Changes in Landscape Patterns and Associated Forest Succession on the Western Slope of the Rocky Mountains, Colorado

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Abstract—*Using repeat photography, we conducted a qualitative and quantitative analysis of changes in forest cover on the western slope of the Rocky Mountains in Colorado. For the quantitative analysis, both images in a pair were classified using remote sensing and geographic information system (GIS) technologies. Comparisons were made using three landscape metrics: total relative cover, mean relative patch size, and number of patches per major vegetation type. We noted several important changes in the pattern of the landscape and the structure of the forests. The relative area covered by interspersed, nonforested rangelands has decreased significantly, and the total forest cover across these landscapes has increased. Statistical analyses (ANOVA) of other landscape characteristics (patch number and patch size distribution) did not detect changes. However, nonstatistical observation of the trends in these data revealed that in many cases, there has been important, observable change in the configuration of the landscape at many of these locations. Furthermore, our field data show that 96% of the sampled forests have a conifer component in the overstory, understory, or both.*

Introduction

Throughout the Intermountain Region, reproduction of aspen (*Populus tremuloides* Michx.) from seed is rare (DeByle and Winokur 1985; McDonough 1985; Kay 1993). Most successful reproduction occurs via suckering from adventitious buds located on lateral roots. Successful regeneration is associated with early seral communities and gaps in the canopy as a result of the limited ability of aspen to compete in low-light environments (Baker 1925; Barnes 1966; DeByle and Winokur 1985). Aspen reproduction is stimulated by disturbance due to the interruption of hormonal growth inhibitors transported through the stems and roots; the current pattern of fire suppression is suspected as an inhibitor of successful aspen reproduction because it increases the interval between disturbance events (DeByle et al. 1987). Fire is known to stimulate aspen regeneration under a variety of conditions (Bartos et al. 1994; Bartos et al. 1991; Bartos and Mueggler 1981; Brown and DeByle 1987). Further evidence of the effects of fire suppression on aspen ecology is provided by recent surveys of aspen stands in the region, which discovered a predominance of mature to overmature age structure in many aspen forests (Mueggler 1989; Shepperd 1990). If aspen is not reproducing successfully, then we should observe a reduction in the presence of aspen on the landscape over time. This study investigates the relationship between successional development and landscape level changes in forest structure as they relate to aspen ecology.

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We used repeat photography to quantify changes in the Colorado landscape. Previously, multi-temporal series of aerial photographs have been used to quantify changes in vegetation patterns in the western United States and elsewhere (Hart and Laycock 1996; Hester and Sydes 1992; Knapp and Soule 1998; Mast et al. 1998; Snodgrass 1997; Wirth et al. 1996; Zampella and Lathrop 1997). These studies use aerial photographs and/or satellite imagery to assess changes in a specific vegetation type, land-use, or the configuration of landscape elements over time. These studies have successfully demonstrated the temporal and spatial variability associated with ecological systems, but they rarely extend beyond 50 years of change; most are much shorter.

Methods

We selected three measurable landscape parameters to quantitatively represent the configuration of the landscape. Trani and Giles (1999) analyzed 24 landscape metrics for their ability to detect known changes in landscape patterns. Fourteen of these metrics showed the ability to recognize the difference between contiguous and fragmented forested landscapes. However, total area, mean patch area, contiguity, and percent interior forest have nearly linear (therefore easily interpretable) relationships with progressive change toward contiguous or deforested landscape. Many other variables are sensitive to these changes, but curvilinear trends with respect to change make interpretation of these variables difficult using only two sample dates. For a simple and accurate representation of the landscape, we chose total area of cover, mean patch area per type, and number of patches per type.

Our expectations are that there has been a change in the extent and pattern of vegetation cover over the last century. Specifically, we expect that coverage by conifers is increasing. And contrary to popular belief, we expect that coverage by aspen has also increased. As a result, montane areas dominated by shrubs and grasses are decreasing (subsequently referred to as rangelands with recognition that these interspersed communities are only a subset of all communities recognized as rangelands). In addition to changes in the spatial extent of these vegetation types, changes should also be evident within the landscape elements as successional development toward mature community structure continues.

Subsequent to analysis of the landscape patterns, we visited each photographed landscape and sampled the forest for composition and size/age structure. We used the transect data to further assess changes in the landscape structure. Structure (age and size) and species composition of the overstory were compared to the composition of the understory. In this manner, we deduced recent successional patterns in the same forests described by the landscape photograph analysis. Further, we considered the understory composition to be the potential composition of these forests in the future.

Using this landscape level approach and considering patterns of forest development, we hypothesize that:

- Aspen cover has changed significantly since the turn of the century, resulting in more total cover and larger continuous patches of aspen than was found on the landscape near the turn of the last century (circa 1900).
- Conifer cover has increased in the last 90 to 100 years. We do not expect that conifers have replaced aspen on the landscape in this period.

- The cover of open rangelands (interspersed, nonforested shrublands and meadows), within the forest matrix or forested mosaic, has decreased. This is necessary if both aspen and coniferous forest cover have increased.
- Reproductive success of shade-tolerant conifers will outpace the success of aspen reproduction in these closed canopy forests.

The photographed locations in this study are distributed, in two distinct clumps, across a 100-mile portion of the western slope of the Rocky Mountains in Colorado. They are concentrated in the West Elk Mountains of the Gunnison National Forest and the San Juan Mountains of the Uncompahgre National Forest, separated by the Gunnison River Valley, Blue Mesa Reservoir, and the Black Canyon of the Gunnison. These data points are not random; they were determined by the intended subject of the original photographers. In this case, the subjects were geologic features. The authors considered all photographs available in the local collection as potential sample sites, but images picturing nonforested landscapes were removed from consideration. There was not, therefore, intentional bias from the original photographers or the current investigators on the distribution of sample points for the assessment of forest cover. The sample locations resulting from this process are concentrated in the upper montane and subalpine ecoregions.

We collected photographs from the archives of the United States Geologic Survey (USGS) library in Denver, Colorado, to document the previous condition of the landscape. These photographs originate from survey teams documenting Colorado resources from the years 1885 through 1915. We photographed the landscapes in 1995 from the same locations used by the original photographers. Using the paired photographs, we conducted a qualitative and quantitative analysis of changes in forest cover. Qualitative analysis was facilitated by a description of each photograph followed by direct comparison. For the quantitative analysis, both images in the pair were classified using remote sensing and geographic information system technologies. Statistics on polygons, representing continuous patches of major cover types, were collected to determine the change in several landscape variables between the two photographs. Comparisons were made using these metrics (i.e., total relative cover, mean relative patch size, and number of patches per major vegetation type) to represent the landscapes. In order to distinguish obvious differences in landscape history (i.e., disturbance history), we divided the 24 photographed landscapes into two groups. Twelve locations have direct evidence of recent disturbances; 12 intact sites have no evidence of disturbance in the original photograph or the modern photograph. This procedure is subjective, but the photographic evidence is clear in most instances.

Initially, we compared the photograph pairs to qualitatively assess changes in the landscape (see appendix for a sample pair.) To this end, disturbance events (e.g., fire, logging, and mining activities) and the distribution of the dominant cover types (e.g., conifer, aspen, rangeland, bare soil, rock, dead and down timber, forest regeneration) for each photograph were noted. The photographs were compared to identify differences in the pattern and extent of vegetation cover. Qualitative analysis of the photographs was followed by quantitative analysis. The images were scanned at 300 dots per inch resolution and then imported into a Geographic Information System (GIS). Each image was classified using the major vegetation cover (conifer forest, aspen forest, mixed herbaceous and shrub rangeland, and bare ground). Data for total coverage, number of patches, and mean patch size were collected for each major vegetation type. The data representing landscape vegetation were analyzed using a pairwise ANOVA. Total cover and mean patch size were normalized as percentages of the total value within the image. Changes in the number of patches were calculated using a direct comparison (not normalized) between paired photos. Quantitative comparisons were made using these estimates of the landscape metrics. The F-statistic was calculated for each metric to compare the coverage on the old landscape to the modern landscape. Recently disturbed and intact landscapes were analyzed separately.

Subsequent to analysis of the landscape patterns, we traveled to each photographed landscape to analyze the structure of the forests. We used two 500 m^2 transects (2 m x 250 m^2) on each landscape, in most cases, to sample the size and age structure of the forests. Graphs of forest structure were analyzed in association with the landscape history provided by the photograph pairs. The analyses of these data are not presented here, but some of the data are discussed. An example of a size-age distribution showing abundant fir regeneration is provided in figure 1.

Results

The general trend depicted by the photographic histories is an increase in forest cover (coniferous and deciduous) and a decrease in rangeland cover. The qualitative comparison suggests that 92% of the pairs reveal an increase in the total area covered by conifers and aspen, and a decrease in the area covered by rangelands (figure 2). This is supported by the quantitative analysis of these sites where 96% of the classifications show a net increase in forest cover (figure 2). According to the quantitative comparisons, conifer cover increased on 63% of

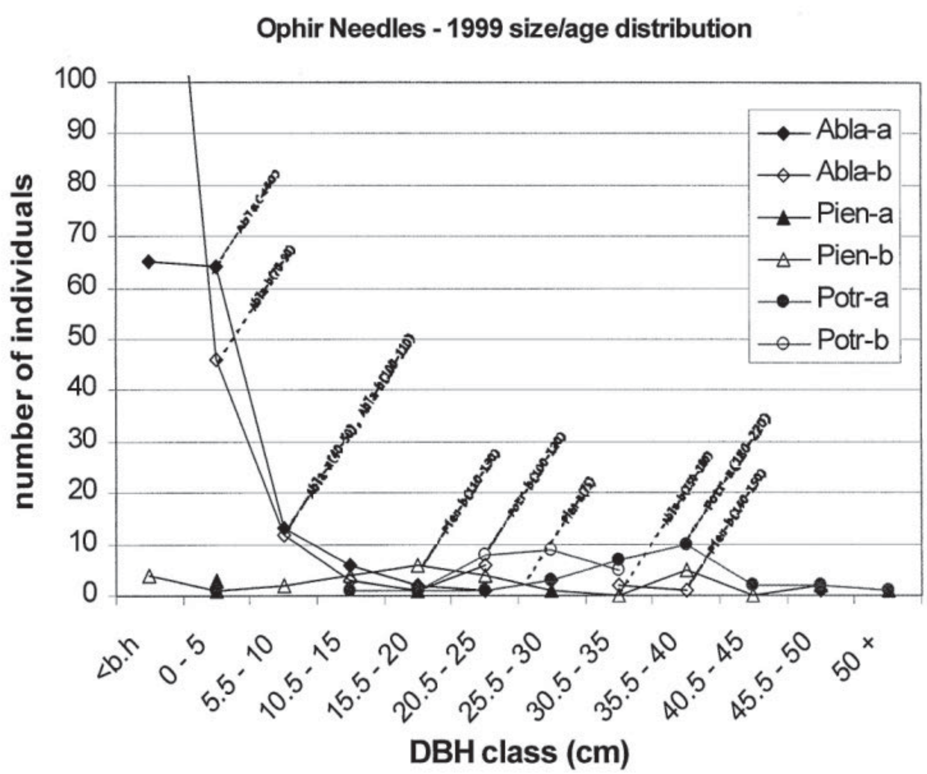

Figure 1—Size-age distribution for Turkey Mesa. Abla = *Abies lasiocarpa*, Pien = *Picea engelmannii*, Potr = *Populus tremuloides*. This example of a size-age distribution used in the analyses was constructed from two transects (designated "a" and "b" on the graph), which stretch across the central portion of the photograph of the mesa in front of the Ophir Needles (Turkey Creek Mesa) (see appendix). The distributions show that although there is an abundance of aspen and conifers in the overstory, the understory composition (recent regeneration and small, older individuals) is dominated by *Abies lasiocarpa*. The maximum age (at breast height) of sampled trees was 220 years. The distributions were created based on the size distributions, and the corresponding ages were added using size-age distributions determined by coring a minimum of 10% of each size class.

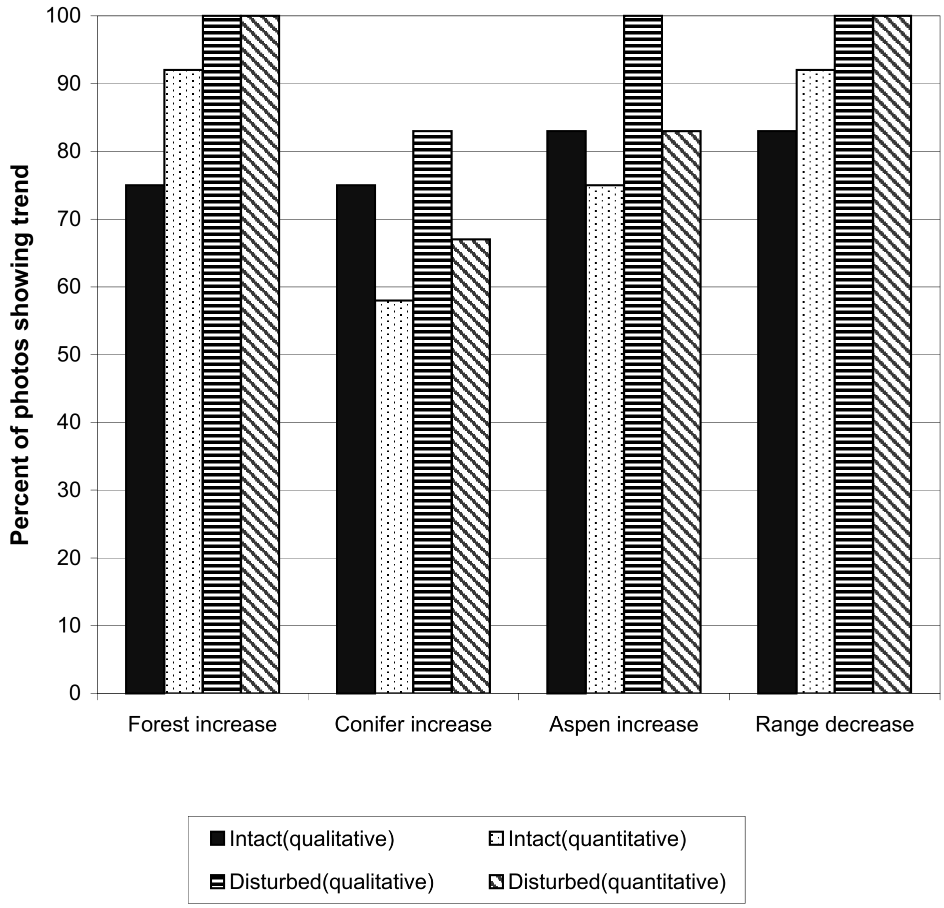

Figure 2—Summary of the changes in total cover, by cover type. Patterns described qualitatively and quantitatively are distinguished; the differences between these values indicate changes apparent to the observer but not detected in the GIS generated data. Note that the change in nonforested rangelands is a decrease, while the changes in forest cover types are increases. This is the cause and effect relationship described in the text.

all sites; aspen cover increased on 79% of all sites; and coverage by rangelands decreased on 96% of all sites (figure 2). The decrease in coverage of open range is significant ($F_{disturbed} = 5.03$, $P_{disturbed} = 0.006$; $F_{intact} = 3.76$, $P_{intact} = 0.003$; df = 11), but there is not a corresponding increase in conifer and aspen coverage. The lack of significance in the statistical analyses of the other cover types is due to the high variability between sites. Simply stated, the relative cover of coniferous and aspen forests and mixed rangeland patches varies more depending on which slope, valley, or watershed you observe than it does over time across these same locations.

Upon sampling the photographed landscapes we discovered that the range of forest ages (based on the age distributions of canopy dominants) was similar for both sets of data. The maximum age for landscapes classified as "intact" was 150–250 years, despite our previous distinction. (Although large, old "remnant" individuals were observed in many of these landscapes, they were rare enough to miss detection in our sampling.) This suggests that these landscapes were disturbed more recently than was apparent in the photography. Further, the patterns in landscape age predicted by photographic interpretation were not as strong as predicted. Our data confirm that many of the sampled forests are entering, or have entered, stages of succession when shade-tolerant conifers have a competitive edge over less-tolerant aspen. These data show that 96% of the sampled forests have a conifer component in the overstory, understory, or both. Twenty-one percent (21%) of the forests have distributions with many young conifers (especially fir); this suggests recent colonization and future competition for aspen. These data suggest that there are two components to landscape level changes in forest cover and composition: (1) expansion of stand borders as trees establish in formerly open meadows, and (2) the expansion of shade-tolerant (later seral) species under the canopy of existing forest dominants.

Discussion

This study is unique because it quantifies changes in landscape pattern over an 80- to 100-year period. The time span is consistent with other repeat photography studies in this region (e.g., Veblen and Lorenz 1991; Houston 1982; Gruell 1983; Progulske 1974) and near to the limit of the photographic history, which extends back to 1866 in some areas (Hart and Laycock 1996). However, these studies have not quantified the change. Although our statistical analysis fails to detect most of the observed differences in the landscape, several significant, and many nonsignificant, quantified changes were observed. Analyses suggest that there is an inverse relationship between relative total forest cover (increasing) and the relative area covered by open rangelands (decreasing). The statistical analysis of other landscape characteristics does not detect changes in patch number or patch size distribution. However, a comparison of individual pairs of images and observation of the trends in the data reveal that in many cases, there has been important, observable change in the configuration of the landscape at many of these locations. (See the images in the appendix for an example of one such area.) The wide range of values in the analyzed variables (variability among sites) is primarily responsible for the reduced statistical significance of the variables. This is reflected in the statistical analysis; further, the wide range in cover type distributions can be easily observed in the images. The details of landscape configuration (i.e., patch size, shape, and distribution) are variable at a more local scale than that used for this analysis and reflect local competition, environmental conditions, and management factors more strongly than a generalized pattern of change. Total cover, an apparently more uniform variable, does demonstrate the significance of the trend of forest increase and rangeland decrease.

Although there is a wide range in the distribution of successful aspen reproduction, there is a strong trend (among all sample locations) for reproductive success of shade-tolerant species. The evidence is the presence of abundant conifer regeneration in half of the forests dominated, or codominated, by aspen (96% of all sampled forests). Thus, it is possible to recognize the expansion of aspen across some landscapes while remaining concerned for the future survival and reproductive success of aspen. The success of shade-tolerant species is often at the expense of the less competitive species (i.e., succession toward later seral stages). These are the same patterns predicted by systemic models of succession in aspen communities (Bartos et al. 1983).

The ability for aspen to reproduce (considered from a landscape perspective) was not strongly influenced by parameters documented in the site histories. This is evidenced by the prominence of aspen regeneration on both disturbed and mature sites. Surprisingly, a higher percentage of aspen stands were found to be reproducing successfully on the intact sites than on recently disturbed sites. Furthermore, even recently disturbed sites show a greater abundance of conifer regeneration than aspen regeneration. These patterns suggest that modern disturbances have had a different effect on forest structure and regeneration than those typical 100 years ago. The patterns are similar to those documented by

Mueggler (1989) and Shepperd (1990) in the Rocky Mountain and Intermountain Regions. This condition must be a concern as we address the long-term persistence of aspen on the landscape. Presumably, as an increasing amount of the landscape develops dense forest cover, the reproductive success of aspen will continue to decrease.

Conclusions

At the present time, and in the landscapes surveyed, there has not been a decrease in the coverage of aspen forest. Instead, our study suggests that there has been an increase in forest cover across the region. We presume that this is primarily the result of fire suppression, but other land uses and land management practices in these areas may also be responsible. The landscape level implication is that early seral communities (those created by recent disturbances resulting in regeneration and recolonization without competition from later seral species, namely conifers) are becoming rare on the landscape. This conclusion is supported by our field data, which suggest that reproduction by shade-tolerant species is prolific under the canopies of mid-seral communities. Regeneration of forests following the major disturbances associated with European settlement of western Colorado is impressive, but it is distinctly different from the patterns created by historical fire regimes. We have entered an era where the control of landscape level disturbances has created a different landscape than that which existed before our management of these forests. Future research and management needs to address the potential paucity of early seral communities. The importance of these communities with respect to their composition (species diversity), their role in wildlife habitat (forage production and nutrition), and their role in forest structure (a range of generations) needs to be elucidated. We need research and management practices, which ensure that the landscape of the future includes multiple generations of forest communities and the species composition and age structure necessary for perpetually healthy forests. Particularly, the distribution of these different communities needs to be addressed from a landscape perspective. Only from this broad perspective can we study, monitor, and manage the distribution of various community types to ensure that our national lands provide the needed structural diversity to ensure healthy systems and the continued availability of wood products, wildlife habitat, and recreational opportunities into the future.

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Appendix follows on next page

Appendix: Ophir Needles and Turkey Mesa, San Miguel County, Colorado

A (top): Original photo by C.W. Cross, 1899, United States Geologic Survey.

B (bottom): Recent photo by D.J. Manier, 1995.

The camera is facing east; the photographed aspect faces west. Elevation ranges between 10,200 feet (3,100 m) and 12,500 feet (3,810 m). The original photo shows a characteristically patchy landscape south of Telluride, Colorado, along Colorado Highway 145. The interspersion of different-sized patches is probably the result of the historical disturbance regime. The contemporary photograph shows extensive forest cover across the mesa. Coverage of aspen has obviously increased through expansion of patches and consolidation of previously isolated clones. Coniferous forest persists interspersed within the aspen matrix. Most open patches (i.e., nonforested, rangeland patches) are gone; some of the large meadows persist in the contemporary image. Forest expansion has reduced the abundance of open patches within the forest. The size of forest patches has increased due to small, isolated patches growing together and occupying former open, grassy patches.