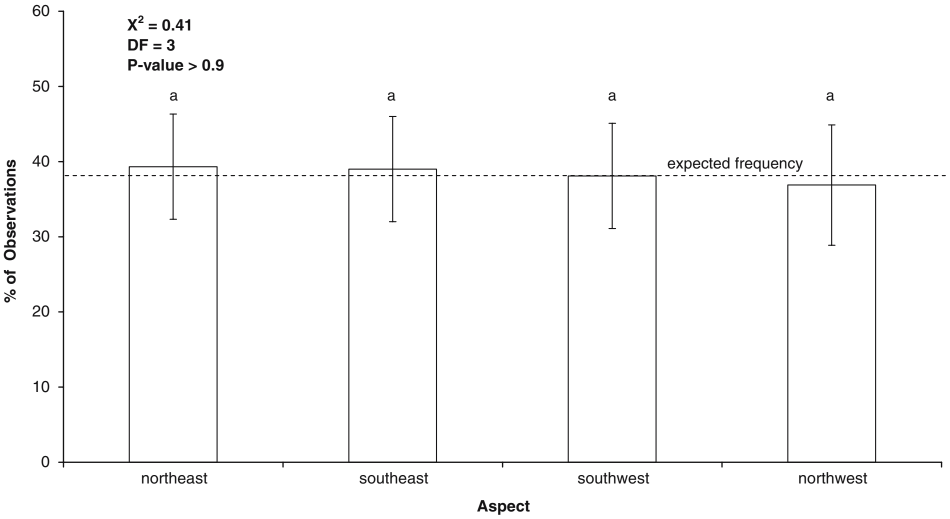

Figure 5. Frequency of conifer cover increase by solar aspect class. *Dashed line* represents the expected frequency. The Chi-square statistic is reported at the *top left* along with its corresponding *p*-value. Frequencies are shown with Bonferonni corrected 95% confidence intervals. Frequencies with the same letter do not differ significantly. Northeast = 1°–90°; Southeast = 91°–180°; Southwest = 181°–270°; Northwest = 271°–360°.

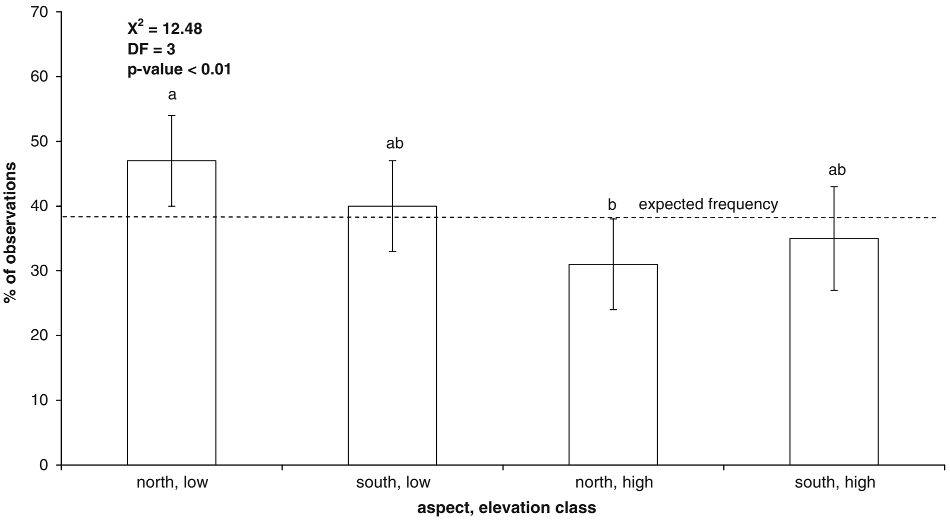

Figure 6. Frequency of conifer cover increase by elevation, aspect class. *Dashed line* represents the expected frequency. The Chi-square statistic is reported at the *top left* along with its corresponding *p*-value. Frequencies are shown with Bonferonni corrected 95% confidence intervals. Frequencies with the same letter do not differ significantly. Low elevation < 2,316 m < High elevation; Northerly Aspects = 271°–90°; Southerly Aspects = 91°–270°.

Finally, the interaction between vegetation type and biophysical setting accounted for significant variability in the frequency and rate of conifer cover increase. The observed frequencies of conifer cover increase by vegetation type, elevation, and aspect strata were significantly different than expected (Figure 9). 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. The rate of conifer cover increase was significantly higher for lower elevation, northerly aspect conifer woodlands than for all grassland–shrubland strata (Table 1).

DISCUSSION

Conifer cover change was widespread across the GYE during the period 1971–1999, occurring in nearly half of all samples. Although the high frequency in the decrease of conifer cover associated with fires and other forest disturbances was expected, the nearly equal frequency of conifer cover increase was highly revealing. In samples that were not recently burned or logged, and were not already closed canopy, conifer cover increase was

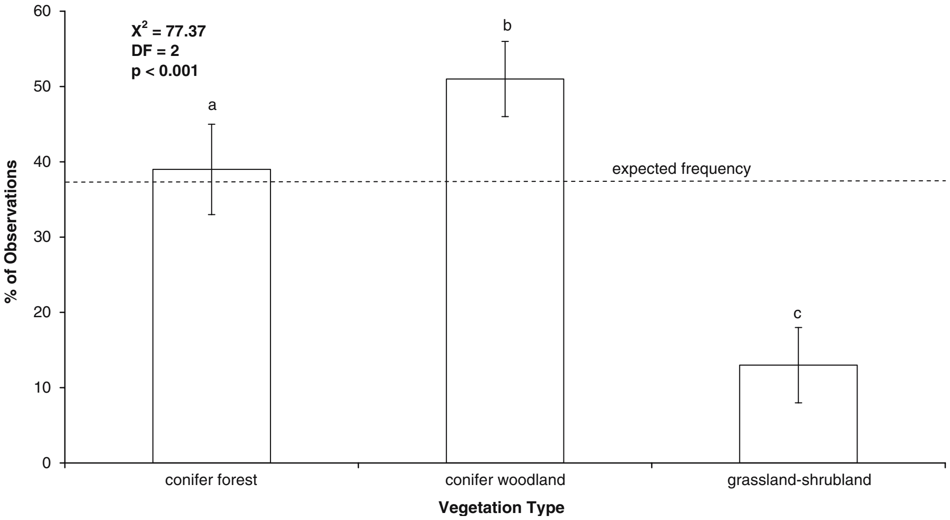

Figure 7. Frequency of conifer cover increase by vegetation type. *Dashed line* represents the expected frequency. The Chi-square statistic is reported at the *top left* along with its corresponding *p*-value. Frequencies are shown with Bonferonni corrected 95% confidence intervals. Frequencies with the same letter do not differ significantly.

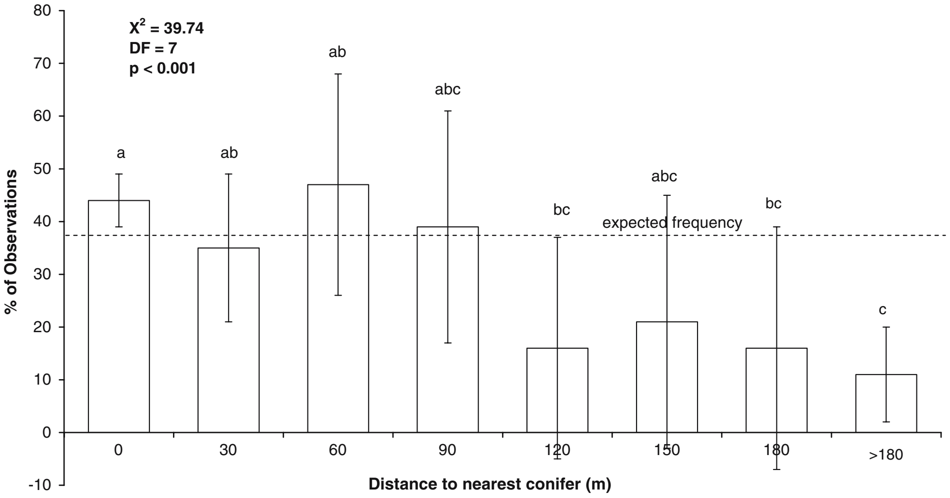

Figure 8. Frequency of conifer cover increase by distance to nearest conifer stand. *Dashed line* represents the expected frequency. The Chi-square statistic is reported at the *top left* along with its corresponding *p*-value. Frequencies are shown with Bonferonni corrected 95% confidence intervals. Frequencies with the same letter do not differ significantly.

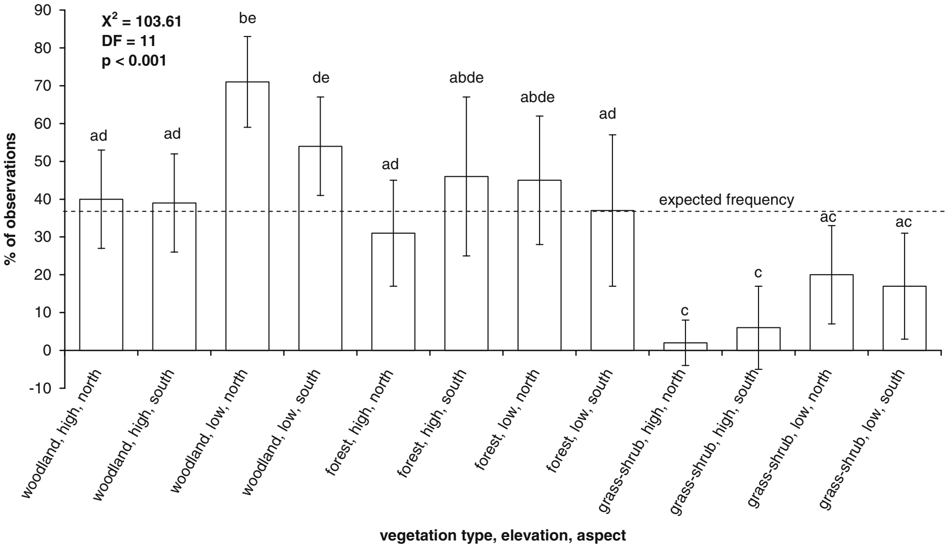

Figure 9. Frequency of conifer cover increase by vegetation type, elevation, and aspect. *Dashed line* represents the expected frequency. The Chi-square statistic is reported at the *top left* along with its corresponding *p*-value. Frequencies are shown with Bonferonni corrected 95% confidence intervals. Frequencies with the same letter do not differ significantly.

common across the GYE during the period 1971–1999, occurring in nearly 40% of samples, at an average annual rate of 0.22%. These results strongly suggest that the structure and composition of conifer forests and conifer–grassland ecotones in the GYE are rapidly changing through a host of dynamic processes, both conspicuous and subtle.

Our measures of conifer cover increase are generally consistent with other studies, but are difficult to compare directly because of methodological differences. The one study that we know of from the GYE that documented the rate of increase in conifer forests over time was from a single watershed in the Centennial Mountains west of Yellowstone National Park (Gallant and others 2003). There, researchers simulated a 0.26% average annual rate of increase in conifer forest cover over 140 years. This is consistent with our GYE-wide estimate of a 0.22% average annual rate of conifer cover increase over 28 years. Our 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 and others 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 areas, rather than across a wide range of biophysical settings. In comparison, the rates of conifer cover increase for the fastest changing settings in our study were over 0.50% per year.

Although 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. Approximately 60% of all eligible samples that were not recently burned or logged did not increase in conifer cover between 1971 and 1999. We 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 our prediction that conifer cover increase was not occurring uniformly across the region, but rather only in certain locations and at highly variable rates. This prompted us to examine which aspects of the biophysical environment influenced the variability of conifer cover increase.

We expected that elevation and aspect, as proxies for temperature, precipitation, solar radiation, and evaporative demand, would associate strongly with the frequency and rate of cover increase, but we were surprised that neither variable alone was strongly related. Although the highest frequency and rate of conifer cover increase were observed at lower elevations, the trend across elevation classes was inconsistent, suggesting that temperature and precipitation alone were not highly limiting factors for conifer cover increase. We did, however, observe a threshold drop in frequency above 3,000 m, as samples were five 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 possible explanations for this pattern. Conversely, more favorable temperatures and longer growing seasons at lower elevations potentially explain the higher rate of conifer cover increase between 1,751 and 2,000 m. Contrary to our 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 in itself 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 and others 1997). As noted earlier, however, this result likely reflects the narrower range of biophysical settings considered in this study, compared to ours.

The interactive effect of elevation and aspect strongly influences plant available moisture conditions. In the GYE, 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 of biophysical settings across the study area, elevation and aspect combined were strongly associated with the frequency and rate of conifer cover increase in the GYE. Northerly aspects at lower elevations exhibited more frequent and rapid conifer cover increase than northerly aspects at higher elevations. This result potentially underscores the importance of adequate moisture conditions at lower elevations, compared to less favorable conditions at higher elevations, where conifer establishment, growth, and survival are potentially limited by colder temperatures and excessive moisture.

Although broad moisture and temperature gradients are important factors, variability in the frequency and rate of conifer cover increase are also significantly associated with local site factors, such as the surrounding vegetation. The rate of conifer cover increase was significantly higher in conifer woodlands than in either conifer forests or grasslands–shrublands. In fact, densification of conifer woodlands occurred in more than 50% of all eligible sites, although expansion of conifers into nearby grassland–shrubland occurred on only 13% of sites. This result potentially demonstrates the importance of proximity to conifer forest for seed availability and site amelioration. Nearby forest provides shade that improves soil moisture conditions, buffer from the elements, and protection from browsing and trampling, all increasing the probability of seedling survival and enhancing growth (Sindelar 1971). The significant difference in frequency of increase between conifer woodlands versus conifer forests suggests that as the canopy nears closure, light, nutrients, and water become limiting for understory seedlings and saplings. Lower density conifer woodlands are therefore more likely to exhibit conifer cover increase than higher density conifer forests.

Apart from the type of surrounding vegetation, the actual proximity to conifer forest explained a significant amount of variation in the frequency and rate of conifer cover increase. Within the 28-year span of observations, conifer cover increase was more than four times 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). Further, if conditions are suitable for continued reproduction, seedling establishment, growth, and survival, the number of individuals increases and seed sources become abundant, fostering a biological inertia (Knapp and Soulé 1998).

Implications for Determinants of Conifer Cover Increase

Although this study did not directly examine the underlying causes of conifer cover increase in the GYE (changes in climate, atmospheric composition, fire regimes, and grazing regimes), it did examine the biophysical patterns of cover increase. These patterns offer insight into how conifer reproduction, seedling establishment, growth, and survival might be influenced by the underlying causes of conifer cover increase. Climate variability directly influences the physical conditions of a site, rendering soil moisture more or less favorable for conifer seedling establishment (Jakubos and Romme 1993; Patten 1963). Research indicates that on sites susceptible to drought, conifer cover increase is likely triggered by cooler and wetter conditions, whereas 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 been hypothesized to improve water use efficiency in plants (Romme and Turner 1991; Soulé and others 2003). Improved water use efficiency potentially has the effect of extending the range of a species into warmer and drier locations than where it presently occurs (Graham and others 1990). Fire suppression (Arno and Gruell 1986) and grazing (Richardson and Bond 1991) directly influence growth and survival of conifers. Fire suppression removes a direct source of conifer mortality, allowing vegetation succession to proceed unchecked (Sindelar 1971). Grazing, by reducing fine fuels, is a de facto form of fire suppression (Butler 1986). At high grazing levels, however, trampling of conifer seedlings is a direct source of mortality, whereas at intermediate levels, grazing influences the competitive balance between conifers and other life-forms.

Spatial variability in the frequency and rate of conifer cover increase suggests multiple drivers of change in forest structure and composition. Human land use impacts and natural disturbance regimes are considerably different in lower elevation forests than in 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, 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 more widespread and rapid in cooler, moister locations. Much longer fire return intervals and less intense land use in higher elevation forests of the GYE have rendered a greatly reduced impact of fire suppression and grazing on forest structure and composition. Higher elevation conifer cover increase is potentially driven by climate variability, and to a lesser extent by fire suppression and grazing regimes, and is more widespread and rapid in warmer, drier locations.

Limitations and Scope

Few previous studies have attempted to answer fundamental questions about the frequency, rate, and spatial variation of conifer cover increase across regions as large and complex as the GYE. Other studies on this subject have dealt with smaller areas, encompassing a narrower range of biophysical conditions. The limitations to a study such as ours include the difficulty of obtaining accurate spatial datasets. For example, variables such as plant available soil moisture are difficult to measure over large areas and long time frames. Despite the use of coarse-scaled proxies, and largely univariate analyses, we have shed light on a widespread, but poorly quantified issue. Due to the correlational nature of this study, we have not explicitly examined the factors that cause conifer cover increase, but we have taken considerable steps towards interpreting the biophysical footprint of the phenomenon. Despite these caveats, we have presented a method for quantifying the frequency, rate, and spatial variation of conifer cover increase over a large region. This study, therefore, lays the groundwork for further study of the mechanisms that underlay the patterns.

Research and Management Implications

Forest research and management in the GYE have historically focused on the effects of stand replacement disturbances like fire and logging. Although these conspicuous disturbances continue to be widespread across the GYE, more subtle changes are occurring in the opposite direction that at least partially mitigate the loss of conifer forest cover. The ultimate consequences of the widespread and rapid changes brought about by conifer cover increase in the GYE remain unknown and require additional research. Potential consequences span from biogeochemical cycling (Houghton and others 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 the expanding conifer forests of the region. The magnitude of such a sink, however, remains a question, and accurate quantification hinges upon consideration of biophysical variability. This study, therefore, lays the foundation for determining the full extent of conifer cover increase across the GYE, and the consequent magnitude of carbon sequestration. Studies from other regions suggest that conifer cover increase leads to fuel accumulation, potentially altering fire behavior (Allen and others 2002). This might result in higher intensity fire and the loss of stored carbon. Further research is required to better understand the relationships between conifer cover increase, fuel accumulation, fire behavior, and carbon storage.

ACKNOWLEDGMENTS

We thank the NASA Land Cover Land Use Change Program for funding this study. We also thank Jeremy Lougee, Nick Lyman, Lew Stringer, and Jason Bruggeman for aerial photo interpretation in support of this study. Special thanks to Monica Turner and her support from NSF for use of aerial photos for Yellowstone National Park. We also thank Lisa Graumlich, Rick Lawrence, Jay Rotella, and three anonymous reviewers for their thoughtful comments on manuscript drafts.

REFERENCES

Allen CD, Savage M, Falk DA, Suckling KF, Swetnam TW, Schulke T, Stacey PB, Morgan P, Hoffman M, Klingel JT. 2002. Ecological restoration of southwestern ponderosa pine ecosystems: a broad perspective. Ecol Appl 12:1418–33.

Archer S, Schimel DS, Holland EA. 1995. Mechanisms of shrubland expansion–land-use, climate, or CO_2. Climatic Change 29:91–9.

Arno SF, Brown JK. 1989. Managing fire in our forests–time for a new initiative. J Forestry 87:44–6.

Arno SF, Gruell GE. 1983. Fire history at the forest–grassland ecotone in southwestern Montana. J Range Manage 36:332–6.

Arno SF, Gruell GE. 1986. Douglas-fir encroachment into mountain grasslands in southwestern Montana. J Range Manage 39:272–5.

Arno SF, Smith HY, Krebs MA. 1997. Old growth ponderosa pine and western larch stand structures: influences of pre-1900 fires and fire exclusion. Research Paper INT-RP-495. USDA Forest Service Intermountain Research Station.

Barbour MG, Fernau RF, Benayas JMR, Jurjavcic N, Royce EB. 1998. Tree regeneration following clearcut logging in red fir forests of California. Forest Ecol Manage 104:101–1.

Barrett SW, Arno SF. 1982. Indian fires as an ecological influence in the northern Rockies. J Forestry 80:647–51.

Brown DG. 2003. Landuse and forest cover on private parcels in the Upper Midwest, USA, 1970 to 1990. Landscape Ecol 18:777–90.

Butler DR. 1986. Conifer invasion of subalpine meadows, central Lemhi Mountains, Idaho. Northwest Sci 60:166–73.

Dando LM, Hansen KJ. 1990. Tree invasion into a range environment near Butte, Montana. Great Plains-Rocky Mountain Geograph J 18:65–76.

Daubenmire RF. 1943. Soil temperature versus drought as a factor determining lower altitudinal limits of trees in the Rocky Mountains. Botanical Gazette 105:1–13.

Daubenmire RF. 1968. Soil moisture in relation to vegetation distribution in the mountains of northern Idaho. Ecology 49:431–8.

Despain DG. 1990. Yellowstone Vegetation. Boulder: Roberts Rinehart: Consequences of environment and history in a natural setting, p 239.

Gallant AL, Hansen AJ, Councilman JS, Monte DK, Betz DW. 2003. Vegetation dynamics under fire exclusion and logging in a Rocky Mountain watershed: 1856–1996. Ecol Appl 13:385–403.

Graham RL, Turner MG, Dale VH. 1990. How increasing CO$_2$ and climate change affect forests. BioScience 40:575–87.

Gruell GE. 1983. Fire and vegetative trends in the northern Rockies: interpretations from 1871–1982. Gen. Tech. Rep. INT-158. USDA Forest Service Intermountain Forest and Range Exp. Station.

Hansen AJ, Rotella JJ, Kraska MPV, Brown D. 2000. Spatial patterns of primary productivity in the Greater Yellowstone Ecosystem. Landscape Ecol 15:505–22.

Hernandez P. 2004. Demographic change in the new west: Exurban development around nature reserves [thesis]. Bozeman (MT): Montana State University. 164p.

Houghton RA, Hackler JL, Lawrence KT. 2000. Changes in terrestrial carbon storage in the United States. 2: The role of fire and fire management. Global Ecol Biogeography 9:145–70.

Houston DB. 1973. Wildfires in northern Yellowstone National Park. Ecology 54:1111–7.

Jakubos B, Romme WH. 1993. Invasion of subalpine meadows by lodgepole pine in Yellowstone National Park, Wyoming, USA. Artic Alpine Res 25:382–90.

Knapp PA, Soulé PT. 1998. Recent *Juniperus occidentalis* (Western Juniper) expansion on a protected site in central Oregon. Global Change Biol 4:347–57.

Kullman L, Engelmark O. 1997. Neoglacial climate control of subarctic *Picea abies* stand dynamics and range limit in northern Sweden. Arctic Alpine Res 29:315–26.

Lawrence RL, Ripple WJ. 2000. Fifteen years of revegetation of Mount St. Helens: a landscape-scale analysis. Ecology 81:2742–52.

Littell JS. 2002. Determinants of fire regime variability in lower elevation forests of the northern Greater Yellowstone Ecosystem [thesis]. Bozeman (MT): Montana State University. 122p.

Loope LL, Gruell GE. 1973. The ecological role of fire in the Jackson Hole area, northwestern Wyoming. Quart Res 3:425–43.

Mast JN, Veblen TT, Hodgson ME. 1997. Tree invasion within a pine/grassland ecotone: an approach with historic aerial photography and GIS modeling. Forest Ecol Manage 93:181–94.

Meagher M, Houston DB. 1998. Yellowstone and the biology of time: photographs across a century. Norman: University of Oklahoma Press, p 287.

Miller EA, Halpern CB. 1998. Effects of environment and grazing disturbance on tree establishment in meadows of the central Cascade Range, Oregon, USA. J Vegetat Sci 9:265–82.

Pacala SW, Hurtt GC, Baker D, Peylin P, Houghton RA, Birdsey RA, Heath L, Sundquist ET, Stallard RF, Ciais P, Moorcroft P, Caspersen JP, Shevliakova E, Moore B, Kohlmaier G, Holland E, Gloor M, Harmon ME, Fan S, Sarmiento JL, Goodale CL, Schimel D, Field CB. 2001. Consistent land- and atmosphere-based U.S carbon sink estimates. Science 292:2316–20.

Parmenter AP, Hansen AJ, Kennedy R, Cohen W, Langner U, Lawrence RL, Maxwell B, Gallant A, Aspinall R. 2003. Land use and land cover change in the Greater Yellowstone ecosystem: 1975–95. Ecol Appl 13:687–703.

Patten DT. 1963. Vegetational pattern in relation to environments in the Madison Range, Montana. Ecol Monogr 33:397–406.

Richardson DM, Bond WJ. 1991. Determinants of plant distribution: evidence from pine invasions. Am Naturalist 137:639–68.

Romme WH. 1982. Fire and landscape diversity in subalpine forests of Yellowstone National Park. Ecol Monogr 52:199–221.

Romme WH, Despain DG. 1989. Historical perspective on the Yellowstone fires of 1988. BioScience 39:695–9.

Romme WH, Turner MG. 1991. Implications of global climate change for biogeographic patterns in the Greater Yellowstone Ecosystem. Conserv Biol 5:373–86.

Rosenstock SS, Van Riper III C. 2001. Breeding bird responses to juniper woodland expansion. J Range Manage 54:226–32.

Rupp TS, Chapin III FS, Starfield AM. 2001. Modeling the influence of topographic barriers on treeline advance at the forest-tundra ecotone in northwestern Alaska. Climatic Change 48:399–416.

Sahin V, Hall MJ. 1996. The effects of afforestation and deforestation on water yields. J Hydrol 178:293–309.

Sindelar BW. 1971. Douglas-fir invasion of Western Montana grasslands [dissertation]. Missoula: University of Montana, p 130.

Soulé PT, Knapp PA, Grissino-Mayer HD. 2003. Comparative rates of Western Juniper afforestation in south-central Oregon and the role of anthropogenic disturbance. Professional Geographer 55:43–55.

Steinauer EM., Bragg TB. 1987. Ponderosa pine (*Pinus ponderosa*) invasion of Nebraska Sandhills prairie. Am Midland Naturalist 118:358–65.

Turner JS, Krannitz PG. 2001. Conifer density increases in semi-desert habitats of British Columbia in the absence of fire. Northwest Science 75:176–82.

Turner MG, Romme WH, Gardiner RH, Hargrove WW. 1997. Effects of fire size and pattern on early succession in Yellowstone National Park. Ecol Monogr 67:411–33.

Turner MG, Romme WH, Tinker DB. 2003. Surprises and lessons from the 1988 Yellowstone fires. Frontiers Ecol Environ 1:351–8.

Zimmerman GT, Neuenschwander LF. 1984. Livestock grazing influences on community structure, fire intensity, and fire frequency within the douglas-fir/ninebark habitat type. J Range Manage 37:104–10.