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DISSERTATION

FOREST ECOLOGY OF QUAKING ASPEN IN ROCKY MOUNTAIN NATIONAL PARK: A LANDSCAPE SURVEY, A RECONSTRUCTION, AND A PREDICTIVE MODEL

Submitted by

Margot Wilkinson Kaye

Graduate Degree Program in Ecology

In partial fulfillment of the requirements

for the Degree of Doctor of Philosophy

Colorado State University

Fort Collins, Colorado

Summer 2002

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WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY MARGOT WILKINSON KAYE ENTITLED FOREST ECOLOGY OF QUAKING ASPEN IN ROCKY MOUNTAIN NATIONAL PARK: A LANDSCAPE SURVEY, A RECONSTRUCTION, AND A PREDICTIVE MODEL BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

Committee on Graduate Work

Advisor

Department Head/Director

ABSTRACT OF DISSERTATION

FOREST ECOLOGY OF QUAKING ASPEN IN ROCKY MOUNTAIN NATIONAL PARK: A LANDSCAPE SURVEY, A RECONSTRUCTION, AND A PREDICTIVE MODEL

Ecology and management issues of quaking aspen in western forests have come to a pinnacle in the region of Rocky Mountain National Park, Colorado. Human land-use practices over the past century have altered both fire regimes and elk populations, two factors that play important roles in the life history of aspen. Fire suppression diminished the number of new aspen stands, most aspen stands have reached 100 years of age, and many stands are succeeding to conifers. Previous studies of aspen in the Park have concluded that intensive elk browsing has brought about a decline in the aspen population. A survey of 240 hectares of the Park revealed that elk browsing has a highly localized effect on aspen populations in the heart of the elk winter range, but on a broader spatial scale, conifer invasion is more prevalent. A dendrochronological reconstruction of the dynamics of conifer invasion of aspen stands indicated that conifer trees replace aspen via sub-canopy establishment and longevity rather than directly causing a decline in aspen growth or an increase in aspen mortality. Forest succession from aspen to conifer forests primarily occurs due to differential life history traits of the species involved, rather than species interactions. Tree-ring data were used to create an age-

structured model for aspen in the Park. The model projects aspen density through time under varying recruitment scenarios. Aspen stands sampled in this study require between 100 and 300 stems ha-1 recruitment each decade to maintain current stand density (500 to 1500 stems ha-1). With no future recruitment, aspen stands would not persist longer than 100 years. Periodic pulses of recruitment lead to an aspen stand structure that is highly dynamic through time.

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DEDICATED

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LUCINDA PINA WILKINSON

TABLE OF CONTENTS

CHAPTER 1: OVERVIEW

QUAKING ASPEN IN THE FRONT RANGE, COLORADO

Quaking aspen (*Populus tremuloides* Michx.) qualifies as a leader in the charismatic mega-flora of the central Rocky Mountains. From afar, light-green and brilliant yellow patches of aspen on the landscape contrast the surrounding matrix of dark-green conifer forests. From within, aspen patches provide lush refuge for plants and animals from homogenous conifer forests that represent over 90% of the forested landscape. As early as the 1950's, ecologists noted the higher floral and faunal diversity in aspen forests, especially when compared to surrounding conifer forests (Hoff 1957). Subsequent studies have documented that aspen forests tend to have higher diversity than conifer forests of mammals (DeByle 1985), birds (Turchi et al. 1995), herbaceous species (Hoff 1957, Stohlgren et al. 1999), and butterflies (Simonson 1998), as well as lower flammability (Brown and Simmerman 1986). Stohlgren et al. (1999) labeled aspen patches as "hotspots" of diversity. Additionally, aspen forests are valued for their aesthetic beauty (Johnson et al. 1985).

The management of aspen in the Front Range is polemical due to land management issues and the species' life history. Aspen covers a small percentage of the landscape (<10%) and has a highly varied structure, which makes it difficult for managers to target a desired population structure. Establishment of aspen patches is integrally related to forest fires (Baker 1925, Bartos and Mueggler 1981, Bartos et al.

1994), which have been suppressed since early in the 20th century. The high-profile population of elk (*Cervus elaphus*) in Rocky Mountain National Park has been blamed for damaged portions of the Park's aspen population (Packard 1942, Olmsted 1979, 1997, Baker et al. 1997). Forest fires and elk populations in the central Rocky Mountains remain unsolved management issues themselves, and decisions concerning management practices for aspen cannot be completed without progress in these two arenas.

THE SCOPE OF THIS STUDY

The 20th century alteration of fire regimes and elk populations directly influenced the aspen population in Rocky Mountain National Park, Colorado. Ecology and management issues of aspen in western forests have come to a pinnacle in the Park. Since the late 1960's, National Park management has been dictated by the policy of natural regulation. Under this policy, active management within the Park is kept to a minimum so that "natural regulation" can proceed within the ecosystems. The degree of "naturalness" is unclear given the absence of the three major predators of elk (humans, wolves, and grizzly bears). In Rocky Mountain National Park, natural regulation has brought about a dramatic increase in elk population due to the prohibition of herd culling or hunting and absence of natural predators of elk. In addition to changes in the elk population, fire suppression throughout the central Rocky Mountains has removed the primary disturbance within the Park landscape.

I chose to conduct my research within Rocky Mountain National Park because of the current management issues surrounding aspen, the history of previous studies of aspen within the Park (Packard 1942, Olmsted 1979, Parker and Parker 1983, Turchi et al. 1995, Baker et al. 1997, White et al. 1998, Suzuki et al. 1999), and the opportunity to

treat the population of aspen within the Park as representative in climate and geomorphology for the Front Range of the Colorado Rocky Mountains. Within the Park, many studies have concluded that aspen forests are in decline due in part to excessive browsing by elk (Packard 1942, Olmsted 1979, Baker et al. 1997). These studies focused on portions of the elk winter range within the Park, which is only a fraction of the landscape within the Park.

The elk winter range represents the area in the Park that is most likely to be highly impacted by elk (DeByle 1985). Large numbers of animals (approximately 2000 head in 1999) rely on these low-elevation areas for winter forage (another 2000 elk overwinter within the adjacent town of Estes Park). The browsing of stems and shoots of aspen trees by elk both removes new growth and creates wounds for pathogen infection in old stems (Krebill 1972, Hinds 1985). The summer range is much larger; extensive high-elevation areas have lower elk densities and higher forage availability. The spatially variable foraging patterns of elk should lead to varying impacts across the landscape of the Park.

I began my research by describing the aspen population in Rocky Mountain National Park and then used the results from the description to continue research on key issues concerning the aspen population. My goals for the description were to determine the amount of aspen on the landscape, the structure of the aspen stands, and the degree to which the population had been affected by elk browsing. This descriptive study revealed that conifer invasion in aspen stands was evident throughout Park, while elk browsing was highly localized (see also Suzuki et al. 1999). Based on these results, I concluded that conifer invasion could be a more pressing issue in the population-scale management of aspen. Therefore, my next research project was a dendrochronological reconstruction

of the dynamics of conifer invasion in aspen stands. The goal of this study was to identify the mechanisms driving conifer invasion of aspen stands. I also created an age-structured model to project current aspen stand structure into the future to explore the implications of these ecological factors on the future of aspen in Rocky Mountain National Park.

CHAPTER 2: A SPATIAL SURVEY OF THE QUAKING ASPEN POPULATION IN ROCKY MOUNTAIN NATIONAL PARK, COLORADO

ABSTRACT

Elk, fire, and climate have been affecting the aspen population in the Rocky Mountains, but mostly subjective studies have characterized the influences of these factors. A broad-scale perspective may shed new light on the status of aspen in the region. I collected field measurements of aspen patches encountered within 40 randomly located transects in 340 km^2 of Rocky Mountain National Park, Colorado, to quantify the aspen population and determine the effects of elk browsing. Aspen covered 5.6% of the area in the transects, much more than previously expected. The distribution and structure of aspen patches were highly heterogeneous throughout the study area. Of the 123 aspen patches encountered in the 238 ha surveyed, all but one showed signs of either conifer invasion or elk browsing. No significant difference occurred in aspen basal area, density, regeneration, and patch size between areas of high elk use (elk winter range) and areas of lower elk use (elk summer range). Two-thirds of the aspen patches contained conifer invasion. I concluded that elk browsing may have highly localized impacts on aspen patches, however conifer invasion is a greater landscape-scale influence on aspen persistence between fires.

INTRODUCTION

The future of quaking aspen (*Populus tremuloides* Michx.) forests in the Rocky Mountains is the subject of widespread debate. Human land-use practices over the past century have altered both fire regimes and elk populations, two factors that play important roles in the life history of aspen (Jones and DeByle 1985, DeByle et al. 1987, Romme et al. 1995). In addition, aspen dynamics are influenced by fluctuations in climate (Romme et al.1995, Singer et al. 1998). Ecologists do not agree on the extent to which elk, fire, and climate have been affecting the aspen population in the Rocky Mountains. Some argue that the damage has been severe (Packard 1942, DeByle 1985, Wagner et al. 1995), and that restoration of past disturbance regimes and elk densities is not sufficient to preserve aspen (Berry et al. 1997, White et al. 1998). They cite lack of aspen recruitment, damage to existing aspen stems, absence of new stand establishment, and extensive conifer invasion as symptoms of the decline of aspen. From another point of view, the dynamic characteristics of aspen may allow it to persist through varying conditions (Parker and Parker 1983). Indeed, it may be the versatility of aspen's life history and structure that has in part caused the disagreement concerning the status of the species.

Structure and function of aspen patches

Aspen exists in many forms across the Rocky Mountain landscape, ranging from large stands of pure aspen to isolated patches consisting solely of a few stems. Aspen patches can be found on meadow edges, in riparian corridors, and buried deep in expanses of other forest types such as lodgepole pine or mixed conifer. Aspen is a clonal species, so the trees we see aboveground are ramets connected by an extensive

belowground root mass (Barnes 1966, Jones and DeByle 1985). An individual stem or ramet of aspen usually lives less than 200 years, though aspen clones can persist on the landscape for a much longer time (Barnes 1966). Ramets (referred to as stems for purpose of this paper) can establish as single or multiple cohorts in a clone (Betters and Woods, 1981). Aspen forests are both a rare and important habitat type for many floral and faunal species of the Rocky Mountains (DeByle 1985, Turchi et al. 1995, Stohlgren et al. 1997a and 1999), they are the only widespread deciduous forest type of the region (Peet 1988), and they are valued for their aesthetic beauty (Johnson et al. 1985). The full range of aspen forms on a landscape must be assessed to understand aspen dynamics and the future of the species in the Rocky Mountains.

Elk Browsing

Patterns of elk browsing are stratified between the elk's lower elevation winter range and higher elevation summer range. The impacts of elk browsing on aspen are more severe within the elk winter range with large numbers of animals in small areas with limited forage (DeByle 1985). Browsing in the elk summer range has less impact as the herds are distributed over larger areas in a season with higher forage production. Ecologists have suggested that aspen stands heavily impacted by elk will have lower stem basal area, density, and number of sprouts than those with little elk browsing (DeByle 1985, White et al. 1998).

Comparative aspen data

The data collected in this study can provide a baseline description of a population of aspen in the central Rocky Mountains. Two types of comparable data are available for aspen in the Rocky Mountain region. The first type of data comes from field

measurements of aspen stands. The limitation of these data lies in small number of stands sampled and the selectivity in types of stands sampled. The second type of data comes from high-resolution remote sensing. For example, a GIS of the central portion of Rocky Mountain National Park was created based on aerial photographs (1:15,840) taken in the Park in 1987 (M. Kalkhan, Natural Resource Ecology Laboratory, Colorado State University). The minimum mapping unit of these data limit their ability to detect the diverse forms of aspen patches (Stohlgren at al. 1997b).

Study objectives

Pessimistic predictions for the future of aspen forests in the central Rocky Mountains have been based on data collected from a hand-picked or small sample of stands (e.g., Baker et al. 1997, Olmsted 1979, 1997, Packard 1942). A broader-scale, objective perspective may shed new light on the status of aspen in the region (Suzuki et al. 1999, Barnett and Stohlgren 2001,). Remote sensing and field collections are two possible methods to collect the appropriate data. For this study, I used randomly located belt transects to describe the population of aspen in 340 km^2 of Rocky Mountain National Park, Colorado. This method maximized the area of the Park I could survey and the grain of the spatial resolution of the data. I collected field measurements of aspen patches encountered within the randomly-located transects to: (1) characterize the structure of aspen patches in the Park; (2) assess the impacts of elk on the structure of aspen forests by comparing measurements between the elk winter and summer ranges; (3) compare the structure of aspen stands in the Park with similar measurements collected for aspen throughout the Rocky Mountains; and (4) compare the results of the ground survey with remotely sensed data collected from the same area.

METHODS

Study area

Rocky Mountain National Park is located in the Front Range of the Colorado Rocky Mountains and covers an area of approximately 107,500 ha and elevations ranging from 2390 m to 4300 m. The Park straddles the continental divide, with half the area above tree line. Average annual minimum and maximum temperatures near Estes Park ($105^0$30', $40^0$24'; at 2390 m elevation and the east-side entrance to the Park) are –1.5 and 14.0 °C. Growing season (May-October) temperatures average 4.0 to 21.0 °C with annual precipitation of 350 mm. Vegetation types are typical of the Central Rocky Mountains and include ponderosa pine (*Pinus ponderosa*), lodge pole pine (*P. contorta*), mixed conifer (*P. ponderosa*, *P. contorta*, *Pseudotsuga menzesii*, *Abies lasiocarpa*, *Picea engelmannii*), and spruce-fir forests (*A. lasiocarpa*, *Picea engelmannii*), as well as wet and dry meadows, riparian corridors, and alpine tundra (Peet 2000).

Field methods

The survey was conducted between June 1998 and October 1999. I randomly located 40 points within the forested area of the central portion of the Park. To locate the points, an X and Y coordinate grid was laid over aerial photographs (1:15,840) of a 33,933 ha area. Two hundred pairs of randomly generated X and Y coordinates were located on the maps, and 40 of those points fell within forested regions of the park. Of the 40 points, I eliminated any point that fell within 1000 m of a previously established point.

Points were located in the field using United States Geologic Survey (USGS) 1:24,000 topographic maps and a hand held Global Positioning System. I sampled belt

transects from 36 of the 40 randomly located points because three points were within 1000 m of another point and the fourth was inaccessible due to impassible terrain and rivers. Two perpendicular belt transects were run from each point. The azimuth of the first belt transect was randomly selected and the second transect was either plus or minus 90 degrees based on a coin toss. Each belt transect was 50 m wide and 1000 m long, when possible. If I encountered topographic barriers such a cliffs, lakes, or breaks in forest cover greater than 50 m, I truncated the transect and recorded the length. Transect locations and lengths were mapped onto USGS topographic maps and positions were recorded for each transect origin and end point.

Data were collected for all aspen patches intersected within the belt transects. I recorded the GPS position at the center of each aspen patch, the dimensions and shape of the entire patch and the area of the patch within the transect, dominant aspect and slope of each patch, and classified the topographic position by drainage, basin, gentle slope, rocky slope, steep slope, steep and rocky slope, rock outcrop, and ridge top. All aspen patches were mapped onto USGS topographic maps based on field orienteering and GPS positions. Elevation of each patch was calculated from the topographic maps.

I subjectively located 25 m^2 (5 m x 5 m) plots within each aspen patch encountered in the transects to quantify the structure of the patch. I sampled between one and six plots according to the heterogeneity of aspen structure within the patch. Within each plot I recorded (for stems >1.5 m tall): number of stems, diameter at breast height (taken at 1.4 m), height, and a visual estimate of percent bark browse up to 1.5 m. Elk browsing leaves a distinctive scar on the bark of aspen stems (Hinds 1985), and I estimated the percent of the stem that was covered with such scars. I counted the number

of stems <1.5 m tall as "aspen regeneration", and recorded the number of stems that showed evidence of elk browsing. Chronically browsed aspen regeneration often sprout many stems in tight clumps from a single root node. I counted each clump as a single regenerating stem because it was unlikely that more than one of the sprouts would successfully grow to full size (Romme et al. 1995). Due to the mixed tree composition of many aspen patches, I estimated the percentage of aspen and conifers in the canopy by counting the number of trees of aspen and conifers in the canopy and converting the count to a percent. I used this percentage to represent the degree of conifer invasion in an aspen patch. If an aspen patch was smaller than the plot size, its dimensions were recorded and all plot data were collected except percent aspen in the canopy.

Data analysis

Area of aspen patches was calculated using geometric equations based on the patch shape and measured dimensions. Area covered by each transect was calculated by multiplying the transect length (in meters) by its width (50 m). Percent cover of aspen within the forested area of the Park was calculated based on the total area covered by the belt transects and the area of aspen patches within transects. I calculated the percent aspen cover as a function of elevation based on the area covered by transects at a given elevation and the area of aspen patches at that elevation. The distribution of topographic positions of aspen patches was calculated to identify any pattern in aspen patch location.

Data from the 25 m^2 plots were used to calculate density, basal area (BA), average bark browse, and regeneration. All data were scaled to a per-hectare basis for analysis, and I calculated a weighted mean for patches with more than one plot. Elk winter and summer range boundaries were mapped from a 5-year monitoring of elk movements

within the Park (F. Singer, Natural Resource Ecology Laboratory, Colorado State University, pers. comm.). I overlaid the location of the patches on the boundary map and classified each patch as occurring either in the elk summer or winter range. Percent bark browse, basal area, density, regeneration, and patch size were compared between stands within and outside of elk winter range with a one way ANOVA (alpha=0.05).

Aspen cover measured by the ground survey was compared with values measured by a GIS created from high-resolution color aerial photographs (1:15,800) of a 10,000 ha area around Beaver Meadows in the Park. Average aspen cover measured in the six transects that fell within the 10,000 ha area was compared with the 6.4% cover calculated by the GIS for the same area.

RESULTS

The 36 randomly located transects were distributed throughout the forested area of Rocky Mountain National Park, with half the transects on either side of the Continental Divide (Fig. 2.1). I surveyed 238 hectares within the belt transects and encountered 123 aspen patches. Aspen patches covered 5.6% of the transect area throughout the study area, and 6.3% and 4.9% of the area on the east and west sides of the Continental Divide respectively.

Aspen patches were found from the lowest elevations in the Park (2560 m) to tree line (3200 m). Percent cover of all aspen peaked at three elevation ranges: 2580-2610 m, 2740-2820 m and 2930-3050 m (Fig. 2.2). On the east side of the Park (east of the Continental Divide), percent aspen cover peaked at 2930-3050 m. On the west side of the Park, percent aspen cover peaked at slightly lower elevations (2850 m-2960 m). Aspen cover was consistently low above 3100 m, with most on the west side (Fig. 2.2).

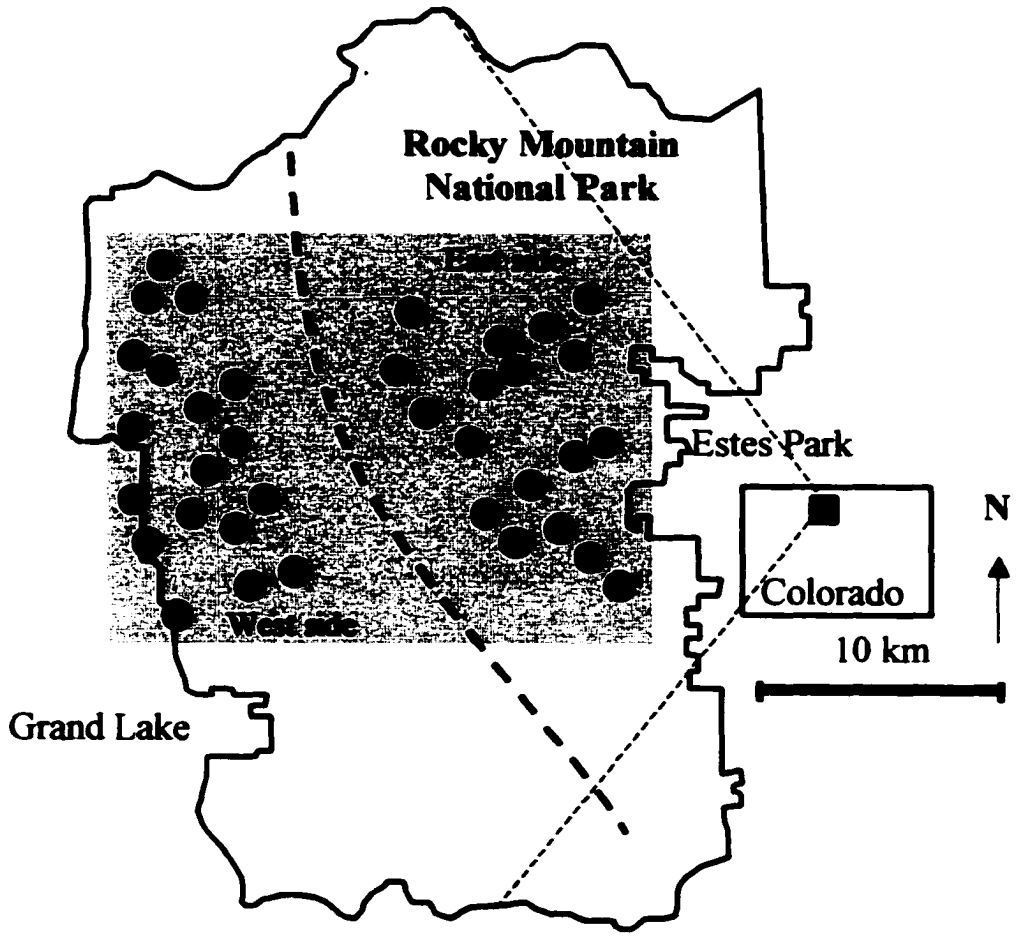

Figure 2.1. Map of study area within Rocky Mountain National Park, Colorado. Shaded box represents 340 km^2 area in which 36 points (black circles) were randomly located. From each point, two perpendicular belt transects (50 m X 1000 m) were surveyed for aspen. The Continental Divide runs through the Park (dashed line).

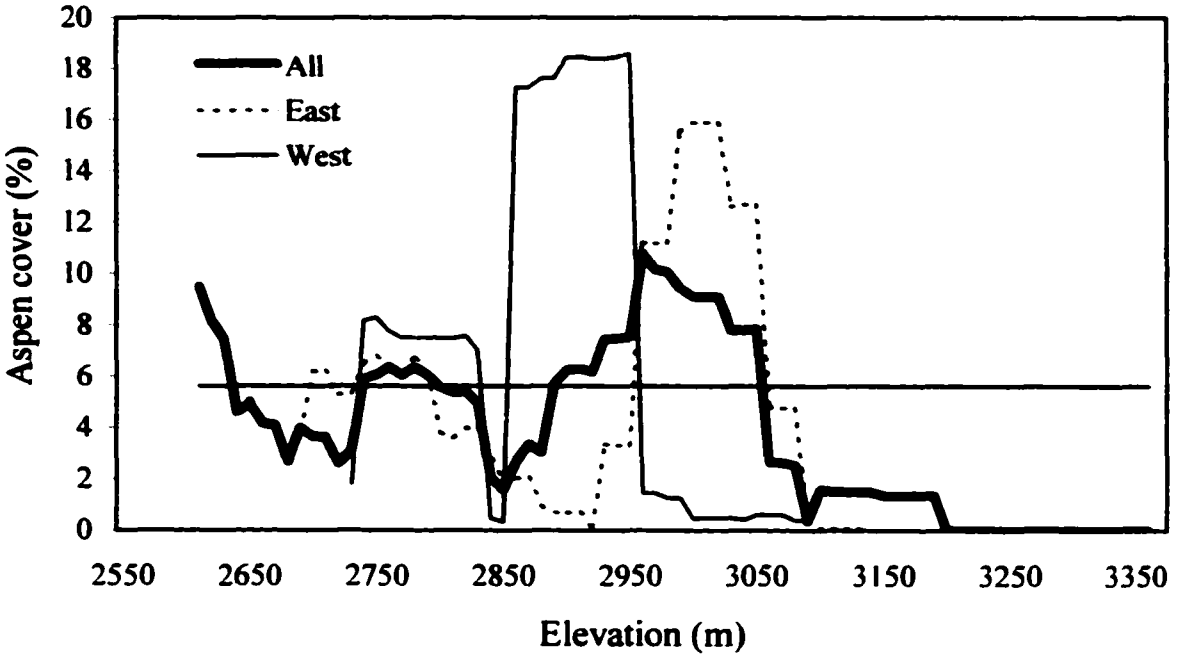

Figure 2.2. Distribution of percent aspen cover across an elevation gradient. The dark solid line represents percent cover for all aspen, the thin solid line represents the distribution of percent aspen cover on the west side of the park and the dashed line represents percent aspen cover on the east side. Percent aspen cover for aspen all throughout the Park was 5.6% (horizontal line).

Aspen patches occurred most frequently on gentle and rocky slopes, however patches were found in all topographic positions (Fig. 2.3). Patches were evenly distributed across all aspects. I found patches on slopes ranging from 0 to 50 degrees, with 50% of the patches on slopes of less than 10 degrees.

Aspen patches ranged in area from < 1 m^2 to >1 ha (Fig. 2.4a). Stands >1ha were complex in shape and were difficult to accurately measure with the design used in this study. I plotted frequency of all patch areas and those between 1 m^2 and 200 m^2. Patch areas were distributed throughout this range, with over 12% of all patches having an area <10 m^2 (Fig. 2.4b). Mean patch area peaked at 2900 m and 3000 m elevation (Fig. 2.5).

Conifer invasion was found in aspen patches throughout the Park. Only 1/3 of patches contained pure aspen in the canopy and another 1/3 had less than 50% aspen in the canopy (Fig. 2.6). The amount of conifer trees was weakly correlated to aspen basal area and density ($r^2 < 0.2$, $P<0.01$, Fig. 7), and the relationships were significant ($p<0.01$) (Fig.2.7).

Aspen characteristics were similar among the 47 stands in the elk winter range and 62 stands in the elk summer range; only percent bark browse differed significantly (Fig. 2.8). Aspen was more commonly found on gentle slopes in the summer range (36% of patches) than in the winter range (23%) (Fig. 2.3). Elk browsing was evident in 93% of the patches throughout the Park; with a large number of patches showing over 80% bark browse (Fig. 2.9).

The six transects that fell within the 10,000-ha forested area surrounding Beaver Meadows in the Park had an average aspen cover of 8.6%. The GIS calculated an aspen cover of 6.4% for the same area.

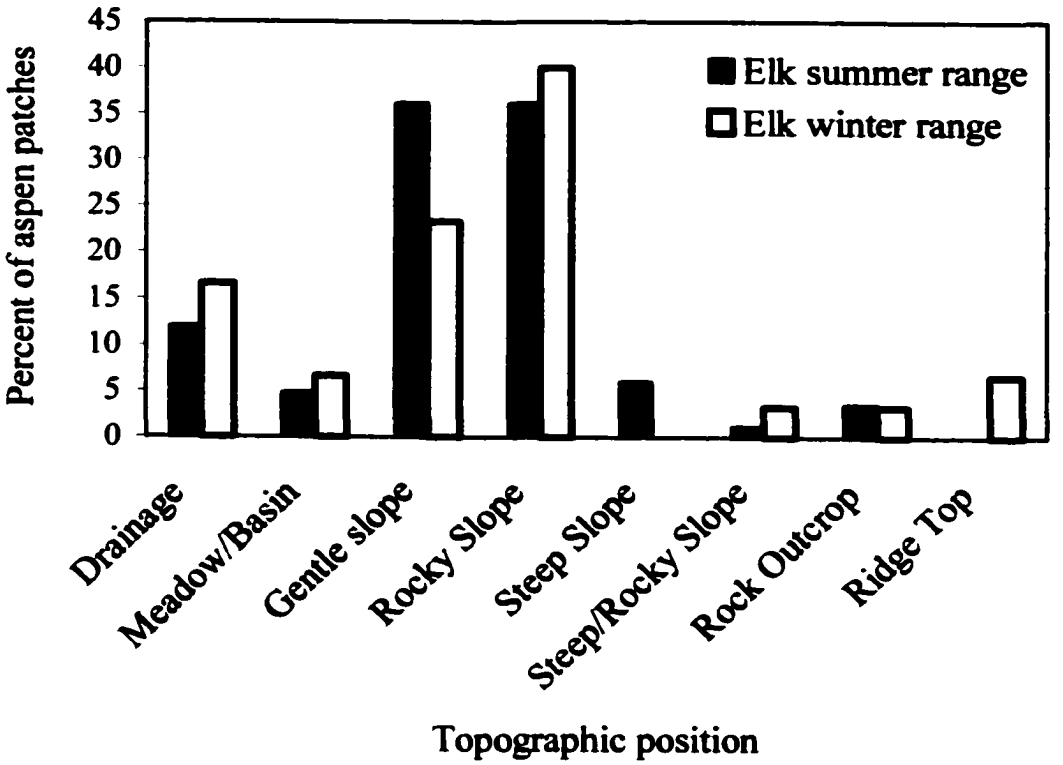

Figure 2.3. Topographic positions of aspen patches encountered within the transects. Forty-two of the patches are located in the elk winter range and 67 in the summer range.

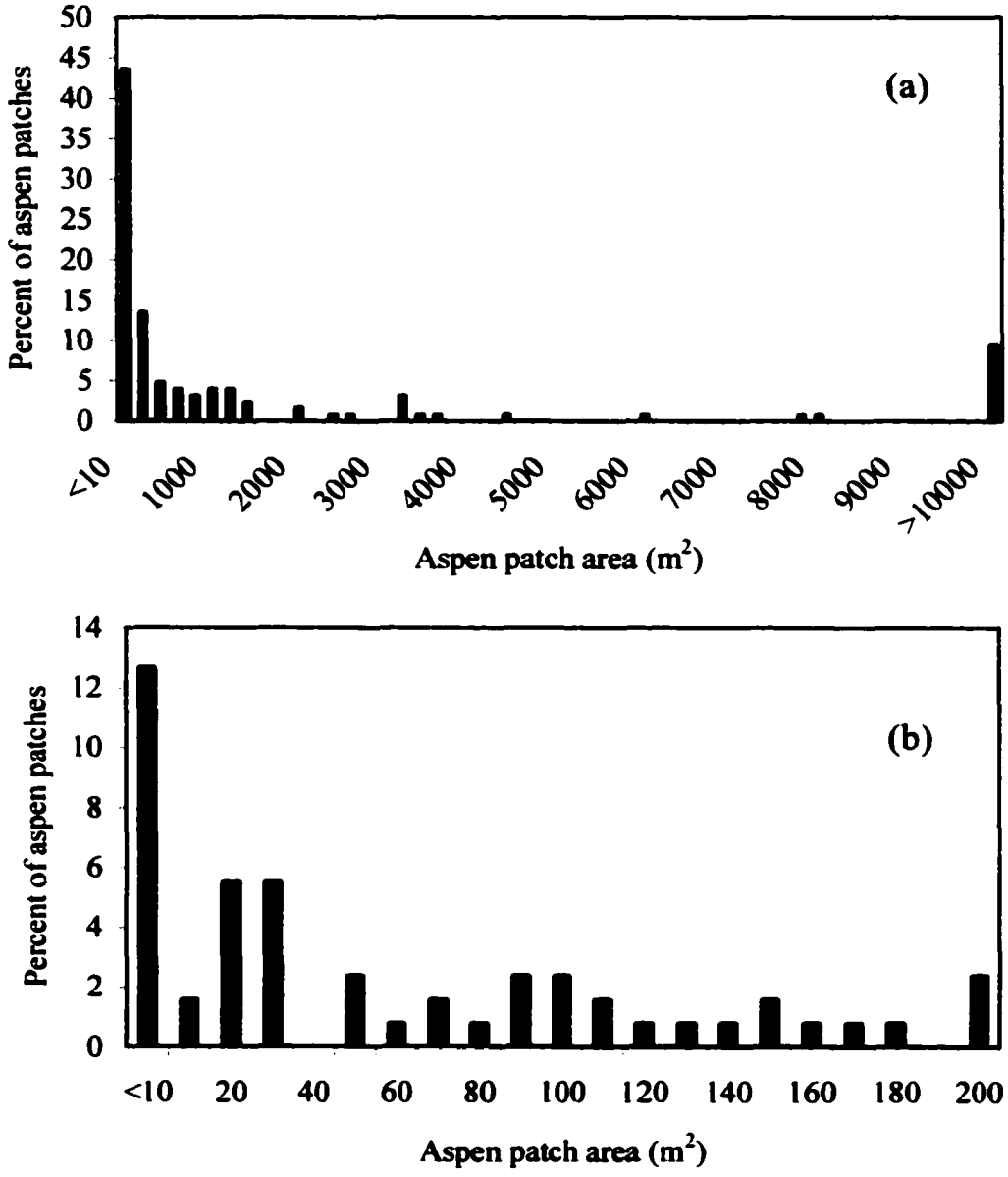

Figure 2.4. Aspen patch area (m^2) of the 123 patches encountered with the belt transects. Nearly 10% of the patches were larger than one hectare, which was the maximum patch size measured accurately with this study design. Over 40% of patches were smaller than 200 m^2 (a), so I plotted the distribution of patch areas between 1 and 200 m^2 (b).

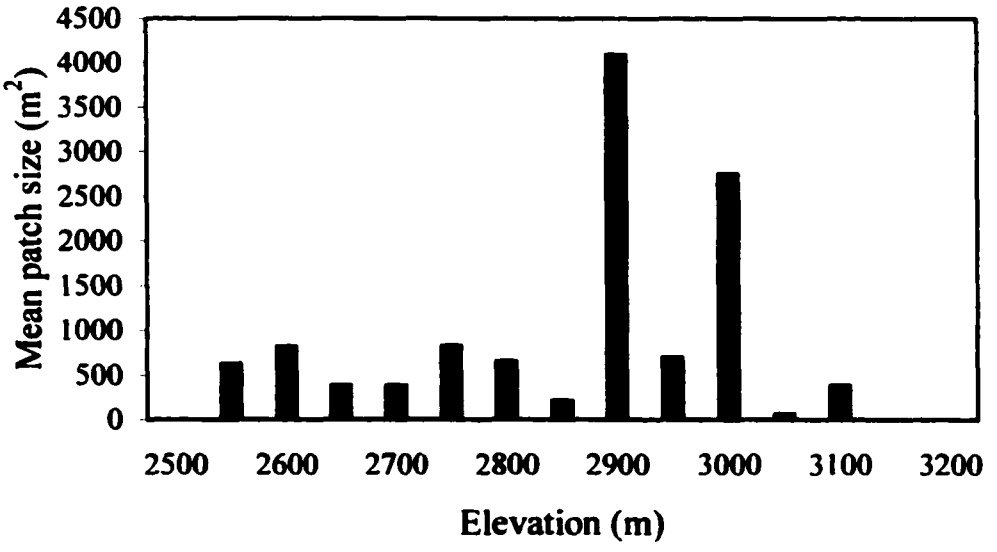

Figure 2.5. Mean aspen patch size (m^2) across an elevational gradient. Mean patch size between 2900m and 3100m elevation may be underestimated because at those elevations I encountered aspen patches larger than one hectare in area.

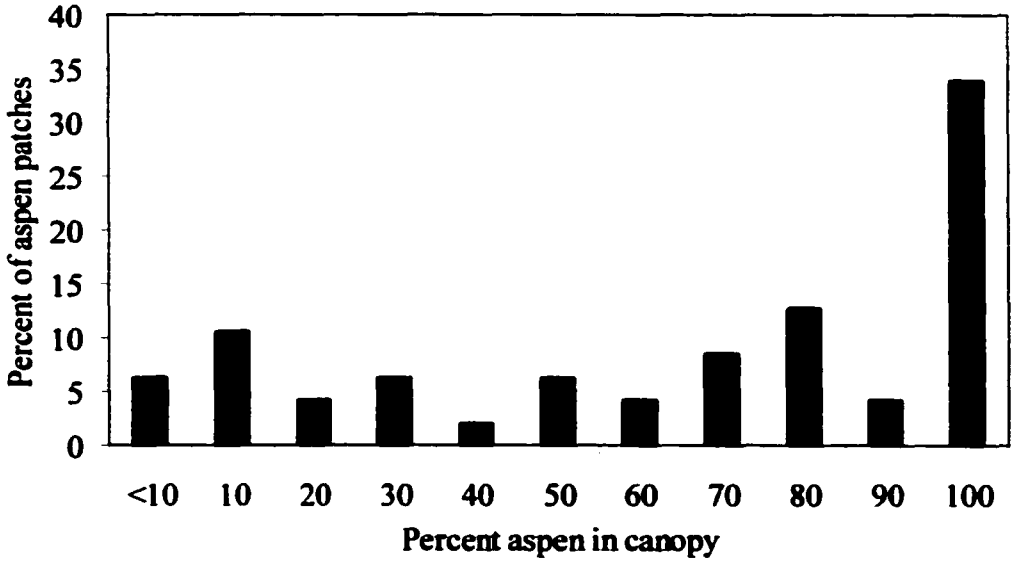

Figure 2.6. Percent aspen in the canopy of forest patches that were identified as aspen within the belt transects. Conifer species occupying the remaining percentages of the canopy were: *Picea engelmanii*, *Abies lasiocarpa*, *Pinus contorta*, and *Pseudotsuga menzesii*.

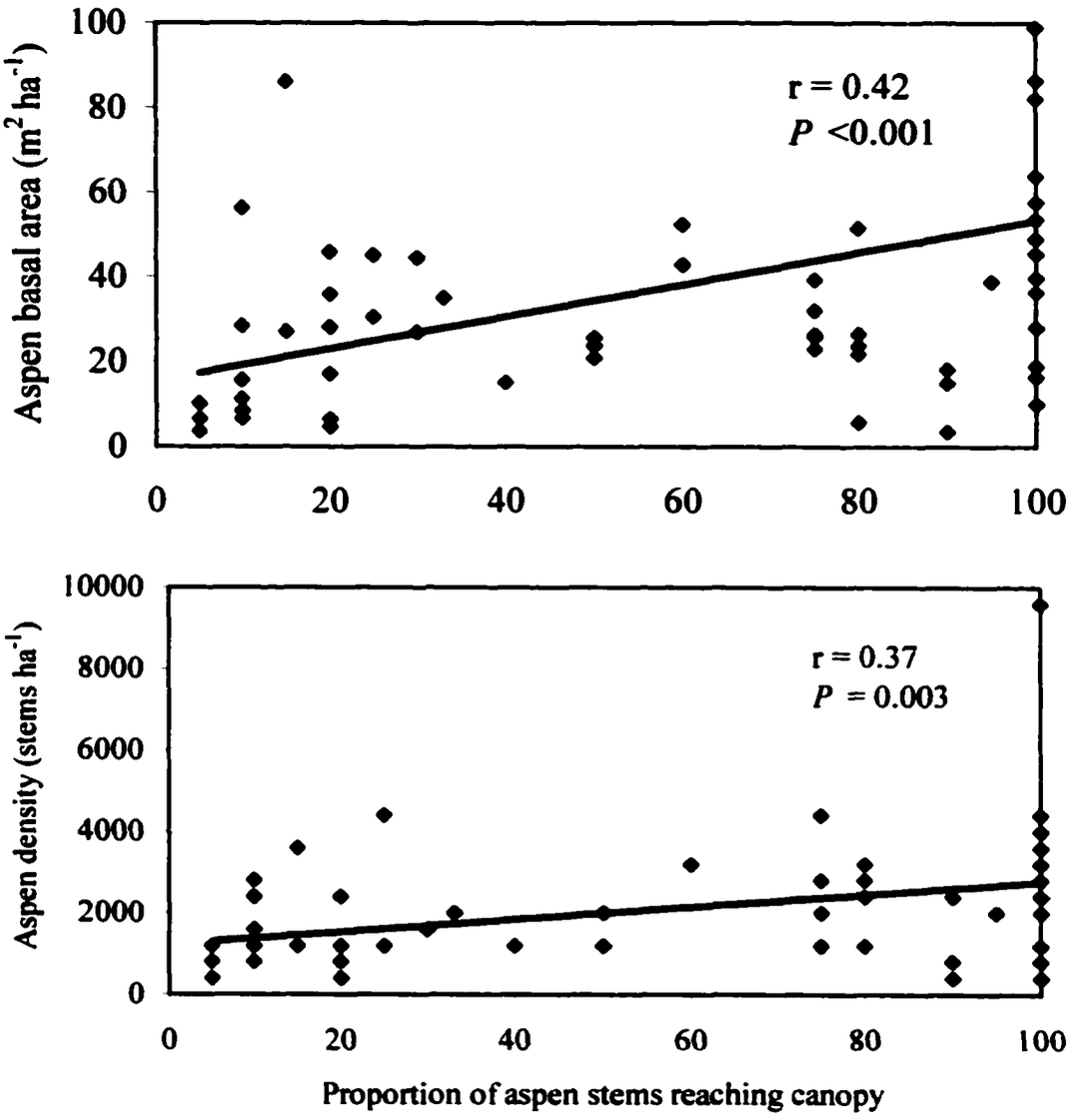

Figure 2.7. Correlations of percent aspen in the canopy with aspen basal area (BA) and density (n=61).

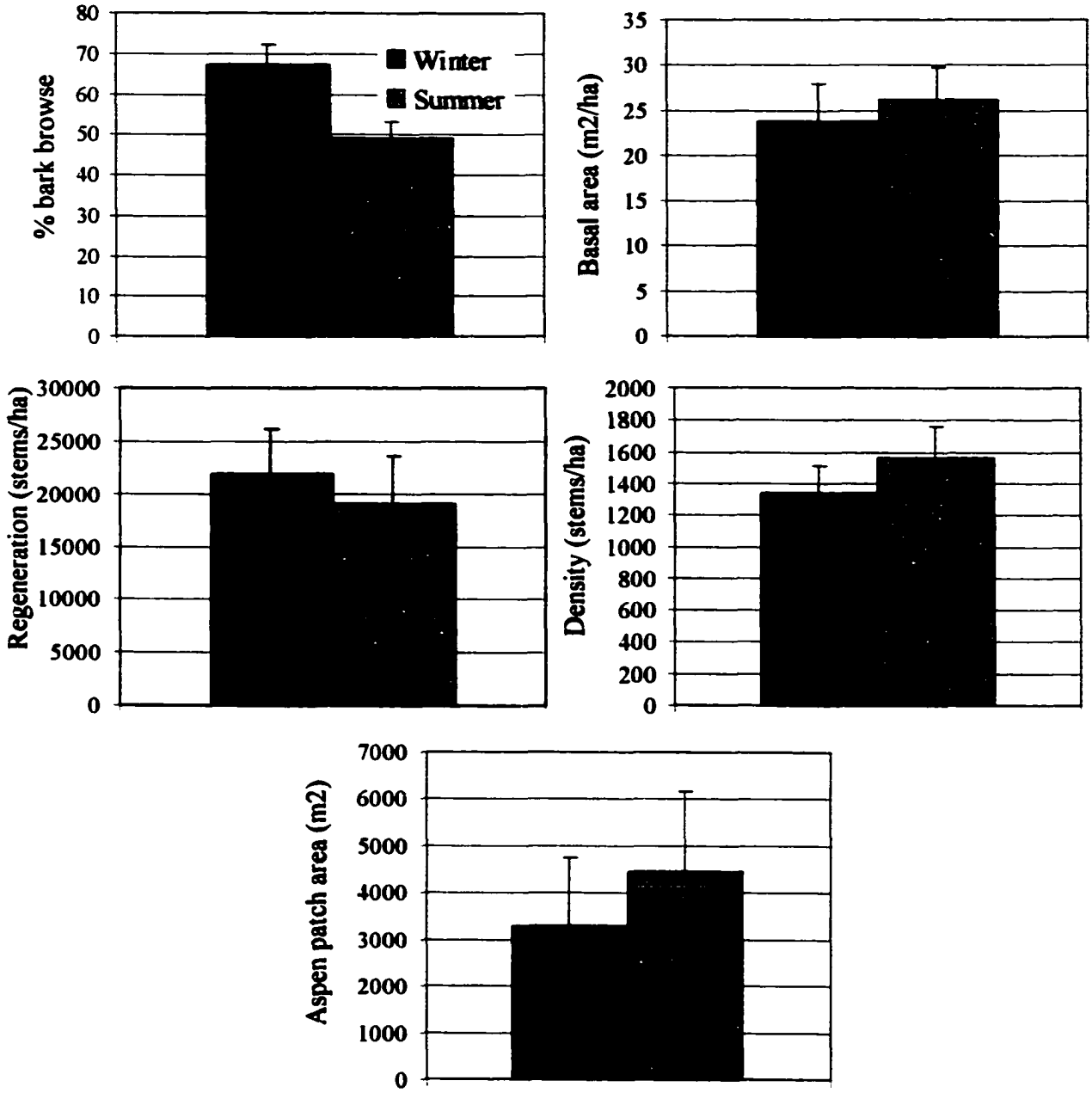

Figure 2.8. Mean and stand errors for aspen patch characteristics in the elk winter (black) and summer (striped) ranges. t-tests compared the following characteristics between aspen patches in the elk summer (n=62) and winter (n=47) ranges: percent bark browse on aspen stems ($P<0.01$), basal area of aspen stems ($P=0.67$), regeneration (stems <1.5m tall) of aspen stems ($P=0.65$), density of aspen stems ($P=0.44$), and area of aspen patches ($P=0.62$).

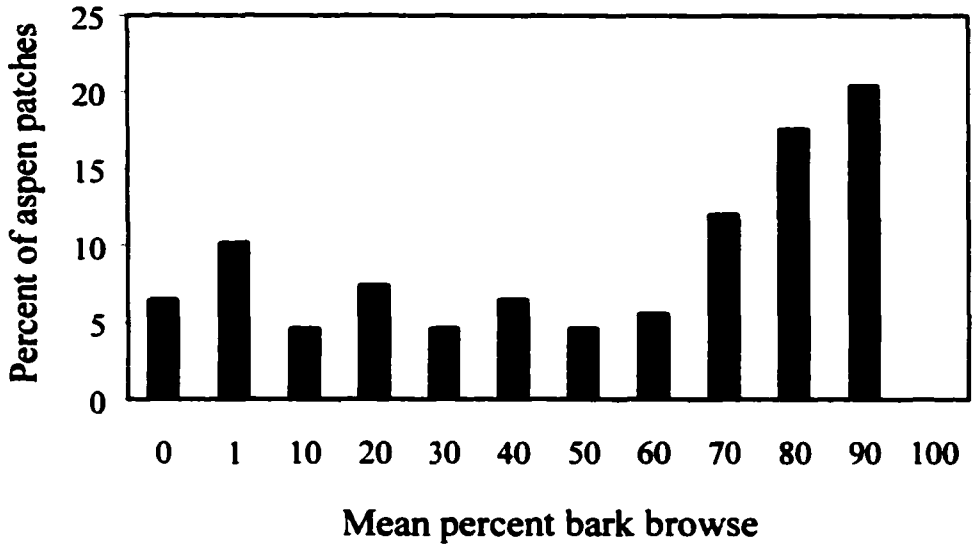

Figure 2.9. Percent bark browse of aspen patches encountered in the belt transects. Mean percent bark browse was calculated per patch by averaging values from each aspen stem measured within the 25 m^2 plots sampled within each aspen patch. If the patch was smaller than 25 m^2, I measured all stems within the patch. Fifty percent of patches had an average of over 70% bark browse. Only 7 of the 123 patches showed no bark browse.

DISCUSSION

The status of aspen in Rocky Mountain National Park

The results of the ground survey emphasized the futility in describing a "typical" aspen patch for the central Rocky Mountains (Figs. 2.2-2.4). For example, I encountered aspen at tree line in krummholtz form, as large patches (> ¼ ha) persisting on rocky outcrops, and on gentle topography such as meadow edges and mild slopes. Aspen patches ranged in size from a single stem to several hectares. Most likely, the high quality habitat associated with aspen usually refers to larger stands of pure aspen. However, each form of aspen patches contributes to the population as a whole. Small patches of aspen may represent relicts of older stands that have been replaced by conifer trees and are likely connected to a larger root matrix. In the case of a forest disturbance such as fire, small aspen patches may expand rapidly and colonize a large area via asexual reproduction (Mueggler 1989). In time, this patch may become one of the high-quality habitat stands. Though I can speculate on the function of all types of aspen patches, further research is needed to understand the processes associated with the structural diversity of aspen forests.

The heterogeneity of aspen structure in the central Rocky Mountains has been largely overlooked in ecological studies. Most of the research conducted on aspen has focused on a narrow range of stand types (e.g. Packard 1942, Olmsted 1979, Betters and Woods, 1981, Parker and Parker 1983, Mueggler 1989, Turchi et al. 1995, Olmsted 1997). Generally, these studies either focused on stands in a small study area or stands of a certain type (e.g., >1 ha, no conifer invasion, single cohort). Conclusions from these studies are limited due to the scope of their data. Two recent studies of aspen

regeneration randomly selected stands for sampling in large study areas and reported results that conflicted with previous subjective studies (Suzuki et al. 1999, Barnett and Stohlgren 2001). This study was a further attempt at an objective quantification of the range of characteristics of the aspen population as a whole to better understand its current status.

I found almost three times more aspen cover (5.6%) in the transect area than values cited in previous studies (2%) in Rocky Mountain National Park and the central Rocky Mountains (Stohlgren et al. 1997a, Suzuki et al. 1999). Earlier estimations of aspen cover were based on aerial images that are only capable of recognizing areas where aspen was a dominant portion of the canopy. This approach likely missed whole patches and areas of larger patches where aspen was not the dominant forest canopy species. These elusive aspen patches contribute both to the overall percent aspen cover and to the dynamics of the aspen population.

The status of the aspen population within the study area can be better understood by looking at patch location, size and distribution across an elevation gradient than percent aspen cover alone. Mean patch size (Fig. 2.5) and percent aspen cover (Fig. 2.2) both peaked between 2900 m and 3100 m elevation. Aspen cover on both the east and west side of the Park followed that same pattern of peak coverages at higher elevations. The greater aspen cover and patch size at higher elevations may be explained by variations in fire regimes of the surrounding conifer forest and by winter browsing by elk in lower elevations. High elevation conifer forests such as mixed-conifer and spruce-fir tend to have lower frequency, higher intensity, and larger fires due to the productivity and fuel loadings of the systems (Mutch 1970, Wright and Bailey 1982). This type of

disturbance regime would be likely to initiate large aspen stands. The surface-fire regimes of lower elevation forests such as ponderosa pine are less likely to initiate large aspen stands because they do not create forest opening for aspen to colonize. At lower elevations (<2650m), percent aspen cover was above average (Fig. 2.2) and mean patch size was small (<1000m^2, Fig. 2.5). In these areas, many smaller aspen patches are distributed across the landscape. Throughout the elevation range, the majority of aspen patches were located on gentle topography such as slopes and drainage basins (Fig. 2.3), however the species is capable of growing in more severe locations such as rock outcrops and ridge tops. Stands growing in these harsher locations tended to have smaller basal areas than those in more favorable locations (data not shown).

The range of basal area and density values for aspen patches encountered in the transects documented a much larger variation in patch structure than reported in other studies of aspen in the Rocky Mountains (Table 2.1). Mean basal area of patches in this study area was similar to other stands but their range showed values much smaller and larger than expected. Maximum stocking for aspen stands has been estimated at 50 m^2/ha (Jones et al. 1985), however I found 10% of the patches in this study area had basal areas over this value. Mean stem density within the study area fell below the range of most of the values reported in other studies (Table 2.1). Additionally, the maximum stem density in this study is not as high as densities reported by other studies. The mean and range of basal area and density values measured in this study represent the range of aspen patch types in the population of aspen patches in the Park. These values could differ for other populations of aspen throughout the Rocky Mountains because of local variations in climate, disturbance regimes, topography, surrounding forest types, and browsing history.

Table 2.1. Review of basal area (m^2) and density (stem ha^{-1}) values for aspen forests throughout the Rocky Mountains. Values represent means (†), individual values found in the literature (‡), and ranges of values (*).

Reference	Location	BA (m^2 ha^{-1})	Density (stems ha^{-1})
This study	Rocky Mountain National Park, Colorado, USA	24.9† 0.4-99.1*	1455† 30-9600*
Fornwalt and Smith. (pers. comm.)	Southern Wyoming, USA	11.9‡[a] 46.6‡[b]	4400‡[a] 12326‡[b]
Chen et al. 1998.	British Columbia, Canada	15.9† 4.6-36.3*	1906† 450-4150*
Parker and Parker, 1983.	Bierstadt Moraine, Rocky Mountain National Park, Colorado, USA	19.1†	2800†
Kemperman and Barnes, 1976.	Fish Lake, Sevier County, Utah, USA		1327‡ 790-2051*
Gosz, 1980.	Santa Fe, New Mexico, USA	36.4-38.1*	2270-3070*
Baker 1925[c]	Central Rocky Mountains, USA	19.15† 15.8-22.3*	

a: Single-storied stand., b: multi-storied stand, c: taken from Jones et al. 1985.

Elk browsing and conifer invasion

Despite the variability in aspen patch structure and location, external factors such as conifer invasion and elk browsing show no discrimination in their effects on aspen structure. All but one of the 123 aspen patches I encountered had conifer invasion, elk browsing, or both. Of these two factors, elk browsing has received much more research attention, especially in the elk winter ranges of the Greater Yellowstone Ecosystem and Rocky Mountain National Park (Packard 1942, Olmsted 1979, Romme et al. 1995, Wagner et al. 1995, Baker et al. 1997, Berry et al. 1997, Olmsted 1997, White et al. 1998, Ripple and Larsen 2000, Barnett and Stohlgren 2001). In both parks, the policy of natural regulation adopted in 1968 was followed by a dramatic increase in elk populations (e.g., from under 500 animals in the 1960s to approximately 3000 in the late 1990s in Rocky Mountain National Park; Romme et al. 1995, Baker et al 1997, Ripple and Larsen 2000, F. Singer, Natural Resource Ecology Laboratory, Colorado State University, pers. comm.). Ecologists and Park managers are concerned for the future of aspen because of the visible impacts of elk on aspen in some areas of the elk winter range. Studies of aspen in the winter range have confirmed aspen decline in this area, but broader-scale studies have refuted the dire predictions (Suzuki et al. 1999, Barnett and Stohlgren 2001, this study).

There was little difference in aspen condition between the elk winter and summer ranges in Rocky Mountain National Park. I would expect to see differences in measures of aspen vigor such as regeneration, basal area, density, bark damage, and patch size between patches in the summer and winter ranges if 30 years of intensive elk browsing

were causing a decline in aspen (Bartos and Campbell 1998, White et al. 1998). Percent bark browse showed the only significant difference between the two ranges (Fig. 2.8). Bark scarring is the most notable effect of elk browsing on aspen patches. The prevalence of bark browsing on aspen stems in the elk winter range may fuel the concern over aspen in that area. However, the effects of elk browsing on important stand characteristics such as basal area, density, regeneration, and patch size are not evident in the results. It should be noted that this lack of differences in stand characteristics may be due to confounding factors other than elk range such as elevations, microsite conidition, and stand history.

Few data exist for the extent of conifer invasion in aspen forests in the Rocky Mountains, despite its prevalence (but see Shepperd et al. 2001). Bartos and Campbell (1998) estimated that aspen patches are at risk when aspen canopy cover is less than 40%. I found that just under 1/3 of the patches had less than 40% aspen in the canopy. Discussions of conifer invasion of aspen stands often attribute the process to forest succession, where shade intolerant aspen is replaced by shade tolerant conifer species such as spruce (*Picea* spp.) and fir (*Abies* spp.) (Mueggler 1989, Kay 1997). The frequent occurrence of conifer invasion in aspen stands on today's landscape may be a legacy of 80 years of fire suppression in the intermountain West (Loope and Gruell 1973, Houston 1982, Romme et al. 1995). During the past 100 years, conifers have been replacing older aspen patches and almost no new aspen patches are being initiated by fire (Ripple and Larsen 2000). This results in an aspen population such as the one in Rocky Mountain National Park that consists of many patches with conifer invasion and fewer without. Unlike elk browsing, conifer invasion seems to be related to patterns in aspen

basal area and density (Fig. 2.7). Aspen patches with the greatest basal area and density have 100% aspen in their canopies. Further research is needed to determine if conifer invasion is affecting aspen basal area or whether invasion tends to occur in areas of lower aspen basal area and density.

A comparison of two methods

Most of the parameters I used to describe the status of aspen in Rocky Mountain National Park are not measurable from remotely sensed data. Key descriptors of the status of aspen forests such as aspen basal area, density, browsing by elk, and conifer invasion cannot be detected with remote sensing. Those parameters that are measurable, such as patch area, may not be accurate when measured from an aerial perspective. This is demonstrated by the underestimation of aspen cover by the GIS of forest cover developed from high-resolution aerial photographs (1:15,800). Therefore, I believe the ground survey is an effective approach to quantifying the aspen cover type and adds critical information to our understanding of the status of aspen forests in the Park.

In a direct comparison between measures of aspen cover in 10,000 ha area around Beaver Meadows in the Park, the ground survey detected 25% more aspen cover (8.6%) than estimated in the GIS (6.4%). The smallest aspen patch identified by the aerial photos was 10 m^2, which can be considered the grain of that data type. The distribution of aspen patch sizes shows that 13% of the aspen patches encountered were smaller than 10 m^2. These small patches cannot account for the difference in percent aspen cover found between the two methods, however they do represent a part of the aspen population that is effectively lost in remotely sensed data at 10 m^2 resolution. Conversely, the spatial extent of the ground survey was one hectare. The size and shape of aspen patches

>1ha can be better measured by remote sensing. The 25% underestimation of aspen cover calculated from remotely sensed data was likely due to the sum of aspen cover missed in small aspen stands, stands that were not identified as containing aspen because of the high levels of conifer invasion, and the difficulty in accurately defining the perimeter of an aspen patch from aerial photographs.

CONCLUSIONS

The description of the aspen population in the central portion of Rocky Mountain National Park helps resolve some of the debate over the status of the species in the central Rocky Mountains. All but one of 123 patches showed evidence of elk browsing or conifer invasion, supporting the idea that elk browsing and fire suppression are factors affecting the aspen population. Elk browsing of aspen stems appears to have had little effect on aspen patch characteristics. This indicates that elk browsing has not (yet?) damaged the aspen population as a whole.

Extensive conifer invasion in aspen stands in the Park led me to suggest that further research needs to be done on its effects on aspen structure. I found conifer invasion in two thirds of the aspen patches that I randomly encountered in the ground survey. This high frequency of conifer invasion may be a legacy of 80 years of fire suppression in Rocky Mountain National Park. The timing, extent, and effects of conifer invasion in aspen patches are little understood.

This study presents a snapshot in time of the population of aspen in the central portion of Rocky Mountain National Park. Today's variability of aspen structure and the prevalence of elk browsing and conifer invasion can help guide future management and research choices for aspen in the Rocky Mountains. The ubiquity of conifer invasion in

the aspen population indicated that fire may be needed to initiate new aspen stands before the majority of current stands are replaced by conifers. Newly initiated aspen stands in the elk winter range would need to be protected from elk browsing to ensure successful aspen establishment. Managers need to recognize the importance of small, remote aspen patches in the dynamics of aspen population. The data I was able to obtain from a ground-survey provided useful information concerning the status of aspen in the Park that would be augmented by future data collected with remote sensing.

CHAPTER 3: EFFECTS OF CONIFER INVASION ON THE ESTABLISHMENT, GROWTH, AND MORTALITY OF QUAKING ASPEN STANDS IN THE FRONT RANGE OF COLORADO.

ABSTRACT

Widespread conifer invasion of quaking aspen (*Populus tremuloides* Michx.) stands in the Front Range of the Rocky Mountains has been attributed to a combination of 80 years of fire suppression and natural forest succession. I examined the effects of conifer invasion on the establishment, growth, and mortality of five aspen stands in Rocky Mountain National Park. I used tree rings to reconstruct the timing of aspen and conifer establishment and mortality, as well as growth. Three stands with conifer invasion showed no aspen establishment in the past 50 years, while two stands without conifer invasion had small amounts (<100 stems ha^{-1} $decade^{-1}$). Aspen stands with conifer invasion showed no decrease in total basal area increment, whereas increment declined in stands without invasion. Maximum aspen growth related negatively to conifer basal area and basal area increment. Aspen mortality was independent of conifer invasion and was highly correlated with aspen density ($r = 0.93$, $P=0.017$). Conifer trees replaced aspen via sub-canopy establishment and longevity rather than directly causing a decline in aspen growth or an increase in aspen mortality. Forest succession from aspen to conifer

species primarily occurs due to differential life history traits of the species involved, rather than species interactions.

INTRODUCTION

The long-term dynamics of quaking aspen stands in the Rocky Mountains can be summarized into two general trajectories: self-replacing aspen stands and aspen stands that are successional to conifer stands. Self-replacing aspen stands persist with periodic pulses of aspen sprouting into the stand. Aspen stands that are successional to conifer tend to shift species dominance as shade-tolerant conifer species successfully invade into aspen stands and gradually dominate. Recent surveys of aspen stands throughout the Rocky Mountain States report that an increasing number of aspen stands are being invaded by conifers (Mueggler 1989, Kay 1997, Bartos 2001, Manier and Laven 2001). Documentation of more frequent conifer invasion can be complemented by a long-term perspective on the dynamics of aspen succession to conifers.

Widespread conifer invasion of aspen stands has been attributed to a combination of 80 years of fire suppression and natural forest succession (Jones and DeByle 1985, Bartos 2001). Aspen stands often establish rapidly via root sprouting following a stand-replacing forest disturbance, such as fire (Grant and Mitton 1979, Jelinski 1993). Aspen may persist as a pure stand (Betters and Woods 1981, DeByle and Winoker 1985, Cryer and Murray 1992, Crawford et al. 1998), but shade-tolerant conifer species commonly establish in the under story of aspen (DeByle and Winoker 1985, Cryer and Murray 1992). If conifer species continue to establish and live longer than aspen, conifer dominance will develop over time. Fire suppression in the twentieth century has drastically diminished the number of new aspen stands, most aspen stands have reached

100 years of age, and many stands are succeeding to conifers (Mueggler 1989). In this study, I used tree rings to reconstruct patterns of forest stand structure and growth over the past one and a half centuries to evaluate the dynamics of conifer invasion in quaking aspen stands in the Front Range of the Rocky Mountains, Colorado.

Detailed reconstructions of forest structure provide insights into how forests change through time (Henry and Swan 1974, Wipple and Dix 1979, Lorimer 1980, Foster 1988). In the Rocky Mountains, tree species tend to be long-lived (100 to 500+ years) and reconstructions reveal long-term dynamics that short-term studies may not accurately represent. Chronosequences examine long-term forest dynamics by assuming that space can be substituted for time. Dendrochronology, the study of tree rings, can retrospectively reconstruct stand history with a location, avoiding the assumptions of chronosequences (Fastie 1995, Mann et al. 1995). The establishment, growth, and mortality of the majority of tree species in the Rocky Mountains can be assessed by their annual growth increments. Analysis of information logged in tree rings allows ecologists to reconstruct past forests dynamics (Johnson and Fryer 1989, Donnegan and Rebertus 1999).

What are the mechanisms that allow conifers to replace aspen? Ecologists have attributed plant succession to factors ranging from species and community interactions (including resource competition) to individualistic behavior by the species involved. Some models of succession focus on species interactions such as facilitation, tolerance, inhibition, and resource competition (Clements 1936, Connell and Slatyer 1977, Tilman 1985). Other models identify individual species behavior and life history as a driving variable (Gleason 1939, Drury and Nisbet 1973, Walker et al. 1986, Huston and Smith

1987, Chapin et al. 1994). More recent studies have emphasized the importance of stochastic events in succession (Binkley et al. 1997, Donnegan and Rebertus 1999). Realistically, the potential driving variables of succession are not mutually exclusive and predictable changes in species composition may be the result of many combinations of species interactions, species characteristics, and stochastic events (McCook 1994).

In the case of aspen succession to conifers, does competition with conifers contribute to aspen decline? Or do the life-history traits of conifers (such as shade-tolerance and a long lifespan) simply allow conifers to gradually replace aspen? An understanding of these dynamics can provide useful information to the management of western aspen forests, and add to our ecological portfolio of field studies of forest succession (Bartos et al. 1983, McCook 1994).

I predicted that conifer invasion in aspen stands should influence the establishment, growth, and mortality of aspen. Aspen establishment would decrease with increased amounts of conifers due to the shade intolerance of aspen; aspen growth would decline due to competition for resources with invading conifers; and aspen mortality would increase as longer-lived and younger conifer trees persist after aspen die. Aspen establishment, growth, and mortality would also have predictable relationships with stand age. In the absence of conifer invasion, establishment and growth would decrease and aspen mortality would increase as stands age.

Tree-ring data from aspen stands in Rocky Mountain National Park and Roosevelt National Forest, Colorado were used to test my predictions. I reconstructed aspen and conifer establishment, growth, and mortality with tree-rings in five stands in the Front Range. Conifer basal area and basal area increment were used as measures of conifer

invasion. The number of years since the earliest aspen establishment date represented stand age. Aspen basal area increment was used as a measure of aspen growth (Biondi 1999, LeBlanc 1992). I focused solely on stands with conifer invasion to report the effects of the invasion on aspen and focused on stands without conifer invasion to present the effects of stand age on aspen.

METHODS

Study area

The study area was between 2400 and 2900 m elevation in the eastern side of Rocky Mountain National Park and Roosevelt National Forest, in the Colorado Front Range of the Rocky Mountains. Average annual minimum and maximum temperatures near Estes Park ($105^0$30'W, $40^0$24'N) at 2400 m elevation are –1.5 and 14.0 °C. Growing season (May-October) temperatures average 4.0 to 21.0 °C, with an average of 350 mm yr^{-1} precipitation. Vegetation types are typical of the Central Rocky Mountains and include ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.), lodgepole pine (*P. contoria* Dougl. es Loud.), mixed conifer, and spruce-fir forests (*Picea engelmanii* Parry ex Engelm. and *Abies lasiocarpa* Hook. Nutt.), as well as wet and dry meadows, riparian corridors, and alpine tundra (Peet 2000).

Field and laboratory methods

I identified 24 aspen stands within the study area with aerial photographs (1:15,800). These stands were randomly ordered and assessed in the field for seven requirements:

(1) >20 m radius

(2) minimal evidence of elk browsing

(3) non-riparian slope position

(4) moderate topography

(5) aspen basal area between 25 and 45 m^2 ha^{-1}

(6) aspen density between 500 and 1500 stems ha^{-1}

(7) if conifer trees are within an aspen stand, their establishment post-dated aspen establishment and can be classified as conifer invasion of the aspen stand

These requirements were used to eliminate stands with major influences by processes that were not the focus of this study (e.g., elk browsing, hydrology, species range, or extreme microsite conditions). If a stand fulfilled these requirements, it was chosen for sampling. If not, I continued reconnaissance with the next stand on the list until five stands were selected.

In each of the five selected stands, I established a circular plot ranging from 10 to 18 m radius (314 to 1018 m^2) to sample a minimum of approximately 100 trees per plot and to encompass uneven spatial clumping of aspen and conifer trees. Within each plot, tree-ring samples were taken from all living and dead aspen and conifer stems (>1.5 m tall and >4 cm diameter at core height) at 20-30 cm above the root collar. I collected increment cores or cross-sections cut with a handsaw from all dead aspen and conifer stems with bark or beetle galleries to assure my ability to identify the last year of cambial growth of each dead tree. The presence of beetle galleries on a dead aspen stem assures that the outermost ring on the tree is preserved because bark beetles build their galleries in the vascular cambium, which is located between the outer-most ring (xylem) and inner-bark (phloem). Diameter and core height, bark thickness, and tree species were recorded for each sample.

Core samples were mounted and cores and cross sections were sanded with progressively finer sand paper ranging from 250 mm to 15 micron grit to maximize tracheid and vessel definition and the ability to distinguish between annual growth rings. Samples were examined under a binocular microscope, skeleton plotted, crossdated, and calendar years were assigned to each ring (Stokes and Smiley 1968). If a radius did not intercept the pith, I used concentric circles to estimate the number of rings between the innermost rings and the pith (Applequist 1958, Biondi 1999). I assigned (estimated) establishment dates to all samples and year of the outmost ring for all dead samples. For each sample, I created a ring-width series by measuring annual rings with a slide stage micrometer of 0.01 mm accuracy interfaced to a personal computer. The program COFECHA (Holmes 1986) was used for quality control of the cross-dated tree-ring series.

Data analysis

Establishment and mortality dates of aspen and conifers were aggregated into decadal frequencies (due to the resolution of establishment and death dates; Veblen 1992), and decadal frequencies of establishment and mortality within the plot were scaled to a hectare basis.

I used tree-ring data to reconstruct stand basal area (m^2 ha^{-1}), basal area increment (BAI; m^2 ha^{-1} yr^{-1}), and tree density (stems ha^{-1}) for conifers and aspen for each stand from the time of stand establishment to the present. To calculate basal area and BAI, I began by calculating the radius of a tree for each year starting with the radius I measured in the field. I used the following calculations:

$$R_y = (DCH_y/2)-BT_y$$

$$R_{(y-t)} = R_{(y-t+1)} - RW_{(y-t)}$$

where, y = the year the stand was sampled (either 1999 or 2000), t = number of years prior to y, ranging from 1 to the age of the oldest aspen stem, R_y = tree radius measured in the field for year y, DCH_y = tree diameter at core height for year y, BT_y = bark thickness measured in the field in year y, $R_{(y-t)}$ = tree radius for t years before y, $RW_{(y-t)}$ = ring width measurement for year y-t. I then converted the annual radius of a tree for each year into annual basal area with the following geometric equation:

$$BA_{(y-t)} = R_{(y-t)}^2 * \pi$$

where, $BA_{(y-t)}$ is tree basal area for year y-t. Annual basal area increment was calculated based on annual basal area:

$$BAI_{(y-t)} = BA_{(y-t+1)} - BA_{(y-t)}.$$

where, $BAI_{(y-t)}$ is the tree BAI for year y-t.

To create a time series of aspen and conifer growth, I summed the basal area and BAI of all trees in the plot for each year. A count of the number of trees living in each year produced a time-series of tree density. Plot-level basal area, BAI, and density were converted to a hectare basis for comparison between stands. Decadal averages of basal area, BAI, and density were calculated, as well as a 10-year running mean centered on the fifth year, to accentuate lower-frequency (>10yrs) variability in aspen and conifer growth due to stand dynamics rather than high-frequency (<10yrs) variability due to annual climate fluctuations. Time since death of samples was evaluated within the plots to determine how far back in time aspen establishment, growth, and mortality could be reconstructed reliably (Johnson and Fryer 1989).

Regression models were fit with conifer invasion (as quantified by conifer basal area and basal area increment) as the independent variable and aspen establishment, growth, or mortality as the dependent variable. Due to the large number of decades during which aspen establishment was zero (61% of all potential decades of establishment), I chose to regress conifer basal area with maximum aspen establishment recorded for a given basal area (e.g., a maximum aspen establishment of 199 stems ha^{-1} were recorded for conifer basal areas between 10 and 20 m^2 ha^{-1}). I tested the null hypotheses that there was no relationship between conifer basal area and aspen establishment, BAI, and mortality with polynomial regressions. The alternative hypotheses were that with increasing conifer basal area, aspen establishment and growth decreased and aspen mortality increased.

RESULTS

I visited thirteen aspen stands before finding five that met the criteria; the class of stands I chose to sample apparently represented less than half of the stands identified from photos of the area. Of the five stands sampled, four had varying amount of conifer invasion and one had no invasion. Plots with an 18-m radius were sampled in two stands and with 10-m radius in three. In total, samples were collected and analyzed from 304 living aspen, 401 dead aspen, 176 living conifers, and 31 dead conifers. The mean inter-series correlation of ring-widths for both aspen and conifer were above r=0.5, and I was able to crossdate all but four tree cores, all of which were from dead trees. For these samples I substituted ring-width series of samples with the same diameter and core height and degree of decay. Pith year was estimated on 34% of the samples because the cores did not include the pith on the sample; less than five years were estimated on over 99% of

the samples. Error introduced by pith estimates and a coring height of 20-30 cm should be taken into account when interpreting the results of this study.

Period of the reconstruction

Dead aspen stems were preserved for up to 92 years within the stands. The relationship between diameter of dead stems and the number of years since death can be summarized by the equation $DBH = 16.29e^{-(0.013 * \text{years since death})}$ ($r^2=0.34$, $P<0.0001$). Twelve percent of dead stems were smaller than 5 cm diameter. The persistence of dead aspen stems and the diameter of preserved stems indicated that few dead and decayed samples were missing from the early years of stand development when thinning of small stems occurred. No conifer mortality was recorded in three of the four stands with conifer invasion. This was more likely due to the young age and low densities of conifers rather than rapid decay of dead stems.

Patterns of aspen stand development

Aspen establishment peaked 20 years after stand initiation and quickly dropped to low levels at 30 years (Fig. 3.1a). Aspen basal area gradually increased over the first 100 years of stand development, and then maintained a value of approximately 30 m^2 ha^{-1} for the following 30 years (Fig. 3.2a). Aspen BAI reached approximately 0.5 m^2 ha^{-1} yr^{-1} after 40 years of stand development and decreased to 0.4 m^2 ha^{-1} yr^{-1} over the last 40 years of stand growth (Fig. 3.2b). Aspen density peaked at approximately 2000 stems ha^{-1}, then declined (Fig. 3.2c). The density of the first 30 years may have been greater than the values recorded in this study because of the loss of small diameter trees (<4 cm DCH) that died many decades ago.

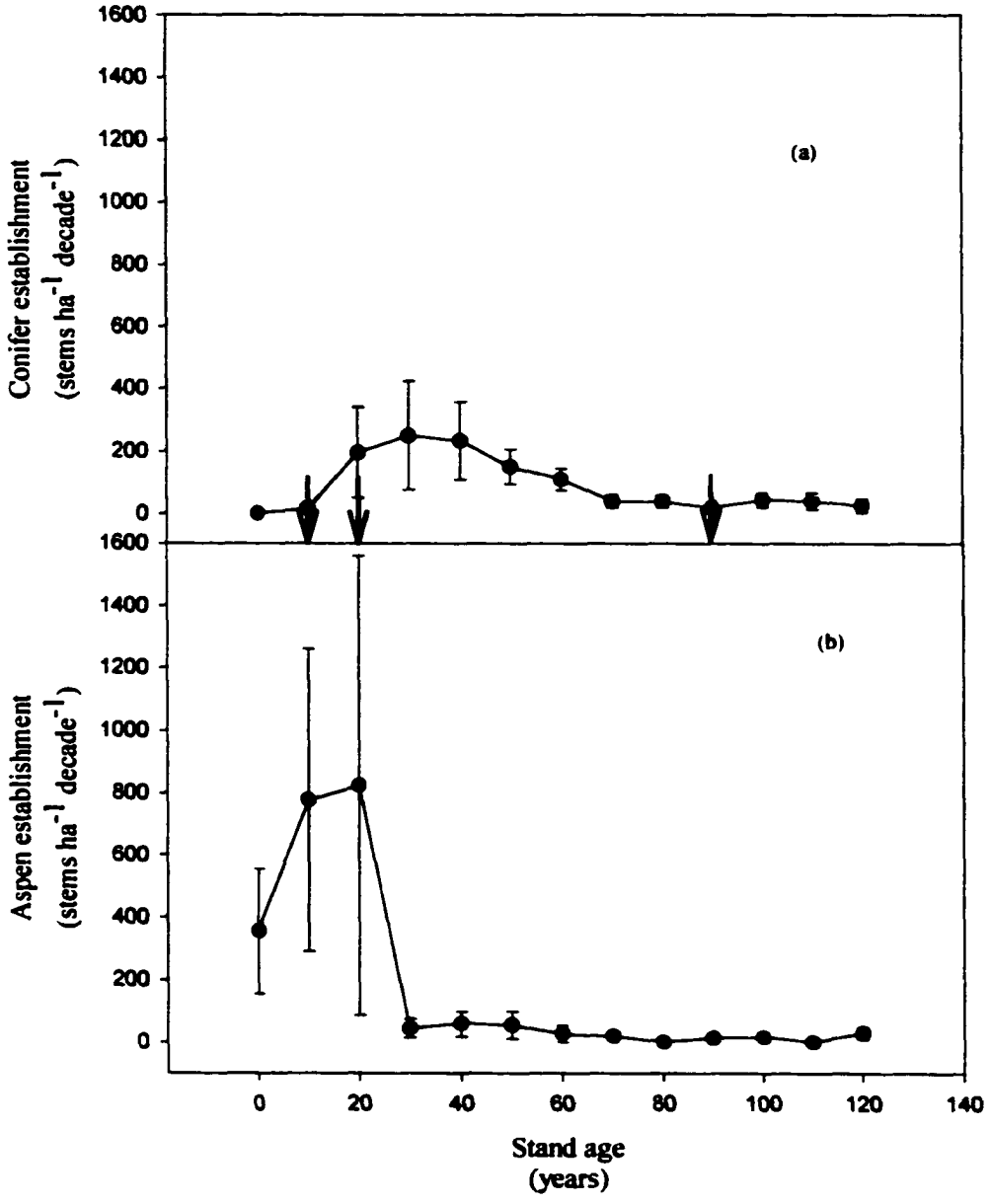

Figure 3.1. Timing of conifer invasion (a) and aspen establishment (b) in five aspen stands in Rocky Mountain National Park. The solid line represents mean establishment (stems ha^{-1} $decade^{-1}$) and the vertical bars represent standard errors. Vertical arrows in (a) represent the stand age at the beginning of conifer invasion for a stand.

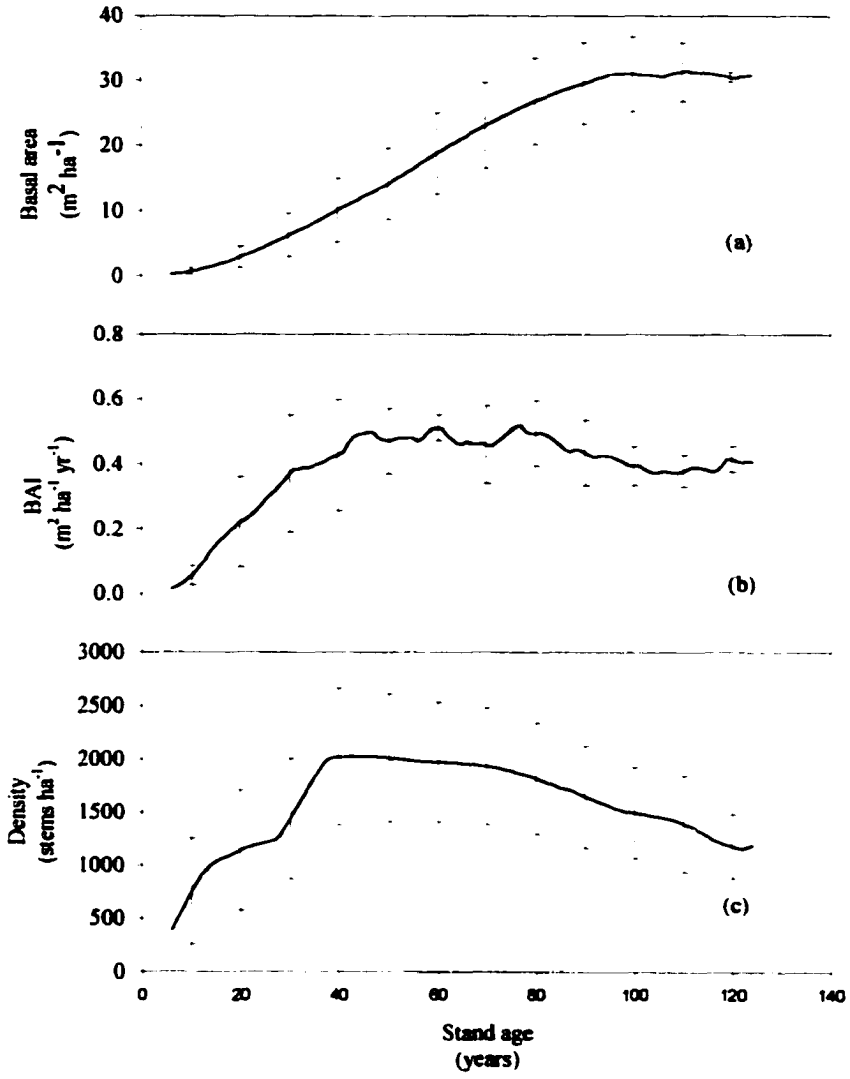

Figure 3.2. Mean basal area (a), basal area increment (b), and density (c) of five aspen stands in Rocky Mountain National Park over 130 years of stand development. Lines represent a 10-year running mean, centered on the fifth year and vertical bars represent standard errors values at 10-year intervals.

Patterns of conifer invasion

Conifer establishment occurred between 10-120 years after initial aspen establishment and peaked after approximately 30 year (Fig. 3.1b). The on-set of first conifer invasion began between 10 and 90 years after aspen stand initiation (Fig. 3.1b). Three of the five stands experienced conifer invasion, one stand had minimal amounts of conifer invasion (40 years after the first conifer established, conifer basal area had not yet reached 2 m^2 ha^{-1}), and one stand had no conifer invasion. Aspen growth data were averaged for the three stands with conifer invasion and for the two stands with little or no conifer invasion. Averages were compared to determine differences in aspen growth trends with the presence or absence of conifer invasion. Future sampling of more stands would greatly improve the reliability of pooled data from multiple and variable aspen stands.

Influences of conifer invasion

Conifer basal area related linearly with decreasing maximum aspen establishment (P=0.018; Fig. 3.3). No stand had aspen establishment when conifer basal area was greater than 30 m^2/ha. However, there are only four data points above this level of conifer invasion. Stands with conifer invasion had no aspen establishment after 70 years of stand age (mean=0 stem ha^{-1} per decade), which was significantly less than the amount of aspen establishment in stands without conifer invasion (mean=137 stem ha^{-1} per decade after 70 yrs; P<0.001).

Although aspen BAI did not relate to conifer BAI (Fig. 3.4a) or conifer basal area (Fig. 3.4b), conifer invasion appeared to relate to maximum aspen growth. In the absence of conifer invasion, aspen BAI reached over 0.8 m^2 ha^{-1} yr^{-1}, but dropped by over half when conifer BAI and basal area reached their maximum (Fig. 3.4).

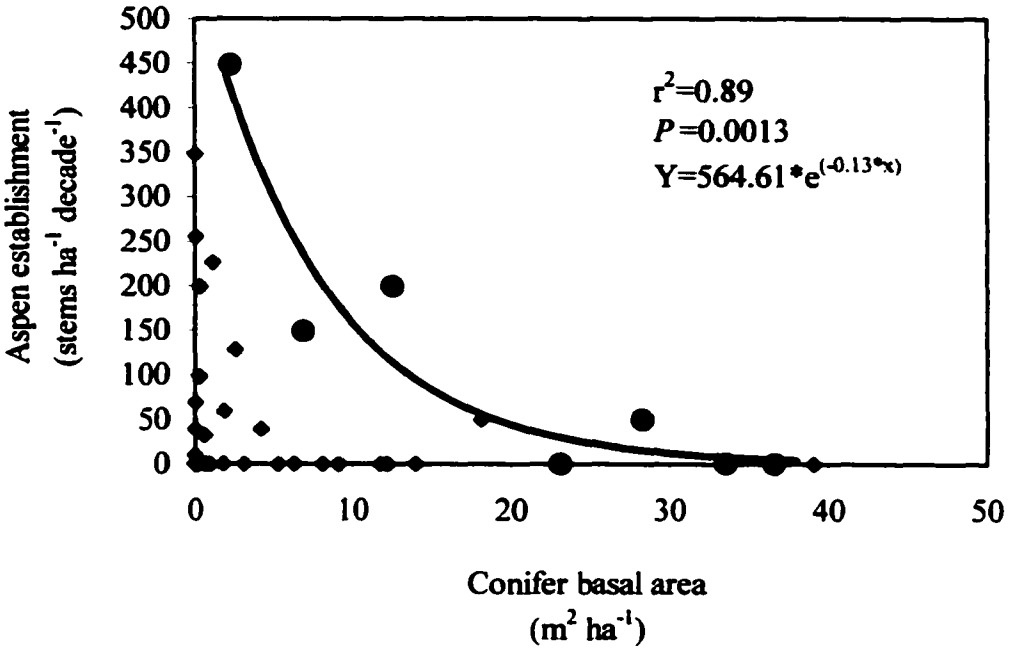

Figure 3.3. Relationship between conifer basal area and aspen establishment in three stands in Rocky Mountain National Park. Solid line represents the regression between conifer basal area and maximum aspen establishment for each 5 m^2 ha^{-1} range of conifer basal areas (shown in larger, round symbols).

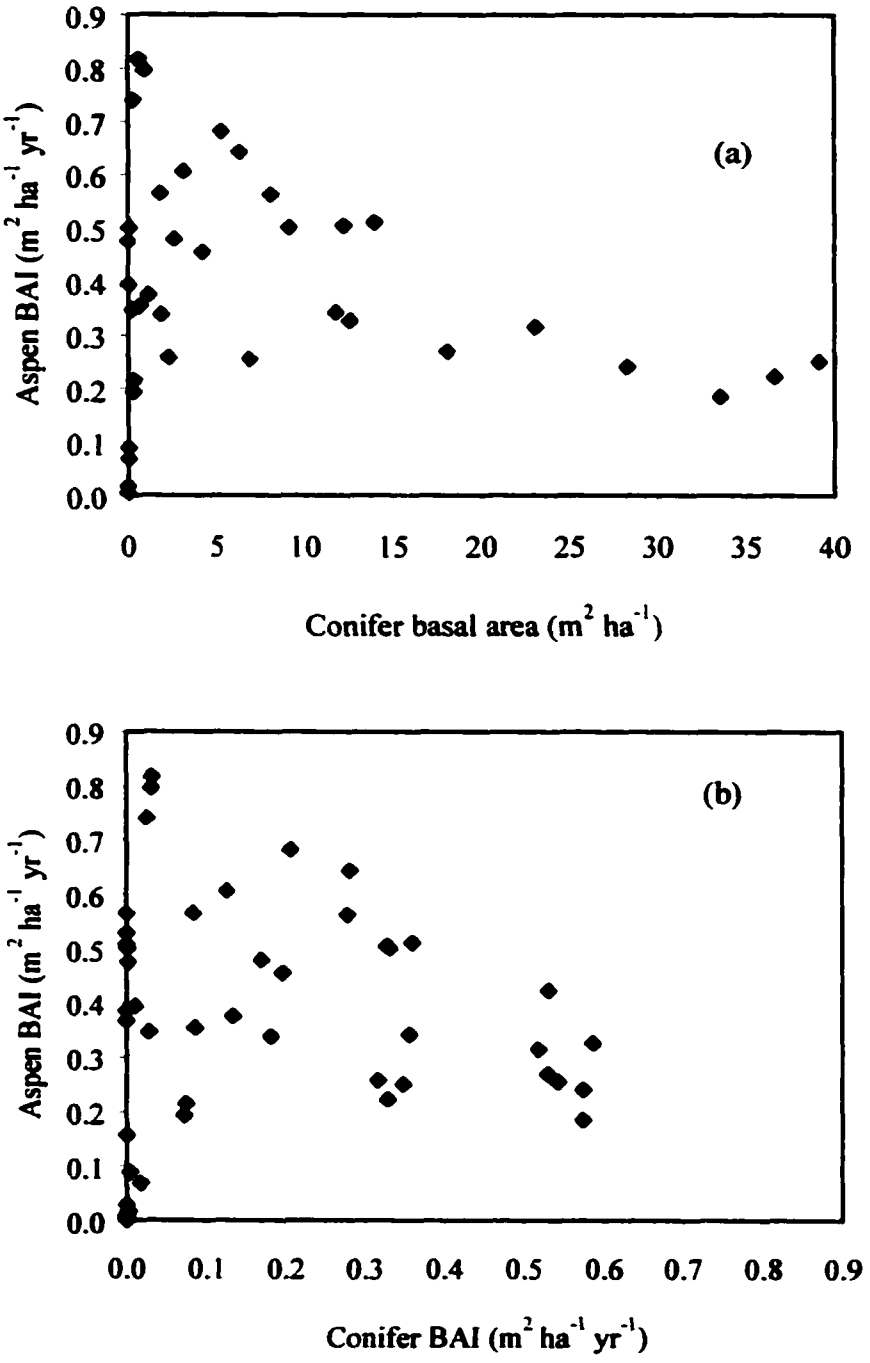

Figure 3.4. Relationship between conifer invasion and aspen growth. No significant correlation existed between aspen BAI and conifer basal area (a) or BAI (b) however both relationships indicate that there is a limit of aspen growth as conifer growth and basal area increase.

In stands without conifer invasion, aspen growth (BAI) appeared to decline after 50 years (Fig. 3.5a), whereas it remained constant in stands with conifer invasion (Fig. 3.5b). Total stand increment (the sum of aspen and conifer BAI) plateaued after 70 years in stands with conifer invasion (Fig. 3.5b).

Conifer basal area did not relate to aspen mortality. Percent aspen mortality increased with peak aspen density in the last 50 years of stand growth (P=0.017; Fig. 3.6).

DISCUSSION

Stand-level reconstructions of aspen dynamics revealed that aspen stands in the Front Range of Colorado can remain as pure aspen stands or can be invaded by conifer species. Typically, forest ecologists describe aspen rapidly regenerating an area following disturbance with an even-aged cohort. Following establishment of the initial cohort establishment, an aspen stand could follow two trajectories: shade tolerant conifers invade and eventually replace the aspen or cohorts of aspen continue to establish, creating a self-replacing, multi-cohort aspen dominated stand (Betters and Woods 1981, Mueggler 1989, Crawford et al. 1998). Despite the extensive criteria I imposed on site selection to isolate aspen-conifer interactions, I found that no two stands sampled were alike in their patterns of aspen and conifer establishment and growth (Appendix A). Initial aspen establishment occurred as a cohort in three of the stands I sampled, while the other two stands experienced prolonged aspen establishment spanning over 50 years. In one stand, conifer establishment began only a decade after initial aspen establishment, while in another stand conifer establishment began 90 years later (Fig. 3.1). Leiffers et al. (1996) found conifer establishment followed aspen establishment by 10 to 50 years in west

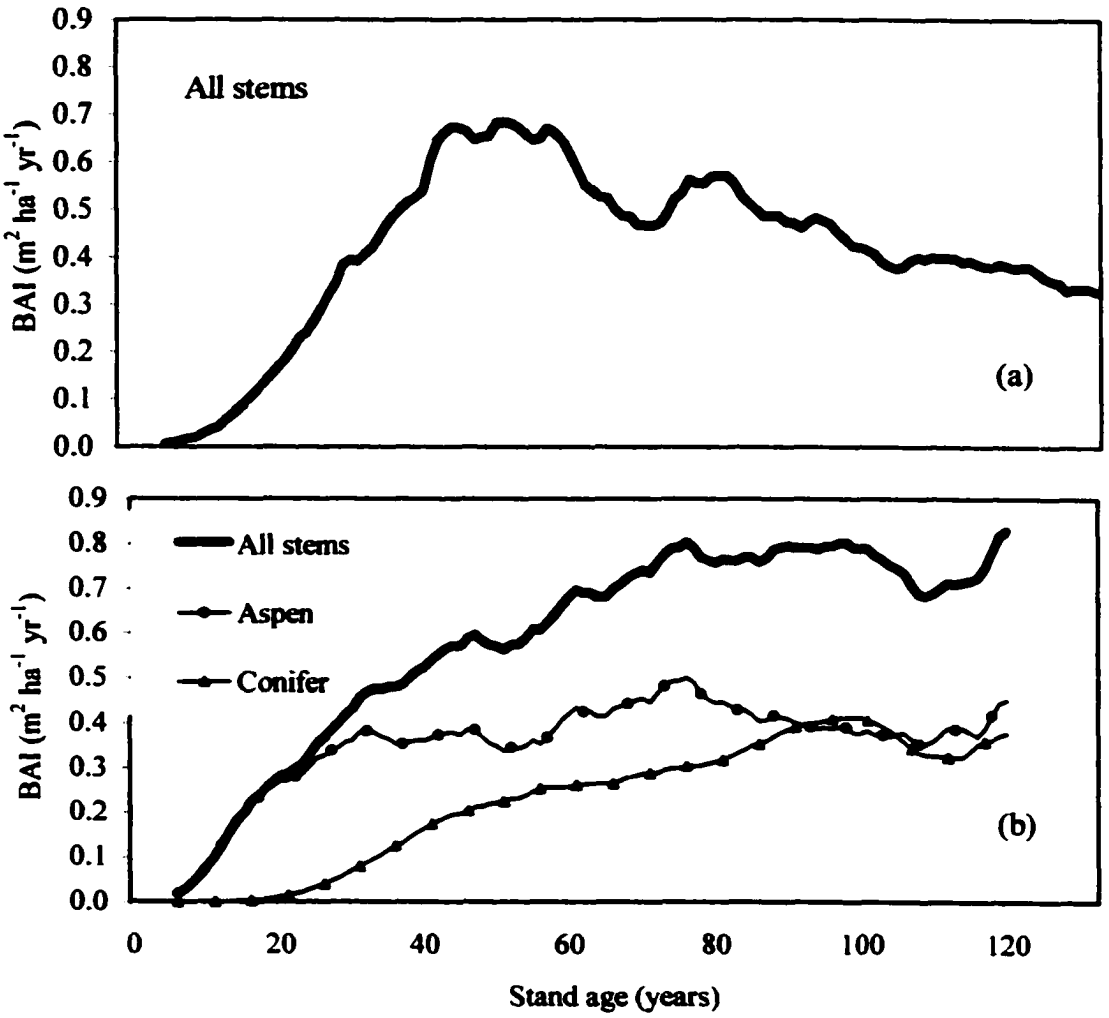

Figure 3.5. Mean stand increment over time for pure aspen stand (a) and a mixed stands (b). In mixed stands, increment of both aspen and conifer shown.

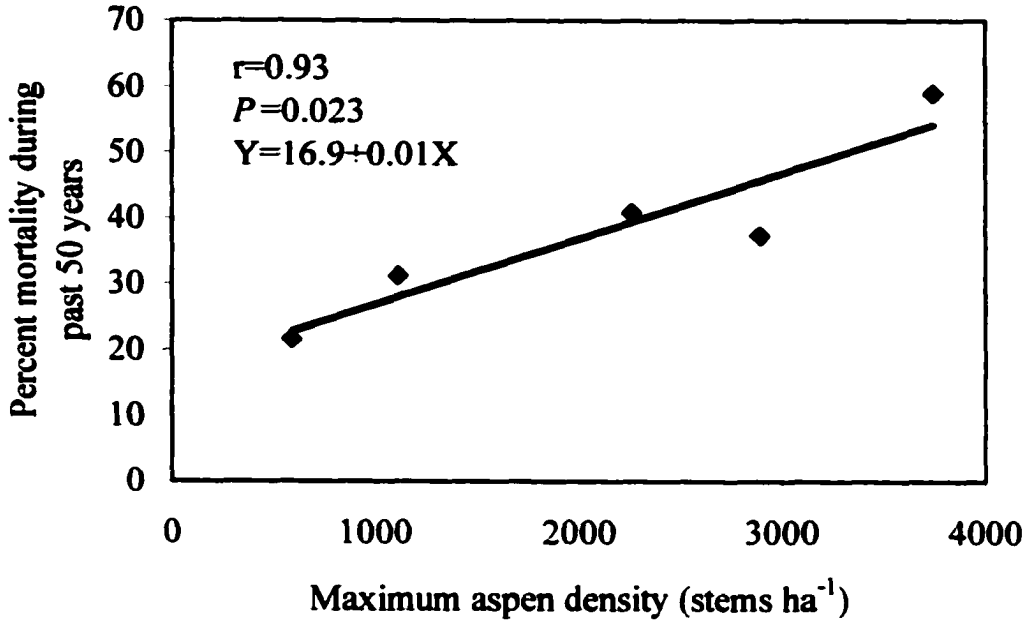

Figure 3.6. A linear regression comparing percent aspen mortality in a stand and the stand's peak aspen density showed a significant relationship and 86% of the variance explained.

-central Alberta. Based on the variability in the stands I sampled, it is clear that a larger number of sample stands in the study area is needed to characterize the spatial variability of conifer invasion in aspen stands. However, based on the data from five stands in the Colorado Front Range, tentative patterns of conifer invasion and aspen establishment, growth, and mortality can be discussed.

I expected a decline in aspen growth (Shepperd et al. 2001) and an increase in aspen mortality to be two mechanisms in the succession of aspen to conifers, but found little evidence supporting these patterns. In fact, the data from hundreds of trees showed that stands with conifer invasion tended to have greater basal area than those without conifer invasion and that aspen mortality tended to decrease with increasing conifer invasion. These patterns were likely due to differences in soils or site factors in the stands I sampled, rather than cause and effect relationships between conifer invasion and aspen growth and death. Conifer basal area and BAI seemed to impose a limit on maximum aspen growth (Fig. 3.4), however this relationship does not seem to have had an effect on aspen basal area (Fig. 3.5). Bartos and Campbell (1998) suggested that aspen is threaten when its canopy cover is <40%. In sites 4 and 5, aspen canopy cover dropped below 40%, however aspen growth was not in decline.

Interestingly, if I had analyzed the basal area data collected in the field as a chronosequence of stands ranging in age from 90 to 120 years, I would have concluded that aspen basal area was declining in stands with conifer invasion (Fig. 3.7). Conclusions concerning the effects of conifer invasion on aspen growth would have been different, despite the reality that the change in basal area over time was likely due to site

differences and aspen growth rates. These data accent the difficulty in using a chronosequence approach to studying long-term dynamics (Fastie 1995).

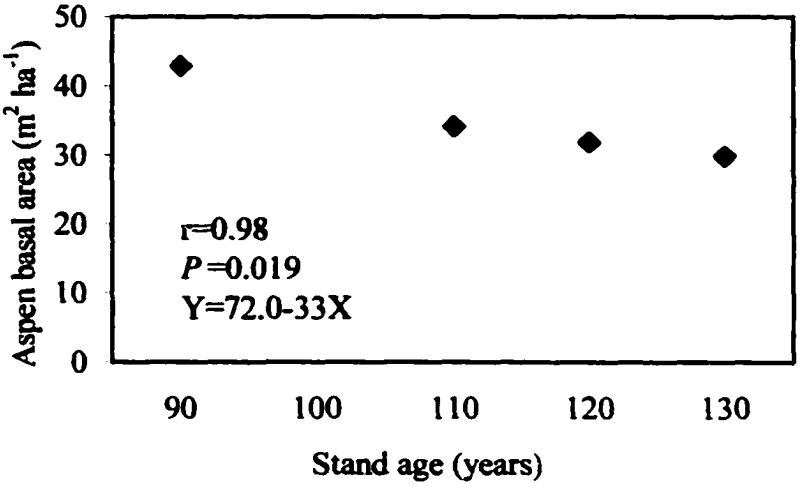

Figure 3.7. Aspen basal area from five aspen stands plotted as a chronosequence of stands ranging age from 90 to 130 years. Aspen basal area for stand age 110 is the average of two stands that were 110 years old when sampled.

In contrast to aspen growth and mortality, aspen establishment was significantly related to conifer invasion. As conifer invasion increased, maximum aspen establishment decreased (Fig 3.3); no stands had aspen establishment when conifer basal area exceeded 30 m^2 ha^{-1}. This conifer basal area may represent a limit beyond which aspen can no longer establish, however more data needs to be collected to test this potential limit. Finally, over the past 50 years aspen only established in stands without conifer invasion. Although the establishment rate in these stands was low (<100 stems ha^{-1} per decade), continued establishment would ensure the persistence of aspen in these stands.

Aspen mortality had a stronger relationship with aspen density than conifer invasion. I found no significant relationship between aspen mortality and conifer basal area, and in fact saw a trend of decreasing aspen mortality with increasing basal area.

This trend may be a function of lower amounts of mortality in stands with conifer invasion than stands without. In contrast, peak aspen density of a stand explained almost 90% of the variance in percent aspen mortality (Fig. 3.6).

The intraspecific pattern of aspen mortality can be put into the context of a classic, albeit controversial, ecological concept: the –3/2 thinning rule (also known as the self-thinning rule or the $3/2^{th}$ power law of self thinning; Yoda et al. 1963). According to the rule, plant density declines as plant size increases in monospecific, even aged stands. More specifically, the slope of the line regressing the natural log of mean plant size to the natural log of plant density is consistently –3/2 once canopy closure has been reached in the stand. Consequently, the rule represents density-dependent mortality among plants. This –1.5 slope has been touted as one of the only documented generalization in ecology, however reviews of relevant data sets often find conflicting evidence in support or contradiction the universal slope (for extensive reviews of this subject, see Weller 1987, Lonsdale 1990). The three even-aged stands in this study showed a strong relationship between density and mean stem basal area (Fig. 3.8), however the slope of the regression between the natural log of these two variables was greater than –3/2 (Table 3.1). Therefore, the aspen stands sampled in this study showed a slower rate of self thinning that expected from the self-thinning law. These data can be considered further evidence of the inadequacy of the self-thinning law (Lonsdale 1990). Variability in species and site-specific characteristics are usually greater than a single power function can encompass (Zeide 1987).

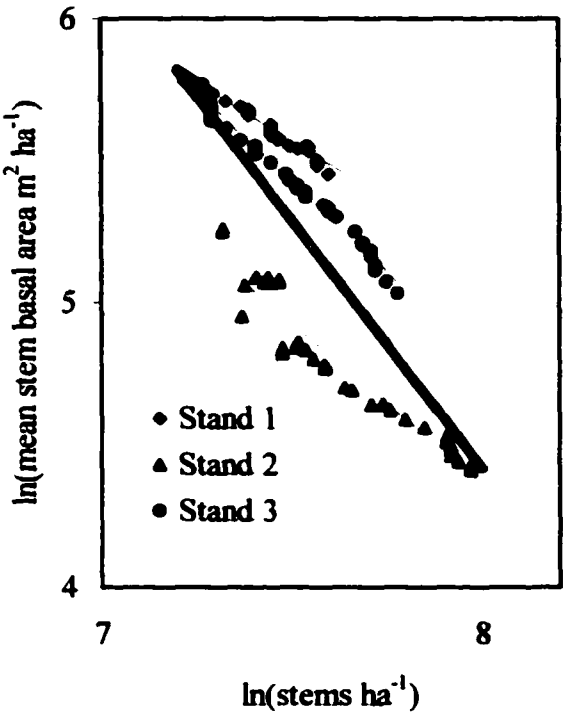

Figure 3.8. Self-thinning patterns of even-aged aspen stands. A linear regression comparing the natural log of aspen density and mean stem basal area. Table 3.1. summarizes slopes of self-thinning lines for each stand. Heavy black line represents aggregated self-thinning slope for the three stands.

Table 3.1

Summary of regression equations testing the –3/2 thinning rule. The independent variable was the natural log of aspen stem density (stems ha^{-1}) and dependent variable was the natural log of mean aspen stem diameter (cm^2). Analysis included Stands 1-3, the only even-aged aspen stands I sampled.

Data	Slope	r^2
Expected	*-1.5*	
Stand 1	-0.84	0.97
Stand 2	-1.13	0.95
Stand 3	-1.27	0.98
Stands 1, 2 and 3	-1.75	0.80

A simplified model based on data of conifer invasion and aspen establishment, growth, and mortality can summarize the dynamics involved in conifer invasion of aspen stands. The timing and amount of initial aspen establishment, subsequent aspen growth, and conifer invasion are highly variable throughout the study area. However, once conifer species begin to invade an aspen stand, aspen establishment decreases. As the stand matures, aspen mortality appears to be a function of aspen density and its duration a function of aspen longevity (Franklin et al. 1987). Generally, aspen stems in the Front Range of Colorado reach a maximum age of approximately 150 years. Concurrently, conifer species such as Engelmann spruce, subalpine fir, and Douglas fir (*Pseudotsuga menzesii*) would be establishing and growing, first in the understory and eventually achieving canopy dominance. These species are shade tolerant and longer-lived than aspen (Aplet et al. 1988, Veblen et al. 1991). Over time and with the absence of aspen establishment, aspen stems would disappear from the stand and conifer species would dominate. Belowground, aspen root systems may remain intact despite a strong presence of conifers aboveground (Shepperd et al. 2001). Crawford et al. (1998) suggested that the eventual replacement of aspen stems by conifer species could take centuries; however the data I collected indicated that the replacement could occur more rapidly in some stands. The timing of this process would depend on site characteristics and history (Donnegan and Rebertus 1999). Insect outbreaks in conifer forests and fires, which both occur frequently and at large scales in parts of the study area (Veblen et al. 1994), could alter this successional pattern (Veblen et al. 1991). Additionally, elk browsing in aspen stands may accelerate conifer invasion if the elk preferentially browse the aspen and avoid the conifer species. The model of forest succession presented above does not differ

greatly than what has previously been described for quaking aspen in the Rocky Mountains. However, the understanding that conifer replacement of aspen may occur via exclusion of aspen establishment rather than interactions with mature aspen is novel. This relationship needs to be tested with further data collection.

The results from this study indicate that forest succession from aspen to conifer forests primarily occurs due to differential life history traits of the species involved, rather than species interactions such as competition. Life history traits such as mode of reproduction, shade tolerance, and longevity account for changes in species composition over time. Aspen's ability to sprout from previously existing roots gives it an advantage over conifers in rapid site recolonization. Shade tolerance of conifer species allow them to establish in the understory of the aspen canopy, while shade intolerance of aspen does not favor their establishment below a conifer canopy. Aspen's short life-span (for stems, not clones) causes mortality of aspen sooner than mortality of conifers, and conifer species longevity allow it to persist on a site long after the majority of aspen stems have died. For aspen to persist on a site, it would require repeated establishment, and data from this study indicate that aspen establishment is reduced by conifer invasion. The division between life-history traits and species interactions is not always clear (e.g., for example, aspen could be considered to "facilitate" conifer invasion by creating a closed canopy that favors conifer over aspen establishment), however I found that this example of forest succession corroborates with other studies that list life-history traits as a principal driving variable in forest succession (Dix and Swan 1971, Drury and Nisbet 1973, Walker et al. 1986, Huston and Smith 1987, Chapin et al. 1994).

A common theme from the data is limits imposed by conifer invasion on aspen dynamics (e.g. maximum aspen establishment; Fig. 3.3 and maximum aspen BAI; Fig. 3.4). Limits on aspen establishment set by conifer invasion seem to have impacted aspen dynamics more than limits on aspen growth. This is demonstrated by the lack of aspen establishment in stands with conifer invasion. In contrast, the limits of conifer invasion on aspen growth have not brought about declining aspen basal area in stands with conifer invasion (Fig. 3.5a). However, as time passes, reduced growth of aspen as a result of conifer invasion may begin to cause a decline in aspen basal area.

In aspen stands without conifer invasion, changes through time of aspen establishment, growth, and mortality were similar to the expected patterns. Initial aspen establishment occurred as a pulse within the first 20 years of stand development (Fig. 3.1a). I did not expect a 10 to 20-year lag between stands initiation and the peak in aspen establishment. This lag may be due more to the methods than ecological phenomenon (Veblen 1992). I extracted tree-ring samples at 20-30cm height on the bole. The time it took aspen stems to grow to that height was variable and I may have placed stems that established within the first 10 years in the category of stems that established between 10 and 20 years.

Aspen growth, as represented by BAI, varied little over the period of stand development, however it did show a slight decrease with stand age (Fig. 3.2b). The aspen stands were reaching 130 years of age, and the growth of mature stems in these stands may have been slowing down due to old age. Concurrently, aspen mortality was increasing rapidly. A combination of reduced growth and increased mortality of aspen in older stands indicates that these stands may be declining. Unfortunately, I only had data

from two aspen stands without conifer invasion, and I suggest that further data be collected from additional stands. In the area of Rocky Mountain National Park, it was difficult to find aspen stands without conifer invasion or elk browsing.

The variability in timing of aspen establishment and dynamics of conifer invasion indicates that the mechanisms driving these processes are complicated (Leiffers et al. 1996). I was not expecting to find as much variation in stand development, and consequently did not collect suitable data to quantify potential driving variables (e.g., site productivity or records of stand initiating disturbance). The timing and amount of initial aspen establishment and the subsequent growth of aspen may be a function of preceding forest disturbance, the availability of availability root mass for aspen sprouting, site productivity, and current climate conditions (Hoff 1957, Dix and Swan 1971, Mitton and Grant 1980, Baker et al. 1997, Chen et al. 1998). The timing of conifer invasion may be a function of factors such as aspen density, patch size, seed source, site productivity, and current climate (Leiffers et al. 1996). Further research addressing these influential factors would lead to a better ability to describe the mechanisms behind succession of aspen forests to conifers and predict aspen-conifer dynamics. Predictable patterns in forest succession are likely to be overrun at times by stochastic variables such as fire, insect outbreaks, and other factors (Binkley et al. 1997).

Based on the data I have collected to date, the invasion of conifer species into previously existing aspen stands appeared to decrease the amount of aspen establishment in the stands, but had little effect on growth and mortality of existing aspen stems. The mortality of aspen stems was highly correlated with peak aspen density within the stands. I conclude that the succession of aspen stands to conifer was a function of the life history

characteristics of the species involved. Asexual reproduction, shade-intolerance, and short life spans of aspen and shade-tolerance and longevity of conifer species account for the early and rapid establishment of aspen into recently disturbed area and the eventual replacement of aspen by conifers. The future of aspen in these Rocky Mountain forests can be ensured with successful aspen regeneration because aspen growth appears to be resilient to competition from invading conifer trees (Shepperd et al. 2002). Successful aspen regeneration may result from natural environmental changes (e.g., climate and disturbance) or human manipulation of the system (e.g., forest thinning and stimulation of root sprouting).

CHAPTER 4: AN AGE STRUCTURED MODEL PROJECTS THE FUTURE OF QUAKING ASPEN STANDS IN ROCKY MOUNTAIN NATIONAL PARK, COLORADO

ABSTRACT

Multiple resources associated with quaking aspen in the central Rocky Mountains require conflicting management strategies. Models of the temporal dynamics of aspen in the region can facilitate multiple management decisions. The objective of this study was to project the density of individual aspen stands through time with an age-structure model of aspen based on life-table analyses, current stand structure, and variable recruitment levels meant to reflect various ecological and management scenarios. In five stands sampled in Rocky Mountain National Park, current stand density could be maintained if between 80 and 230 stems ha^{-1} reached 10 years of age during each decade. No stand would persist longer than 100 years without recruitment into the stands. If recruitment occurred in episodic pulses, stand densities would fluctuate an order of magnitude (between 10^1 and 10^2 stems ha^{-1}) and all stands would persist.

INTRODUCTION

Quaking aspen (*Populus tremuloides* Michx.) is the most widely distributed tree species in North America and the most common deciduous species in the Rocky Mountains. Aspen forests provide important habitat for birds and mammals (DeByle

1985, Turchi et al. 1995), they have been called "hotspots" of diversity for plant species (Stohlgren et al. 1999), and are valued for their aesthetic beauty. Over the past 60 years, some ecologists have speculated that aspen would disappear from parts of Rocky Mountain National Park owing to elk browsing and fire suppression (Packard 1942, Olmsted 1979, Baker et al. 1997, White et al. 1998). These speculative predictions have not been born out. Packard (1942) predicted that browsing by elk would eliminate aspen from Beaver Meadows; "It is almost certain that in comparatively few years all of these aspen will have died, and there is little chance that they will be restored in the near future, thereafter" (p. 480). Aspen stands persisted in this area through the 20th century and 20 to 50% of aspen stands contain recently recruited stems (Suzuki et al. 1999).

A science panel on vegetation management of elk winter range of Rocky Mountain National Park suggested several expanded studies on the status of current and potential aspen stands (Berry et al. 1997). It suggested that the persistence time of current stands should be estimated and an appropriate number of aspen patches should be protected from elk browsing to ensure sustainability of the vegetation type. This information can be obtained through ecological modeling.

Ecological models are mathematical expressions of the patterns and processes that join organisms and their environment. A key pattern in the ecology of aspen is the role of life history traits in the temporal dynamics of aspen (Chapter 3; this dissertation). Therefore a model based on life history characteristics of aspen may improve predictions of the future of the species within the Park.

In this study, I used past dynamics of aspen forests to develop a quantitative model to forecast the future of aspen stands in Rocky Mountain National Park. The

projected variable of this study was density of trees in individual aspen stands through time based on an age-structure model of aspen. The model was developed with age-specific survivorship values calculated from a static life table, the current age structure of aspen stands, and a recruitment parameter. I manipulated the recruitment parameter to reflect various ecological and management scenarios (e.g., reducing elk herd size, building elk exclosures, introducing prescribed fires), and then modeled the effects on future stand structure. My primary questions were:

(1) What level of aspen recruitment was necessary to maintain current stand density?

(2) How long would current aspen stands persist without recruitment?

(3) How would periodic pulses in recruitment affect long-term dynamics of stand structure?

Results from the model projections can direct managers within and around the Park in their development of plans to preserve aspen, whether it be for particular aspen stands, clones, or the population.

METHODS

Study area

Rocky Mountain National Park is located in the Front Range of north-central Colorado, straddling the Continental Divide. The Park covers an area of approximately 107,500 ha and elevations ranging from 2,300 m to 4,300 m. Aspen covers approximately 6% of the forested area of the Park, is found at all forested elevations, and occurs as pure stands and in mixtures with conifers (see Chapter 2; this dissertation).

Model development

Three types of input data were necessary to develop the model: (1) current age structure of aspen stands; (2) survivorship values in 10-year age classes for aspen in the Park; and (3) number of new stems recruiting into aspen stands (Fig. 4.1). The model was developed to project aspen density through time and each run of the model began at time zero, which is the decade during which the field data were collected (1990s). Each time step of the model represented 10 years.

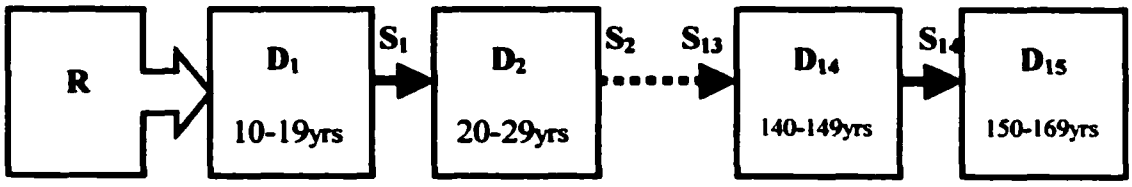

Figure 4.1. Box diagram of age-structured model of aspen in Rocky Mountain National Park. Recruitment (R) represents the number of stems/ha entering the first age class (10-19 years) with each time step of the model. D_i represents the number of stems/ha in age class *i*. S_i represents the age specific survivorship: the probability a stem in age class D_i survives to age class D_{i+1}. See Table 4.2 for parameter values.

Age structure data

Five aspen stands on the east side of the Park were randomly selected from the population of stands greater than 1,000 m^2 in area, between 2300 and 2900 m elevation, and with little evidence of elk browsing (for a more detailed description of site selection see Chapter 3; this dissertation). In each stand, a circular plot with a radius between 10 m and 18 m was established. Within the plot, increment cores or cross sections were sampled from every living aspen stem at approximately 20-30 cm above the root collar.

In the laboratory, wood samples were mounted and surfaced to ensure maximum visibility of annual ring boundaries with a binocular microscope. Each sample was

crossdated (Fritts 1976) and pith dates were assigned. If the pith was not intersected with the sample, a pith estimator of concentric circles was used to extrapolate the number of rings between the innermost ring on the core and the pith (Applequist 1958, Biondi 1999). Current age structure of each stand was calculated by aggregating individual tree age data into 10-year age classes and converting the data to a per-hectare scale.

Survivorship values

Age-specific survivorship values for aspen in Rocky Mountain National Park were calculated using a static life table (Table 4.1; Deevey 1947, Kimmins 1987). I used age data from 825 aspen trees (419 in the elk winter range and 406 in the summer range) in 74 randomly selected aspen stands in and around Rocky Mountain National Park (Suzuki et al. 1999) to create three static life tables based on 10-year age classes. Age-specific survivorship rates calculated with the life table analyses represented the probability that a tree would pass from one 10-year age group to the next with each time step of the model. Assumptions made with life table analyses include constant birth and death rates for each age class (Caughley 1976, Johnson et al. 1994).

Recruitment values

I manipulated the recruitment parameter of the model to create three scenarios that reflect different management and environmental scenarios. Recruitment represented the number of stems per hectare that reached the first age class (10 to 19 years) in each time step of the model. In Scenario I, I modeled constant recruitment over 13 time steps of the model (130 years) for recruitment values ranging from 0 to 500 stems ha^{-1} $decade^{-1}$. For Scenario II, I modeled zero recruitment over 13 time steps. In

Table 4.1. Description and calculation of columns in a static life table as outlined by Smith and Smith (1998). Parameter "l_x" was used as the age-specific survivorship value in the age-structured model of aspen in Rocky Mountain National Park.

Column in Life table	Definition	Calculation
x	Age class	x+1 is the following group x-1 is the previous group
n_x	Raw data	No. of survivors in x. n_{x0}= no. of samples in first age group
l_x	**Survivorship**	$= n_x/n_{x0}$
d_x	Deaths	$= l_x - l_{(x-1)}$
q_x	Mortality rate	$= d_x/l_x$
L_x	Average life of all individuals	$= (l_x + l_{(x+1)})/2$
T_x	Time units left for all individuals from x	= sum (L_x to last age group).
e_x	Further expectation of life (no. of age groups)	$= T_x/l_x$

Scenario III, I varied the amount of recruitment entering a stand by drawing each recruitment value from a distribution of values ranging from 0 stems ha^{-1} (the most frequent value of recruitment per decade) to 1000 stems ha^{-1}. This distribution of recruitment values reflected numbers found in this study and by Suzuki et al. (1999). To validate the model, I began with the reconstructed age structure of the five stands for the 1950s, ran the model for four time steps, and added the same amount of recruitment per decade that I measured in the stand reconstructions. Under these conditions, the model should project similar stand densities for the 1960s, 1970s, 1980s, and 1990s to those measured with the stand reconstruction. The first validation of the model revealed that it was consistently underestimating stand densities. Elevated mortality rates per age class could account for the underestimation, so I investigated the input data to identify a potential cause of overestimated mortality. The age structure data used to calculate the survivorship values were based on stands found throughout the Park, in areas of both high and low elk use (Suzuki et al. 1999). The five stands sampled for this study showed no evidence of elk browsing. Elk browsing has the potential to decrease survivorship of aspen stems because of the increased opportunity for pathogen invasion into aspen stems via browsing wounds (Krebill 1972, Hinds 1985). Due to this potential impact on survivorship values, I recalculated the life tables based on age data from aspen trees found in areas of high and low elk use (elk winter and summer ranges, respectively). I then used these data to validate the model and see if stratification by stand history helped me better estimate observed changes in stand density.

RESULTS

Model development and validation

The age distribution of the five stands spanned 130 years and no stand showed a stable age distribution (Fig. 4.2), which is also true of other aspen stands sampled in the central Rocky Mountains (Betters and Woods 1981, Mueggler 1989). Stands 1, 2, and 3 initiated with large pulses of aspen recruitment within the first 40 years and only Stands 1 and 2 had any recruitment in the past 50 years. Aspen in Stands 4 and 5 established regularly, but a low levels, over a 30 to 80 year period (for further discussion of stand age structure see Chapter 3; this dissertation).

For the life table analyses, the assumption of constant births through time was supported by aspen establishment dates throughout the Park (Fig. 4.3). The assumption of constant mortality in a stand had not been tested. The youngest tree sampled was 5 years and the oldest was 161. Survivorship vales were calculated for age classes from 10-19 years to 160-169 years (Table 4.2). Aspen in the Park have a Type 1 survivorship curve (Deevey 1947), where survival probability was highest for the younger age classes and decreased with older age classes (Fig. 4.4). Aspen trees from areas of low elk use had higher survival rates than trees in areas of high elk use for all age classes except 100-109 and 110-119 years (Fig. 4.4).

Survivorship values based on all stands in the Park, and those based on only stands in areas of low elk impact, yielded underestimations of stand density in the model validation (Fig. 4.5). However, the survivorship values from stands with lower elk use produced significantly less underestimation, so I used those values for the modeling of the three recruitment scenarios.

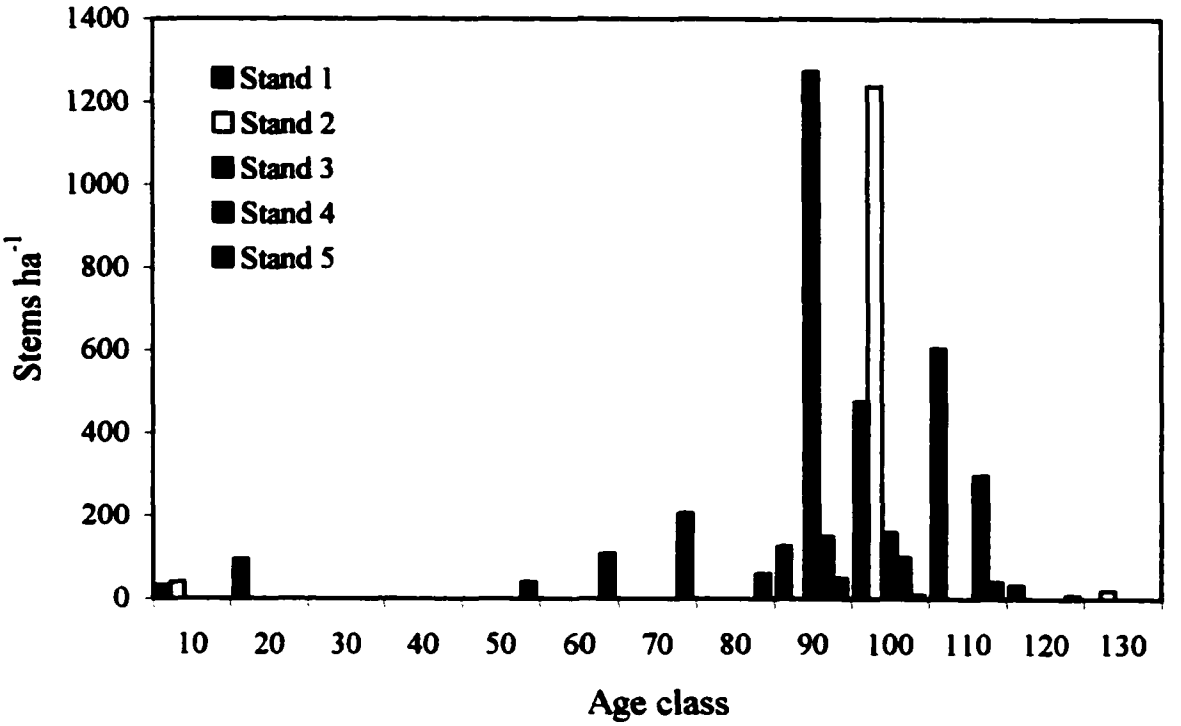

Figure 4.2. Age distribution of five aspen stands in Rocky Mountain National Park. Each bar represents the number of stems/ha in each 10-year age class, beginning with the youngest age class, 10-19 years.

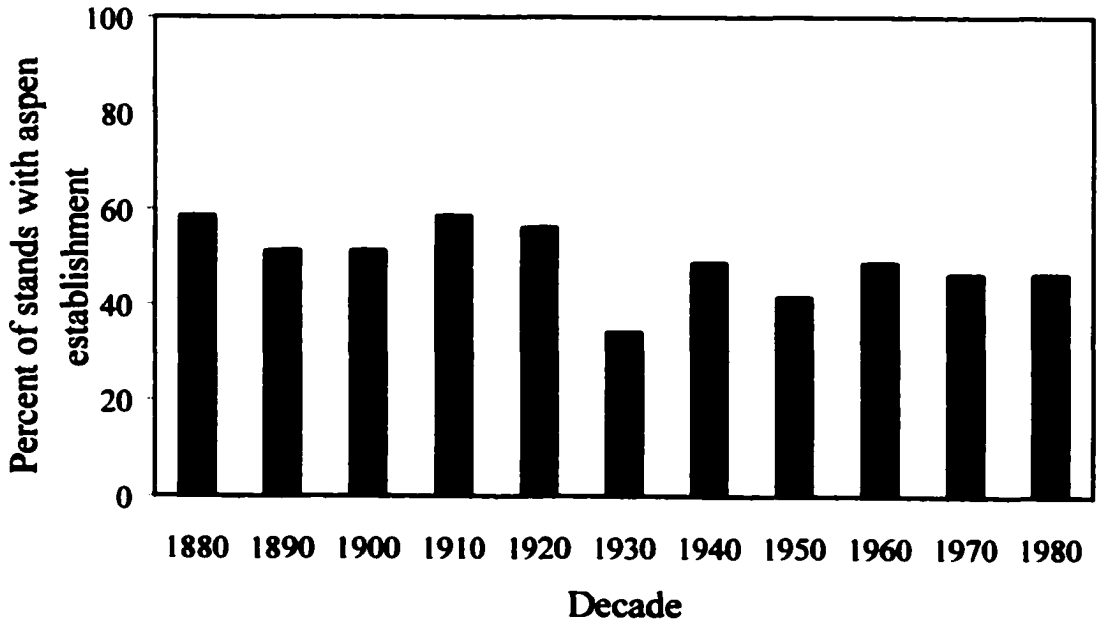

Figure 4.3. Percent of stands sampled by Suzuki (1997) in Rocky Mountain National Park that had aspen recruitment for a given decade.

Table 4.2. Age classes and survivorship values (lx) used in the age-structured model for aspen in Rocky Mountain National Park. Survivorship values were calculated from a static life table with data collected by Suzuki (1997).

Age classes			**Survival probability (Lx)**			
Model parameter	**From (years)**	**To (years)**	**Model parameter**	**All stands**	**Stands with low elk impact**	**Stands with high elk impact**
D_i			R			
D1	10	19	S1	0.99	0.99	0.99
D2	20	29	S2	0.88	0.91	0.84
D3	30	39	S3	0.76	0.84	0.69
D4	40	49	S4	0.70	0.77	0.63
D5	50	59	S5	0.63	0.69	0.57
D6	60	69	S6	0.59	0.64	0.53
D7	70	79	S7	0.53	0.57	0.49
D8	80	89	S8	0.45	0.47	0.43
D9	90	99	S9	0.38	0.39	0.37
D10	100	109	S10	0.30	0.27	0.32
D11	110	119	S11	0.22	0.20	0.23
D12	120	129	S12	0.10	0.13	0.07
D13	130	139	S13	0.04	0.06	0.02
D14	140	149	S14	0.01	0.01	0.01
D15	150	159	S15	0.00	0.00	0.00

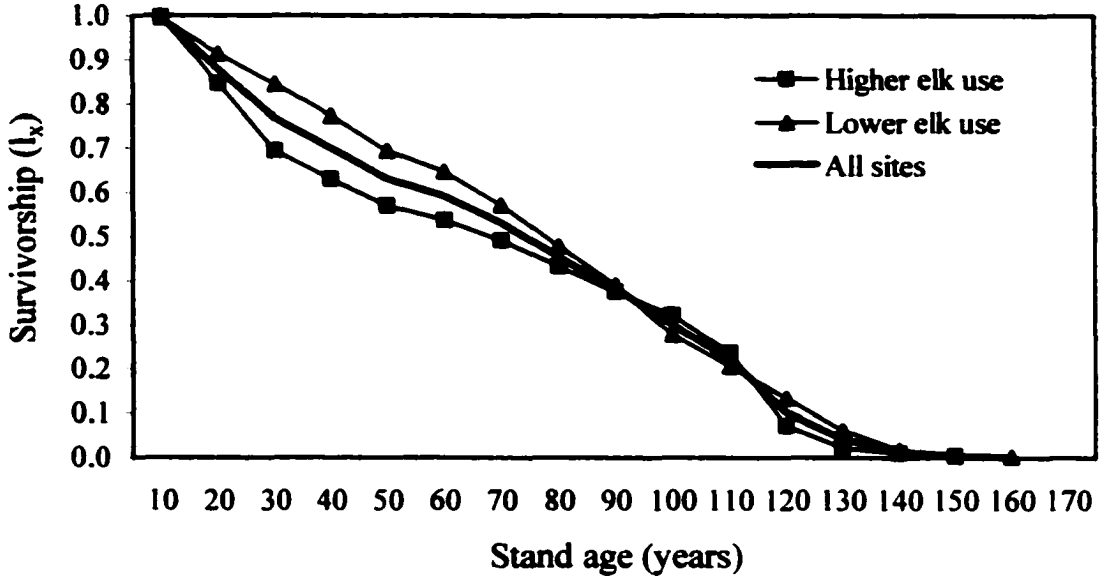

Figure 4.4. Age specific survivorship values for aspen throughout Rocky Mountain National Park (solid line). Survivorship values were also calculated for stands in areas of high elk browsing (squares) and low browsing (triangles). Survivorship values (l_x) were calculated with a static life table (Table 1, Smith and Smith 1998).

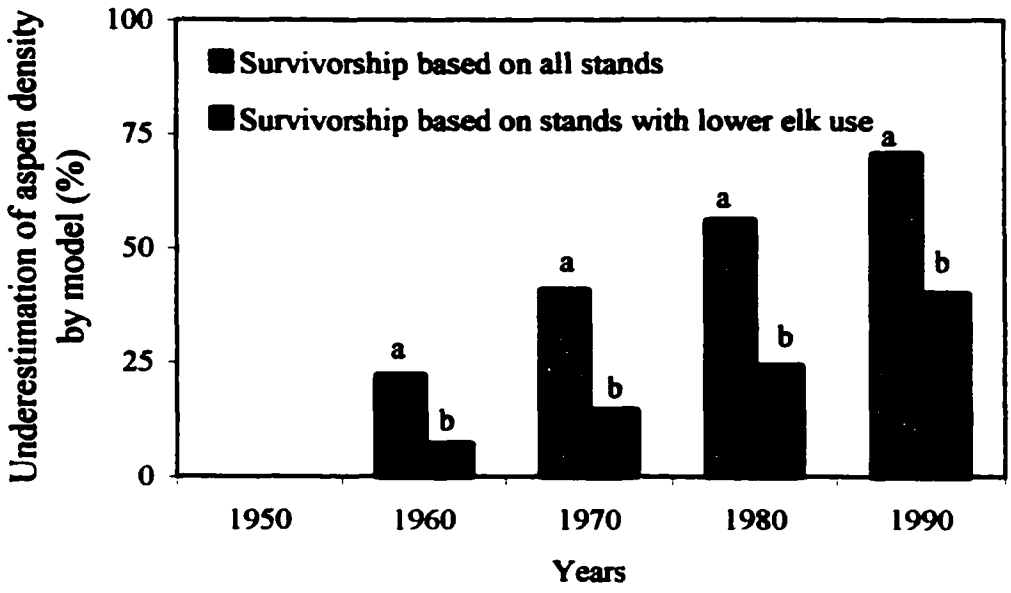

Figure 4.5. Model validation results. The age-structured model based on survivorship values from all stands in Rocky Mountain National Park (striped bars) consistently underestimated actual stand density more than the model based on survivorship values from areas of low elk browse in the Park (solid bars).

Recruitment Scenario I: constant recruitment through time

Constant rates of recruitment led to the same temporal pattern of stem density among stands (Fig. 4.6), although the values of density (the scale of the Y axis) varied between stands. At time zero, aspen density was equal to that which was measured in the field (Fig. 4.6; region a). Aspen density then decreased, reached a minimum, and began to increase, usually within 50 years (Fig. 4.6; region b). This initial decrease in aspen density was due to the absence or low levels of aspen recruitment in all five stands in the past 50 years (Fig. 4.3). In the first 50 years of model projection mid-aged classes had almost no stems and aspen mortality exceeded aspen recruitment. Within 50 years, the constant recruitment entering a stand with each time step of the model had increased the number of stems in younger and mid-aged classes and mortality rates remained constant. After approximately 100 years, aspen stand density reached a steady state because both inputs (recruitment) and outputs (mortality) were constant (Fig. 4.6; region c).
The linear equation $Y = 6.21*X$ represented the recruitment necessary (X) to maintain the current stand density measured in the field (Y; Fig. 4.7). In the five stands, recruitment values between 80 and 230 would maintain the densities measured in the field. These scenarios were based on constant recruitment through time, which is unlikely based on observed stand structure.

Recruitment Scenario II: no recruitment

No stand would persist more than a century without future recruitment of new stems (Fig, 4.8). Stands 1 and 2 would persist the longest because of the minimal amounts of recruitment that had occurred in the past 30 years (Fig. 4.3).

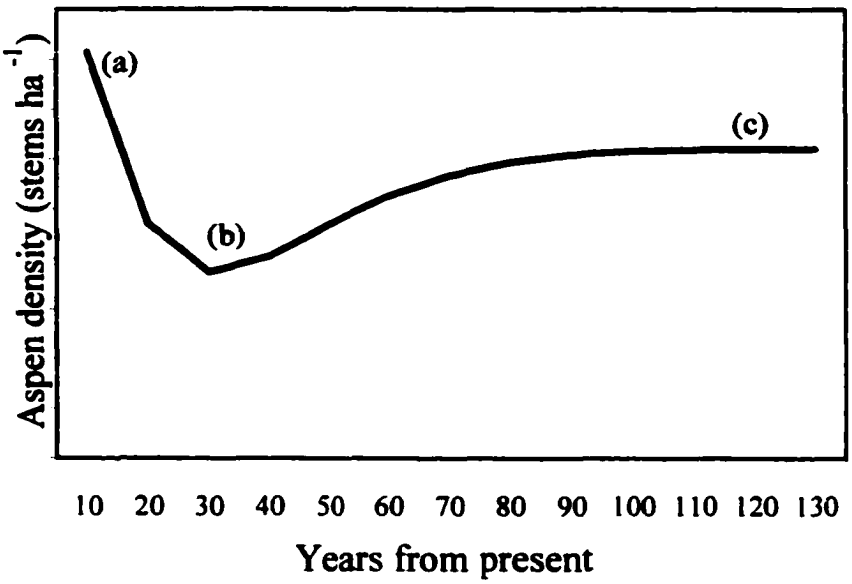

Figure 4.6. Representative graph of the age-structured model projection when recruitment remains constant through time. Aspen density begins at time zero with the density measured in the field (a). Within the first few decades, aspen density declines due to the gap in recruitment that has occurred over the past 50 years (b). Eventually, aspen density reaches a steady state as establishment and mortality become constant (c). This pattern was observed in all five stands, however the scale of the Y axis changes between stands.

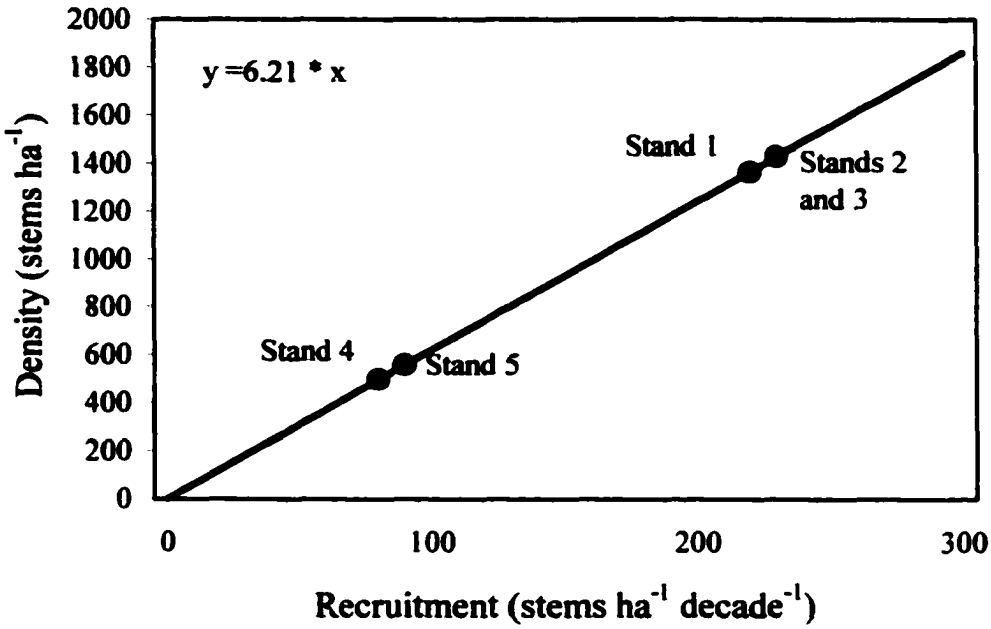

Figure 4.7. Linear relationship between the number of stems ha^{-1} $decade^{-1}$ necessary to maintain a given stand density. The recruitment necessary to maintain density measured in the five stands in Rocky Mountain National Park is represented by black dots.

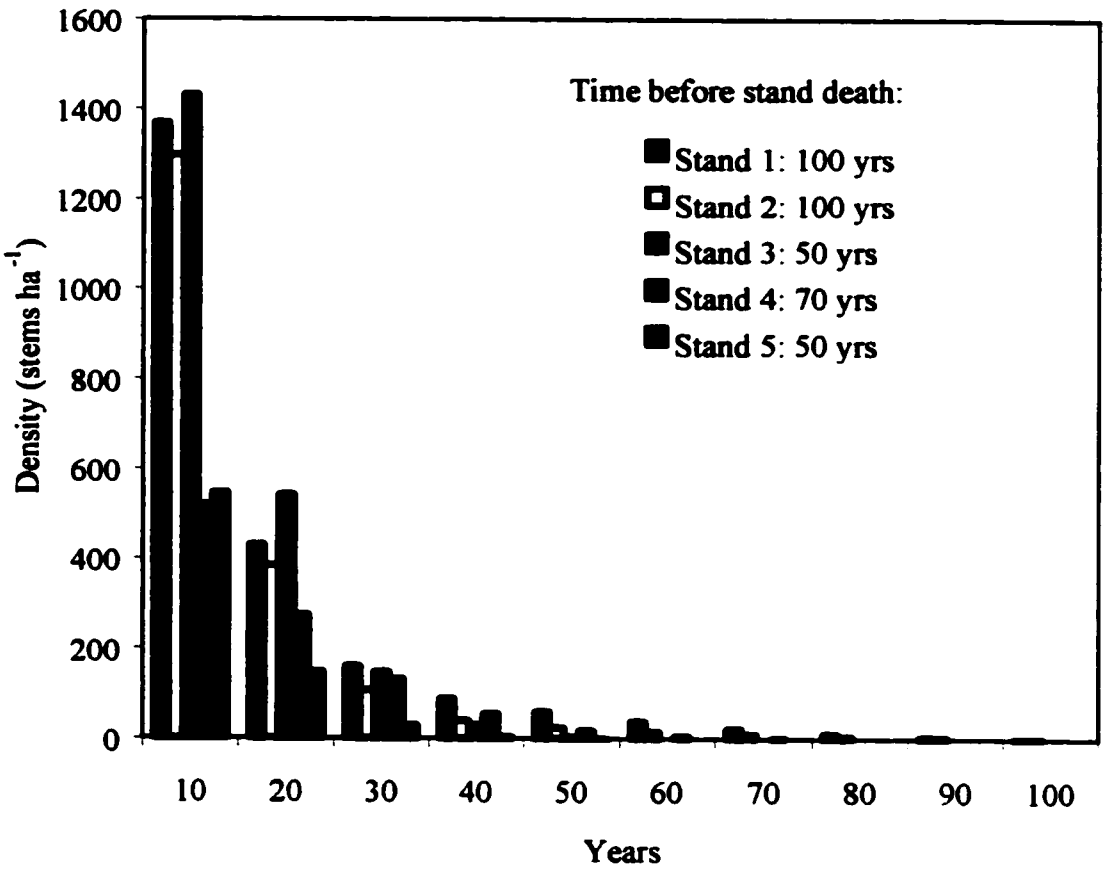

Figure 4.8. Decrease in aspen density with time when the age-structured model is run with no recruitment entering the stands.

Recruitment Scenario III: continued periodic recruitment

The amount and timing of recruitment clearly affected the long-term dynamics of stand density (Fig. 4.9). All stands showed the same initial decrease in stem density in Scenario I, which was due to the absence or low levels of recruitment over the past 50 years. The distribution of recruitment values reflected the range of recruitment values occurring in the five sampled stands over the past 100 yrs. Randomly drawn recruitment produced episodic pulses in aspen recruitment (dashed line, Fig. 4.9). The resulting stand density (solid line, Fig. 4.9) fluctuated over an order of magnitude. The maximum density reached by any stand was 1747 stems ha^{-1} and the minimum was 30 stems ha^{-1}. Over the 100-year period of model projection, no stand experienced complete mortality of all stems (i.e., a density of 0 stems ha^{-1}).

DISCUSSION

Forecasts of the future of aspen stands in Rocky Mountain National Park need not be based solely on speculation, given the records of stand dynamics that are found in tree rings. The quantitative age-structured model developed in this study for quaking aspen showed potential for projecting the future of aspen dynamics in and around the Park. I chose the amount of recruitment entering aspen stands as the main parameter of manipulation to reflect different environmental and management conditions and ran the model for 130 years into the future because it is unlikely that predictions of the condition of an aspen stand in Rocky Mountain National Park could be reliable past this point. This is due to the increased probability of unpredictable events occurring as more time goes by (e.g., a large-scale stand-replacing fire such as the one that occurred in

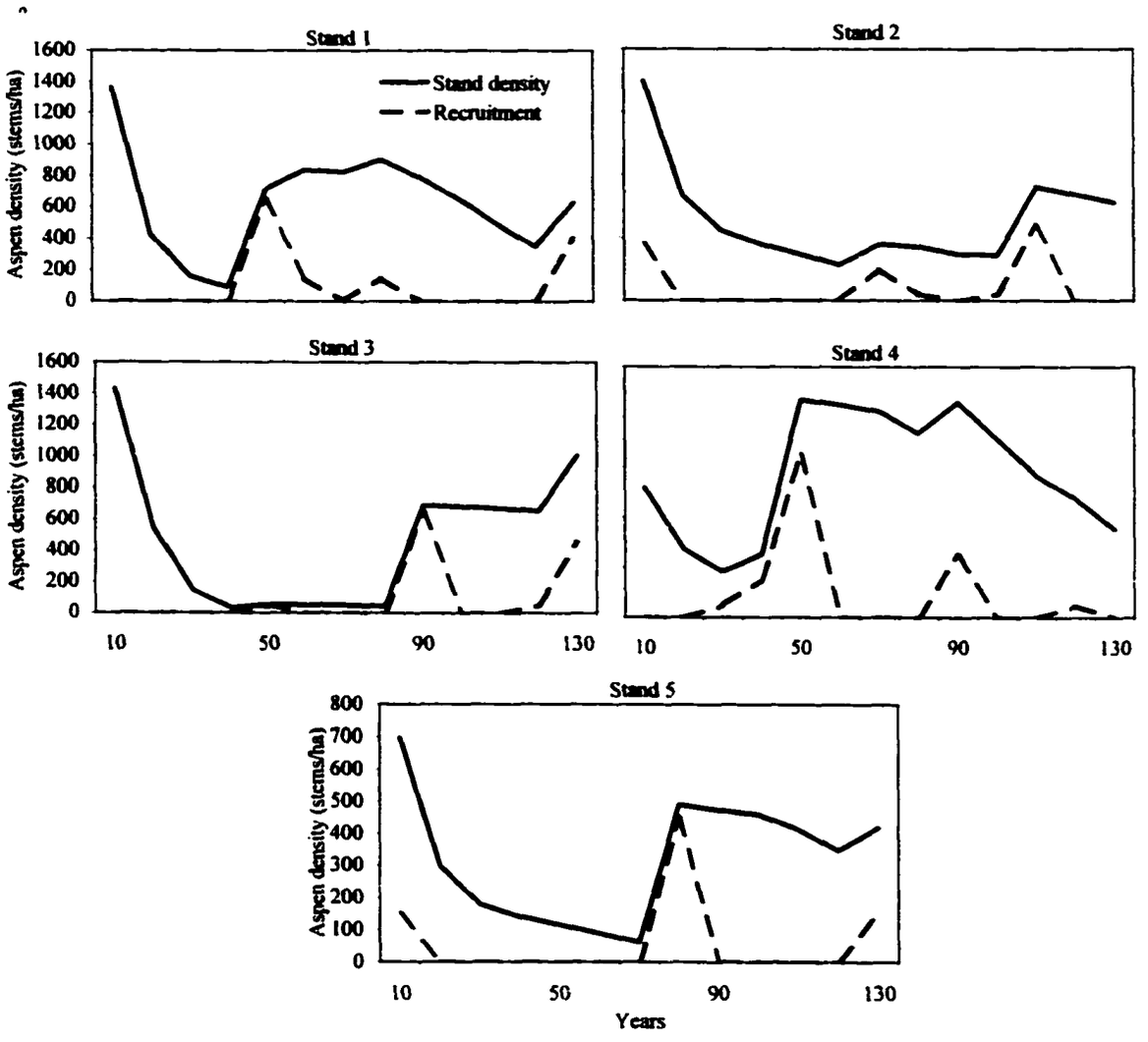

Figure 4.9. Projection of aspen density (solid line) with the age-structured model. Recruitment (dashed line) ranged from 0 to 1000 stems/ha and was episodic.

Yellowstone National Park in 1988) and the relatively short-lived nature of aspen stems (not clones).

Several assumptions were made to develop and run the model. Life-table analyses assumed constant establishment and mortality through time. The life-table data was representative of the population of aspen within the Park because Suzuki et al. (1999) randomly selected the aspen stands they sampled. At this level, aspen establishment remained consistent over the past 100 years (Fig. 4.2), however there are no population-scale mortality data. Age structure data from the five stands sampled in this study showed that aspen establishment and mortality has not been constant over time at the stand level. These data indicated that at certain scales, the assumptions may have been met, and at others they may not. Ultimately, it is essential that the assumptions of static life table analyses be addressed (Johnson and Fryer 1989, Johnson et al. 1994). In addition to the assumptions made for the life-table analyses, I assumed in Scenarios I and II that recruitment would be constant over time, whether it was as a single value or as zero. Although these scenarios were unlikely due to variations in climate, disturbance regimes, and other factors affecting the ecology of aspen (Romme et al. 1995), they provide a concept of the effects of recruitment on future stand persistence and density.

The model validation demonstrated that survivorship values were influenced by stand history, which indicated that further stratification of life-table analyses could yield more accurate projections of aspen stand density. I was able to calculate survivorship values for aspen stands in areas of high elk browsing (elk winter range) and low browsing (elk summer range) and the model validation showed that survivorship values from the elk summer range were more appropriate for the five stands I sampled. The browsing of

aspen stems by elk causes wounding to the bark and inner cambium, and a passageway for pathogens into the wood of the tree (Hinds 1985, Krebill 1972). This may be the mechanism by which elk browsing was correlated with lower survivorship values in aspen for the majority of age classes (Fig. 4.4). The modeling approach taking in this study allowed me to identify elk browsing as a variable that affected aspen survivorship.

If browsing history brought about differences in aspen survivorship, other stand characteristics should be taken into account in future model development. For example, aspen stand elevation and density are likely to have an effect on aspen survivorship (Chapters 2 and 3; this dissertation). Field collections should focus on potential factors such as these to compute survivorship values for specific types of aspen stands. The resulting age-structured model could project the density of specific types of aspen stands (e.g., those with high degrees of elk browsing or conifer invasion).

The benefits of an age-structured model for forested systems are two-fold: (1) past aspen regeneration and survivorship can be used to project the future of individual aspen stands; and (2) regeneration and survivorship levels can be manipulated to simulate the effects of particular land management decisions. To maximize the usefulness of this model, I selected recruitment as the sole parameter of manipulation. The three recruitment scenarios present possible conditions in the near future in Rocky Mountain National Park.

Values of recruitment on a per-area basis were difficult to find in the literature, therefore I relied on results from only one other study and from this one to select appropriate recruitment values. The majority of recruitment values documented in other studies was either presented without an aerial unit, on a per plot basis (even if plot size

varied), or as stem diameter size classes rather than age classes (e.g., Olmsted 1979, 1997, Betters and Woods 1981, Parker and Parker 1983, Baker et al. 1997, Crawford et al. 1998, Hessl 2000). Suzuki et al. (1999) recorded recruitment values in the Front Range of Colorado between 0 and 1000 stems ha^{-1} $decade^{-1}$ (Suzuki 1997), with an approximate average of 500 stems ha^{-1} $decade^{-1}$. This study recorded recruitment values between 0 and 1200 stems ha^{-1} $decade^{-1}$ (Fig. 4.4), with an approximate mean of 600 stems ha^{-1} $decade^{-1}$. In both data sets, recruitment was episodic, rather than continuous.

The goal of modeling constant recruitment through time was to identify a target recruitment level for preserving current aspen stand density. A science panel on vegetation management of elk winter range of Rocky Mountain National Park proposed that current aspen stands within the elk winter range be preserved, and one approach would be to build elk exclosures around aspen patches (Barry et al. 1997). The exclosures would prevent elk from damaging existing stems and future recruitment, however active steps may be necessary to ensure that sufficient recruitment occurs within the exclosure. Based on the results of the model, the equation:

$$\text{Current Density} = 6.2 * \text{Recruitment (stems } ha^{-1} decade^{-1})$$

could be used to approximate the amount of recruitment that would be necessary to preserve any stand at a given density. Additionally, measurements of recent recruitment into a stand could indicate if a stand is aggrading or degrading in stem density by comparing it with the above equation.

In some stands in the Park, it is possible that no future recruitment would occur. Aspen is considered to be shade intolerant, so recruitment may not occur in a closed-canopy stand. External factors such as elk browsing, unsuitable climate, or a deep forest

floor also inhibit aspen recruitment (Romme et al. 1995, Baker et al. 1997). Three of the five stands sampled have not experienced any recruitment over the past 50 years, so continued absence of recruitment would not be unexpected. None of the five stands would persist as long as a century without recruitment, and Stands 3 and 5 might persist only fifty years (Fig. 4.8). When the age-structured model was applied to five stands sampled by Suzuki et al. (1999) in the Park and Roosevelt National Forest, the model projected that without recruitment the stands would decline from almost 4000 stems ha^{-1} to 0 stems ha^{-1} in 100 years (Fig. 4.10).

In contrast, episodic recruitment modeled in Scenario III would allow aspen stands to persist despite large fluctuations in stem density (Fig. 4.9). This Scenario is likely the most realistic of the three because aspen recruitment has been pulsed and varied through time (Fig. 4.4). Patterns in periodic recruitment would be driven by stand specific and regional factors such as browsing history, fire, and climate. The degree of elk or cattle browsing (outside the Park) would have an inverse relationship with aspen recruitment, with increased browsing leading to decreased recruitment due to consumption of aspen sprouts by animals. Fire regimes also influence aspen recruitment (Bartos and Mueggler 1981, Bartos et al. 1994). Stand-replacing fires create conditions

suitable for aspen establishment, however once an aspen stand has established, it is considered difficult to burn because of fuel type and moisture (Brown and Simmerman 1986). Therefore, in already existing stands, fire may not have much influence on pulses of recruitment. Decadal fluctuations in aspen establishment are influenced by variations in climate as well (Baker et al. 1997, Romme et al. 1995). These external variables, in addition to the life history of aspen, dominate the timing and extent of episodic aspen

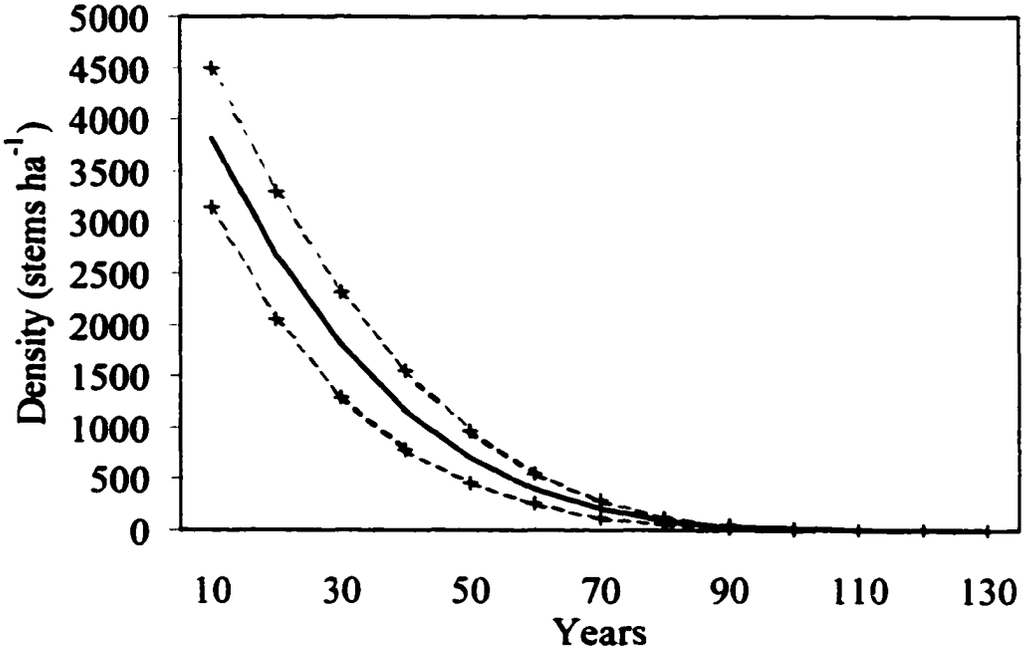

Figure 4.10. Age-structured model applied to five aspen stands sampled by Suzuki et al. (1999) in Rocky Mountain National Park. Solid line represents mean of five stands, and dashed lines represent standard errors.

recruitment, and the potential for aspen to persist on the landscape.

The persistence of aspen on the landscape can be considered at two levels: as the persistence of a multi-aged stand with continuous recruitment ensuring the constant presence of aspen as the dominant tree species (Scenario I), or as the persistence of the aspen clone, where the abundance of aspen stems may drastically fluctuate through time, but the clone depends on its root system to persist (Scenario III; Burton 1966, Grant and Mitton 1979). Park managers must decide at what level they want to preserve aspen, and then make prescriptions to ensure it. For example, for the stand to persist, exclosures and mechanical sprout stimulation may be necessary to ensure constant decadal recruitment. To ensure clone persistence, landscape-scale disturbance regimes and elk population management may be necessary.

The direst situation projected by the model is that current aspen stands experience no more recruitment, and that these stands disappear within the next 100 years (Fig. 4.8). Suzuki at al. (1999) found that approximately 50% of the stands they sampled in the Front Range had no regeneration since the 1960's, a time of active fire suppression. If failed aspen recruitment continued in these stands, the amount of aspen on the landscape would decline. For the population of aspen patches to maintain its abundance, new aspen stands need to be initiated. Historically, fire was the primary means to initiate new stands (Baker 1925, Bartos and Mueggler 1981, Bartos et al. 1994). Throughout the 20th century, fire in western forests has been a highly debated subject. However, the reintroduction of fire may be necessary to stimulate new aspen patches. At the landscape scale, the population of aspen stands and clones may remain at a steady state, while individual stands establish and die.

The age-structured model presented in this study could be expanded into a landscape-scale model of the structure of the aspen population. This model could be developed by linking a GIS of aspen stands in the Park with the age-structured model. To complete the landscape-scale model, a stand initiation parameter would need to be added so that as current stands decline or die, new stands enter the population. This larger scale model would provide greater insight for management of the population of aspen in the Park and surrounding regions.

CONCLUSIONS

The age-structured model of quaking aspen provides a tool to view potential future scenarios of aspen stands for managers of Rocky Mountain National Park. They can estimate the time a given stand will persist without any new recruitment or the amount of recruitment necessary to maintain current stand density. They can manipulate the recruitment parameter in the model to reflect particular management decisions or environmental conditions. In the future, the scale of the model can be expanded to project the structure of the entire population of aspen stands in the Park. Collecting more recruitment data and calculating aspen survivorship values that take into account stand history such as elk browsing, conifer invasion, and elevation could further improve the model.

The three model scenarios presented in this paper demonstrated a wide range of possibilities for aspen stands within the Park. In the five stands, current stand density could be maintained if between 80 and 230 stems ha^{-1} reached 10 years of age every decade. This could be achieved with natural fire regimes, prescribed fire, insect outbreaks where conifers are invading aspen stands, mechanical stimulation of aspen

recruitment and, in areas of high elk impact, exclosures to protect the aspen recruitment. If no recruitment were to occur within the stands, no stand would persist as long as 100 years. The same is true of five aspen stands studied by Suzuki et al. (1999). If episodic pulses of recruitment continued to occur, stand densities would fluctuate an order of magnitude (between 10^1 and 10^2), yet no clone would disappear from the landscape.

It seems likely that aspen recruitment will be absent in only a handful of stands in and around the Park despite both external (e.g., elk browsing, fire suppression; Suzuki et al. 1999) and intraspecific (e.g., shade intolerance) factors. These aspen stands will become extinct by the turn of the next century and new stands need to be initiated. Stand initiation is most likely to be achieved through the reintroduction of fire to the landscape, in conjunction with suitable climate conditions and reduced elk impacts (Romme et al. 1995). Despite the loss of a few stands from lack of recruitment, the population of aspen stands can be maintained by both natural and human induced impacts.

CHAPTER 5: SYNTHESIS

Many general concepts of the structure and dynamics of quaking aspen stands did not seem to apply uniformly to aspen in the Front Range and the aspen population was more dynamic and variable than expected. The variability in aspen structure makes management decisions even more complicated than previously thought. However, certain generalization concerning the population in Rocky Mountain National Park could be made based on the research conducted in this study.

Life-history traits of quaking aspen accounted for many of the dynamics in aspen stands. Principally, the clonal nature of aspen allowed it to rapidly colonize recently disturbed areas with sprouts from the aspen's root matrix. This behavior explained the presence of most of the aspen on the landscape in the central Rocky Mountains. However, once aspen has established, other life-history traits came into play such as shade intolerance, a short life span for individual stems, and density-dependent mortality (see Chapter 3; this dissertation). These traits helped account for the conifer invasion found throughout aspen stands in Rocky Mountain National Park. However, life history traits were not the sole influencing factors on aspen dynamics.

External factors such as disturbance, climate, and elk browsing played a large role in the landscape-scale structure of aspen forests. I focused my research on the spatial influence of elk browsing on aspen forests in the Park. Elk browsing had a localized impact on aspen stands unlike fires, insect outbreaks, and climate that had widespread

impacts. In certain areas of the elk winter range, where approximately 3000 head of elk over-winter, the evidence of elk browsing was severe. However, it seemed that elk browsing had yet to effect stand dynamics such as basal area, density, or regeneration (see Chapter 2; this dissertation). Although I did not directly study the relationship between aspen and fire in the Park, the large number of aspen stands with conifer invasion suggested that 80 years of fire suppression has left its legacy in the aspen population. The reintroduction of forest fires in the Park would be one means to initiate new aspen stands.

The three research projects encompassed in this dissertation spanned broad spatial and temporal scales (Fig. 5.1). The description of the aspen population covered broad spatial scales, however it was a snapshot in time. A long-term aspen monitoring program within the Park could expand the temporal scale of this project. In contrast, the study of conifer invasion covered longer temporal scales (+100 years), yet was limited on a spatial scale due to the labor-intensive approach to the reconstruction. Repeating the methods used in this project on more aspen stands in the Park may improve the potential to generalize about conifer invasion and therefore increase the applicability of the results of this study. Finally, the age-structured model encompassed a long temporal scale, however it currently only projects the structure of one aspen stand at a time. Future model development could include the union of the age-structured model with a GIS of aspen stands. This new model would encompass both large spatial and temporal scales.

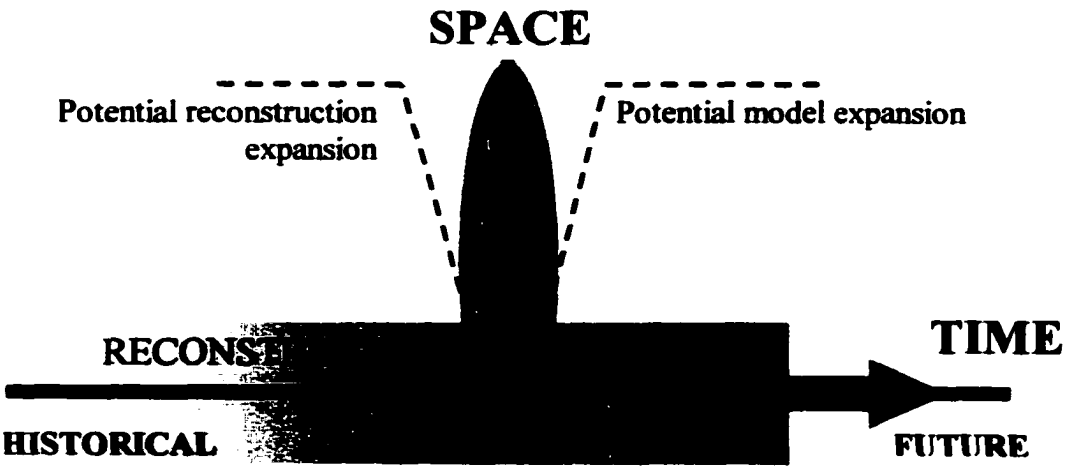

Figure 5.1. A schematic diagram representing the spatial and temporal scales of the research conducted in this dissertation. Shaded polygons represent the scale of data that I collected. The black dashed lines represent potential future expansions in the scale of these research projects. Ideally, the stand reconstruction and the age-structured model could both be expanded to broader spatial scales.

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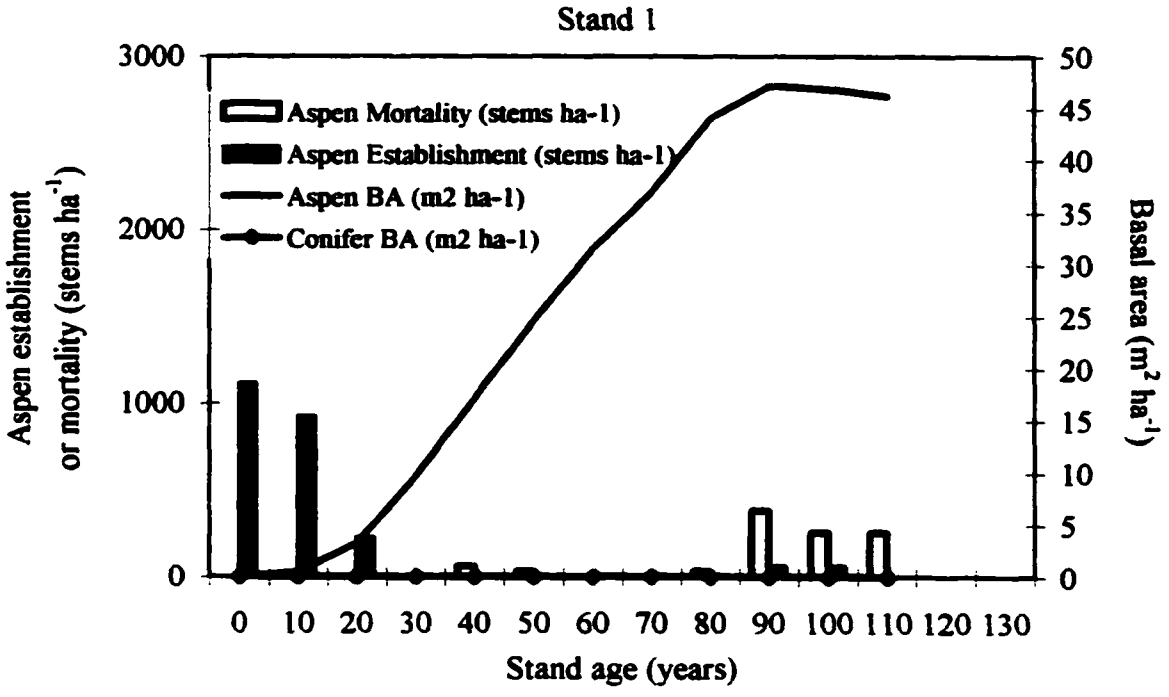
APPENDIX A

Reconstructed establishment, mortality, and basal area for quaking aspen (*Populus tremuloides*) and basal area for conifer species in five stands in Rocky Mountain National Park, Colorado. Establishment and mortality data are presented as 10-year sums and basal area as a 10-year average.



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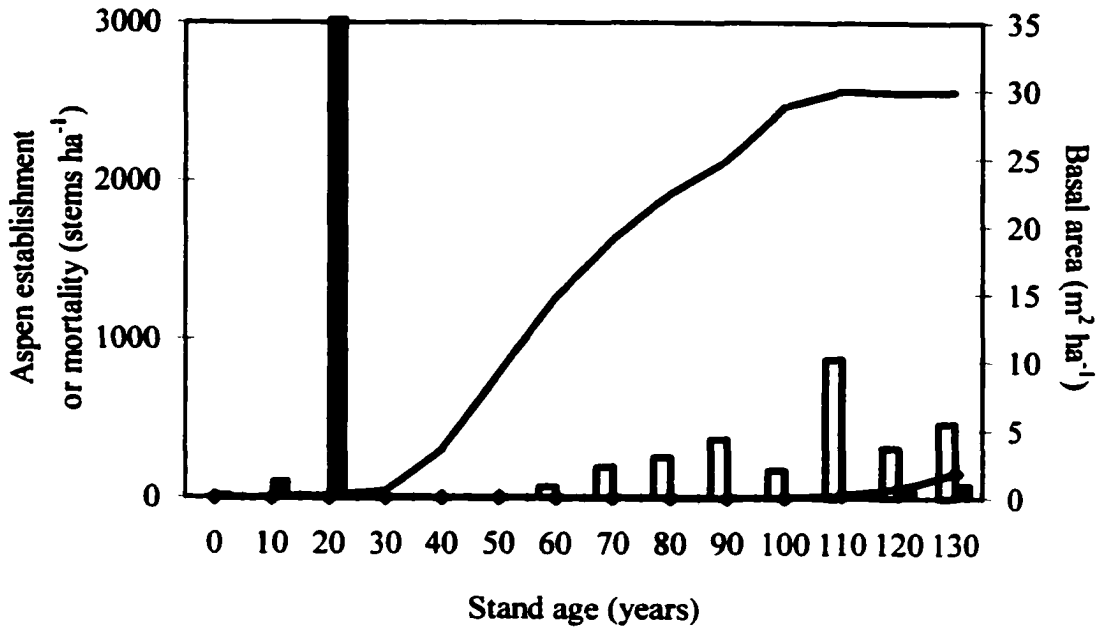

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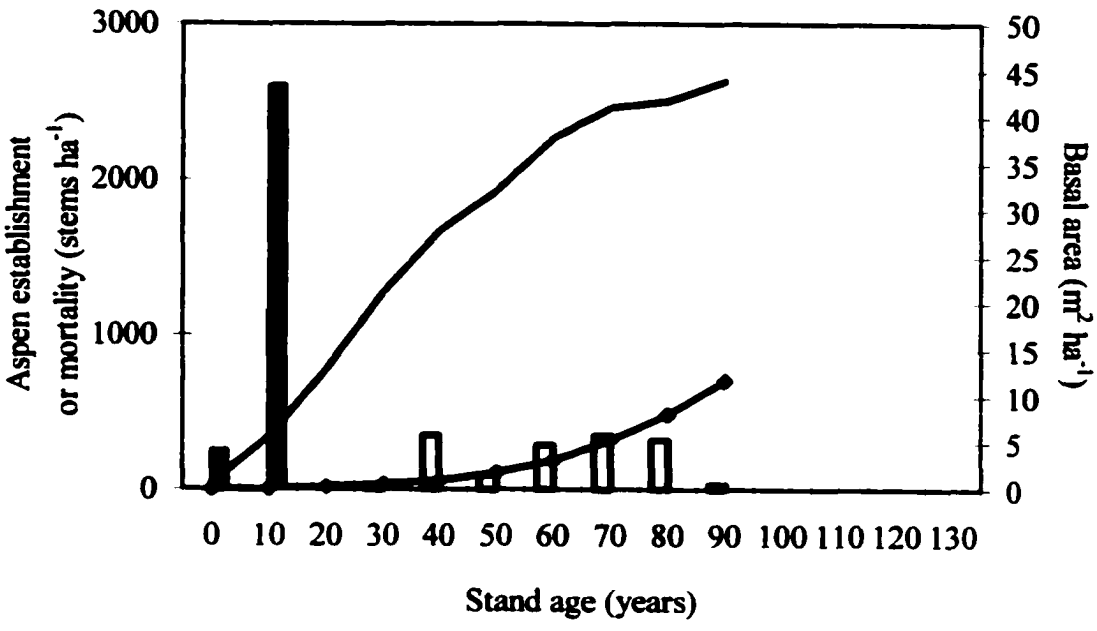

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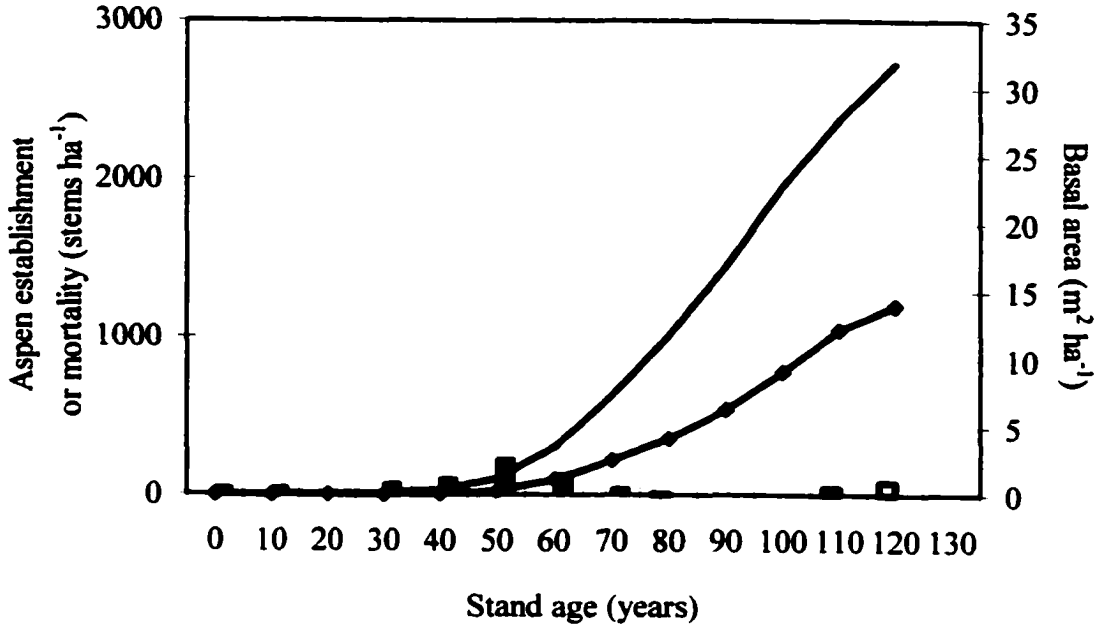

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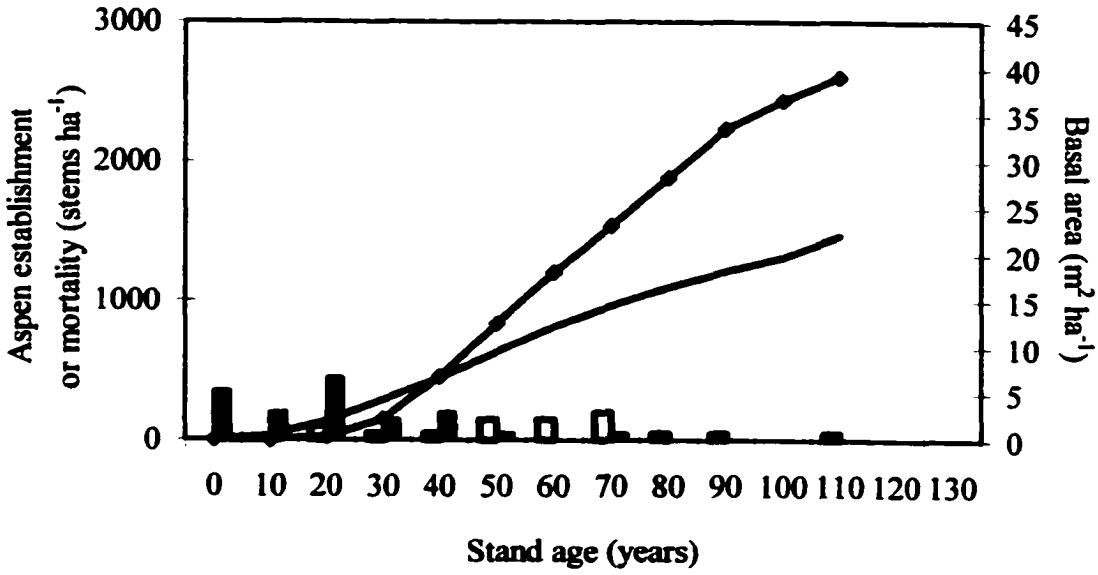

APPENDIX B

Reconstructed conifer invasion by species for two aspen stands with conifer invasion in Rocky Mountain National Park, Colorado. Conifer invasion is represented by basal area over time.