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DISSERTATION

Changes in landscape patterns and associated forest succession on the western slope of the Rocky Mountains, Colorado:

Submitted by
Daniel J. Manier
Department of Forest Sciences

In partial fulfillment of the requirements
of the Degree of Doctor of Philosophy,
Colorado State University,
Fort Collins, Colorado
Spring 2000

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We hereby recommend that the dissertation prepared under our supervision by Daniel J. Manier entitled, "Changes in landscape patterns and associated forest succession on the western slope of the Rocky Mountains, Colorado," be accepted as fulfilling, in part, the requirements for the degree of Doctor of Philosophy.

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Abstract

Changes in landscape patterns and associated forest succession on the western slope of the Rocky Mountains, Colorado

I address the prediction that fire suppression has resulted in a decline in the presence of aspen (*Populus tremuloides* Michaux) on the landscape. Repeat photography and size-age distribution analyses are used to assess changes in major vegetation types (coniferous forest, aspen forest, rangelands) on the western slope of the Rocky Mountains, Colorado, U.S.A. The photographs span a period of 80 to 110 years, thus representing a century of change since the large mining-related disturbances associated with European expansion and the subsequent suppression of wildfires in the region. Photos are compared using parameters representing landscape characteristics (i.e., total cover area, number of patches, mean patch size) estimated from geographic information system representations (GIS coverages). Comparisons of these documented landscapes suggest that forest cover (both aspen and coniferous) has increased across the region. Pairwise ANOVA procedures reveal significant increases in the relative total cover of aspen and conifers and a decrease in the relative coverage of rangelands. However, the number of patches and mean, relative patch size showed little significant change. High variability among sites reduces the significance of trends that are apparent in qualitative assessments and quantified trends. Analysis of size-age distributions reveal that aspen is reproducing successfully in some areas. However, my data suggest that many aspen forests are aging with limited reproductive success. In most areas, aspen populations exist within a coniferous matrix, and shade-tolerant conifer species (especially *Abies lasiocarpa* Nutt. and *Picea engelmanii* Engelm.) are abundant in the understory. Even in areas with successful aspen regeneration, successional development, which has ensued since the last major disturbance, favors reproduction by shade-tolerant species over aspen. Closed canopy aspen and conifer forests have expanded across the landscape at the expense of early seral communities. Similar data in other studies suggest that this pattern is widespread across the region. While it is apparent that the distribution of aspen on the landscape has not decreased in the last century, the structure of most of these forests is evidence of ongoing colonization by conifers. Closed canopy aspen and conifer forests have expanded across the landscape at the expense of early seral communities.

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Special thanks go to my advising committee. Denis Dean and Melinda Laituri assisted me in developing G.I.S. representations of the photographs, and they provided valuable insights for editing the manuscript. Fredrick (Skip) Smith provided valuable advise on sampling designs and stand structure analyses, and valuable insights towards the editing of the manuscript. I am grateful for their patience and assistance.

Thanks to the United States Geologic Survey Library, Denver for providing the original photographs. The photographic records preserved by their diligent efforts enable this and other similar projects to occur. Thanks go especially to the original photographers (now deceased): C. W. Cross, E. Howe, W. T. Lee, and C.W. Purington. And, thanks to Joe McGregor, photographic librarian, for his assistance with identifying, locating, and attaining reproductions of the old photographs.

Finally, I give many thanks to my parents, James and Karen Manier, who have continually supported me in my pursuit of this degree and everything leading up to it. Without their support, guidance and understanding my life would be very different today. Thanks to my brother and sister, Greg and Mollie, who share and support my passion for wild places and the aspiration to know life. And I thank my wife, Heather; her patience and unbounded support have allowed me to pursue a lengthy career as a student. Without the support of my family, this dissertation could not exist.

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Chapter 1: Introduction

1.1 Overview

The successful suppression of wildfires in the Rocky Mountains, and throughout the western United States, has interrupted the regeneration of aspen trees (*Populus tremuloides* Michaux). The result is a decline in the percent of aspen cover on the western landscape (Brown and DeByle 1987). Studies that address this issue are rare. This project addresses this premise by using time series photographs (repeat photography) to compare the coverage of major vegetation types (coniferous forest, aspen forest, and mountain rangelands) between dates 80 to 110 years apart. In addition, I sampled the structure of the forests that appear in the photographs to document the stand development patterns associated with changes in landscape structure and pattern.

The United States Geologic Survey (USGS) library in Denver, Colorado supplied the original photographs. These photographs originate from survey teams documenting Colorado resources from the years 1885 through 1915. I photographed the landscapes in 1995 from the same locations as the original photographs. Using the paired photographs, I make a qualitative and quantitative analysis of changes in forest cover. Qualitative analysis is facilitated by a description of each photograph followed by direct comparison. For the quantitative analysis, both images in the pair are classified using remote sensing and geographic information system technologies. Statistics on polygons, representing continuous patches of major cover types, are collected to determine the change in several landscape variables between the two photographs. Comparisons are 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.

My expectations are that there has been a change in the extent and pattern of vegetation cover over the last century. Specifically, coverage by conifers is increasing. Contrary to popular belief, coverage by aspen has increased; and as a result, areas dominated by shrubs and grasses are decreasing. In addition to changes in the spatial extent of these vegetation types, changes should also be evident within the landscape elements as successional development towards mature community structure, i.e. competitive exclusion stages.

This study is unique because it quantifies changes in landscape pattern over an eighty to one hundred year period. The time span is consistent with other repeat photography studies in this region (e.g., Veblen and Lorenz 1991, Houston 1982, Gruell 1980, 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. Multi-temporal series of aerial photographs have been used to quantify changes in vegetation patterns (Vuttera et al. 1998, Brown and Carter 1998, Knapp and Soule 1998, Zampella and Lathrop 1997, Snodgrass 1997, Mast et al. 1997, Wirth et al. 1996, Hart and Laycock 1996, Demers et al. 1995, Hester and Sydes 1992).

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, however they rarely extend beyond 50 years of change; most are much shorter. My study is also limited by the time span of the photography, however the time frame afforded by using ground photography is longer (by approximately 50 years) than is typical for aerial photography. Furthermore, I quantify the landscape information provided in the imagery, thus distinguishing it from other repeat photography studies.

My technique provides valuable insight into former forest conditions, however it has several limitations. Many potentially relevant details regarding land use, disturbance, and climate data are not available for each datum point, i.e. each photographed location. Important details regarding site histories are described using the record preserved in the photographs; however, this information is restricted to two points in time. Regional history and climate data are used to describe the general patterns associated with the region, based on data from three nearby locations. I must assume that this information reflects the climate conditions and local history similarly for each study site.

In addition, the procedure of classifying and comparing data from oblique photographs (ground photos versus aerial photos) results in the combination of two otherwise distinct variables, the shape of individuals (i.e. crown shape) and the shape of patches (i.e. patch perimeter). This reduces the meaning of several typically measured landscape variables such as stand perimeter or a convexity index for this study. Trani and Giles (1999) analyze 24 landscape metrics for their ability to detect known changes in landscape patterns. Fourteen of these metrics show 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 towards contiguous or de-forested 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. I selected three variables which are deemed to reflect changes in landscape configuration (Trani and Giles 1999) as both measurable using my techniques and relevant to my questions regarding landscape change. These variables are: total area of cover, mean patch area per type, and number of patches per type.

Angular distortion created by the use of oblique photographs also affects vertical (aerial) photographs and has a regular (predictable) effect on changes in patch area, i.e. as the angle increases, the area decreases. The effect is similar for all patches. The shape of a stand is also distorted when the crowns of the trees protrude from patch borders. This results in a small distortion of patch area, but a large and unpredictable distortion of patch shape. Area suffers from this effect because overlap of adjacent stands may result in overestimates of the near stand and an underestimate of the background stand; this area is small relative to the entire patch area, and losses on one side are usually offset by increases on the other. Therefore, patch area assessed using this technique is believed to represent the actual footprint of the patch. The top (photograph perspective) border of the silhouette of the stand is characterized by angles created by the shape of individual tree crowns. This means that the polygon shapes derived from this method are not representative of the perimeter dependent landscape elements that are typically analyzed using patch perimeter as a component, e.g. convexity and total edge. Respective of these potential difficulties, I address the previously mentioned questions regarding trends in the landscape using a few, simple variables, which are indicative of changes in forest cover.

A final issue of bias is that the data points are not established randomly, they were established by photographers working for the U.S.G.S. near the turn of the last century (1900 C.E.). This is a typical problem for use of historical data, because information is restricted to the locations where they are preserved, i.e. not distributed regularly or randomly across the landscape. I collected a large, photograph set using photographs from several different photographers and expeditions. In this way, biases of the original photographers have been reduced in their affect on my analyses. I must assume that the biases of the original photographers have not introduced significant bias into the sampling of the landscape using these locations in order to extrapolate any of these results onto the surrounding landscape. However, due to the limited sampled area and the high variability in aspen communities, any extrapolation should be conducted with skepticism.

Field sampling, subsequent to the repeat photography analysis, provides size and age structure information for the forests that appear in the photographs. The sampling design is subjective. Transects are located on the landscape that lies in the central portion of each photograph. Use of two transects for each photograph (most locations) allows us to sample across a broad portion of this landscape. Thus, transects do not necessarily represent the structures of single stands, instead they often crossed stand boundaries. This unconventional approach is designed to directly sample the structure of the landscape, as opposed to piecing together the structure of each stand, measured independently, to reconstruct the landscape structure. Thus, whether forest dominants are reproducing in the understory or expanding into adjacent canopy openings, I will detect their reproductive success. The site history provided by repeat photography in conjunction with forest size and age structure provides a detailed picture of landscape patterns and associated changes in community structure.

1.2 Aspen ecology

1.2.1 Aspen communities

Aspen is the most widely distributed deciduous tree in North America. Its range extends across the entire continent, Pacific coast to Atlantic coast, and from New Mexico and Arizona up through Canada to Alaska. However, its role in forest community structure, percent cover and successional role, varies considerably across this range (DeByle and Winokur 1985). In the intermountain region of the Rocky Mountains, aspen is commonly associated with ponderosa pine (*Pinus ponderosa*) at low elevations, Douglas-fir (*Pseudotsuga menzeisii*) and lodgepole pine (*Pinus contorta*) at mid-elevations, and spruce-fir (*Picea pungens, Picea engelmanii*, and *Abies lasiocarpa*) mixed forests at high elevations.

The ability of aspen to compete for resources varies with its life history characteristics relative to other species (e.g. relative shade tolerance, reproductive strategies, and growth rates) and environmental determinants such as disturbance regime, precipitation, temperature, slope, and aspect. At high elevations and throughout most of the intermountain region, aspen is generally considered seral to conifers (Mueggler 1976, Bartos et al. 1983). At lower elevations, aspen can be seral to coniferous species, or it can be a self-replacing dominant (Mueggler and Campbell 1982). Elevational trends vary with latitude; the zone of suitable habitat is higher in the south, and lower in the north. In Colorado and Utah, aspen generally occupies intermediate elevations; in the southern part of this region, aspen occupies elevations of 2300m to 3200m (7,500ft. - 10,500ft.) and the northern habitat ranges from 1800m to 2800m (5900ft. - 9200ft.) (Mueggler and Campbell 1986).

In addition, the aspen community is characterized by a highly productive understory (Woods et al. 1982), which produces habitat and forage for wild and domestic species of ungulates, small mammals, birds, and other wildlife. The high floral and faunal species diversity associated with aspen forests is often in stark contrast to the surrounding coniferous forests on the landscape (Mueggler 1985). The persistence of these communities is important for human and wildlife interests, based on the biological diversity and grazing potential.

1.2.2 Aspen populations

DeByle et al. (1987) suggest that aspen is in decline on the western landscape because of reproductive difficulties, namely a lack of natural disturbance to initiate stand regeneration. Throughout the intermountain region, aspen reproduction from seed is rare (DeByle and Winokur 1985, McDonough 1985, Kay 1993). Less than optimal conditions of temperature, substrate, and competition are not well tolerated by the rapidly aging seeds (McDonough 1985). The only recent documentation of regeneration from seed in this region was discovered after the Yellowstone fire of 1988 (Kay 1993). The apparent limitation is moisture, but aspen rarely survives on saturated soils (Kay 1993). Romme et al. (1998) describe the "unique" circumstances of bare mineral soil and abundant soil moisture that contributed to this reproductive success. These observations suggest a narrow range of conditions that are suitable for successful seedling survival and growth, and which are often not met in the Rocky Mountain region.

However, aspen is highly successful at vegetative reproduction. Aspen produces adventitious shoots (suckers) that grow from nodes in the lateral root system. Shoot production, suckering, is suppressed by auxin produced in the apical meristem of the standing trees. This usually limits the number of new suckers and can eliminate successful reproduction. Most successful (beyond sapling stage) reproduction, in clones with live canopy trees, occurs near the perimeter of a clone where the concentration of hormones is lower and light availability is higher (Jones and DeByle 1985).

Vegetative reproduction by aspen is heavily influenced by disturbance, especially fire (Brown and DeByle 1987). Low intensity, surface fires are common in the aspen ecotype. They generally kill the standing trees but leave the root system alive. The death of live trees in the canopy results in prolific production of suckers the first growing season after the fire. Fire interrupts the hormonal inhibitors (auxin), and it increases light and temperature at the surface; the combination of these factors results in abundant proliferation of aspen (Schier 1976, DeByle and Winokur 1985). The combination of disturbance stimulated reproduction in aspen, fire suppression in all of its natural habitat, and documentation of development of later seral stages results in the common belief that aspen is generally not regenerating, and therefore its status on the landscape is declining. " In the past, fire played a prominent role in the perpetuation of quaking aspen (*Populus tremuloides* Michaux) forests. In contrast, today the existence of aspen in threatened by lack of fires in areas of the west" (Brown and DeByle 1987, p.1100).

This theory is not fully supported by the literature. One study by Wirth, et al. (1996) indicated a 45% decline in aspen cover between 1947 and 1992. This study focused on a 460,000-acre area in the southwest corner of Montana's Beaverhead-Deerlodge National Forest; this is only a small fraction of the distribution of aspen in North America (i.e. a range extending from Alaska to Arizona, British Columbia to Quebec, California to Maine,). Similar studies for other areas do not exist.

Given the diverse associations (Jones and DeByle 1985) and broad range (Mitton and Grant 1996) of aspen across the continent, there are not sufficient data to extrapolate to the extent of aspen habitat, even within the western region. Where, then, does the idea of aspen decline get its basis? Wirth et al. (1996) suggest that historical records can be used to estimate a 75% decline in aspen cover across the Rocky Mountains, however no document exists to date that compiles this information.

Community models suggest conversion to conifer-dominated forests due to forest succession (Bartos et al. 1983). In addition, the lack of disturbance, e.g. fire, is associated with the loss of reproductive vigor and reduction of the competitive advantage aspen derives from growth in early seral communities (DeByle et al. 1987). Documentation of mature age structure in many stands throughout the region (Shepperd 1990, Mueggler 1989) add support to this suspected trend in Rocky Mountain aspen communities.

1.2.3 Succession, Disturbance, and Community Patterns

Bartos et al. (1983) used a deterministic model to describe the general successional trends exhibited in communities occupied by aspen, conifers, shrubs, and herbaceous species. The model summarizes the theoretical basis for secondary succession (initiated by disturbance, i.e. fire) in mixed aspen and conifer forests. It assumes there is available aspen root structure on the site, and a readily available source of conifer seedlings. The growth patterns are based upon long-term averages of growth rates and inhibition factors in the intermountain region. Growth of each vegetation type is affected by the growth and regeneration of the other types. The results of this model, although they are not supported by the confidence inferred from field data, do indicate the general relationships and growth patterns expected given current knowledge of succession. Herbaceous species biomass peaks in the first few years; shrubs peak after 20 to 100 years, and conifers increase slowly to possible "equilibrium" after 400 years; aspen biomass peaks at 100 to 150 years and then begins to decline (Fig. 35 *in* Bartos et al. 1983, p. 29). Subsequent simulations and manipulations suggest that competition with conifers for resources has a powerful effect on aspen populations. In addition, a simulated disturbance after 300 years causes a new peak in aspen biomass and suggests an oscillating pattern of forest biomass division between herbaceous species, shrubs, aspen and conifers (Fig. 34 *in* Bartos, et al. 1983, p.29). Although this model is based upon many estimates, "the model yields believable results for the forest system simulated, whether that forest was undisturbed or subjected to various manipulations" (Bartos, et al. 1983, p.45).

The pattern of aspen decline after 100 to 150 years in this model gives rise to the suggestion that aspen in the Rocky Mountains, deprived of large disturbances for at least 100 years, is either entering this stage or is well into the stage of decline. Shepperd (1990) conducted a classification of aspen stands in the central Rocky Mountains. The classification included 14% young stands (< 40 yr.), 23% middle aged stands (50-60 yr.), 60% mature stands (80-100 yr.), and 4% old stands (140+ yr.). While this study was not designed to systematically sample the landscape, it provides strong field evidence for an aging trend in aspen communities across the landscape. Mueggler (1989) surveyed 713 aspen stands in Idaho, Utah, and Wyoming. He found 62% in a condition of mature or over-mature age structure. Thus, the trends predicted by Bartos et al. (1983) are apparently supported by field evidence of stand development.

1.2.4 Patch structure and spatial pattern

There is a growing body of literature in the fields of community and landscape ecology that describes natural disturbance as a deterministic component of the temporal and spatial variability of community structure (Pickett and White 1985). Much of the research on and modeling of community dynamics focuses on fine scale dynamics, exhibited in small tree-fall gaps within the canopy (Shugart and Seagle 1985). These models focus on the interactions between individuals and species in various phases of life, e.g., establishment, growth, and mortality. The results generally reflect the growth pattern of each individual and "project consequences of species attributes to the forest ecosystem dynamics" (Shugart and Seagle 1985, p. 358).

More recent efforts examine the dynamics of populations and communities with explicit incorporation of disturbance as a determinant of structure and pattern. Studies of patch dynamics address the temporal and spatial dynamics of the landscape as determined by disturbance and the pattern of regeneration which occurs following the disturbance. Turner, et al. (1993) describe the effects of the disturbance interval relative to the recovery interval (temporal) and small versus large portions of the landscape (spatial). Variation in these variables allows prediction of disturbance conditions that lead to different landscape dynamics. These predictions are in agreement with the pattern observed on several landscapes. They also describe the differential effects of small, frequent fires in Yellowstone National Park and large, catastrophic fires, i.e. the 1988 fire in Yellowstone National Park (321,000 ha).

According to Turner et al. (1993), small disturbances create small gaps resulting in local effects and patch dynamics within the apparent equilibrium of the larger landscape. The return interval for large disturbances, such as the 1988 fires in Yellowstone, is approximately 300 years. At this broad spatial and temporal scale, the apparent equilibrium of the landscape is better described as cyclical. It is characterized by periodic, catastrophic disturbance which initiates regeneration patterns across the landscape. Therefore, the size and intensity of fires as well as the interval between fires is directly related to the mosaic pattern created by conifer, aspen, and range covered lands.

Smaller, non-catastrophic disturbances in high elevation forests will create patches that are distinct from the surrounding forest. Species colonize these openings based upon their respective reproductive strategies and local factors such as presence of a seed source, or presence of shade-tolerant individuals in the understory. Thus, periodic, small disturbances maintain small portions of the forest in various stages of development and affect the overstory structure (Veblen et al 1994, Aplet et al. 1988). Large disturbances affect species differently based simply on their size. The distance a seed must travel to colonize central portions of large openings as well as the availability of seed (or in the case of aspen, surviving roots) to colonize the newly available space (Parker and Parker 1983). In this manner, they create a different effect on the landscape than small area disturbances. In addition, the effect of large disturbances varies between community types. For example, spruce and fir populations generally take longer to colonize an area after a fire than do grasses, shrubs, and aspen (if aspen has surviving root structure). The result is a shift in community composition in which forest cover is greatly reduced while herbaceous species dominate along with patches of young aspen. Years later, conifers will colonize, mature, and eventually dominate the area once occupied by grasses and aspen stands.

Veblen et al. (1994) describe the interactions of disturbances such as fire, insect induced mortality, and avalanches. The existence of landscape variability, variations in patch size and age, created by previous disturbances also affects the extent and frequency of subsequent disturbances. Thus, the frequency of small disturbances in the spruce-fir forest affects the frequency and extent of less frequent, large-scale disturbances, and vice versa. From a landscape perspective (i.e. one that recognizes patterns and attempts to associate processes with observed changes in the variables of interest), the change in species composition is determined by fires, age mortality, wind throw gaps, avalanches, and insect infestation. This creates a mosaic where there is variation of age and composition such that all species are not at all locations at all times.

Maarel and Sykes (1993) describe a carousel model where the community exists in various degrees of composition and high variability at a small spatial scale. The apparent stability of the community increases when a larger spatial scale is considered. Small disturbances within a million acre spruce-fir stand will not change the dominance of shade-tolerant conifers across the landscape. However, a large, stand-destroying canopy fire can significantly change the vegetation, soil, and the potential for future fires across the landscape (Romme et al. 1998). These events typically occur less frequently than small disturbances. They require longer periods of time to regenerate to characteristics similar to those before the disturbance. Thus, they create a pattern of stand development that exists across hundreds of years. To summarize, suppression of natural fire regimes is likely affecting forest dynamics at several spatial and temporal scales. Therefore, I can expect the pattern and structure of vegetation cover to change with development of successive stages in the forest structure.

In addition, dynamic community relationships between species are affected by the frequency and extent of disturbance events. Armstrong (1988) documented a disturbance mediated relationship in an investigation of the community dynamics of fungi. He suggests that the ease with which species coexist can depend strongly on the disturbance regime. And, coexistence is facilitated by the increased reproductive success of subordinate species (i.e. less competitive) with respect to the dominant species. The relationship between these fungi bares similarities to the relationship between aspen, conifers, and fire. Aspen is less shade-tolerant than most conifers, which are the long-term dominants, and therefore they may be considered subordinate to them. Fire can mediate the competition between these species by determining stand age.

In another discussion of disturbance affects on species composition, Denslow (1985) addresses the affects of spatial and temporal variability on species coexistence. She suggests that the periodic freeing of resources created by disturbance allows less dominant species to maintain populations in the community, thereby increasing species heterogeneity. This is affected by historic disturbance patterns, and the associated adaptation of local species to disturbance regimes. High elevation interactions between spruce, fir, lodgepole pine, and aspen are different from interactions between grasslands, aspen, and ponderosa pine. The historic fire regime of the former may be frequent small fires, and infrequent large, crown fires, while in the latter a high frequency, surface fire regime is likely. Thus in addition to directly affecting the spatial and temporal distribution of populations and communities, the disturbance regime, the adaptations of each species to this pattern, and the relative growth and colonization abilities of local competitors interact to create long-term structural patterns in communities.

Heinselman (1981) specifically discusses the role of fire as a determinant of forest structure with special attention to aspen, suggesting it is particularly important for the regeneration of even-aged stands. As it is known that wildfires have been successfully suppressed in this region for the last 90-100 years, then I conclude that fire suppression must be affecting the reproduction of aspen. This is of particular concern when considering the current status of aspen on the landscape because aspen occupies a particular location, spatially and temporally (i.e. an early seral stage) in much of its Rocky Mountain range (Mueggler 1985), and there is a documented aging of many existing (Meuggler 1989, Shepperd 1990).

1.3 Sample area and regional history

1.3.1 Study area

This study is conducted on the western slope of the Rocky Mountains, in southwestern Colorado. It includes samples from two national forests, Gunnison National Forest and Uncompahgre National Forest, in three counties, Gunnison, Ouray, and San Miguel. The sample locations, photograph sites, are clumped into two areas separated by extensive rangelands (Figure 1.1). I use the data to indicate trends in forest structure along approximately 100 miles (150 km, north-south) of the western slope of the Rocky Mountains, describing a region of approximately 2500 square miles (6000km^2). This region includes the West Elk Mountain range in the north, and the San Juan Mountains in the south. Details of climate, disturbance, and land-use history are not easily attained

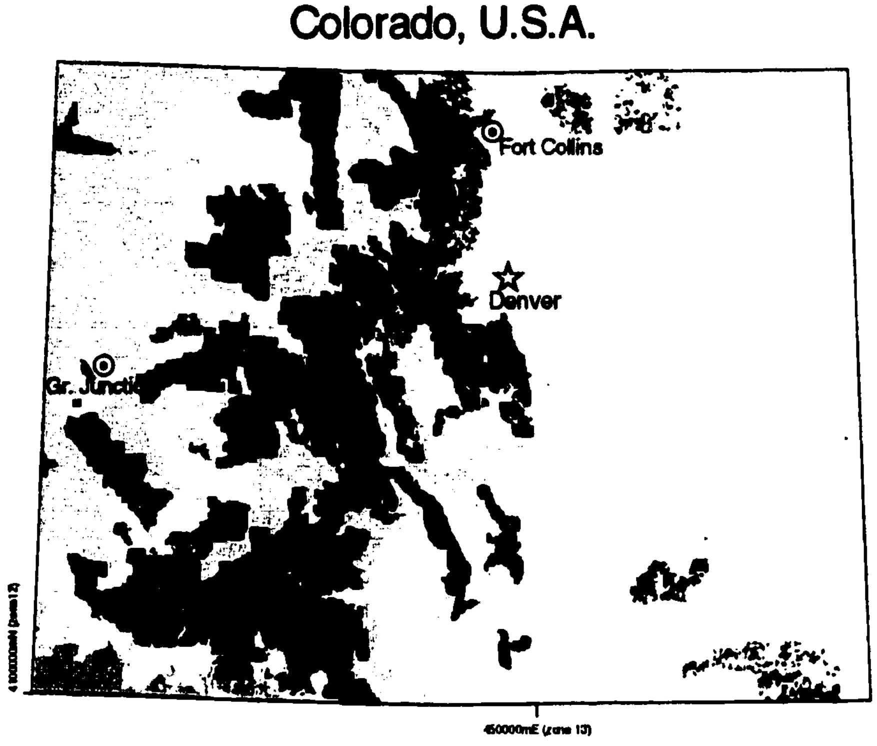


Figure 1.1: State of Colorado with management agency classification (green = Forest Service, Peach = BLM, Blue = Park Service, Pink = military, Beige = state, Orange = Ute reservation). Photograph and sampling locations are defined in red.

1.3.2 Historic use and European colonization

The western half of the Rocky Mountain region, in Colorado, was designated property of the Ute tribes and off limits to European settlers until the 1800's. This does not mean that no Europeans entered the region before that time. Coronado led the first exploration of the region around 1540 (Hart and Hart 1997). Trappers and fur traders traveled extensively throughout the region before official settlement. As early as the 1860's, prospecting parties entered the region, but the Utes drove them out before towns were established (Vandenbusche and Smith 1981). In 1873 the Brunot treaty between the U.S. government and the Utes allowed unhindered exploration and excavations by

1860's, prospecting parties entered the region, but the Utes drove them out before towns were established (Vandenbusche and Smith 1981). In 1873 the Brunot treaty between the U.S. government and the Utes allowed unhindered exploration and excavations by miners in the mountainous regions of the western third of the state. In 1873, the mining towns of Silverton, Ouray, and Lake City, along with many associated camps, were established in the San Juans. Within a few years, agriculture and ranching interests created documented conflicts between European settlers and the native populations. In 1882, settlers moved into the valleys North of Ouray where the towns of Ridgeway and Montrose now exist (O'Rourke 1980). The Denver and Rio Grande railroad reached Gunnison in 1881 providing the transportation link needed to support the new camps in Crested Butte and Gothic. Frank Fossett, speaking in 1880 said that, "until recently [the Gunnison country has] been an unknown land to the world at large and even to the people of Colorado" (Vandenbusche and Smith 1981). By the end of the 1880's the influence of mining and ranching was changing the western Colorado landscape by driving out the former stewards of the land (the Ute tribes) and perpetuating clear-cut logging, mining, ranching, and town development.

When miners were finally permitted to settle the western Colorado mountains in the 1880s, cattle ranchers were not far behind (Vandenbusche and Smith 1981). Clements and Young (1997) address the affect of livestock introductions to Great Basin range systems in the late 1800s. The addition of this herbivory pressure resulted in severe overgrazing, especially near water supplies. "The loss of the perennial grasses left a biological near vacuum in the understory . . ." (Clements and Young 1997, p.133).

These patterns will undoubtedly vary depending on the resilience of the system to grazing and the intensity of the grazing pressures. The introduction of cattle changes the amount of herbaceous vegetation. These types of vegetation (i.e. herbaceous species) are the fine fuels that carry surface fires (Byram 1959). The elimination of fine fuels will greatly reduce the probability that an area will burn.

Just prior to the reduction in the occurrence of natural fires, early European settlement, i.e. mining operations, were marked by the burning of entire mountain sides (after extracting some timber) in order to expose the geologic patterns underlying the vegetation (Vandenbusche and Smith 1981). Several photographs in this study (8 of the 24 photograph pairs) depict the direct effect of the mining industry and associated settlements on the landscape of the region. Most of these samples show entire mountainsides that have been de-forested. In addition, the creation of tailings results in interspersion of perpetually bare slopes and islands of bare rock. As the photographs indicate, these disturbed landscapes have been largely re-occupied by forest in the present landscape.

The modern landscape is marked by continual change in land-use due to urbanization. Some historically mining communities have persisted and expanded as local tourism destinations (e.g. Crested Butte, Ouray, Telluride); other urban centers have expanded with the ongoing migration of modern society into formerly remote regions (e.g. Ridgeway, Gunnison). The construction of homes within the forest matrix, away from community centers creates a distinct new landscape pattern, which creates a new set of influences on the local landscape (e.g. Theobald, et al. 1997). My study does not document the expansion of urban, suburban, or rural human communities. However, the continued presence, and probable expansion, of such communities is evidence that human activities continue to affect many of the wild communities and the landscape patterns in this region.

1.3.3 Fire history

Gruell (1985) conducted a survey of historic journals and literature throughout the western region in order to document the occurrence of fires in the landscape. His survey included six states, Utah, Wyoming, Idaho, Montana, Nevada, and Oregon. Although this analysis conspicuously excludes Colorado, the regions sampled do contain similar ecosystems and many species common to those found in Colorado. Gruell (1985) suggests that, "fire was a major perturbation of the interior west," which is indicated by the spatial and temporal patterns described in the documentation of these fires (Gruell 1985, p.103). In addition, he suggests that, the dominant source of ignition was native American tribes; the Utes in Colorado were known to participate in wildfire ignitions. Scar evidence on aspen in Utah suggested a mean fire return interval of seven to ten years during the period of 1770-1875 (Baker 1925 *in* Gruell 1985). This may be comparable to former fire regimes in southwestern Colorado. "Today, the number and sizes of fires in these regions have been markedly reduced, and large areas have not burned since the late 1800's" (Gruell 1985, p.103). Cattle grazing (fine fuels reduction), displacement of the Ute peoples resulting in removal of the human source for ignition, and suppression of natural ignitions combine to create this change in the disturbance pattern. In 1917, Wallace Hutchinson, of the U.S. Forest Reserve proudly documented,

> Prior to their [the National Forests] creation little or no effort was made to guard the timber on the public domain from fire. But during the past ten years, a most effective system of detection and suppression of fires has been developed by the forest service. Through these various means, the occurrence of disastrous fires has practically been eliminated, and the number of small fires materially reduced.
>
> (Hutchinson 1917, p.563)

Thus, it is apparent that the arrival of European settlers had an important role in changing the historic patterns of fire occurrence on the western landscape. The process of disturbance and regeneration is important to determining the landscape configuration, however it is not the only process that affects these patterns.

1.3.4 Regional climate

Although a thorough climatic study of the region has not been published, data are available from weather stations in the region (Colorado Climate Center). Data from three stations (Crested Butte, Silverton, and Telluride) are selected for their long history (start dates of 1900, 1906 and 1904 respectively) and elevation (8870, 9420, 8750 feet respectively). These time frames and locations are similar to the distribution of the regional photograph pairs in time and elevation. These data suggest that there has not been a trend towards change in precipitation or temperature in the last 100 years, however both of these factors are highly variable during this period. Mean temperature for the region was 36.6°F with an average high of 53.3°F and average low of 19.8°F. There is an average of 266 days when the minimum temperature is 32°F or lower, hence there are an average of 98 frost free days during the growing season. Mean annual precipitation is 24 inches. Variables not analyzed (e.g. length of growing season, and moisture available during growing season) may affect the relative reproductive abilities of aspen, conifers, and herbaceous species in the area. Although specific effects of a changing climate on this region are not documented, the records suggest that there have not been major changes in the climate of this region. Further, the one hundred year time span of this study is probably not sufficient to detect variations in vegetation due to small climate changes. Unless the change is significant enough to cause a massive, rapid die-off of the canopy dominants, changes in the community structure and landscape patterns will not be observable until the current canopy dies allowing successive generations to mature. Considering these species (aspen, spruce, fir) live for 100 to 300 years, or more, the changes observed are not attributed to climate change.

1.4 Techniques and literature review

1.4.1 Using repeat photography for evaluation of changes in landscape patterns

Several studies have been conducted using repeat photography to assess changes in the landscape. Veblen and Lorenz (1991) assessed the vegetation dynamics on the Front Range of the Rocky Mountains in Colorado. Gruell (1980) studied the effects of fire in the Bridger-Teton national forest, Wyoming. Progulske (1974) used photographs from the Custer expedition to assess human impacts on the ponderosa pine forests of the Black Hills of South Dakota. Numerous other studies have been conducted in a similar manner to assess dynamics in other systems (Hastings and Turner 1965, Rogers 1982, Vale 1987, Veblen and Lorenz 1988, Hart and Laycock 1996). The evaluation is conducted by comparing the two photographs for change over time using a qualitative assessment and comparison. These descriptive comparisons reveal much about long-term dynamics of these communities and landscapes, however none have attempted to quantitatively assess the changes in cover.

Studies that quantify change are becoming common in the field of remote sensing. Multi-temporal series of aerial photographs have been used extensively to quantify changes in terrestrial landscapes (Vuttera et al. 1998, Brown and Carter 1998, Knapp and Soule 1998, Zampella and Lathrop 1997, Snodgrass 1997, Mast et al. 1997, Wirth et al. 1996, Hart and Laycock 1996, Demers et al. 1995, Hester and Sydes 1992) as well as coastal and marine communities (Panapitukkul et al. 1998, Robbins 1997, Strong and Bancroft 1994, Deysher 1993). These studies, and others, have demonstrated the temporal and spatial variability associated with many ecological systems. However, few (e.g. Zampella and Lathrop 1977) of these studies extend beyond a few years of change.

In this study, images containing valley and mountain slopes with forest cover were selected as "aspen habitat" from the archives of the USGS. All photographs that include forest cover were considered potential sample sites. However after field investigation, locations that had no aspen within the landscape identified in the photograph were not used in the study. In 1995, each photographed location was visited to survey the current landscape patterns and photograph the landscape again. The result is a series of photographs creating a temporal frame of 80 to 110 years and a broad area within a region of similar vegetation, climate, and human history. These data points are not randomly distributed within the region of interest; they are clumped. This is partially a function of the distribution of forested land (the Gunnison river, Black

Canyon of the Gunnison, and extensive rangelands lie between these two forested regions) and partially a function of accessibility for the original surveyors. Recognizing these limitations, every effort has been made to represent the region accurately by attaining photographs distributed throughout the forested area.

1.4.2 Analysis of photographic records

A comparison of the photograph pairs was conducted to qualitatively assess changes in the landscape. Descriptions focus on evidence of disturbance events (e.g. fire, logging, and mines) and the extent and pattern of dominant cover types, i.e. conifer, aspen, rangeland, bare soil, rock, forest regeneration. Differences in the pattern and extent of vegetation cover between the two photographs were described subsequent to individual photograph descriptions. The set of photograph pairs was divided into two groups based on their disturbance history. Those with direct evidence of a recent, large disturbance event are distinguished from locations without this evidence (intact sites).

Quantitative analysis consists of classifying scanned photographs using remote sensing software (Erdas Imagine, versions 8.2 and 8.3). The resulting raster image is converted to a vector coverage. Data regarding number of patches, total area, and mean, minimum, and maximum patch size for each cover type are attained from the classified polygon representation, then area estimates are normalized as a percent of the total coverage. In this manner, variations in scale among different photographs are removed from the analysis. Data representing specified landscape metrics are analyzed as evidence of changes in landscape pattern.

1.4.3 Relating landscape change to community structure and dynamics

Following analysis of the photograph pairs, I sampled the forests appearing in the images to determine the size and age structures of these forests. My goal is to associate site history information provided by the photograph analysis with specific structural patterns in the forests. Two 500 square-meter belt transects oriented across the landscape represented in the photographs are used to sample the forest structure. Graphs representing the size and age structure of these forests are summarized to assess the current structure of the communities.

By combining the information from these two techniques, I expect to gain a more accurate understanding of the current patterns and ongoing dynamics than if I only used one technique. I expect to find similar age structure (e.g. population ages, reproductive rates) on landscapes with similar histories. Landscapes that experienced major disturbances at the beginning of this century should have a roughly single-aged overstory with rates of regeneration reflecting the composition of the overstory (i.e. little change in composition between old trees and young trees). Conversely, landscapes where fire has been excluded for longer than these recently disturbed sites should have forest age distributions that include an abundance of regeneration of shade-tolerant species and a lack of regeneration of shade-intolerant species (i.e. aspen).

2. Analysis of changes in forested landscapes using repeat photography

2.1 Introduction

Throughout the intermountain region, reproduction of aspen (*Populus tremuloides* Michaux) 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 to the overstory, especially fire; the current pattern of fire suppression is suspected as an inhibitor of successful aspen reproduction (DeByle et al. 1987). If aspen is not reproducing successfully, then I should observe a reduction of the presence of aspen on the landscape over time. This approach looks for changes in the landscape patterns, which are associated with the interruption of the disturbance and regeneration process.

This study investigates changes in forest cover on the western slope of the Rocky Mountains in Colorado, U.S.A. I use eight by ten-inch black and white photographs collected by United States Geological Survey teams near the turn of the last century as baseline data. The contemporary conditions are represented by another image that was photographed in 1995. My analysis is limited because the oblique photos provide slightly distorted estimates of stand shape. Aerial photographs, for example, have this problem to a far lesser degree because the stands are viewed from above with only small distortion towards the perimeter of images. The shape of canopy trees affects the shape of the stand in these images. However the use of precise image re-capture for the creation of paired images allows for accurate comparisons over time at each location. I do not analyze perimeter data because the shape of the crowns of the trees particularly affects this information. I assume area does not suffer from this dilemma because the area of the tops of crowns is small relative to the total patch size. Perimeter is potentially affected at all locations on the margin of a patch (i.e. because of crown morphology); therefore it does not provide information I can use in this study. Quantifying repeat photography comparisons is desirable, despite these limitations, because of the extended period between samples and the confidence ascribed to quantitative analysis. As previously discussed, changes in cover and landscape patterns are typically investigated using aerial photography and satellite imagery. These studies avoid the distortions discussed above, but they have limited temporal extent.

Finally, the distribution of data, especially when using historical information, is an important concern and limitation. 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 (Figure 2.1). These data points are not random; they are determined by the intended subject(s) of the original photographers. In this case the subjects were geologic features. The survey teams traveled extensively by horseback (evidence in photograph no.446 by W. Lee, see Appendix B 18), thus travel was not physically restricted to roads or railroad lines, but many of their photographs depict

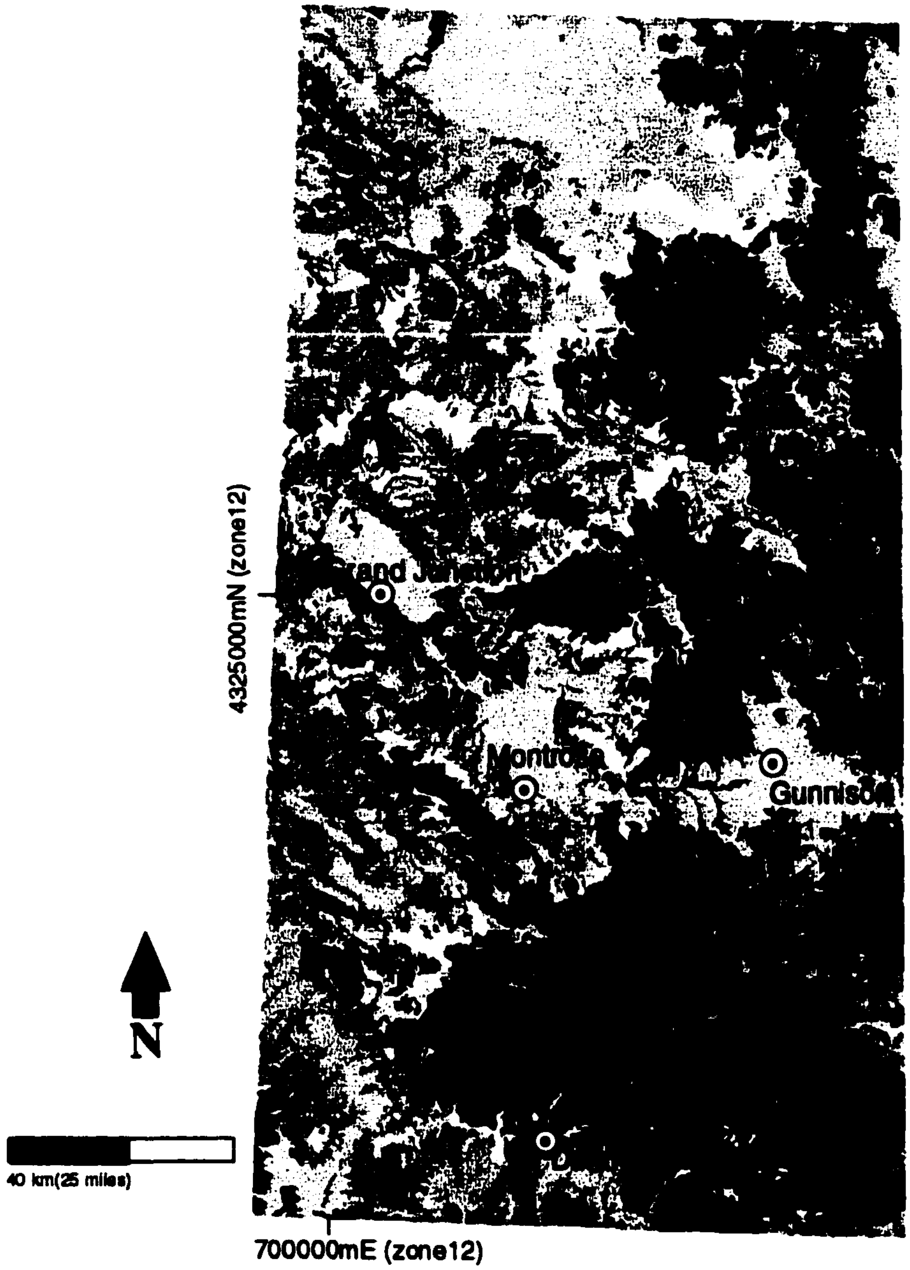


Figure 2.1: Detail of the western slope of the Rocky Mountains in Colorado. Major vegetation types (U.S.D.A. Forest Service GAP data) are identified in the map (green = forest types, yellow and beige = mixed rangelands). Sample locations are represented in red.

areas that are accessible (e.g. wide valleys, close proximity to well traveled routes). There is not, therefore, intentional bias on the assessment of forest cover, but possibly incidental bias toward areas of human interest and use. The remoteness of several of the sample sites is evidence that there is not a consistent bias in the distribution of data points. My expectations are that the century of fire suppression has not resulted in decline of aspen forests on the western slope of Colorado. However, I do expect that this widespread management practice has affected the landscape patterns in which aspen is found. Specifically, I 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; this will be apparent as a significant change in the corresponding landscape characteristics of total cover and mean patch size. I do not expect that conifers have replaced aspen on the landscape in this period.
- The cover of rangelands, within the forest matrix or forested mosaic, has decreased in area and number of patches. This is necessary if both aspen and coniferous forest cover have increased.

While comparisons of individual patches could yield useful information regarding expansion or reduction of these specific patches, my interest is in the trend of change across these units, i.e. across the forested landscape. Thus, I selected landscape metrics (total cover area, mean patch size and number of patches), which are strong indicators of changes in forest, cover (Trani and Giles 1999) to provide a simple, representative assessment of the changes evidenced in the photographs. I estimate the total area of coverage relative to the total classified area, mean patch size relative to the total classified area, and the number of patches for each cover type. In order to distinguish obvious differences in landscape history (i.e. disturbance history), I divided the 24 photographed landscapes into two groups; 12 locations have evidence of recent disturbances; twelve intact sites have no evidence of disturbance in the original photograph or the recent photograph. This procedure is subjective, but the photographic evidence is clear in most instances.

2.2 Methods

2.2.1 Photography techniques

The approximate locations of the sites were mapped using descriptions attached to each original photograph; specific adjustments were made in the field to insure exact image replication. A Nikon 35mm camera with a variable, wide-angle lens (28-45mm) was used to photograph the contemporary landscape. Although the original landscape was photographed using the wide-angle lens and large format cameras, a variable, wide-angle lens on a 35mm camera was able to capture the same area as the original in most cases. Panoramic pairs were used in cases where the range of the lens was not sufficient.

2.2.2 Qualitative analysis

I conduct a comparison of the photograph pairs to qualitatively assess changes in the landscape. Towards 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 are noted. The photographs are compared to identify differences in the pattern and extent of vegetation cover. Recognition of individual patches as well as an overall (across the photographed area) assessment of change between the two times provides an accurate description of changes on the landscape. In most cases these changes are widespread. The assessment of changes in total cover and patch characteristics (number, size, and location of patches) is central to each comparison, however the information regarding these variables is observational, and therefore less specific than that which is provided by the quantitative analyses. The percentage of study sites showing a particular pattern is used to summarize this qualitative information (i.e. net increase in forest cover, increase in conifer cover, increase in aspen cover, decrease in rangeland cover).

2.2.3 Quantitative analysis

The following section describes the techniques used to classify each of the photographs into a vector coverage for quantitative analysis (Figure 2.2).

A. Scan the image (200 dots per inch) to create a raster file from the photograph.

B. Conduct an image-to-image rectification of the new photograph to the original photograph using a first order (linear), nearest neighbor re-sampling algorithm. This procedure corrects small differences in the angle of image capture between the original photograph and the contemporary one. It is similar to the procedure used to geo-rectify aerial photographs. Nearest neighbor re-sampling assures that original data values are not changed, but their location is adjusted.

C. I subset the images to isolate the same analysis area. Because the scale of objects in the foreground and background is different, height growth of individuals in the foreground has a similar quantified effect as expansion of patches in the background. This is a source of error that is difficult to control except by removing extreme portions of the image through sub-setting. To subset the image, a polygon, which circumscribes the central area of the original photograph, is defined. This polygon is used to define the new perimeter for both the original photograph and its photographed mate. This reduces the problem of differences in scale between the foreground and background, but it does not eliminate it. Use of the same polygon to subset both images creates a uniform sampling area for making quantitative comparisons.

D. A supervised classification is performed using the signatures (gray scale intensity) of the dominant cover types using Level I classification modified to recognize Level II classification in the case of forest types (Anderson et al. 1976). Conifer, aspen, dead and down trees, mixed rangeland, bare soil, and rock were common classes, while snow and water were lumped into the surrounding cover type. These classifications require extensive manual editing because of the spectral limitations of a black and white photograph (compared to color, infra-red, or satellite imagery, for example) and overlap of the classification signatures within the photographs (i.e. foreground and background color similarities).

E. The thematic raster image is filtered using a 5x5 pixel majority filter (to remove some of the classification noise), then converted from a raster image to a vector coverage.

F. Editing of the classification is accomplished using on-screen digitizing.

G. Classification accuracy is assessed using the automated procedure in the Imagine program. Test points are generated using a stratified random design and then they are displayed on the original photograph for user identification. Overall user accuracy and the Kappa statistic are generated to describe the accuracy of the classification (Appendix A). Classification accuracy estimates range from 75% to 100% with errors attributed to patch border regions. Tests on the Kappa statistic suggest that standard use (single run tests) may not yield accurate results (Kalkhan, Reich, and Czaplweski 1996). However, time limitations prohibit the use of a boot strapping technique, which requires multiple tests of accuracy for each image (all 48 classified photographs in this case) to create a distribution of accuracy values, which then represent the accuracy of the classified image.

H. The completed classification is used to generate statistics for number of patches, total area (represented by a pixel count), mean, minimum and maximum patch size, and variability of patch size for each cover type.

I. Data are summarized using change in percent cover (total cover and mean patch size) and the number of patches to make comparisons between photograph pairs.

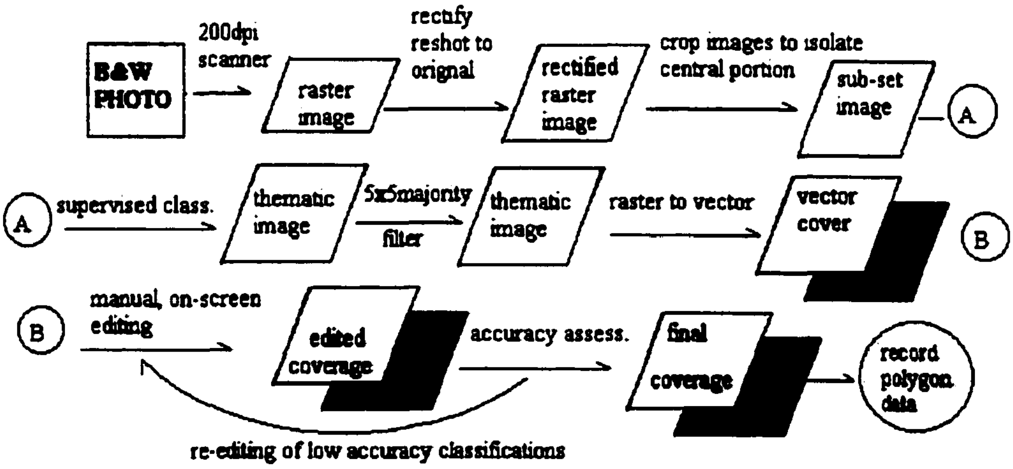


Figure 2.2: a flow chart of the image classification process.

2.2.4 Statistical analyses

A pairwise analysis of variance (ANOVA) procedure was used to compare the former conditions with the current landscape configuration (Ott 1993). The twenty-four classified images are separated into the same two populations of twelve samples each as described in the qualitative assessment. Photograph pairs that depict broad disturbance events (e.g. standing dead, large canopy openings with widespread regeneration of trees, and dead and down trees) with extensive overstory mortality are grouped together in the recently disturbed category (i.e. they were burned immediately prior to the successful implementation of wildfire suppression policy)(see examples in Plates 1 and 2). Photographs, which showed small disturbances or inconclusive evidence of recent disturbances, are categorized as intact landscapes. The landscape patterns may suggest disturbance in the site history, but evidence of a recent disturbance (i.e. one that is apparent in the photographs) was not observed (see examples in Plates 3 and 4). I make this distinction to recognize and explicitly address the role of recent disturbance in determining landscape pattern.

The 'F' distribution was used to assess the significance of differences between paired photographs (same location) in total cover, number of patches, and mean patch size. Raw values are attained directly from the vector coverage attribute files. Total cover and mean patch size are normalized as percentages of the total value within the image. Changes in the number of patches are calculated using a direct comparison (not normalized) between paired photos. Quantitative comparisons are made using these estimates of the landscape metrics.

Plate 1.

Site: **L 459**

The Castle

a. Original photo by W. Lee 1909.

b. Recent photo by D. Manier 1995.

Aspect is to the southeast.
Elevation ranges between 9600 feet and 10,000 feet.

The original photo shows evidence (e.g. standing dead, and dead and down) of an extensive, high intensity fire in the recent past (a presumed natural event due to the remoteness of this location). Conifer forests at the top of the slope remain mostly unaffected. The lower slopes have sparsely distributed surviving individuals. The contemporary photograph contains extensive aspen cover with small patches of conifer forest within the aspen matrix. Remnant aspen patches have expanded and regenerated to create the current closed canopy aspen forests. Conifers are limited in distribution to location and extent of remnant stands (in the central portion of the photo); their total cover and mean patch area have changed little since the fire. Regeneration of the foreground forest (left) demonstrates more varied species composition (conifer *and* aspen). Based on spatial extent, aspen dominates the increase in forest area (total cover and patch size) on this site.

Plate 2.

Site: **Cr 472**

North face of Red Mountain #2 at Ironton

a. Original photo by C.W. Cross 1900.

b. Recent photo by D. Manier 1995.

Aspect is to the North-northwest.
Elevation ranges between 10,200 feet and 13,500 feet.

Most of the forest cover has been removed by heavy mining and related logging activities on the landscape depicted in the original photo. Sparse to dense regeneration is apparent in some areas, especially the lower slopes. The town of Ironton, established in conjunction with the local mines, extends across the foreground, and mines dot the background slopes. The influence of major, human induced disturbance is obvious here. This area has regenerated into a mixed conifer / aspen forest with patches of aspen interspersed and widespread within the coniferous matrix. Aspen distribution is similar but not limited to the regions of regeneration in the original. Forest cover and extent have increased and the number of forest patches has necessarily increased as there was little forest standing in the original photograph. The former town of Ironton contains two structures now, however several mining companies continue to operate elsewhere in the valley.

Plate 3.

Site: **Cr 246**

Ophir needles

a. Original photo by C.W. Cross 1899.

b. Recent photo by D. Manier 1995.

Aspect is to the west.
Elevation ranges between 10,200 feet and 12,500 feet.

The original photo shows a patchy, i.e. many distinct patch types, landscape. The interspersion of different sized patches is probably the result of the historical disturbance regime (see Chapter 1.2.4). The contemporary photo 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. range 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.

Plate 4.

Site: **Cr 258**

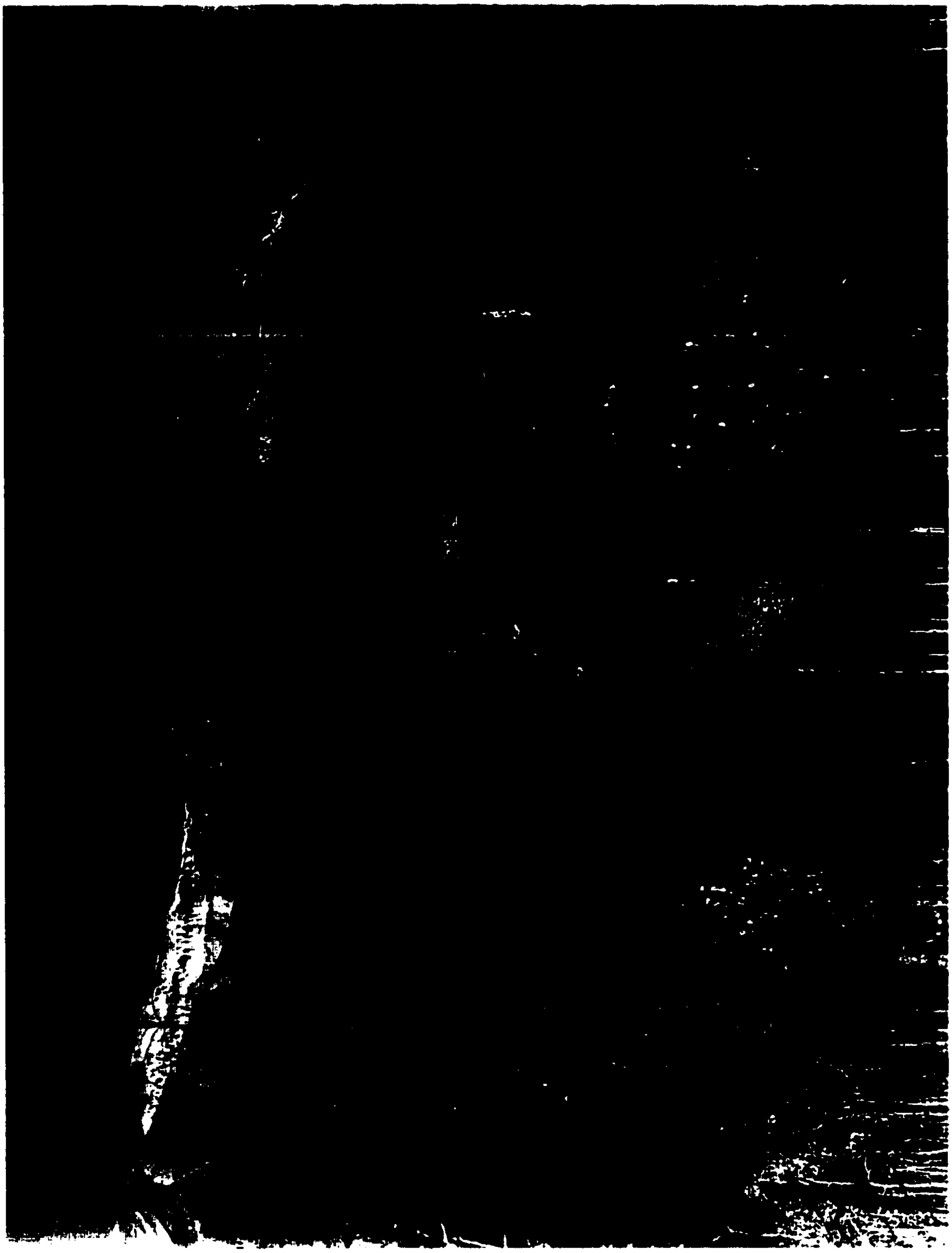
Deep Creek Mesa near Eider Creek

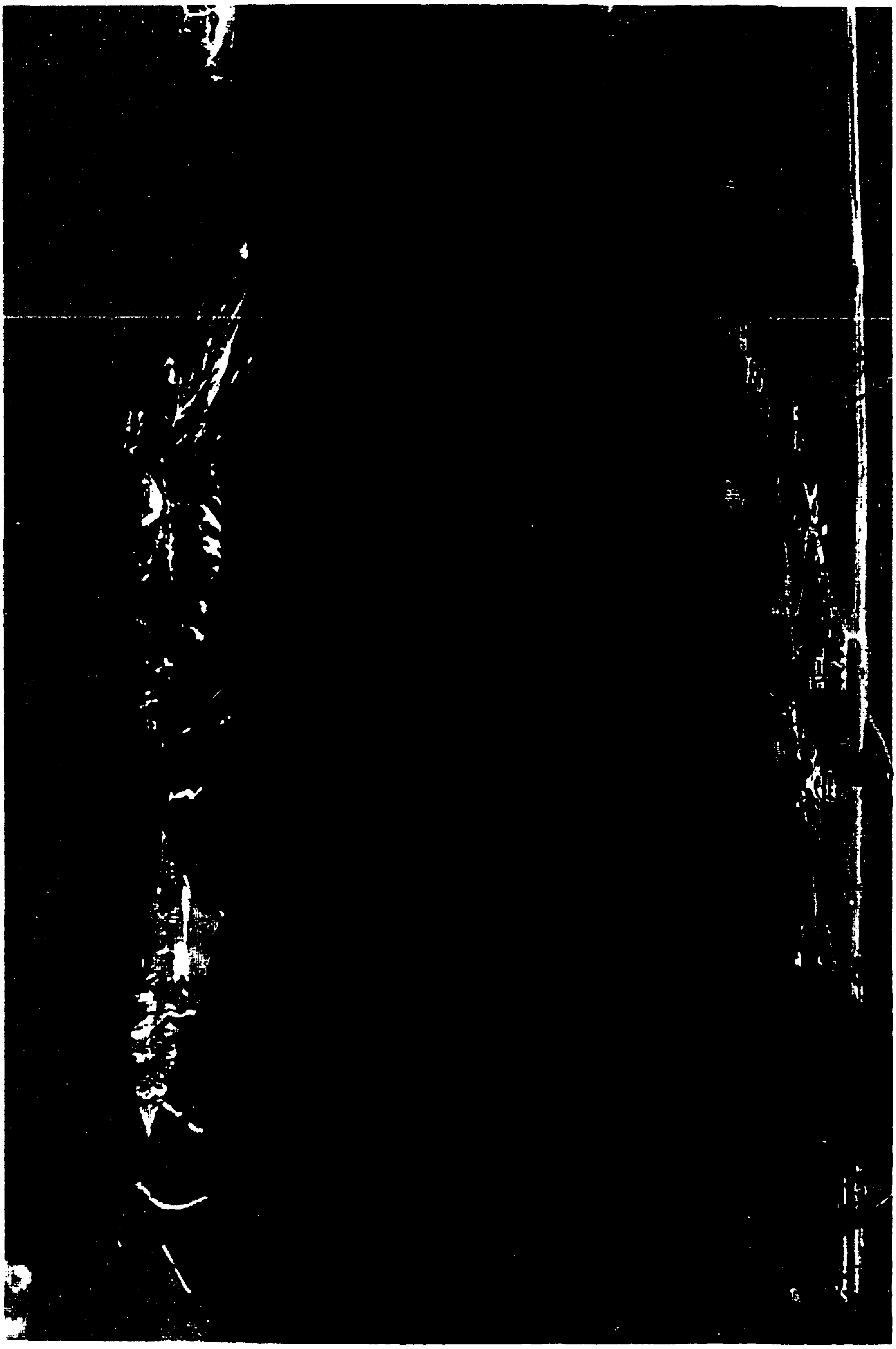
a. Original photo by C.W. Cross 1896.

b. Recent photo by D. Manier 1995.

Aspect is to the south.
Elevation ranges between 10,000 feet and 10,400 feet.

Large aspen stands interspersed with large open, grassy areas visible across the mesa in the original photo. Conifer coverage is primarily restricted to higher elevation slopes and lower drainages. The cabin and road (center-left in the image) confirm human presence, but there is no evidence of extensive affects. Currently, aspen forest blankets the rolling mesa. The large meadows are no longer present. Conifer coverage is extensive in localized areas; it is not prevalent across the landscape. Aspen is prospering here (resulting in expanded canopy coverage and reduced isolation of patches). Forest cover, both aspen and conifer, has increased dramatically here. Continuous forest cover has replaced the variety of cover types apparent in the original conditions. I can expect some age diversity in this forest if the aspen gradually colonized the meadows. However, the current lack of meadow patches (early seral patch types) is an obvious difference in the landscape that developed over the years.





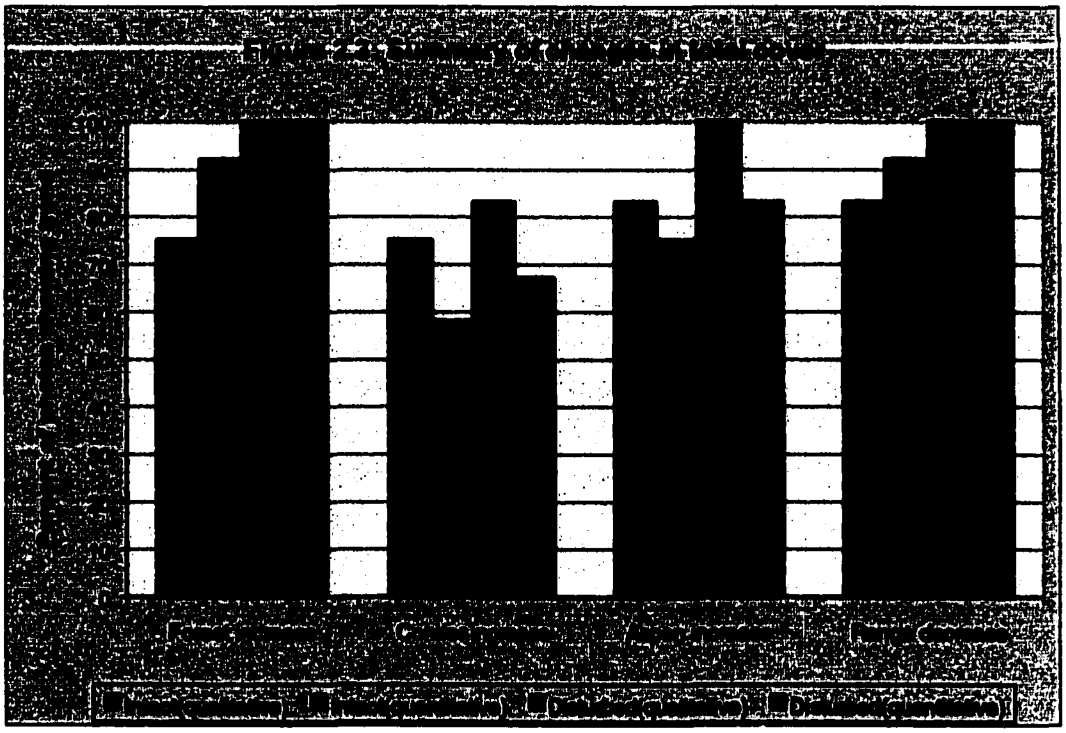
2.3 Results

2.3.1 Overview and results of the ANOVA

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 2.3). This is supported by the quantitative analysis of these sites where 96% of the classifications show a net increase in forest cover (Figure 2.3). According to the quantitative comparisons, conifer cover increased on 63% of all sites; aspen cover increased on 79% of all sites; and, coverage by rangelands decreased on 96% of all sites (Figure 2.3, and Tables 2.1 and 2.2). These changes are significant on the disturbed sites but not on the intact sites (Table 2.3). All (100%) photograph pairs that show a large disturbed area in the original photograph depict large increases in forest cover. Photograph pairs without evidence of major disturbances in the original photo have wide variation in landscape changes ranging from full canopy closure and reduction of patchiness (variety of patch types and sizes), to no observable change in the distribution of patch types. The two assessments agree that most of these sites (82% qualitative, 92% quantitative) do show an increase in forest cover (Figure 2.3).

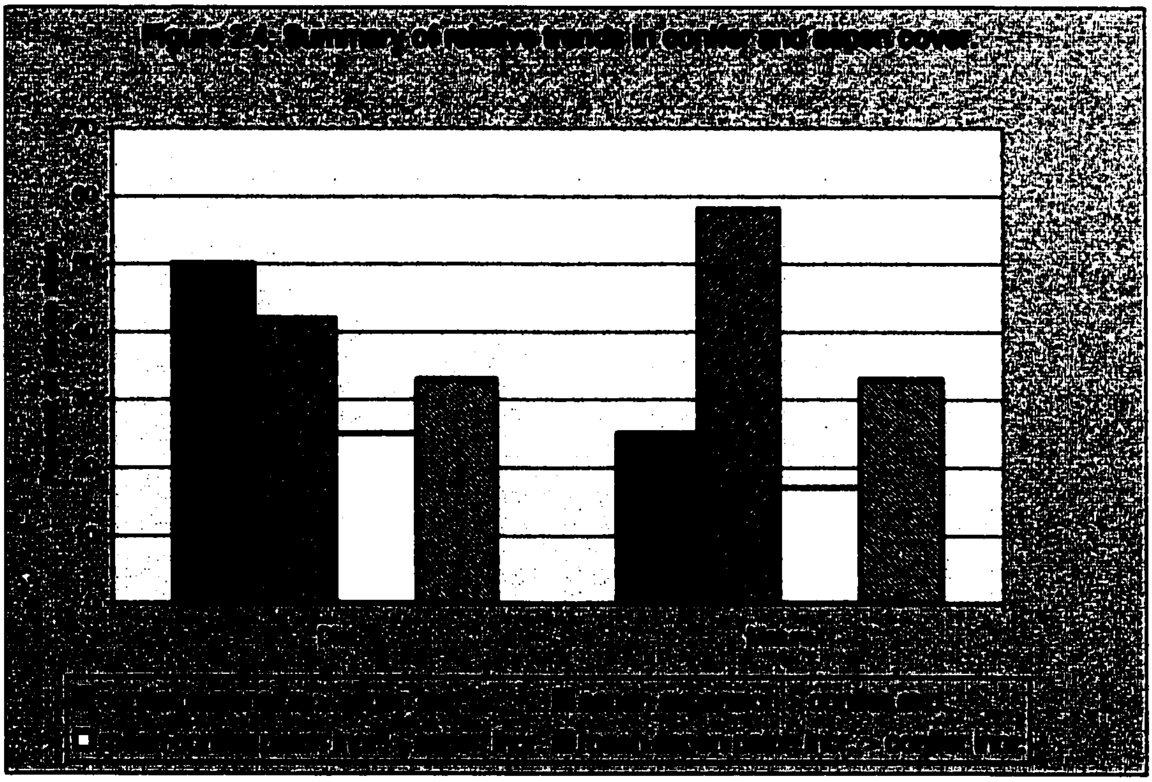
In contrast, the number of patches has not changed significantly among these sites in the last century. ANOVA comparisons detect no significant change in the number patches (Table 2.4) or mean patch size (Table 2.5) either in the recently disturbed or less disturbed sites. However the trends suggested by non-statistical summaries of these data suggest a decrease in the number of conifer patches on most

(58%) disturbed sites and an equal number of increases and decreases on intact sites; whereas, the number of aspen patches decreases on most (58%) intact sites and increases on most (58%) disturbed sites (Tables 2.1 and 2.2). The lack of significance in the statistical analyses is likely traced to the high variability among sites.



2.3.2 Intact sites

Over 80% (qualitative analysis) of the undisturbed sites show an increase in forest cover (aspen and conifer) (Figure 2.3), which is associated with an increase in the contiguity of the canopy (an increase in the average patch size). The remaining 18% showed little change in landscape configuration. Of the twelve intact landscapes, the configuration of nine of them suggests a history of localized disturbance. This is inferred by the size of cover patches (small versus large), and the interspersion of open rangelands within the forest creating a mosaic of types versus the patch and matrix configuration of the contemporary landscape (see Plate 3 for an example). Similar trends are apparent in the quantitative data (Table 2.1). Coverage of most conifer forests shows an increase in total relative area (75% of the areas show an increase and 15% show a decrease). These data show an increase in number of patches in some locations (50%) but no strong trend in the average relative size of patches. Aspen forests also show an increase in total relative coverage (75% of intact sites) as well as an inverse relationship between the number of patches and the average relative size of patches (Table 2.1). Mixed rangeland coverage shows a strong decline; 92% of pairs show a decrease in total relative cover and 50% show a decline in the number of patches. Thus, on the intact sites, both forest cover types display an increasing trend; 58% of these sites show greater expansion of conifer cover than aspen cover; only 25% show greater expansion of conifer cover than aspen cover (Figure2.4). Only one location shows a decrease in forest cover and an increase in rangeland cover. These



data suggest changes in the landscape configuration beyond simple dominance by a particular cover type. The trends suggest the expansion of forest stands (aspen and conifer) into neighboring open habitat resulting in elimination of gaps in the canopy (reducing patch separation). Thus, the mosaic pattern of landscape elements has converted into a more homogeneous structural pattern, i.e. one with less patchiness (see Plate 3 for an example of this pattern).

2.3.3 Recently disturbed sites

All (100%) of the disturbed sites show a dramatic increase in forest cover according to the qualitative analysis. In over half of these cases, aspen expansion exceeds conifer expansion; qualitative assessment recognizes that 27% of these sites show greater expansion of conifer forest than aspen forest; 18% of the pairs showed nearly equal expansion of conifer and aspen stands (Figure 2.4, Table 2.2). According to the quantitative data, 67% of the pairs show an increase in the total relative cover of conifers, and 83% of the pairs show and increase in the total relative coverage of aspen (Figure 2.4, Table 2.2). The number of conifer patches decreased on 58% of the sites, while the number of aspen patches increased on 58% of these sites (Table 2.2). Aspen expansion exceeds conifer expansion in 55% of the disturbed sites, but conifer expansion exceeds aspen expansion on the other sites (Figure 2.4). Thus, large area disturbance events do not appear to simply select the dominance of one cover type over another. Details of change in spatial dominance (i.e. prominence on the landscape) for competing species due to specific fire events (i.e. community level competition mediated by periodic disturbance) requires a more detailed analysis of fire behavior and local regeneration patterns.

Table 2.1: Quantified changes for intact sites.

Photo [illegible]	Range (years)	change in % total cover by type				change in number of patches per type				change in % of area covered by an average sized patch by type			
		conifers	aspen	grass/shr.	rock	conifers	aspen	grass/shr.	rock	conifers	aspen	grass/shr.	rock
Cr102 Anthracite Rng.	1887 - 1995	1	6	-12	5	-25	4	4	0	1	-9	-3	5
Cr246 Ophir needles	1899 - 1995	-4	17	-7	-5	-40	-89	-52	-105	0	51	0	21
Cr248 Ophir loop	1895 - 1995	10	-6	-8	4	-10	-7	-4	8	0	1	-1	2
Cr249 San Miguel R.	1885 - 1995	-9	-21	24	6	9	34	3	-13	0	-7	1	4
Cr258 Dallas Pk.	1896 - 1995	8	14	-30	7	129	-7	2	-4	0	-2	-2	0
CR480 Monument Gl.	1900 - 1995	2	5	-10	3	97	0	5	-1	0	2	-1	0
CR489 Canyon Cr.	1900 - 1995	2	13	-16	1	-9	-11	-16	-2	0	11	0	0
Cr58 Gothic Mtn.	1887 - 1995	10	36	-52	5	-33	-8	6	0	0	20	2	5
H233 El Mandhi mine	1904 - 1995	36	-1	-12	-24	-29	-2	-8	-16	19	0	-1	1
H41 Red Mtn. Valley	1900 - 1995	7	4	-9	-1	34	1	18	-1	0	-3	-6	0
L425 Gothic & Snodgrass Mtns.	1909 - 1995	3	45	-44	-4	27	-6	15	-7	0	24	-39	0
L431 Gibson Rdg.	1909 - 1995	23	13	-33	-3	32	14	26	5	-2	1	-4	1
Average		8	10	-17	-1	15	-6	0	-11	2	8	-5	3

Table 2.2: Quantified changes for disturbed sites.

[illegible]	[illegible]	change in % total cover by type				change in number of patches per type				change in % of area covered by an average sized patch by type			
	Range (year	conifers	aspen	grass/shr.	rock	conifers	aspen	grass/shr.	rock	conifers	aspen	grass/shr.	rock
Cr 11 Cement Cr.	1885 - 1995	1	51	-52	-1	1	-5	-12	-17	0	23	38	0
Cr 18 Mt. Teocalli	1885 - 1995	4	13	-18	1	6	-19	-2	0	0	8	0	0
Cr205 Deep Cr. Mesa	1895 - 1995	-1	31	-9	-21	3	2	16	2	0	12	-1	2
Cr225 Iron spring, Ophir	1895 - 1995	28	3	-25	-6	-6	33	-6	-8	64	0	-3	4
Cr472 Red Mtn. #2 at Ironton	1900 - 1995	68	-5	-57	-6	-12	89	-5	9	5	0	-4	0
Cr473 Corkscrew Gl.	1900 - 1995	42	11	-42	-11	19	62	18	25	1	0	-5	1
Cr475 Red Mtn. #2	1900 - 1995	68	4	-67	-5	-71	11	4	-18	26	0	0	0
H244 Corbett Gl.	1904 - 1995	26	-2	-31	6	-98	-38	-8	-21	3	1	-1	1
L446 Slate R. at Oh-Be-Joyful Cr.	1909 - 1995	44	5	-45	-5	-29	10	18	-35	1	0	-4	0
L459 Castle	1909 - 1995	-5	28	-30	7	7	3	4	5	0	3	-3	0
L729 Telluride - Bear Cr.	1910 - 1995	6	13	-27	8	-40	-16	13	7	0	6	-20	1
P89 Telluride - Boomerange Ridge	1896 - 1995	-6	33	-26	-1	-51	13	-31	-8	3	1	1	0
Average		23	15	-36	-3	-23	12	1	-5	8	4	0	0

Table 2.3: Anova results for change in percent of total cover by type. (df1=2, df2=11)

Cover type	F-value, intact sites	F-value, disturbed sites
conifer	0.336	2.835 *
aspen	0.32	2.931 **
mix. Range	1.498	7.706 ***
mineral	0.086	0.077

Table 2.4 Anova results for change in the number of patches by type. (df1=2, df2=11)

Cover type	F-value, intact sites	F-value, disturbed sites
conifer	0.001	1.281
aspen	0.398	0.432
mix. Range	0.652	0.014
mineral	0.513	0.432

Table 2.5: Anova results for change in the percent area covered by an average-sized patch. (df1=2, df2=11)

Cover type	F-value, intact sites	F-value, disturbed sites
conifer	0.359	0.923
aspen	0.729	1.682 *
mix. Range	0.887	0.002
mineral	0.07	0.107

*** signifies significance at alpha = 0.05 (F = 3.98),
** signifies signifcance at alpha = 0.10 (F = 2.86)
* signifies significance at alpha = 0.25 (F = 1.58)

2.4 Discussion

2.4.1 General trends and statistical analysis

Although the statistical analysis fails to detect most of the observed differences in the landscape, several significant, and many non-significant, changes are observed. Statistical analysis suggests that the relative total forest cover of recently disturbed landscapes has increased, and the relative area covered by rangelands has decreased in the same areas. The analysis of other landscape characteristics does not detect changes in patch number, size, or size distribution. However, a comparison of individual pairs of images and observation of the trends in these data reveals that in many cases, there has been important, observable change in the configuration of the landscape at many of these locations. The wide range of values in the analyzed variables (variability among sites) is primarily responsible for the reduced significance of these variables. This is reflected in the statistical analysis; further, the wide range in cover type distributions can be easily observed in the images. My observation of the development of these landscapes suggests that patterns of community regeneration are not homogeneous within burned areas. Thus, I suggest that 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, site, 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.

2.4.2 Aging forests

The lack of statistical significance in this study contradicts the apparent trend of changes observed in landscape pattern in the photograph pairs. There is a strong tendency across the study areas for an increase in forest cover. This is common to sites with a recent disturbance history and more intact locations. Landscapes with composition and structure that have been determined by fire in the past will demonstrate observable changes over time when that disturbance is excluded. The observable changes are closely related, and they can be observed in two distinct patterns. By watching temporal change in a single stand, I expect a cohort of later successional species, established under the canopy of the early canopy dominants, to replace the less-competitive species (Bartos et al. 1983). Spatially, a similar pattern occurs as slower growing, less prolific species will expand into available patches, i.e., woody species move into range patches (Gruell 1983, Veblen and Lorenz 1991). The periodic occurrence of fire on these landscapes removes woody dominants from some areas allowing temporary dominance by rangeland species and other early seral species.

The original photographs of undisturbed sites provide evidence of the difference in patterns between the present and the past. These sites are characterized by small patch sizes and interspersion of forest and range cover types. After the recent period of fire suppression, the spatial heterogeneity associated with this pattern of inter-spacing is converted to a more homogeneous condition of canopy closure as evidenced in the contemporary photographs. This suggests a difference in the process that created the observed landscape patterns. Figure 2.4 reveals a distinctive difference between the changes on disturbed and intact landscapes. Aspen expansion exceeds conifer expansion on the intact landscapes, but the opposite is true for recently disturbed landscapes. This pattern contradicts the development patterns described by Bartos et al. (1983). According to that model, the older landscape should have greater increases in coniferous species, and vice versa for younger landscapes. This inconsistency is resolved if I consider a spatial component to the patterns Bartos et al. (1983) described. If I assume that the process of succession is similar at all of these locations (disturbed and intact), and the configuration of the landscape (i.e. the pattern of patches) is the primary difference between each of them, then the processes that created the initial patterns may be responsible for the differences in landscape change. Thus, these patterns suggest a difference in the processes, especially a difference in fire behavior, which created the template for my observations of landscape change. AS time passes the recruitment and growth patterns described for a single stand also work to expand forest species into available space, i.e. rangeland.

While losses of aspen over broad areas are not apparent at this time, continuation of the current disturbance regime will likely result in a continuation of progressive change in forest structure; this change can be expected if the success of aspen on the landscapes is associated with expansion into non-forested patches. These patches, created by individual tree deaths (very small gaps) and periodic disturbance (larger patches from a few square meters to hectares), are an opportunity for shade-intolerant, colonizing species to occupy a landscape without tall, slow growing species (spruce and fir) inhibiting the growth of these species.

My data does not support the claim that aspen has been lost from the landscape. In fact, aspen cover has increased in many locations. While I still expect to find variability in the age distribution of aspen across the landscape (ascribed to recent colonization of open patches), the decline in the presence of areas available for reproductive success (i.e. rangeland patches within the forest or thin forest stands where self-replacing regeneration can occur) suggests future regeneration problem. In addition, where aspen and conifers share the landscape, conifers (especially spruce and fir in this region) will, over time, develop in the understory of aspen stands where aspen regeneration is usually unsuccessful. This study provides no direct evidence of this successional pattern, but it identifies a landscape that would support this type of development, i.e. closed canopy forests that favor regeneration of shade-tolerant species over less competitive species.

2.4.3 Regenerated forests

The regeneration of forests after the major disturbances associated with mining and mineral exploration has been extensive and nearly complete in most areas. However, without data regarding the pre-disturbance forest structure, I cannot know if the current forest is similar to the pre-disturbance forest. Only localized patches remain bare, and these are usually associated with harsh soil conditions (e.g., scree and talus slopes, tailings piles and tailing ponds) that limit all plant growth.

Regeneration of these disturbed landscapes is not limited to any particular cover type. The current landscape is dominated by a mix of aspen and coniferous forests. According to the data, the increasing trend in total cover and mean patch size for conifers and aspen is more than twice the percent change in these attributes for the recently undisturbed sites. This finding is not a surprise as many of these disturbed areas were classified as open range or new regeneration (without species differentiation) in the analysis of the original conditions. However, it is excellent testimony of the ability of forest to regenerate after large disturbance events.

Site-to-site variation in species dominance is attributed to between site differences and pre-disturbance conditions. Aspen has reacted with vigorous regeneration following the disturbance events. However, coniferous species have also regenerated dramatically, even in areas with abundant aspen. This suggests that the role of disturbance in the interaction of these species is not simply one of determined successional development following disturbance events that reset the successional clock. I can, and do, observe changes in species dominance within a stand over time. These changes generally reflect the early dominance of rapidly colonizing or regenerating species, followed by a succession of dominance by slower growing species. If I consider colonization patterns, slow-growing, long-lived species may exist throughout the initial community and dominate the canopy when shorter-lived species die; others may persist due to isolated survivors (individuals or clumps of individuals) which facilitate expansion into the rest of the stand over time; others may need to re-colonize from neighboring populations when the distance between the seed source and available habitat is large. Thus, fire behavior and fire induced mortality interact with species life history characteristics to determine future community and landscape structure by affecting the survival of aspen roots, conifer seed sources, soil conditions, and initial forest patterns.

Naturally disturbed sites (e.g. Plates 1,3,4) currently display a higher degree of heterogeneity on the landscape than do those that are affected by widespread human induced disturbance (e.g. Plate 2). The observable difference is the interspersion of open patches of rangeland within the forest mosaic. Although this study provides no direct evidence, analysis of the photos suggests that human induced disturbances of the mining era had a different effect on the landscape than did more natural disturbance events of the same and earlier period.

2.4.4 Conclusions

My suspicion that the century of fire suppression has not resulted in the decline of aspen on the western slope of Colorado is confirmed. However, I did find that this widespread management practice has affected the landscape patterns where aspen is found. Specifically, I hypothesized that aspen cover has increased significantly since the turn of the last century resulting in more total cover and larger continuous patches of aspen than was found on the previous landscape (circa 1900). According to the photographic record I have compiled, most aspen stands in this region have expanded their boundaries into adjacent areas. However, this does not mean that all aspen stands in the region are continuing to reproduce without the threat of conifer invasion. I also discovered that conifer cover has increased in the last 90 to 100 years, and I found that the corresponding landscape characteristics of total cover and mean patch size have increased. In order to accommodate this expansion of forests there has been a corresponding reduction in the cover of rangeland patches within the forest mosaic. This does not necessarily mean that open range is in jeopardy in Colorado. It does suggest that a particular type of range habitat (specifically, meadow patches within the forested matrix) is being lost from the landscape. This could have important implications for wildlife (e.g. for deer which use these patches for forage), recreational uses (e.g. for people who observe flora and fauna, camp, or hunt in these patches) and ecosystem health (e.g. if the identified pattern is one of increasingly old forests and a decrease in young forests and other early seral stages). Although details regarding specific conversions of one cover type to another and patterns of expansion are not part of this analysis, my data and analysis suggest that forest dominants have expanded at the expense of open rangeland patches resulting in a more homogeneous canopy and landscape texture than existed under the previous disturbance regime.

Chapter 3: Size-age structure analyses

3.1 Introduction

Following the characterization of changes in landscape patterns using photography, I examined the structural patterns (size and age distributions) in the same locations that appear in the photographs. Characterization of forested landscapes using size and age distributions has been conducted frequently in Rocky Mountain forests to study population structure (e.g. Whipple and Dix 1979, Knowles and Grant 1983, Parker and Peet 1984, Shea 1985, Mast et al. 1998) and community dynamics (e.g. Stahelin 1943, Day 1972, Veblen 1986, Aplet et al. 1988, Crawford et al. 1998).

My goal for this project is to investigate the relationship between changes in landscape pattern and forest community structure within that landscape. I expect to find older individuals and later seral stages within forests that have not been disturbed recently, compared to those sites that were disturbed near the turn of the last century. This distinction is the same as the separation of the sites for analysis of landscape change (chapter 2). Specifically, I expect to find a lack of regeneration of shade-intolerant species (e.g. aspen) and the current regeneration to be dominated by slower growing, shade-tolerant species (e.g. fir and spruce). The distributions of these shade-tolerant populations are expected to reflect continuous reproductive success resulting in the distribution of individuals across all size and age classes (Day 1972).

Further, I expect that the twelve sites characterized by large disturbances near the last turn of the century are still dominated by the first generation (colonization phase) following the disturbance. Thus, I expect to find predominantly 80-100 year old trees with a similar age distribution (young and middle-aged trees) for all species at the site. I do not expect to find an advanced successional trend towards more shade-tolerant species.

Conversely, the twelve landscapes that show no evidence of a major disturbance 100 years ago (or in the present) have experienced a much longer disturbance-free period of growth. Therefore, these forests should possess a more mature age structure (i.e., exclusion of less competitive species with increasing canopy closure). Closure of the canopy changes the environment in the understory limiting regeneration to shade-tolerant species, or to individuals who have the fortuity of living in a canopy gap. Thus, these communities will have abundant regeneration of spruce and fir producing a second generation under and around the older first generation. I also expect a lack of successful regeneration of shade-intolerant species. These forests are of particular concern for addressing the regeneration and persistence of aspen on the landscape. Specifically, I hypothesize that:

- Stands where disturbance is absent for more than 100 years (i.e., intact sites) will show a lack of aspen regeneration and proliferation of shade-tolerant conifers.
- Sites that were disturbed immediately prior to the fire suppression era have not developed into these later seral stages resulting the continued proliferation of aspen suckers, and very few old individuals, i.e. a continuous distribution of regeneration suggesting perpetuation of the overstory dominants.

3.2 Methods

3.2.1 Sampling design

Using the copies of the contemporary photographs from the previous study, I identified transect locations (two per photograph) to serve as representatives of the landscape portrayed in the photograph. This is a subjective (non-random) procedure focused on providing an accurate representation of the current landscape represented in the images. Transects were located near the center of the photographs in accord with the classified portion of each image. Transects are subjectively located to sample stands that represent the landscape features (cover types) dominating (spatially) in each photograph. Two transects were used in each photograph (except as noted) to cover as much of the photographic frame as possible; four sites were sampled using only one transect because of the limited area represented in the photographs.

3.2.2 Field techniques

I established the starting point for each transect by using landmarks in the photograph and local topographic maps. Specific coordinates were not available because details of the photographs have not been mapped, however most transects can be re-located using the coordinates I established using a geo-positioning system (GPS). These records should allow future researchers to resample these exact locations. All transects were established parallel to the slope contour.

I established 2m by 250m transects to sample all live trees and tallied them by species and size class (five-centimeter increments). I traversed back through each transect and extracted an increment bore at breast height from 10% (minimum) of each size class for constructing size-age relationships. Tallied size data are used to generate species distribution curves. Tree cores are used to generate size-age distributions in the laboratory.

3.2.3 Size-age distributions

I sampled composition and abundance by size class for each transect, then removed increment cores from representatives of each size class in the transect to identify ages associated with each size class. Considering it important to recognize the relationship between size and age for each species on each site, I investigated this relationship. There can be size independent cohorts of aspen (Mueggler and Campbell 1986, Shepperd 1990), and there is a demonstrated lack of correlation between size and age in spruce-fir forests (Aplet et al. 1988). Further, Knowles and Grant (1983) discuss the important role of size for reproductive output suggesting that larger individuals (not necessarily older) reproduce most prolifically. With this in mind, I designed a sampling regime where by collecting information on both size and age, a clear picture of the structure of these forests is gained. I collected size data (using 5-centimeter size classes) for each transect and cored 10% of each size class (with a minimum of 2 per class). By evaluating the size distribution data and the size-age data together, I avoid the error of assuming a small tree is young. In addition, I am able to recognize particular size-age distributions that characterize understory regeneration, e.g. continuous regeneration versus reproduction concentrated in similarly aged cohorts.

Data for each transect are graphed with a best-fit line using either a second order polynomial function, logistic function, or exponential function to help describe the relationship between the variables. As the goal for these data is not to detail the relationship between size and age for each site, I did not conduct regression analyses on these data. Further, continuous distributions can be misleading when interpreting size-age distributions. When establishment patterns result in distinct cohorts, there can be little to no mathematical relationship between size and age distributions. For this reason, subjective, cluster analysis was used to recognize cohorts and distinguish them from continuous, multi-aged regeneration.

3.2.4 Increment core analysis

Cores collected in the field were analyzed in the laboratory. Trees were cored at breast height. Although this may result in loss of some variability in the smallest age class (trees under breast height), the age distribution of individuals under five centimeters at breast height and the five to ten centimeter class, along with the overall regeneration pattern (i.e. cohorts or continuous), are used as a indicators of variability in this smallest class. Core samples that missed the pith were given additional years based on estimations from complete cores of other trees in the same stand (with similar ring densities). Aspen cores were mounted and sanded to make incremental growth rings apparent. Wet (tap water) cores were counted under a dissecting microscope (10x - 20x). Conifer cores were temporarily mounted and rarely sanded in most cases, as the rings are easily apparent with wetting and use of a microscope. Errors associated with missing rings and cores taken at breast height are not regarded as critical to this analysis, because errors of a few years will not change the character of a 90-110 year old cohort, for example.

3.3 Results

3.3.1 Size-age distributions

Structural patterns across the sampled landscapes were summarized by constructing tables that present information regarding forest structure at each site (tables 3.1 – 3.4). The tables isolate overstory and understory components of the forest structure. However, accurate analysis requires consideration of both components together. The information recorded in the tables summarizes the size-distribution data and the size-age distribution data in conjunction. Size-distribution data provide primarily abundance information, while the size-age distributions are used to identify population ages, recognize distinct cohorts, and separate growth variables from stand age information. These distributions were not analyzed using statistical techniques; therefore comparisons discussed in the following sections are not supported by statistical significance.

The forest structure tables are organized to identify several variables important for recognizing present and future forest structure. The 'canopy age' and 'population age' categories identify the age range associated with the mature portion of the canopy population and the understory population, respectively. The conifer data include the species composition of this otherwise broad class. The "Abla" (*Abies lasiocarpa*) designation includes an Engelmann spruce component in most (92%) of the stands. The age distributions of spruce and fir are similar except that the numbers of spruce are fewer, except where specifically noted in the table. "Dominance" is based on the relative number of individuals in each species as reflected in the magnitude of the size-distributions. Dominance falls into three categories, aspen, conifer, or co-dominance,

Table 3.1 - Summary of overstory structure, intact sites.

	Aspen			Conifer			
Site number	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	Population origin
Cr102	(80-100)	Y	old	Abla(25-30)	n	young	Not same
Cr246	(150-200)	CO	old	Abla(100-160)	CO	wide	similar
Cr248	(80-150)	CO	old w/R	Psme(100-150)	CO	wide	similar
Cr249	(80-130)	Y	wide	none			
Cr258	(90-110)	Y	old w/R	Abla(20-30)	n	young	Not same
Cr480	(80-130)	CO	old w/R	Abla(90-130)	CO	wide	similar
Cr489	(90-140)	CO	old w/R	Abla(60-100)	CO	wide	Not same
Cr58	(80-100)	CO	wide	Pico (40-70)	CO	wide	similar
Ho233	(100-120)	CO	old	Abla(80-110)	CO	old w/R	similar
Ho41	(80-110)	1°CO	multi	Abla(70-100)	2°CO	wide	similar
Le425	(80-100)	CO	wide	Pico(150-160) Abla(100-160)	CO	wide	Not same
Le431	(45-65)	CO	wide	Abla(60-100)	CO	young	Not same

Table 3.2 - Summary of overstory structure, disturbed sites.

	Aspen			Conifer			
Site number	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	Population origins
Cr11	(75-125)	CO	wide	Psme(120-180)	CO	wide	Not same
Cr18	(80-100)	CO	old w/R	Pico(80-100)	CO	wide	similar
Cr205	(170-230) (80-140)	Y	multi	Abla(100-130)	n	wide	similar
Cr225	(80-110)	n	old	Abla(70-120)	Y	wide	similar
Cr472	(90-130)	CO	wide	Abla(80-120)	CO	old w/R	similar
Cr473	none			Abla(50-80)	Y	young	similar
Cr475	(70-90)	Y	old w/R	Abla(40-60)	n	wide	similar
Ho244	(70-90)	CO	old	Abco(80-140)	CO	wide	Not same
Le446	(80-110)	CO	multi	Abla(60-100)	CO	old w/R	similar
Le459	(65-95)	CO	old w/R	Abla(70-90)	CO	young	similar
Le729	(100-250)	patch	old w/R	Abla(110-170)	Y	old w/R	Not same
Pu89	(70-100)	patch	old	Abla(70-100)	Y	old w/R	similar

Table 3.3 - Summary of understory structure, intact sites.

	Aspen			Conifer			
Site number	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	Relative distribution
Cr102	low succ.	-	<b.h.	Abla(<20)	Y	multi	Abla>Potr
Cr246	none		old	Abla(<20)	Y	multi	Abla>Potr
Cr248	(<50)	Y	multi	Psme(20-60)	n	wide	Potr>Psme
Cr249	low succ.	n	wide	Abla (<b.h.)	n	<b.h	Abla>Potr
Cr258	(<40)	CO	multi	Abla (<15)	n	young	Abla>Potr
Cr480	(<40)	CO	cohort	Abla (<40)	CO	wide	Potr>Abla
Cr489	(<30)	Y	cohort	Abla(<30)	n	wide	Potr>Abla
Cr58	(<40)	Y	cohort	Abla(20-40)	n	multi	Abla=Potr
Ho233	none		old	Abla(<40)	Y	multi	Abla>Potr
Ho41	(<40) (50-70)	2°CO	2cohort	Abla(<20)	1°CO	2cohort	Abla>Potr
Le425	(<40)	2°CO	cohort	Abla(<60) Pico(<60)	1°CO	few/wide	Abla=Potr
Le431	(<20) (30-40)	n	2cohort	Abla(10-50)	Y	multi	Abla>Potr

Table 3.4 - Summary of understory structure, disturbed sites.

	Aspen			Conifer			
Site number	Population age	Dominance	Age structure	[illegible]	[illegible]	[illegible]	Relative distribution
Cr11	(<25)	Y	multi	none	n	old	Potr>Abla
Cr18	(<40)	Y	multi	Pico/Abla (<20)	n	old	Potr>Abla
Cr205	(40-50)	n	old	Abla(<20)	n	cohort	Abla>Potr
Cr225	none	-	old	Abla(<40)	Y	cohort	Abla>Potr
Cr472	(40-60)	n	old	Abla(<25)	y	2cohort	Abla>Potr
Cr473	none	-	few	Abla(<35)	Y	multi	-
Cr475	(<50)	n	old	Abla(<20)	Y	multi	Abla>Potr
Ho244	none		old	Abla(<40)	Y	multi	Abla>Potr
Le446	(30-50)	n	cohort	Abla(<30), (60-80)	Y	2cohort	Abla>Potr
Le459	(25-35)	n	wide	Abla(<50)	Y	2cohort	Abla>Potr
Le729	(<20)	n	few	Abla(<30), (60-90)	Y	2cohort	Abla>Potr
Pu89	(<20)	n	old	Abla(<60)	Y	2cohort	Abla>Potr

Notation and abbreviations: low succ., low success rates; CO, co-dominance; 1°Co, primary co-dominant; old, aging stands without regeneration; old w/R, aging stands with reproductive success; wide, a wide distribution of ages with low numbers throughout; multi, multiple, recognizable age classes; cohort, regeneration concentrated into distinct groups; <b.h. individuals with unknown ages, all under breast height. Symbols in the relative distribution columns (>,<,=) describe the predominance of conifer or aspen reproduction based on the magnitude of the distributions in the <5cm classes.

with no designation if one component is entirely absent from a location. "Age structure" summarizes the distribution of the relevant forest component (i.e. overstory or understory) with respect to the shape of the distribution of abundance in size and age classes (see Appendix C). "Old" distributions are characterized by an aging overstory with little to no representatives in the small (young) size classes. "Old w/R" designates an aging overstory with decreased numbers in smaller classes, but there is an indication (young individuals) that reproductive efforts are, at least, occasionally successful. "Wide" distributions suggest perpetual, low-level numbers of individuals across the size and age spectrum of the forest, i.e. continuous reproductive success. The "multi" age structure is similar to a "wide" distribution except the range is not necessarily continuous across all sizes and ages and the distribution individuals across size-classes is punctuated by distinct groups. "Cohort" structure is used to describe the presence of a distinct grouping of individuals, which suggests reproductive success concentrated in time.

The range of forest ages (based on the age distributions of canopy dominants) was similar for both sets of data (Tables 3.1 and 3.2). Further, the patterns in landscape age predicted by photographic interpretation were not as strong as predicted. My 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. Sixty-three percent (63%) of the overstory populations in these forests have the same, or similar, ages; this is probably the result of a stand-replacing fire, or another large disturbance, dictating stand age. Twenty-one percent (21%) of the forests have distributions with many young conifers (especially fir); this suggests recent colonization and future competition for aspen.

3.3.2 Intact landscapes

Tables 3.1 and 3.3 summarize the overstory and understory structure for sites that do not show evidence of a recent disturbance in the original photographs, intact sites. Contrary to my expectations, 83% of these distributions demonstrate successful regeneration of aspen. However, aspen is the dominant regenerating species on only 33% of the sites. Fifty percent (50%) of the sample locations have greater regeneration of shade-tolerant species (especially spruce and fir) than aspen. All (100%) of the intact sites have an established shade-tolerant component, in the understory, canopy, or both locations.

The population distributions for these sites reveal that local aspen populations are aging relative to the coniferous competition. Thirty-six percent (36%) of the samples show mature (80-100 years old) or older aspen stands with little to no regeneration (e.g. sites Cr102, Cr246, Ho233; tables 3.1 and 3.3). Only 45% of the intact forests have strong regeneration of aspen (e.g. sites Cr248, Cr480, Cr489; tables 3.1 and 3.3). Seventy-five percent (75%) of these forests have equal or greater regeneration of spruce and fir than aspen.

3.3.3 Recently disturbed sites

Tables 3.2 and 3.4 summarize the forest structure for the twelve sites with a record of disturbance recorded in the original photographs. While 75% of the recently disturbed sites have successful aspen reproduction, only 25% percent of these sample locations demonstrate dominant aspen regeneration. Moreover, 73% of the locations have a greater abundance of young spruce and fir than aspen, and only eight percent (8%) of the locations have aspen without conifers in the understory. Fifty-five percent (55%) of the sites have prolific conifer reproduction such that they will drive future compositional changes because current regeneration surpasses the proportions currently occupied by those species in the overstory. Similarly to the intact forests, most (92%) of these forests also have a presence (if not dominance) of conifers in the understory. Only 25% of the aspen forests have aging populations without successful regeneration. But again, 73% of these forests have regeneration that is more prolific by conifer species than aspen. Thus, while aspen reproductive efforts continue to succeed in these younger forests, there is an increasing presence of shade-tolerant conifers in the understory and overstory, which suggests future reproductive difficulties for aspen.

3.4 Discussion

3.4.1 Disturbed versus intact landscape age structures

The analysis of forest size-age structure does not yield dramatic differences between the two disturbance classes. The mean forest age was similar for both sets of data. This suggests that disturbance, i.e. fire, was more frequent on the landscape (before the suppression era) than anticipated based on the photographic history. Few of these forests have ages greater than 150 years. This similar historical context may explain the similarities in aspen regeneration and conifer invasions between these two landscape categories. Although there is variability in other aspects of forest structure (e.g. success of conifers in the understory) there is a strong trend (among all sample locations) for succession of shade-tolerant species. The evidence is the presence of abundant conifer regeneration in half of the forests dominated, or co-dominated, by aspen.

Sites described as intact landscapes showed a greater percentage of successful aspen reproduction. This may be the result of expansion of aspen clones into adjacent meadows, range patches. However, the relative immaturity of all sampled sites (according to the stand-age data) means that many of the intact and disturbed sites are in similar stages of succession. The abundance of spruce and fir reproduction in forests where these species compete with aspen is confirmation of the successional development of these forests. Thus, regardless of past and current reproductive success, many aspen forests are not following a projection of persistence.

3.4.2 Aspen regeneration and age structure

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 many disturbed and mature sites. However, a higher percentage of aspen stands were found to be reproducing successfully on the intact sites than on recently disturbed sites. Furthermore, more regenerated sites have a greater abundance of conifer reproduction than aspen reproduction than intact sites. This unexpected pattern is likely the effect of two different influences on forest regeneration. One factor is the light reaching the understory. Light availability can limit the success rates for reproduction of aspen under an aspen overstory, or it may enhance the propensity for a clone to expand its boundaries into adjacent, non-forested areas (Jones and DeByle 1985). A second factor is the seed dispersal abilities of the conifers. If the last disturbance event produced large conifer-free areas, then spruce and fir must disperse seed into these areas; presumably, a larger area requires more time for full colonization. Hence, in some areas aspen has continued to expand for the last century and the age structure of these stands reflects this pattern with high numbers in the young age classes. In other areas, light at the forest floor restricts successful aspen regeneration but allows shade-tolerant conifer regeneration as viable seeds germinate and survive. This condition is not an obvious concern as I address the persistence of aspen on the landscape. However, loss (via colonization) of open patches for future colonization may change these age structures in the near future. Thus, when I observe that 50% of the aspen populations on intact sites are being out-reproduced by fir and spruce, then I anticipate a shift in dominance in the near future.

Ninety-six percent (96%) of all sample units have conifers in the understory, overstory, or both. This suggests that conifers will replace aspen as overstory dominants in most of the sampled forests, if succession continues without a major disturbance. It is clearly apparent that 80 to 100 years is sufficient time for conifers to disperse seed into forests where an immediate seed source is not necessarily available; 70% of the stands have conifers present in the overstory providing an immediate seed source. Thus, regardless of past and current reproductive success, many aspen communities are not following a projection of persistence. They are not suffering from age-induced reproductive failure in most cases. Instead, through stand and landscape level succession, I have entered a stage of abundant reproductive success for spruce and fir.

3.4.3 Conifer regeneration and colonization of aspen forests

One hundred percent (100%) of the intact forests, and 92% of the disturbed forests have an observed population of shade-tolerant conifers. This does not necessarily reflect invasion of aspen forest because aspen is often found within a landscape mosaic of lodgepole pine and spruce-fir communities. However, 50% of the intact forests and 73% of the disturbed forests have younger distributions of fir and/or spruce than aspen. In other words, a large percentage of forests with aspen stands have more regeneration of conifers in the understory than young aspen suckers. This is a strong indication of the future structure of these forests.

Careful assessment of the subalpine-fir age distributions suggests that when a portion of the population reaches reproductive maturity (approximately 10-15 centimeters on these sites), reproductive output increases dramatically. Knowles and Grant (1983) suggest that size is a strong determinant of reproductive success. This concept is supported by prolific regeneration at some sites (e.g. sites: Cr102, Cr472, Cr473, Le446, Le459) and much lower numbers at other sites (e.g. sites: Cr18, Cr258). More research into these patterns, both on a species and community level, are needed to elucidate this apparent trend. However, the presence of reproductively active individuals will undoubtedly have an effect on the level of reproductive success for the population. It is clear that fir and spruce are demonstrating an increasing trend in regeneration and population numbers within many of the forests on the western slope of the Rocky Mountains. A study that systematically classifies (e.g. by region, elevation, aspect, forest age and composition) conifer reproductive success could elucidate the details of this success.

4. Conclusion

In the intermountain region of the Rocky Mountains, aspen is commonly associated with ponderosa pine at low elevations, Douglas-fir and lodgepole pine at mid-elevations, and spruce-fir mixed forests at high elevations. However, its role in these different habitats varies with its ability to compete for resources, e.g. relative shade tolerance, reproductive strategy, growth rate, and environmental determinants such as disturbance regime, precipitation, temperature, slope, and aspect. At high elevations and throughout most of the intermountain region, aspen is generally considered seral to conifers.

Regeneration of sites disturbed by wildfires, mining activities, and human induced fires has been impressive. Most of these sites have closed canopies with coniferous forest and aspen forest intermixed. However, these regenerated landscapes do not have the same landscape patterns as the locations affected by historic fire regimes, i.e. the intact sites. Presuming that these locations experienced a mosaic generated by periodic fire and associated regeneration before European settlement, I look to these photographs for examples of "normal" landscape pattern. Naturally disturbed sites (e.g. Plates 3 and 4) currently display a higher degree of heterogeneity on the landscape than do those, which are affected by widespread human induced disturbance. One easily observed difference is the former interspersion, and current absence, of open patches of rangeland within the forest mosaic. Using an understanding of the differential nature of wildfire behavior and its differential effect on forest patterns (Parker and Parker 1983), I infer that some of the heterogeneity perceived in historically disturbed landscapes (e.g. Plate 3) is the product of the differential behavior of fires across that area. Although this study provides no direct evidence, analysis of the photographs suggests that human induced disturbances of the mining era had a more homogeneous effect on the landscape than did more natural disturbance events of the same and earlier period.

Use of repeat photography as an indicator of forest age structure has mixed results. Obvious, general trends, such as those outlined by my hypotheses and expectations, were not revealed. The anticipated trends of conifer invasions in mature forests and continuing aspen regeneration only in recently disturbed forests were not supported. This is attributed to fewer dissimilarities in the long-term site histories between sites than expected, i.e. it has not been very long since most of the intact sites were disturbed (only 150 to 200 years versus 100 years for young landscapes). However, even small differences in stand ages and recent histories provide insights into the succession of mixed aspen, spruce, and fir communities. Fire has the ability to remove the overstory dominants and renew the competition for resources. It does not necessarily selectively remove one species or another from this landscape. It does not create uniform conditions or identical development patterns on different landscapes. It does have a lasting effect on forest age and structure.

The stand-age structure data provided here, in association with the historical and landscape context provided by the photographic history, allows us to consider the development of mixed species communities and landscapes in a manner different from the perspective provided by successional models and single-stand analyses. By explicitly recognizing that species regeneration is not limited to within stands, and by recognizing that expansion (of populations or stands) can be observed on the landscape, I document a spatial component of forest development for analysis. Although this project lacks sufficient spatial and temporal detail to elucidate the all details of a spatial component of succession in these forests, it is apparent that these patterns exist. A study that maps the successional development of a forest (i.e. map the location of individuals of all ages over time) can further elucidate this pattern and the associated processes of seed dispersal, competition, individual growth and forest succession.

The abundance of spruce and fir reproduction in forests where these species compete with aspen is confirmation of the successional development of these forests. Thus, regardless of past and current reproductive success, aspen forests are not following a projection of persistence. This said, I also recognize that the ecological associations of aspen across the landscape are highly varied. They are not suffering from age-induced reproductive failure in most cases. Aspen are part of dynamic communities and landscapes, and changes in this community are potentially induced by the expansion of local competitors (i.e. spruce and fir), disturbance patterns, herbivory, and climate changes. The result is the sequential and systematic exclusion of aspen over time. These forests have not presently reached the stage where aspen is lost from the landscape. They have entered a stage of abundant fir reproductive success. Future management plans and actions need to focus on the role of disturbance across the landscape, not merely stand-by-stand.

Future research into aspen community and landscape ecology should focus on elucidating the details of inter-specific competition both from a community ecology perspective and from a landscape pattern and process perspective. These data suggest that in some communities, aspen and fir do co-exist. However, the forest conditions that distinguish conifer invasion from aspen/conifer co-existence are not well understood. A detailed investigation of each species reproductive strategies in a variety of environmental and successional contexts will elucidate these interactions. Furthermore, spatially explicit investigations of successional development beyond the stand level will allow differentiation of competitive and developmental changes in local gaps from expansion of woody species into earlier seral communities across the landscape.

The results of this study are in agreement with a host of studies from around the world, which document the encroachment of woody cover into shrub and grassland communities (Miller and Rose 1999). This pattern is generally associated with decreased fire frequency and increased grazing by domestic ungulates. However, the details of invasions are associated with several potentially determining factors, i.e. species reproductive and growth capabilities, climate patterns, soil types, disturbance history, grazing pressures, and human land-use patterns (e.g., Turner, et al. 1993, Palik and Pregitzer 1992, Armstrong 1988, Denslow 1985, Roberts and Richardson 1984, Burkhardt and Tisdale 1976), which have different roles in different communities. Subsequent research into the dynamics of aspen and conifer forests in the Rocky Mountains needs to focus on recognition of the patterns and determining the associated processes, which drive the patterns. Thus, our understanding of the patterns described by this project would be enhanced by spatially explicit analyses of these other determining factors and the processes associated with conifer invasion of aspen stands and rangelands and aspen invasion of neighboring meadows.

Finally, my discovery of many individual aspen trees which are 200 years old and older suggests that the current understanding of aspen biology underestimates the potential age of individuals. In addition, the ability of aspen to regenerate under a forest canopy may also be underestimated. A revision of our understanding of aspen biology with respect to growth potential and reproductive abilities would be facilitated by in situ studies of aspen clones.

References cited

Anderson, J.R., E.E. Hardy, J.T. Roach, and R.E. Witmer. 1976. A land use and land cover classification system for use with remote sensor data. U.S.D.I., Geological Survey Professional Paper – 964. United States G.P.O., Washington, D.C.

Aplet, G.H., R.D. Laven, and F.W. Smith. 1988. Patterns of community dynamics in Colorado Engelmann spruce-subalpine fir forests. Ecology 69(2): 312-319.

Armstrong, R.A. 1988. The effects of disturbance patch size on species coexistence. J. Theoretical Biology 133:169-184.

Baker, F.S. 1925. Aspen in the central Rocky Mountain region. USDA Bulletin 1291. Washington, D.C.

Barnes, B.V. 1966. The clonal growth habit of American aspens. Ecology 47: 439-447.

Bartos, D.L., F.R. Ward, and G.S. Innis. 1983. Aspen succession in the Intermountain West: A deterministic model. USDA Forest Service GTR-INT-153, Ogden, UT, 60 pp.

Bartos, D.L., J.K. Brown, and B.D. Booth. 1994. Twelve years biomass response in aspen communities following fire. J. Range Mgmt. 47:79-83.

Brown, J.K. and N.V. DeByle. 1987. Fire damage, mortality, and suckering in aspen. Can. J. For. Res. 17:1100-1109.

Burkhardt, J.W. and E.W. Tisdale. 1976. Causes of juniper invasion in southwestern Idaho. Ecology 57: 472-484.

Byram, G.M. 1959. Combustion of forest fuels. *In* K.P. Davis, editor. Forest fire control and use. McGraw-Hill Co., New York.

Clements, C.D. and J.A. Young. 1997 A viewpoint: Rangeland health and mule deer habitat. J. Range Management 50(2): 129-138.

Colorado Climate Center. Colorado State University, Fort Collins, CO. Historical data records available for public access via world-wide-web: http://ulysses.atmos.colostate.edu/

Crawford, J.L., S.P. McNulty, J.B. Sowell, M.D. Morgan. 1998. Changes in aspen communities over 30 years in Gunnison county, Colorado. Am. Midland Naturalist 140(2): 197-205.

Day, R.J. 1972. Stand structure, succession, and use of southern Alberta's Rocky Mountain forest. Ecology 53(3): 472-478.

DeByle, N.V. and R.P. Winokur, editors. 1985. Aspen: Ecology and management in the western United States. USDA Forest Service GTR-RM-119, Fort Collins, Colo., 283 pp.

DeByle, N.V., C.D. Bevins, and W.C. Fischer. 1987. Wildfire occurrence in aspen in the interior western united states. West. J. Applied Forestry 2(3):73-76.

Denslow J.S. 1985. Disturbance-mediated coexistence of species. pp. 307-323 in S.T.A. Pickett and P.S. White, editors. The ecology of natural disturbance and patch dynamics. Academic Press, Orlando, Fla.

Gruell, G.E. 1980. Fire's influence on wildlife habitat on the Bridger-Teton National Forest, WY, volume 1 – photographic record and analysis. USDA Forest Service Res. paper INT-235, Ogden, Utah.

Gruell, G.E. 1983. Fire and vegetative trends in the northern Rockies: interpretations from 1871-1982 photographs. USDA Forest Service GTR-INT-158. Ogden, Utah.

Gruell, G.E. 1985. Fire on the early western landscape: An annotated record of wildland fires 1776-1900. Northwest Science 59(2): 97-107.

Hart, R.H. and J.A. Hart. 1997. Rangelands of the Great Plains before European settlement. Rangelands 19(1): 4-11.

Hart, R.H. and W.A. Laycock. 1996. Repeat photography on range and forest lands in the western United States. J. Range Management 49(1): 60-67.

Hastings, J.R. and R.M. Turner. 1965. The Changing Mile. University of Arizona Press, Tuscon, Ariz.

Heinselman, M.L. 1981. Fire intensity and frequency as factors in the distribution and structure of northern ecosystems Canadian and Alaskan boreal forests, Rocky Mountain subalpine forests, Great Lakes-Acadian forests. USDA Forest Service GTR-WO-26. Washington, D.C., pp. 7-57.

Houston, D.B. 1982. The northern Yellowstone elk; ecology and management. MacMillan, New York.

Hutchinson, W.I. 1917. Colorado's national forests and mountain parks. Pages 563-588. *In* W.F. Stone, editor, History of Colorado, vol. 2. S.J. Clarke Publishing Co., Chicago, Ill.

Jones, J.R. and N.V. DeByle. 1985. Morphology. Pages 11-18. *In* N.V. DeByle and R.P. Winokur, editors, Aspen: ecology and management in the western United States. USDA Forest Service GTR-RM-119. Fort Collins. Colorado.

Kalkhan, M.A., R.M. Reich, and R.L. Czaplweski. 1996. Statistical properties of measures of association and the Kappa statistic for assessing the accuracy of remotely sensed data using double sampling. *In* Proceedings of the Spatial Acccuracy Assessment Symposium in Natural Resources and Environmental Sciences: Second International Symposium. USDA Forest Service, GTR-RM-277, Fort Collins, Colorado.

Kay, C.E. 1993. Aspen seedlings in recently burned areas of Grand Teton and Yellowstone national parks. Northwest Science 67(2): 94-104.

Knowles, P., and M.C. Grant. 1983. Age and size structure analyses of Engelmann spruce, ponderosa pine, and limber pine in Colorado. Ecology 64(1): 1-9.

Maarel, E. van der, and M.T. Sykes. 1993. Small-scale plant species turnover in a limestone grassland: the carousel model and some comments on the niche concept. J.Vegetation Science 4(2): 179-188.

Mast, J.N., T.T. Veblen, and Y.B. Linhart. 1998. Disturbance and climatic influences on age structure of ponderosa pine at the pine / grassland ecotone, Colorado Front Range. J. of Biogeography 25(4): 743-755.

McDonough, W.T. 1985. Sexual reproduction, seeds and seedlings. Pages 25-28. *In* N.V. DeByle and R.P. Winokur, editors, Aspen: ecology and management in the western United States. USDA Forest Service GTR-RM-119, Fort Collins, Colorado.

Miller, R.F. and J.A. Rose. 1999. Fire history and western juniper encroachment in sagebrush steppe. J. Range Management 52:550-559.

Mitton, J.B. and M.C. Grant. 1996. Genetic variation and the natural history of quaking aspen. Bioscience 46(1): 25-31.

Mueggler, W.F. 1976. Type variability and succession in Rocky Mountain aspen. Pages 16-19. *In* Utilization and marketing as tools for aspen management in the Rocky Mountains: Proceedings of the symposium. USDA Forest Service GTR-RM-29, Fort Collins, Colo.

Mueggler, W.F. 1985. Vegetation Associations. Pages 45-55. *In* N.V. DeByle and R.P. Winokur, editors, Aspen: ecology and management in the western United States. USDA Forest Service GTR-RM-119, Fort Collins, Colorado.

Mueggler, W.F. 1989. Age distribution and reproduction of intermountain aspen stands. Western J. Applied Forestry 4(2): 41-46.

Mueggler, W.F. and R.B. Campbell 1982. Aspen community types on the Caribou and Targhee National Forests in southeastern Idaho. USDA Forest Service Res. Paper INT-294, Ogden, Utah.

Mueggler, W.F. and R.B. Campbell 1986. Aspen community types of Utah. USDA Forest Service, Res. Paper INT-362, Ogden, Utah.

O'Rourke, P.M. 1980. Frontier in Transition: A history of southwestern Colorado. USDI Bureau of Land Managment, Colorado State Office, Denver, Colo.

Ott, R.L. 1993. An introduction to statistical methods and data analysis, 4th edition. Duxbury Press, Belmont, Cal.

Palik, B.J. and K.S. Pregitzer. 1992. A comparison of presettlement and present-day forests on two bigtooth aspen –dominated landscapes in northern lower Michigan. American Midland Naturalist 127: 327-338.

Parker, A.J.and K.C. Parker. 1983. Comparitive successional roles of trembling aspen and lodgepole pine in the southern Rocky Mountains. Great Basin Naturalist 43(3): 447-455.

Parker, A.J., and R.K. Peet. 1984. Size and age structure of conifer forests. Ecology 65(5): 1685-1689.

Pickett, S.T.A., and P.S. White, editors. The ecology of natural disturbance and patch dynamics. Academic Press, Orlando, Fla.

Progulske, D.R. 1974. Yellow ore, yellow hair, yellow pine. South Dakota State University, Agricultural Experiment Station, Bulletin 616. Brookings, S. Dakota

Roberts, M.R. and C.J. Richardson. 1985. Forty-one years of population change and community succession in aspen forests o four soil types, northern lower Michigan, U.S.A. Canadian J. Botany 63: 1641-1651.

Rogers, G. 1982. Then and Now: A photographic history of vegetation change in the central Great Basin Desert. University of Utah Press, Salt Lake City, Utah.

Romme, W.H., M.G. Turner, R.H. Gardner, W.W. Hargrove, G.A. Tuskan, D.G. Despain, R.A. Renkin. 1997. A rare episode of sexual reproduction in aspen (Populus tremuloides Michx.) following the 1988 Yellowstone fires. Natural Areas Journal 17(1): 17-25.

Romme, W.H., M.G. Turner, L.L. Wallace, and J.S. Walker. 1995. Aspen, elk and fire in northern Yellowstone National Park. Ecology 76(6): 2097-2106.

Schier, G.A. 1976. Physiological and environmental factors controlling vegetative regeneration of aspen. Pages 20-23. *In* Utilization and marketing as tools for aspen management in the Rocky Mountains: Proceedings of the symposium. USDA Forest Service GTR-RM-29, Fort Collins, Colorado.

Shea, K.L. 1985. Demographic aspects of coexistence in Engelmann spruce and subalpine fir. Am. J. Botany 72(11): 1823-1833.

Shepperd, W.D. 1990. A classification of quaking aspen in the central Rocky Mountains based on growth and stand characteristics. West. J. Applied Forestry 5(3): 69-75.

Shepperd, W.D., and M.L. Fairweather. 1992. Impact of large ungulates in restoration of aspen communities in a southwestern ponderosa pine ecosystem. USDA Forest Service, Ogden, Utah. pp. 344-347.

Shugart, H.H., and S.W. Seagle. 1985. Modeling forest landscapes and the role of disturbance in ecosystems and communities. pages 353-368 in S.T.A. Pickett and P.S. White, editors. The ecology of natural disturbance and patch dynamics. Academic Press, Orlando, Fla.

Stahelin, R. 1943. Factors influencing the natural restocking of high altitude burns by coniferous trees in the central Rocky Mountains. Ecology 24: 19-30.

Theobald, D.M., J.M. Miller, and N.T. Hobbs. 1997. Estimating the cumulative effects of landscape development on wildlife habitat. Landscape and Urban Planning 39(1): 25-36.

Turner, M.G., W.H. Romme, R.H. Gardner, R.V. O'Neill, T.K. Kratz. 1993. A revised concept of landscape equilibrium: Disturbance and stability on scaled landscapes. Landscape Ecology 8(3): 213-227.

Vale, T.R. 1987. Vegetation change and park purposes in the high elevations of Yosemite National Park. Annals of the Association of American Geographers 77: 1-18.

Vandenbusche, D., and D.A. Smith. 1981. A land alone, Colorado's western slope. Pruett Publishing Co., Boulder, Colo.

Veblen, T.T., and D.C. Lorenz. 1988. Recent vegetation changes along the forest / steppe ecotone in northern Patagonia. Annals of the Association of American Geographers 77: 93-111.

Veblen, T.T., and Lorenz, D.C. 1991. The Colorado Front Range: A Century of Ecological Change. University of Utah Press. Salt Lake City, Utah.

Veblen, T.T., K.S. Hadley, E.M. Nel, T. Kitzberger, M. Reid, and R. Villalba. 1994. Disturbance regime and disturbance interactions in a Rocky Mountain subalpine forest. Journal of Ecology 82(1): 125-135.

Whipple, S.A., and R.L.Dix. 1979. Age structure and successional dynamics of a Colorado subalpine forest, Picea engelmannii, Abies lasiocarpa, Pinus contorta. American Midland Naturalist 101: 142-158.

Wirth, T., P. Maus, J. Powell, H. Lachowski. 1996. Monitoring aspen decline using remote sensing and GIS. Pages 174-183 in J.D. Greer, editor, Proceedings of the 6th Forest Service remote sensing applications conference. American Association for Photogrammetry and Remote Sensing.

Woods, R.F., D.R. Betters, and E.W. Mogren. 1982. Understory herbage production as a function of Rocky Mountain aspen stand density. J. of Range Management 35(3): 380-381.

Appendices

Appendix A:

Results of accuracy assessment for the edited classifications.

Intact sites:

Site code:	gen.	Overall Acc.	Kappa statistic
Cr102	O	85	0.80
	R	88	0.84
Cr246	O	94	0.92
	R	94	0.90
Cr248	O	93	0.92
	R	90	0.88
Cr249	O	98	0.98
	R	83	0.79
Cr258	O	92	0.88
	R	92	0.90
Cr480	O	94	0.92
	R	92	0.90
Cr489	O	100	1.00
	R	94	0.92
Cr58	O	93	0.92
	R	95	0.94
Ho233	O	94	0.92
	R	98	0.97
Ho41	O	92	0.90
	R	91	0.88
Le425	O	83	0.80
	R	88	0.85
Le431	O	84	0.80
	R	95	0.93

Disturbed sites:

Site code:	gen.	Overall Acc.	Kappa statistic
Cr11	O	81	0.76
	R	94	0.90
Cr18	O	*	*
	R	*	*
Cr205	O	95	0.94
	R	97	0.96
Cr225	O	95	0.94
	R	98	0.96
Cr472	O	85	0.80
	R	85	0.81
Cr473	O	92	0.90
	R	86	0.83
Cr475	O	84	0.78
	R	93	0.91
Ho244	O	*	*
	R	*	*
Le446	O	*	*
	R	*	*
Le459	O	*	*
	R	*	*
Le729	O	93	0.92
	R	88	0.85
Pu89	O	94	0.93
	R	95	0.93

*** designates images for which no accuracy assessment was conducted. These files were damaged after the classifications were complete; additional work with them is, unfortunately, not possible.**

Appendix B

Photograph pairs and descriptions:

These are images referred to in the text but are not included in the photograph plates. Copies of the original photographs, both the U.S.G.S. photos, photographers are credited in parentheses at the top-left of each description, and the second in the pair photographed by the author in 1995 are archived in the files of the author.

APPENDIX B 1

Cr102	**Anthracite Range**	1887 - 1995
(C.W. Cross)	Southern aspect	9400-9800ft.

In 1887, the landscape is dominated by expansive coverage of aspen (light color across the far slope) with conifers mixed in especially at the higher elevations. There is interface between conifer forest and rangelands in this image. The second photo also shows extensive forest cover. Aspen has expanded its already dominant role on this landscape by filling in gaps and expanding into lower elevation rangelands. Total forest cover has apparently increased. Patch size is apparently the same (i.e. very large and extending across the field of view) with a possible decrease in the number of patches as expanding patches have connected.

APPENDIX B 2

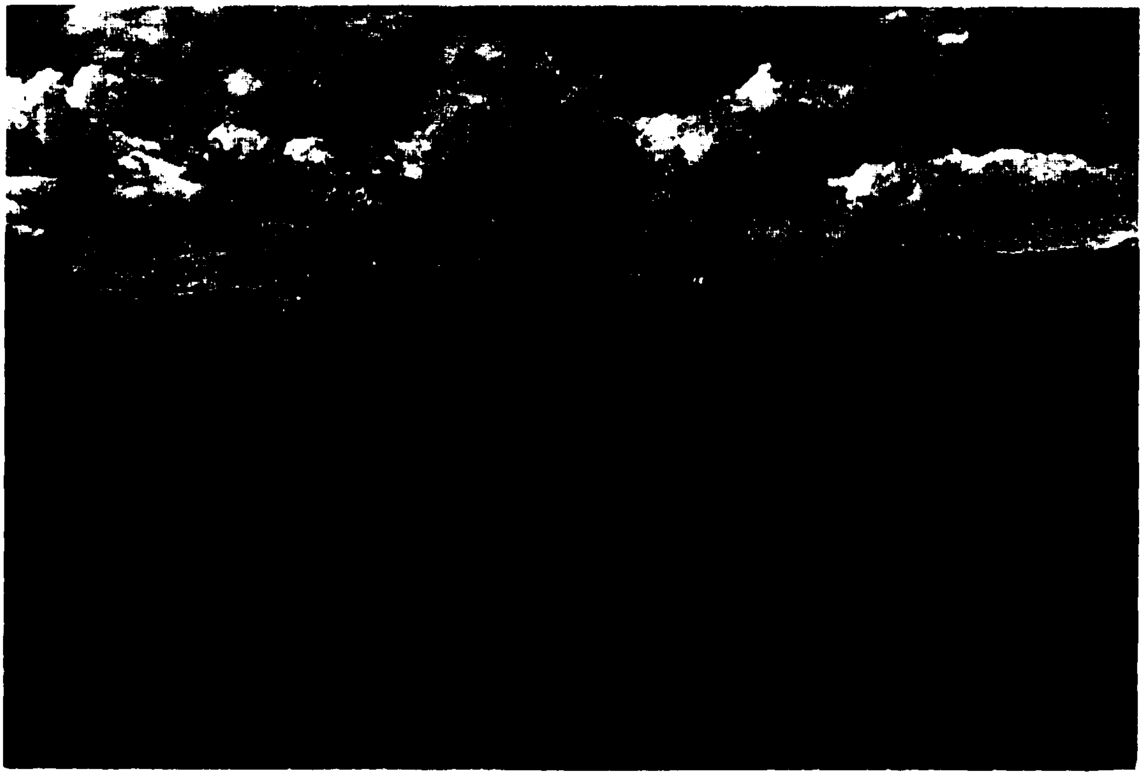
Cr248	**Ophir loop**	1895 – 1995
(C.W. Cross)	Southwestern aspect	9200-9600ft.

The original photo shows interspersion of conifers and many younger (smaller) aspen. The upper part of the slope has two more mature aspen stands. The steep slopes and rock scree appear to limit continuous canopy closure. In the modern photo, there is more extensive forest cover than in the original. Aspen and conifers co-dominate the present canopy. Between the two photographs, a tramway was constructed to service the town of Alta (over the ridge). This apparently had little effect on this forest, since no evidence of clearing or structures is obvious. The landscape pattern is similar in the present to the past, but forest coverage has slightly expanded. Many of the young aspen apparent in the original have grown into mature trees thus increasing canopy height and cover.

APPENDIX B 3

Cr249	**San Miguel River Valley**	1885 – 1995
(C.W. Cross)	Western aspect	8800-9200ft.

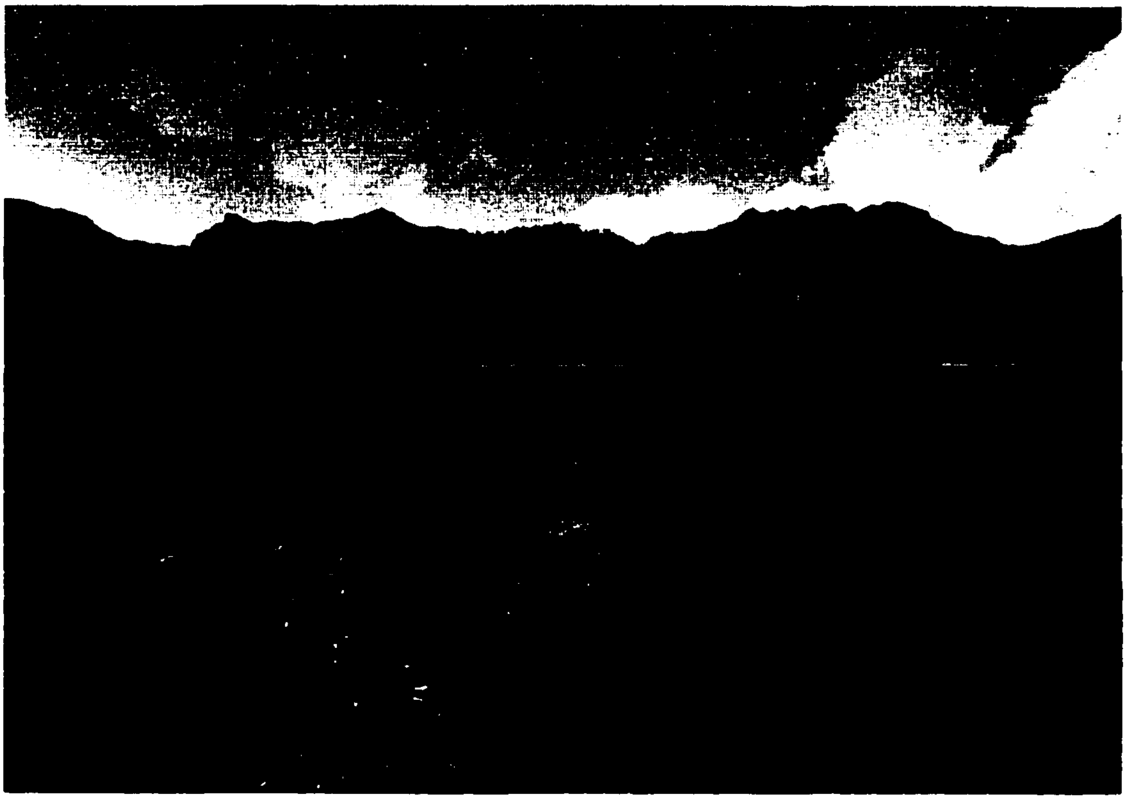
The original and the present landscape are patchy with interspersed patches of conifers, aspen, and open grassy areas. The historic photo is characterized by extensive rangeland interspersed with aspen and conifers. The forest cover appears more extensive down the valley (center rear), but opening in this canopy can be observed. The present photo shows that open meadows and grassy slopes persist here, but forest occupies a more extensive portion of the contemporary landscape. Aspen patches increased density and have expanded across formerly open patches. Conifers persist on the foreground landscape and they have expanded down valley and on the near (left) slope. This results in an increase in total forest cover and in the size of continuous patches over this 110-year time span. Human activities have been extensive in this region (e.g. state highway 145 on the left slope), but tree harvest was not apparently part of these activities (due to the increase in coverage).



APPENDIX B 4

Cr480 (C.W. Cross)	**Aspen covered ridge at Monument Gl.** Southeastern aspect	1900 - 1995 10000-10800ft.

Both photographs show a similar landscape. The original photo shows an aspen covered ridge with variable conifer cover near the top of the ridge. The foreground is mixed rangeland and riparian zone with extensive willow coverage. The mining town of Ironton is visible to the left. This ridge is still covered in aspen with little to no sign of conifers or grass patches. The slopes in the background show an increase in forest cover from a grassy, isolated forest patch pattern in the past. Conifer patches have consolidated resulting in decreased number, but increased size of patches. Much of the rangeland coverage, which appears in the background of the historic photo (currently, invaded by conifers) and the foreground (currently, a 100ft. thick tailings mound), has been lost. Ironton is now a ghost town.



APPENDIX B 5

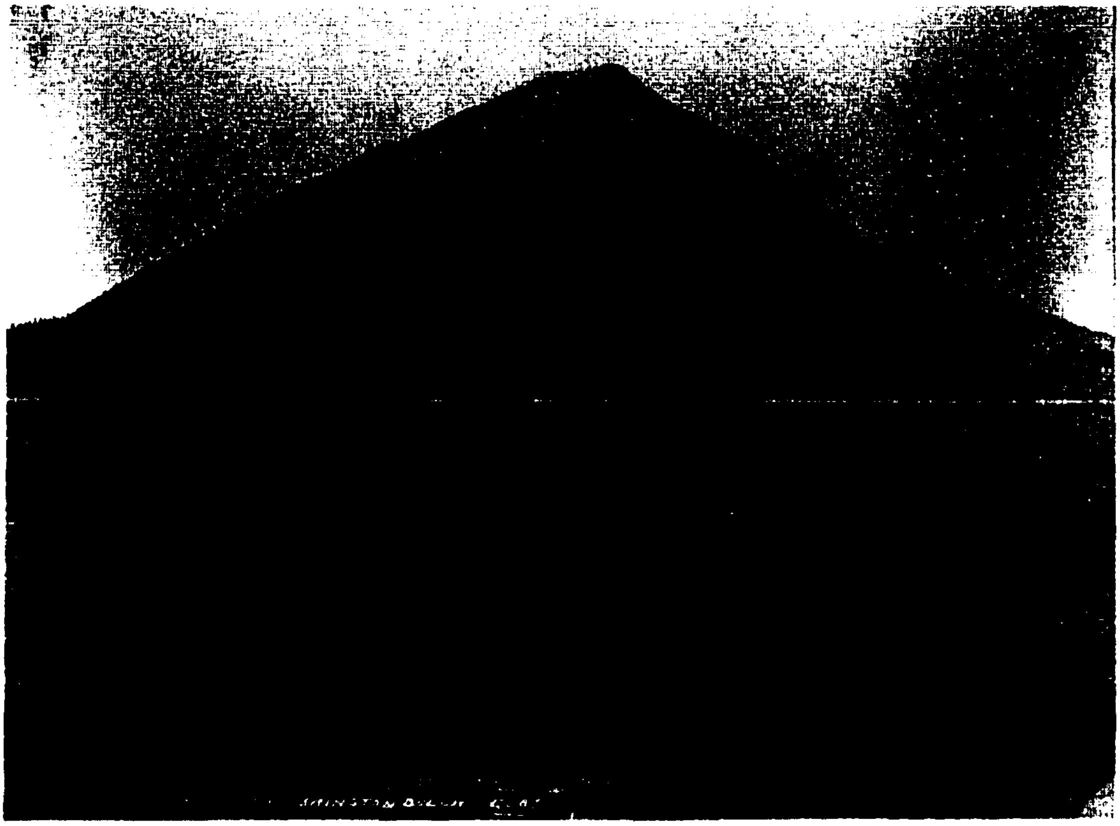
Cr489	**Canyon Creek**	1900 – 1995
(C.W. Cross)	Northwestern aspect	8800-9400ft.

Some human influence on this valley is expected because of the private ranch, converted to vacation homes in the present, most forest development appears to have continued unadulterated. Extensive forest cover characterizes the historic landscape; however, a variety of age structure is suggested by the differences in tree heights across the center (right) slope. The current landscape patterns are similar to the older ones, except that forest cover has become more dominant and more homogenous (fewer gaps and stand borders). Patches that were previously open are now dominated by aspen and conifers. Forest cover (total and mean patch size) has increased except in the maintained meadow.

APPENDIX B 6

Cr58	**Gothic Mountain**	1887 - 1995
(C.W. Cross)	Southern aspect	10200-10600ft.

The historic landscape was photographed in the fall (hence the lack of leaves on the aspen trees). The dispersal of aspen and conifers at the base of the mountain extends across the view. However this coverage is only locally dense, conifer cover is sparse, and multiple open patches are visible within the aspen forest. The current landscape has extensive and dense coverage of aspen; some range patches are visible within the aspen matrix. Conifer cover is restricted to a few patches within the aspen. This pair shows an increase in forest cover due to increased density and expansion of conifers and aspen (primarily aspen) into the meadows. Some large openings have decreased in size and small, previously open patches have been colonized by trees. Total forest cover increased; aspen expanded and formed more continuous canopy closure; the several small conifer patches expanded without major incursions to the surrounding landscape.



APPENDIX B 7

Ho233 **El Mandhi mine at Cow Creek** 1904 – 1995
(E. Howe) Northern aspect 9200-9600ft.

The historic landscape is characterized by forest interspersed with extensive bare rock (presumably a combination of natural erosion and mining activities in this area). The background forest appears more uniform and less affected by mining than the foreground. We expect that the patchy substrate (rock and scree) creates this patchy canopy. However, the current forest cover is continuous across many of these slopes and has expanded even onto scree slopes. The background forest is also closed canopy; it shows an increase in height, density, and extent since the original photo. Forest cover has increased. The pattern of patches in the background is the same in the present as the past, however the foreground has dramatically increased patch size since previously isolated individuals are now part of a large stand. Grass and shrub dominated meadows are not important at this location.

APPENDIX B 8

Ho41	**Red Mountain Valley**	1900 – 1995
(E. Howe)	Western aspect	9800 – 10200ft.

Extensive burning and logging is evident in the foreground of the original, but the slopes down the valley (background) appear largely unaffected by these disturbances. (The foreground of this landscape is assessed in other photo pairs, e.g. appendices APPENDIX B 17-APPENDIX B 18) The background landscape is a patchy mixture of conifer, aspen, and rangeland. The slope on the left shows no evidence of forest cover. Forest canopy cover (conifers and aspen) has increased dramatically in disturbed and undisturbed portions of the landscape. Aspen now covers the slope on the left, where in the past no trees were present. The west aspect (center and right in the photo) shows a dramatic increase in forest cover, especially aspen cover. Total cover and patch size of aspen have increased; conifer patches remain similar; grasslands have decreased in size and distribution. The inset picture demonstrates one type of obstacles to repeat photography of vegetation created by regenerating forests. This obstructed view made it impossible to exactly replicate the original photographer's location for this site.

APPENDIX B 9

Le425	**Snodgrass & Gothic Mountains**	1909 – 1995
(W.T. Lee)	Southwestern aspect	10000-10800ft.

Wide ranging, but sparse forest cover characterizes the historic landscape. The interspersion of young aspen and the extensive grass and shrub dominated meadows suggest a history of disturbance, however no direct evidence for these events is observed. The modern photo shows the extensive aspen stands, which are now, present on the slopes of Snodgrass Mountain (right slope) and Gothic Mountain (rear-center). Conifers are restricted to isolated patches and drainages. Human development currently dominates the valley meadow. Expansion of aspen coverage has been extensive. Total forest cover increased dramatically; previously small patches are consolidated into large continuous stands. The increased forest cover reduces the prominence of open, grassy patches.

APPENDIX B 10

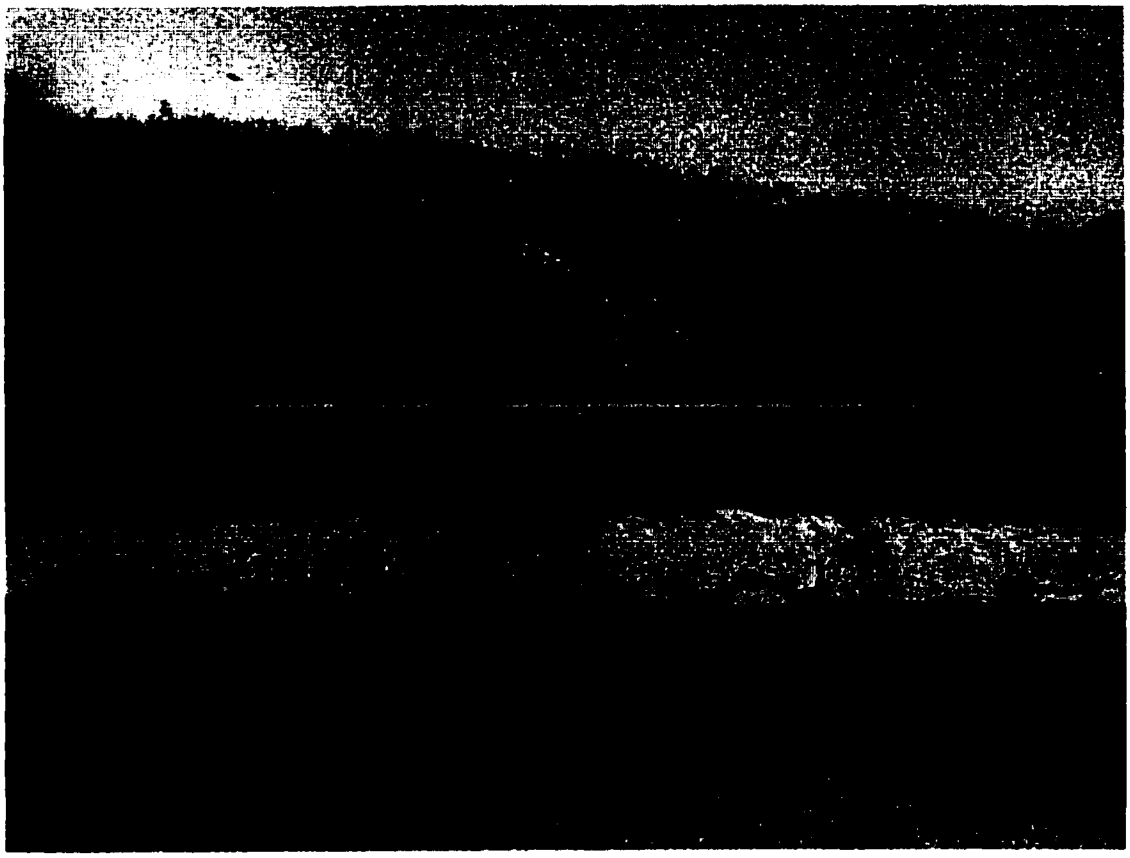
Le431	**Gibson Ridge**	1909 – 1995
(W.T. Lee)	Northern aspect	9200-9600ft.

Some patchy disturbance (logging or fire) is suggested by the narrow openings in the forest in the original photo, however most of this forest remains undisturbed. Forest cover across the top of the mesa and down the valley (rear-right) is more continuous than the foreground. Current forest cover is extensive and nearly continuous. However, the narrow, parallel to the slope, canopy gaps persist in the modern forest. This pattern is likely reinforced by avalanches on these slopes; some of these openings are forested by conifers today. Aspen has increased its cover near the base of the slope, into the meadow both in the foreground and the background. Most forest stands have expanded, but canopy openings remain on this landscape. The human settlement (Crested Butte) has expanded across the valley floor.

APPENDIX B 11

Cr 11	**Cement Creek**	1885 – 1995
(C.W. Cross)	Eastern aspect	9200-9600ft.

The distribution of live trees, i.e. aspen and conifers, in the historical photograph is dispersed and young (e.g. the small aspen on the upper portions of the slope). The charred snags and dead and down stems identify a recent fire as a potential cause of this pattern. The contemporary photograph displays more extensive cover of aspen forest than in the historical image. This forest is still young since much of it was rangeland only 110 years ago (i.e. in the original photograph). Cover of aspen and conifers has increased due to expansion of patches and development of the established clones, i.e. expansion onto former grasslands. Human influences are present (e.g. the ranch in the contemporary photo), but manipulations of the community structure are not apparent or likely. These two frames provide a glimpse of the seral and spatial development of aspen communities after a stand consuming fire event.



APPENDIX B 12

Cr 18	**Mount. Teocalli**	1885 – 1995
(C.W. Cross)	Western aspect	9600-11000ft.

The original photo depicts a landscape mosaic of aspen, conifers, and rangelands. The borders between these types have clearly been defined by previous fire behavior (the finger-like extensions of one type into another provide this evidence). The wide distribution of living trees suggests that several years have passed since the event. The left slope shows the interface of young aspen forest and open grassland. The contemporary landscape patterns remain similar to the pattern determined the fire that burned much of the original photo (right slope). The young aspen forest on the left slope is more extensive now than it was in the original photo. Aspen and coniferous forests in the background (right) have apparently increased in density, but evidence of spatial expansion is limited since aspen covered much of this terrain shortly after the disturbance. Upper and lower treeline are similar. Aspen cover and patch size has increased due to consolidation of some previously separated clones; conifer cover is similar; range has decreased.

APPENDIX B 13

Cr205	**Deep Creek Mesa**	1895 – 1995
(C.W. Cross)	East-southeastern aspect	10200-10600ft.

The original photo shows a logging operation in progress (extensive dead and down stems surrounding the small structure at lower left are the evidence). Large areas of the forest apparently remain unaffected, but the combination of human and other disturbances have created a heterogeneous landscape with many distinctive cover types. Forest cover in the recent photograph is much more continuous and extensive than in the original photograph. Aspen and conifer coverage have increased in this area, however conifer is more similar to previous the distribution (circa 1895) than do the aspen clones, i.e. they have expanded less. The remnant stand (left side of the original photo) remains distinct on the present landscape, but the matrix surrounding it has changed. The increase in aspen cover is attributed to expansion into open patches. Thus patch size of aspen increases and patch size of rangelands decreases as expanding aspen clones meet at their perimeters. Conifer stands have changed little with respect to their landscape characteristics (location and size), but dispersed individuals are apparent in the regenerated portion of the forest.

APPENDIX B 14

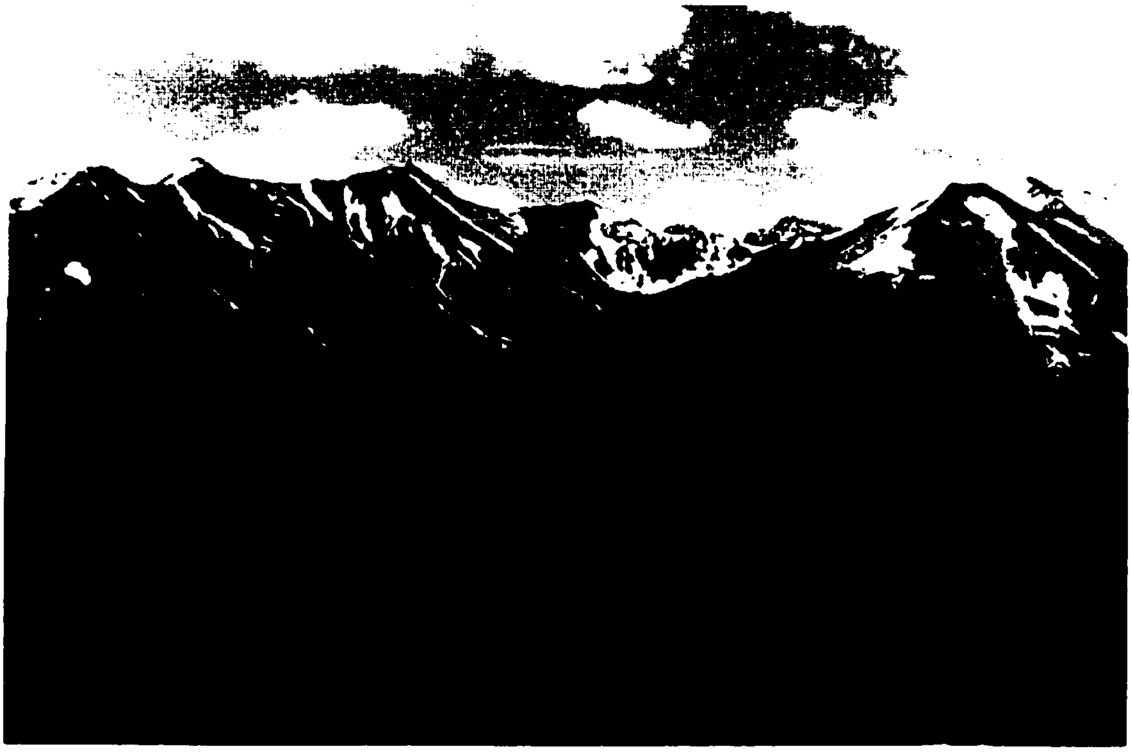
Cr225	**Iron spring, Ophir**	1895 – 1995
(C.W. Cross)	Northern aspect	10000-10400ft.

The landscape portrayed in the original photograph is divided into two distinct age (structural) groups by the border induced by a recent disturbance. Post-disturbance (dead and down stems and standing dead are evidence of the event) regeneration has already begun in the original photo. The right slope is a mixture of conifer and aspen regeneration. The center and background portions of the photo were apparently not effected by the disturbance. The contemporary forest is dominated by spruce and fir. The prolific aspen regeneration suggested in the original photo is not in evidence in the current landscape patterns. The aspen in the contemporary landscape are restricted to several isolated patches (center-right). The first generation of conifer regeneration has apparently out-competed the supposedly rapid growing aspen suckers to establish their dominance on this site. This creates an interesting disparity with the anticipated trends.

APPENDIX B 15

Cr473 **Corkscrew Gulch** 1900 - 1995
(C.W. Cross) North-northwestern aspect 10000-14000ft.

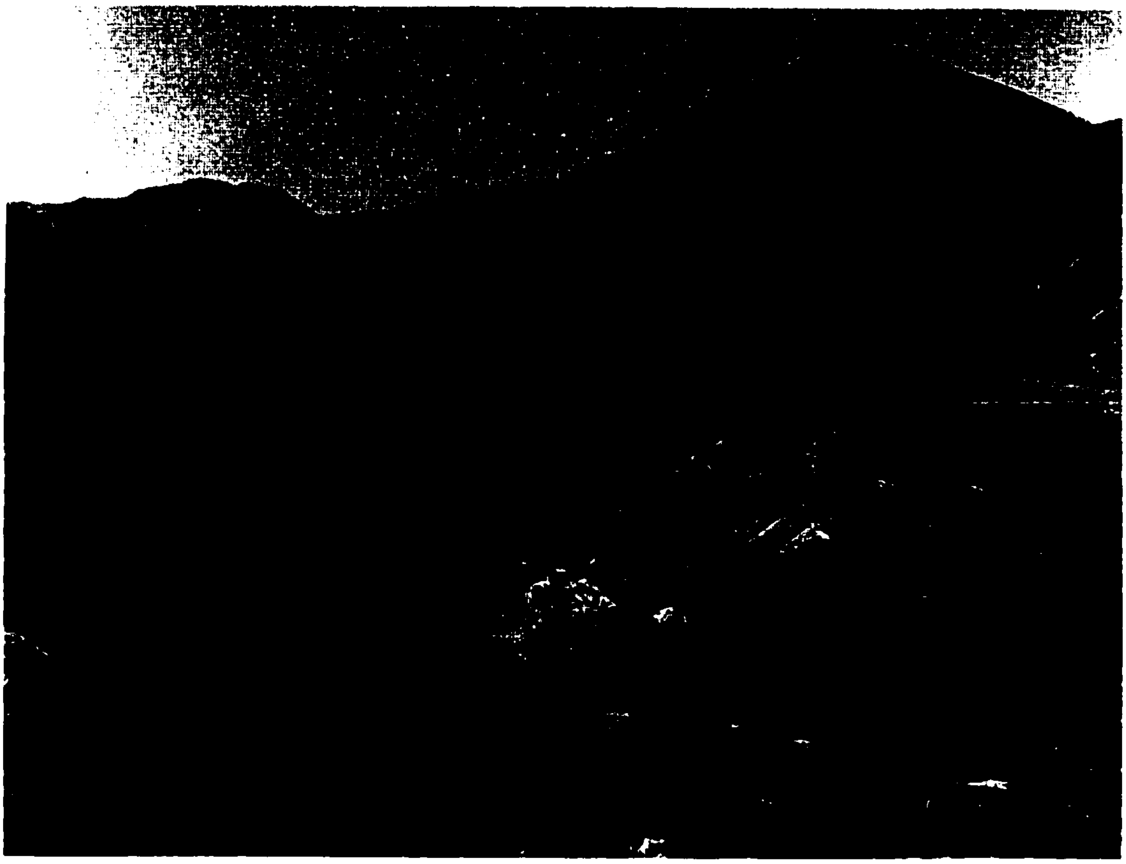
Similarly to other pairs in this region, the extensive disturbance from mining, logging, and fires is evident in the original photo. Undisturbed forests are restricted to upper portions of the slopes and the less accessible gulch (Corkscrew Gulch) in the background. The species composition of regeneration (on the lower slopes) is not easily observed, but we believe it is mixed aspen and conifer. The contemporary landscape has regenerated into a mix of aspen patches and conifer forest. Aspen patches are restricted to lower portions of the slope; knowledge of the previous landscape patterns may help explain these patterns, but our evidence does not explain them. Mine tailings still have little to no vegetation, however immediately adjacent landscape has dense forest cover. The total cover and mean patch size of conifer and aspen stands has increased with forest cover.



APPENDIX B 16

Cr475	**SW face of Red Mountain. #2**	1900 – 1995
(C.W. Cross)	Southwestern aspect	10800-11200ft.

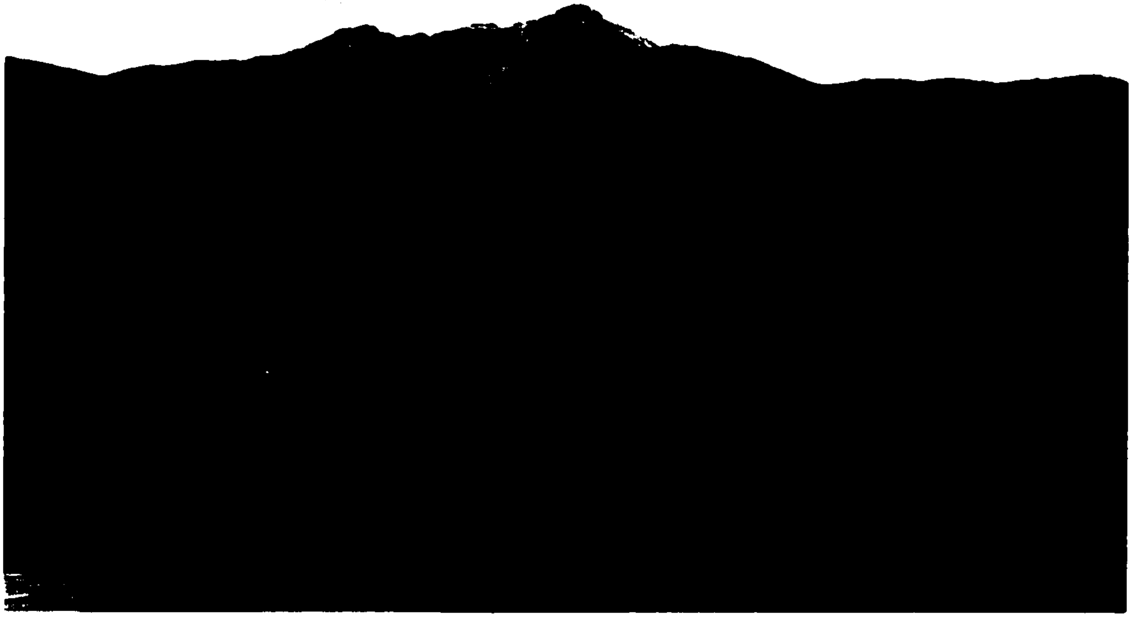
Forest cover has been removed nearly 100% in the historical photograph. Only a few remnant patches of conifers remain on these slopes. The clearing of forest for mining, logging, and fires has regenerated into a mix of aspen patches and conifer forest, however the coverage of aspen is not as extensive as depicted in previous photographs in this area (Appendices APPENDIX B 17 and APPENDIX B 18). Mine tailings have little to no vegetation, however adjacent portions of the forest show dense forest cover. Total cover and mean size of conifer patches have increased reflecting the general increase in forest cover. Aspen have also increased their coverage of the landscape, but their distribution is restricted to a few isolated patches.



APPENDIX B 17

H244	**Corbett Gulch**	1904 – 1995
(E. Howe)	Northeastern aspect	8000-8400ft.

The highly variable landscape depicted in this photograph is the product of two distinct portions of the landscape. The patches, standing dead and sparsely populated stands in the central portion of the photo are distinct, spatially, from the continuous forest cover in the background. Standing dead associated with a large fire is apparent in the background (center); it is clear that this was a fire and not leafless aspen when we consider the present lack of forest cover in part of this area on the contemporary landscape. The contemporary photograph also shows nearly continuous forest cover, both in the foreground and background. Regeneration of this area has, presumably, not been uniform with respect to cover or species composition since the disturbance in the original did not affect the foreground community. However, the result is similar from our perspective, i.e. the heterogeneous landscape patterns observed across the historical landscape have been replaced by a more homogeneous landscape. Age distribution, as one traverses the landscape, is expected to be wide in these circumstances because of the interspersion of old and new stands.



APPENDIX B 18

L446	**Slate River at Oh-Be-Joyful Creek**	1909 – 1995
(W.T. Lee)	Northern aspect	9200-9600ft.

Extensive dead and down stems suggest a fire on both slopes pictured suggest an expansive disturbance event in the recent past; most likely, this was a fire. Avalanches are another, possibly frequent, disturbance to these slopes. Members of the U.S.G.S. survey team are included in the picture. The present photograph contains more extensive forest cover than the old photograph. Conifer cover and aspen cover have increased since the original photo, but the patchy distribution of cover types remains on the present landscape. While some locations have regenerated into closed canopy forests, neighboring locations remain rangelands. Forest cover and patch size have increased since the last major disturbance, but heterogeneity of landscape pattern is conserved. This heterogeneity of patch composition (e.g. species composition, or seral stage), size, and shape is what we expect to find on a landscape maintained by disturbance.

APPENDIX B 19

Le729	**Boomerang ridge**	1910 – 1995
(W.T. Lee)	Northeastern aspect	9200-10000ft.

Although it is not easily apparent due to shadows, the lower portions of the near slopes of the mountain south of Telluride (left) are not forested. The more distant portions of the ridge are forested. The presence of the mining town and the roads (or trials) apparent in the photo suggest that this area had been logged. However, the area of regeneration also appears to be created by a fire due to the extent and stand border patterns; direct evidence for either event is lacking. These slopes, which are occupied by the ski resort on the contemporary landscape, show less forest cover in the past than in the present. The presence of aspen is extensive on lower slopes, and the distant slope is obviously patchy with aspen and conifers. Present conditions show a more uniform forest, but there is still a strong distinction between aspen and conifer stands. The presence of maintained skiing runs has little direct effect on forest cover, however this management approach likely disturbs only the designated areas. The riparian zone east of the town in the original photograph has been covered with thick mine tailings. Thus, these two features restrict natural functioning systems. Forest cover is largely the same on the upper slopes (undisturbed); it has dramatically increased on the lower, disturbed, slopes.

APPENDIX B 20

Pu89	**Bear Creek and Ridge**	1896 – 1995
(W.T. Purington)	Northeastern aspect	10000-10400ft.

The original photo shows the coniferous forests limited to higher elevations with shrubs and/or young aspen growing on lower slopes. The upper slopes are covered by spruce-fir forest. This pattern is likely the result of fires possibly set by miners seeking to expose geologic patterns. The road in the lower right portion of the photo shows is evidence that miners (or loggers) were active on these slopes. The same lower slopes are currently covered by aspen forest while the upper slopes remain mixed conifer. Conifer cover is similar, possibly with a slight increase; Aspen cover has increased in total area and mean patch area from a few scattered patches to extensive closed-canopy forest.