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Running head: Variability of aspen in Rocky Mountain NP

Title: Aspen structure and variability in Rocky Mountain National Park, Colorado, USA.

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ABSTRACT

Elk, fire, and climate have influenced aspen populations in the Rocky Mountains, but mostly subjective studies have characterized these factors. A broad-scale perspective may shed new light on the status of aspen in the region. We collected field measurements of aspen (*Populus tremuloides* Michx.) patches encountered within 36 randomly located belt transects in 340 km² of Rocky Mountain National Park, Colorado, to quantify the aspen population. Aspen covered 5.6% of the area in the transects, much more than expected based on previously collected remotely sensed data. 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 elk browsing or had conifer species mixed with the aspen stems. No significant difference occurred in aspen basal area, density, regeneration, browsing of regeneration, and patch size, between areas of concentrated elk use (elk winter range) and areas of dispersed elk use (elk summer range). Two-thirds of the aspen patches were mixed with conifer species. We concluded that the population of aspen in our study area is highly variable in structure and that, at a landscape-scale, evidence of elk browsing is widespread but evidence of aspen decline is not.

Key words: Aspen, belt transects, conifer invasion, elk browsing, *Populus tremuloides*.

1. 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 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, Hessel and Graumlich 2002). 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 (Hessl 2002). 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, Hessl 2002). They cite lack of aspen recruitment, damage to existing aspen stems, absence of new stand establishment, and extensive conifer invasion as symptoms of aspen decline. From another point of view, the dynamic characteristics of aspen may allow it to persist through diverse conditions (Parker and Parker 1983; Romme et al. 2001). Indeed, it may be the diversity of aspen's life history and structure that has in part caused the disagreement concerning the status of the species.

1.1 Structure and function of aspen patches

Aspen communities exist 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 seen above ground 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).

Superimposed over the inherent variability in aspen stand structure are differential impacts of 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 concentrated in small areas of limited

forage (DeByle 1985). Browsing in the elk summer range has less impact as the herds are dispersed over larger areas in a season with higher forage production. Ecologists have suggested that aspen stands heavily impacted by elk have lower stem basal area, density, and number of sprouts than those with little elk browsing (DeByle 1985; White et al. 1998).

Aspen forests are both a rare and important habitat type for many floral and faunal species of the central Rocky Mountains (DeByle 1985; Turchi et al. 1995; Stohlgren et al. 1997a and 1999; Chong et al. 2001), they are the only widely distributed deciduous forest type of the region (Peet 2000), 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.

1.2 Study objectives

Pessimistic predictions for the future of aspen forests in Rocky Mountain National Park have been based on data collected from a hand-picked or small sample of stands (e.g., Packard 1942; Olmsted 1979, 1997; Baker et al. 1997). Packard (1942) proposed over 50 years ago that it was unlikely that any aspen would survive in a low-elevation area of concentrated elk use. He attributed the observed high levels of aspen mortality and the lack of aspen regeneration to elk browsing. Interestingly, the same aspen stand described by Packard still existed in 1999. Two more recent studies of aspen in the Park's elk winter range predicted the probable disappearance of aspen in the elk winter range due lack of aspen regeneration from elk herbivory (Olmsted 1979, 1999). Baker et al. (1997) found aspen stands in the elk winter range of the Park to be declining because aspen was not regenerating during periods of high elk abundances. These previous studies used sampling strategies that either drew from a limited number of stands in Estes Valley (Fig. 1), a small area of the Park where elk concentrations are considered to be the highest, or they used a

sampling strategy that biased the aspen regeneration data towards older trees (Hessl and Graumlich 2002). A study of aspen regeneration in 32 aspen stands located throughout the Park's elk winter range found that 20% of aspen stands in Estes Valley had regeneration in the past 30 years, while 45% of aspen stands in other areas of the winter range experienced regeneration in the same period (Suzuki et al. 1999). The authors concluded that localized areas of aspen in the winter range may be declining, but they found no evidence of decline at a landscape-scale (Suzuki et al. 1999).

A broader-scale 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 large-scale data. 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). However, the minimum mapping unit of these data limit their ability to detect the diverse forms of aspen patches (Stohlgren et al. 1997b).

For this study, we used randomly located belt transects to describe the population of aspen in 340 km² of Rocky Mountain National Park, Colorado. This method maximized the area of the Park we could survey and the grain of the spatial resolution of the data. The survey encompassed over 1/3 of the total area of the Park and over half the forested area within the Park. We collected field measurements of aspen 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 by comparing measurements between areas of concentrated and dispersed elk browsing; (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. In this study the term aspen patch is used to describe any forest area

that has aspen stems present, with no minimum or maximum size restrictions. As will be described in later sections, aspen patches in this study ranged from single sub-canopy stems to aspen stands greater than several hectares in size.

2. METHODS

2.1 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°30', 40°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* var. *latifolia*, *Pseudotsuga menziesii*, *Abies lasiocarpa*, *Picea engelmannii*), spruce-fir forests (*A. lasiocarpa*, *Picea engelmannii*), and quaking aspen (*Populus tremuloides*), as well as wet and dry meadows, riparian corridors, and alpine tundra (Peet 2000).

2.2 Field methods

The survey was conducted between June 1998 and October 1999. We 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. Forested regions defined on the aerial photographs included all areas that contained a visible tree canopy layer that ranged from open to closed. The

forested regions included conifer forests, aspen forests, riparian corridors, and woodlands at meadow edges. Of the 40 selected points, any point that fell within 1000 m of a previously established point was eliminated.

Points were located in the field using United States Geologic Survey (USGS) 1:24,000 topographic maps and a hand held Global Positioning System. We 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 we encountered topographic barriers such a cliffs, lakes, or breaks in forest cover greater than 50 m, we 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 with the belt transects. Aspen patches were defined as discrete units when they were separated from other aspen stems by more than 25 m. We 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 that fell 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. The topographic position of rocky slope described areas of gentle slopes that are littered by many large rocks (e.g. >1 m diameter), which may effect the ability of vegetation to establish. 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.

A 25 m² (5 m x 5 m) plot was located at the center of each aspen patch encountered (which could be outside of the belt transect) to quantify the structure of the patch. Several aspen patches were large and complex in shape and structure and a single 25m² plot was not sufficient to represent the patch. In these cases, we sampled as many as six plots evenly distributed throughout the patch depending on the heterogeneity of aspen structure within the patch. Plots could fall outside the perimeter of the belt transect. Within each plot we 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 we estimated the percent of the stem that was covered with such scars. The number of stems <1.5 m tall was counted to represent “aspen regeneration”, and the number of stems that showed evidence of elk browsing was recorded. Chronically browsed aspen regeneration often sprout many stems in tight clumps from a single root node. Each clump was counted 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, we 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. This percentage was used 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.

2.3 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 (usually 1000 m) 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. We 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 a possible pattern in aspen patch location. Aspen patch characteristics such as patch area, aspect, and topographic position describe entire aspen patches while percent aspen cover was based solely on the area of aspen patches that fell within the 50m-wide transect.

Data from the 25 m² 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 a weighted mean for patches with more than one plot was calculated. 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.). We 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, percent of regeneration browsed, 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.

3. 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. 1).

We surveyed 238 hectares within the belt transects and encountered 123 aspen patches. Aspen 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). 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 of the high elevation patches occurring on the west side (Fig. 2).

Aspen patches occurred most frequently on gentle and rocky slopes, however patches were found in all topographic positions (Fig. 3). Patches were evenly distributed across all aspects. Patches were found 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 $< 1 \text{ m}^2$ to $>1 \text{ ha}$ (Fig. 4a). Stands $>1 \text{ ha}$ were complex in shape and were difficult to accurately measure with the design used in this study. Frequency of all patch areas and those between 1 m^2 and 200 m^2 were plotted. Patch areas were distributed throughout this range, with over 12% of all patches having an area $<10 \text{ m}^2$ (Fig. 4b). Mean patch area peaked at 2900 m and 3000 m elevation (Fig. 5).

Conifers mixed in the aspen canopy and understory were 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. 6). The amount of aspen in the canopy 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. 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. 8). Aspen was more commonly found on gentle slopes in the summer range (36% of patches) than in the winter range (23%) (Fig. 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. 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% of the forested area. The GIS calculated an aspen cover of 6.4% for the same area.

4. DISCUSSION

4.1 The structure and variability of aspen in Rocky Mountain National Park

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, 1997; Betters and Woods 1981; Parker and Parker 1983; Mueggler 1989; Turchi et al. 1995). 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 (Hessl 2002), however they can be appropriate for describing particular types of stands. Two recent studies of aspen regeneration presented data from randomly selected stands chosen to represent large study areas and reported results that conflicted with previous subjective studies (Suzuki et al. 1999; Barnett and Stohlgren 2001). This study was another approach to the quantification of the range of characteristics of the aspen population as a whole.

The results of the ground survey emphasized the futility in describing a “typical” aspen patch for the central Rocky Mountains (Figs. 2-4). For example, we encountered aspen at tree line

in krummholtz form, as large patches ($> \frac{1}{4}$ ha) persisting on rocky outcrops, and on gentle topography such as meadow edges and mild slopes. Aspen ranged from a single, isolated stem to patches up to several hectares in size. Most likely, the high quality habitat (e.g. high floral and faunal diversity) documented in many aspen stands occurs in the 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, such a patch may become one of the high-quality habitat stands. Though we 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.

Despite the variability in aspen patch structure, some general patterns emerged. Mean patch size (Fig. 5) and percent aspen cover (Fig. 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 (Veblen 2000, Veblen et al. 2000) due to the productivity and fuel loadings of the systems (Mutch 1970; Wright and Bailey 1982). This type of stand-replacing 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 (< 2650 m), percent aspen cover was above average (Fig. 2) and mean patch size

was small ($<1000 \text{ m}^2$; Fig. 5). In other words, many smaller aspen patches are distributed across the landscape in these areas. Throughout the elevation range, the majority of aspen patches were located on gentle topography such as slopes and drainage basins (Fig. 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 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 $50 \text{ m}^2 \text{ ha}^{-1}$ (Jones et al. 1985), however we 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 1). This is likely due to our inclusion of aspen patches mixed with conifer species. 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.

4.2 Elk browsing and conifers

Despite the variability in aspen patch structure and location, external factors such as conifer mixing and elk browsing impacted aspen patches throughout the study area. All but one of the 123 aspen patches we encountered were mixed with conifers, had 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, 1997; Romme et al. 1995; Wagner et al. 1995; Baker et al. 1997; Berry et al. 1997; White et al. 1998; Ripple and Larsen 2000; Barnett and Stohlgren 2001, Romme et al. 2001, Hessel and Graumlich 2002). 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; Hessel and Graumlich 2002; 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 some highly visible areas (Parker 1942; Olmsted 1979, 1999; Baker et al. 1997) 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, although evidence of elk browsing was found in over 70% of the stands. We expected to see differences in measures of aspen vigor such as regeneration, browsing of 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). Over 70% of aspen regeneration showed evidence of elk browsing in the summer and winter ranges. These data could indicate that aspen regeneration has suffering throughout the Park due to elk browsing, but average regeneration in both ranges was over 20,000 stems ha^{-1} (Fig. 8). Therefore, approximately 5000 stems ha^{-1} escape elk browsing in aspen patches in both ranges. Percent bark browse showed the only significant difference between

the two ranges (Fig. 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 patch characteristics may be due to confounding factors other than elk range such as elevation, microsite condition, and stand history.

Few data exist on the extent to which aspen mixes with conifer species in the Rocky Mountains, despite the frequency of mixed-species forests (but see Shepperd et al. 2001). Mixed stands of aspen and conifers can result from co-establishment of aspen and conifers or the invasion of aspen by conifers. Bartos and Campbell (1998) estimated that aspen patches are threatened when aspen canopy cover is less than 40%. We 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). Fire regimes of forests in the central Rocky Mountains have changed drastically over the past century (Brown et al. 1999, Kaufmann et al. 2000, Veblen 2000, Veblen et al 2000, Donnegan et al. 2001). 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 process can contribute to an aspen population such as the one in Rocky Mountain National Park that consists of many aspen patches mixed with conifers and fewer without conifers. Unlike elk browsing, the amount of conifers mixed into aspen patches seems to be related to patterns in aspen

basal area and density (Fig. 7). Aspen patches with the greatest basal area and density have 100% aspen in their canopies. Further research is needed to determine if conifers are affecting aspen basal area or whether conifers tend to occur in areas of lower aspen basal area and density. Additionally, further research needs to be conducted to determine how many of the mixed-species patches are the result of species co-establishment or conifer invasion of aspen patches.

4.3 A comparison of two methods

We found almost three times more aspen cover (5.6%) in the transect area than values cited in previous studies (2% of the forested area) 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.

Most of the parameters we 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, we 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 m², 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 m². 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 may be unidentified by remotely sensed data with a 10 m² 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% lower estimation 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 number of conifers, and the challenge of defining the perimeter of an aspen patch from aerial photographs.

5. CONCLUSIONS

Aspen patches in the central portion of Rocky Mountain National Park are highly variable across the landscape. The amount of aspen in forested areas of the Park (5.6%) is almost three times greater than the 2% cited by previous research. Aspen can be found at all elevations below upper timberline and topographic positions and ranged in patch size from <1 m to > 1 ha. All but one of 123 aspen patches showed evidence of elk browsing or were mixed with conifer species. Aspen's tolerance for diverse conditions may allow it to persist through highly variable climate, disturbance, and browsing regimes. Most studies have not considered small, isolated aspen patches or aspen patches mixed with conifers that we documented in this study. It may be these types of aspen patches that guarantee the persistence of aspen in the central Rocky Mountains.

The majority of aspen stands in our study area showed evidence of elk browsing, however our data indicate that elk browsing has not (yet?) brought about a decline in aspen vigor throughout the elk winter range. Based on over 50 years of reports of declining aspen in the elk winter range,

we expected to measure decreased aspen vigor in the elk winter range due to decades of increased aspen mortality and decreased aspen regeneration. Measures of aspen vigor (such as basal area, density, and regeneration) for patches in the elk summer and winter ranges showed no significant differences and both ranges showed basal area and density values consistent with other aspen stands throughout the Rocky Mountains. A study of aspen regeneration in the elk winter range of Rocky Mountain National Park found that 20-45% of patches have aspen regeneration during the past 30 years (Suzuki et al. 1999). Regeneration and vigor in aspen patches in the elk winter range of Rocky Mountain National Park indicate that aspen may be declining in a limited area (e.g. Estes Valley as documented by Olmsted 1979, 1999; Baker et al. 1997). Romme et al. (2001) suggested that the long-term persistence of aspen may be threatened in areas of marginal habitat for aspen that have heavy elk browsing. These conditions are met in only a small area of Rocky Mountain National Park. At a landscape-scale, evidence of browsing is wide-spread but evidence of aspen decline is not.

The large percent of aspen stands that are mixed with conifer species in the Park (over 2/3 of the stands we sampled) indicates that further research needs to be done on the effects of conifers on aspen structure. The timing, extent, and effects of conifer invasion in aspen patches are little understood. The high frequency of mixed-species stands may be a legacy of 80 years of fire suppression in Rocky Mountain National Park.

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

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

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

FIGURES

Figure 1. Map of study area within Rocky Mountain National Park, Colorado. Grey box represents 340 km² 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). Grey circle represents general area of Estes Valley.

Figure 2. Distribution of percent aspen cover across an elevation gradient in Rocky Mountain National Park. 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 all aspen throughout the Park was 5.6% (horizontal line).

Figure 3. Topographic positions of aspen patches encountered within the transects in Rocky Mountain National Park. Forty-two of the patches were located in the elk winter range and 67 in the summer range.

Figure 4. Aspen patch area (m²) of the 123 patches encountered with the belt transects in Rocky Mountain National Park. 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 m² (a), so the distribution of patch areas between 1 and 200 m² was plotted (b).

Figure 5. Mean aspen patch size (m²) across an elevation gradient in Rocky Mountain National Park. Mean patch size between 2900 m and 3100 m elevation may be underestimated because at those elevations we encountered aspen patches larger than one hectare in area.

Figure 6. Percent aspen in the canopy of forest patches that were identified as aspen within the belt transects in Rocky Mountain National Park. Conifer species occupying the remaining percentages

of the canopy were: *Picea engelmannii*, *Abies lasiocarpa*, *Pinus contorta*, and *Pseudotsuga menziesii*.

Figure 7. Correlations of percent aspen in the canopy with aspen basal area (BA) and density (n=61) in aspen patches in Rocky Mountain National Park.

Figure 8. Mean and standard errors for aspen patch characteristics in the elk winter (black) and summer (striped) ranges in Rocky Mountain National Park. 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 ($P = 0.65$), percent browse of regeneration ($P = 0.26$), density of aspen stems ($P = 0.44$), and area of aspen patches ($P = 0.62$).

Figure 9. Percent bark browse of aspen patches encountered in the belt transects in Rocky Mountain National Park. Mean percent bark browse was calculated per patch by averaging values from each aspen stem measured within the 25 m² plots sampled within each aspen patch. If the patch was smaller than 25 m², all stems within the patch were measured. Fifty percent of patches had an average of over 70% bark browse. Only 7 of the 123 patches showed no bark browse.

Figure 1

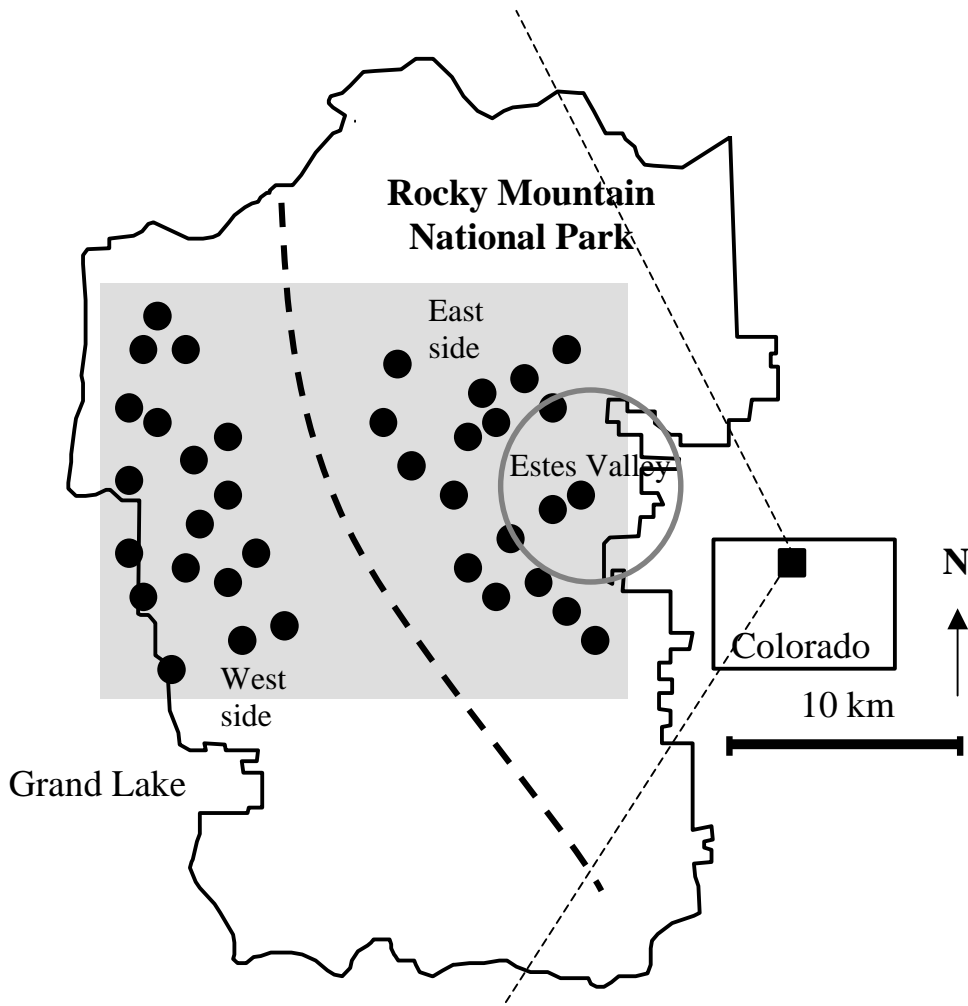


Figure 2

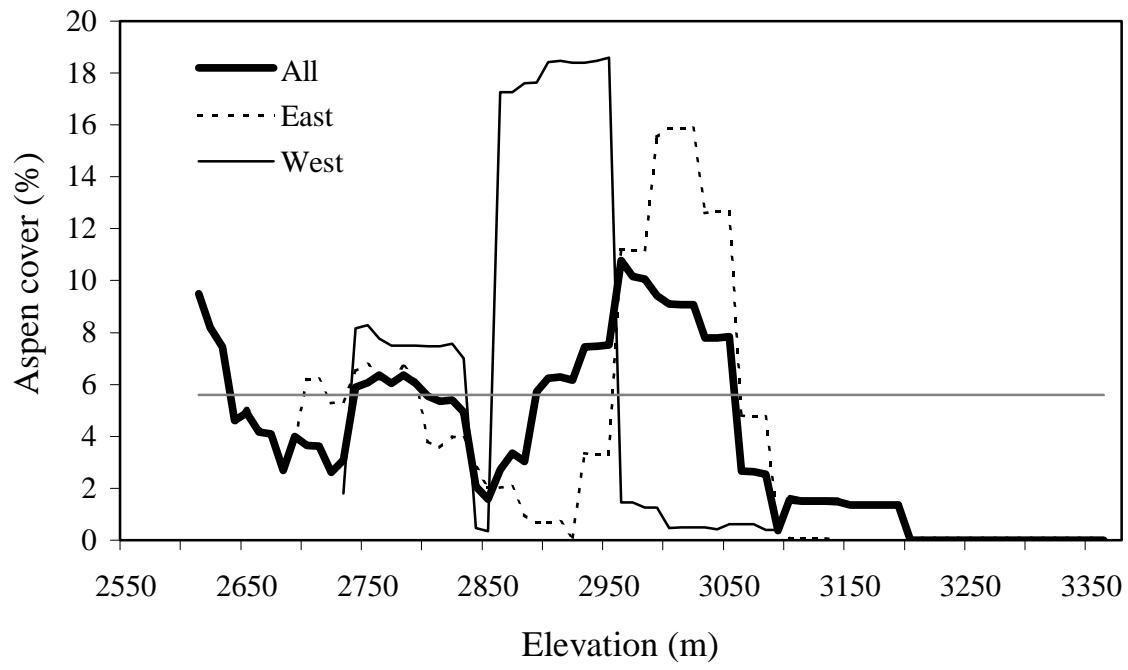


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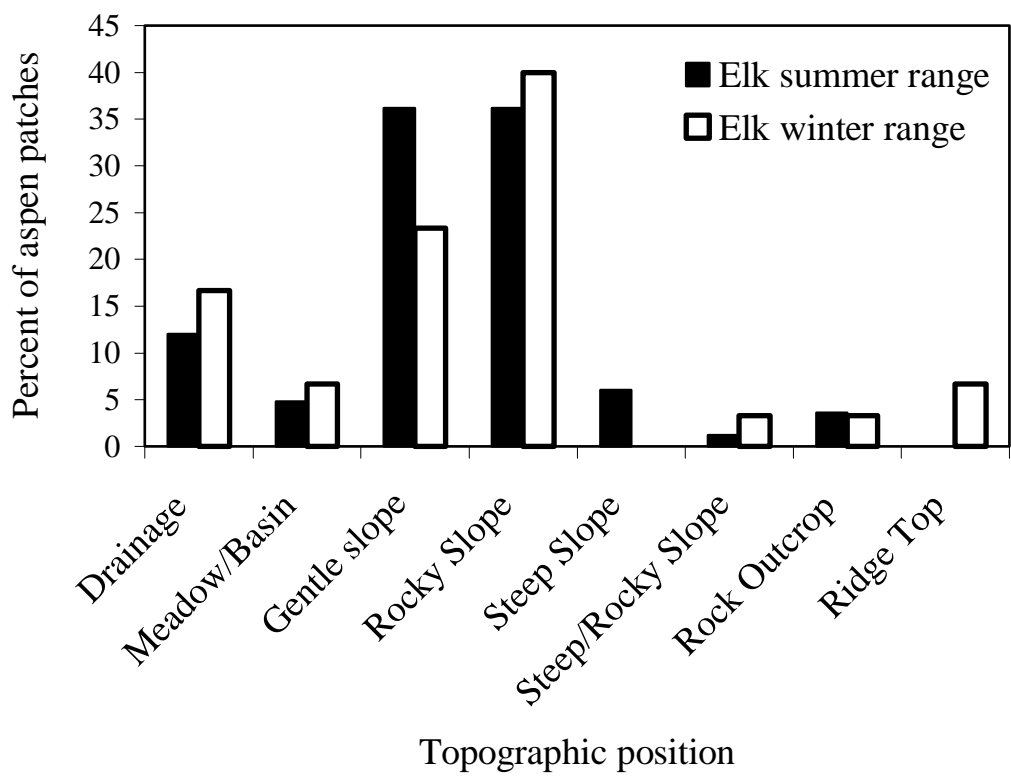


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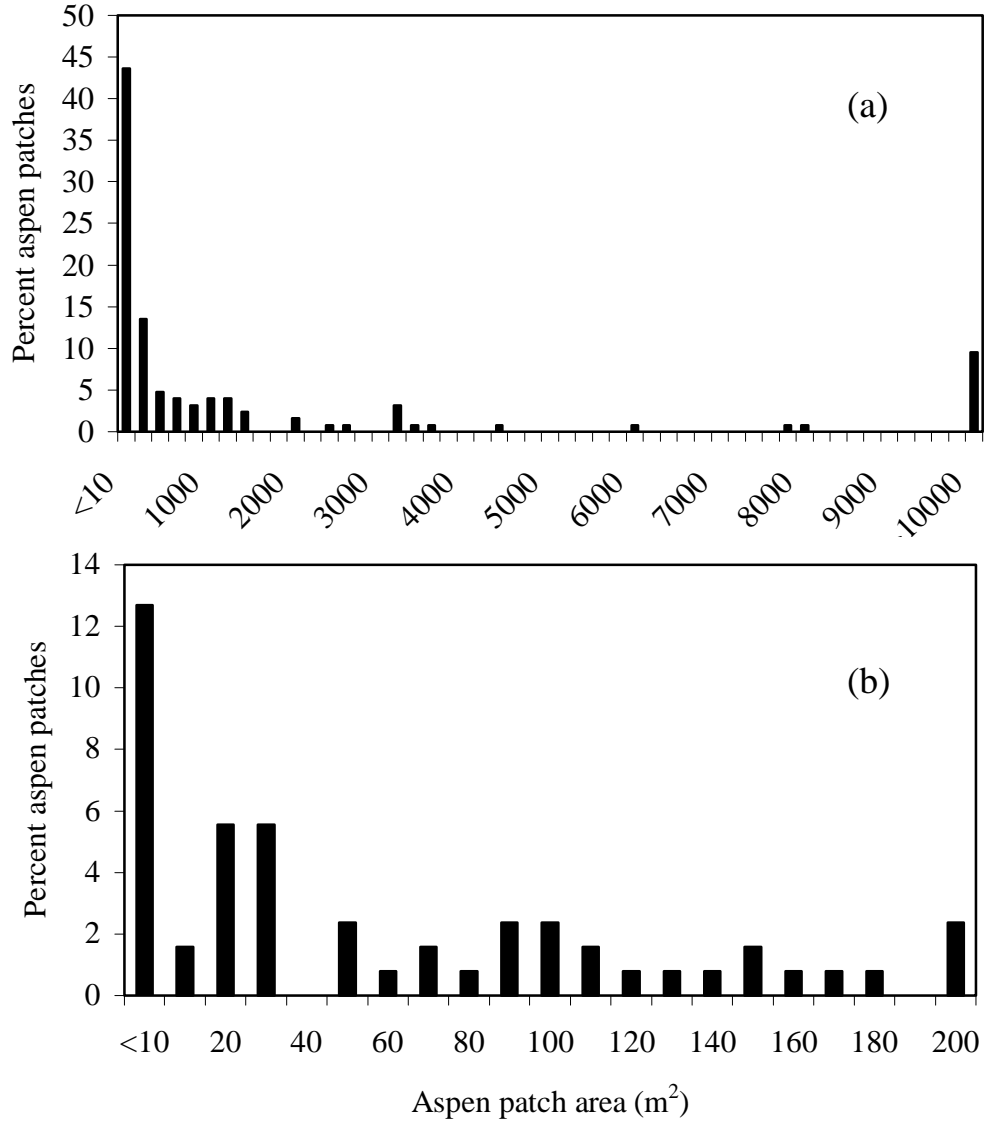


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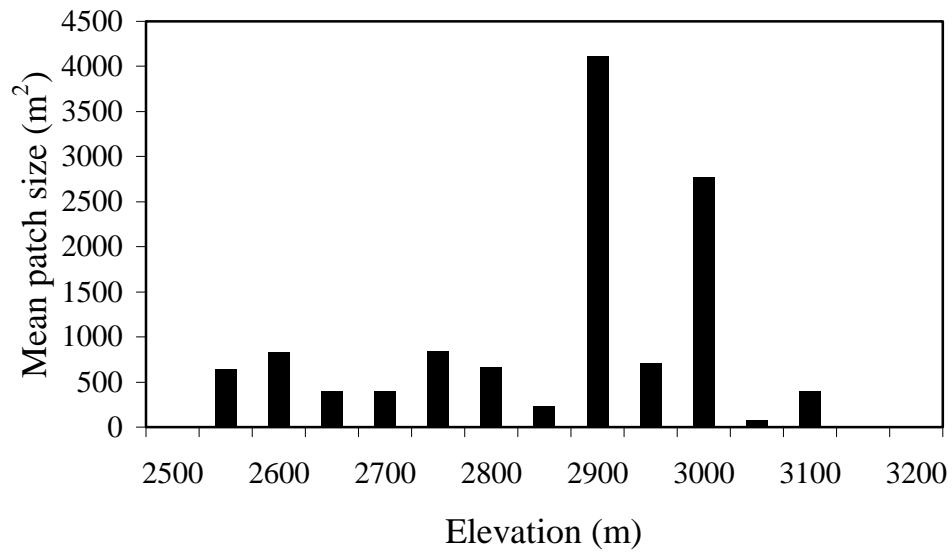


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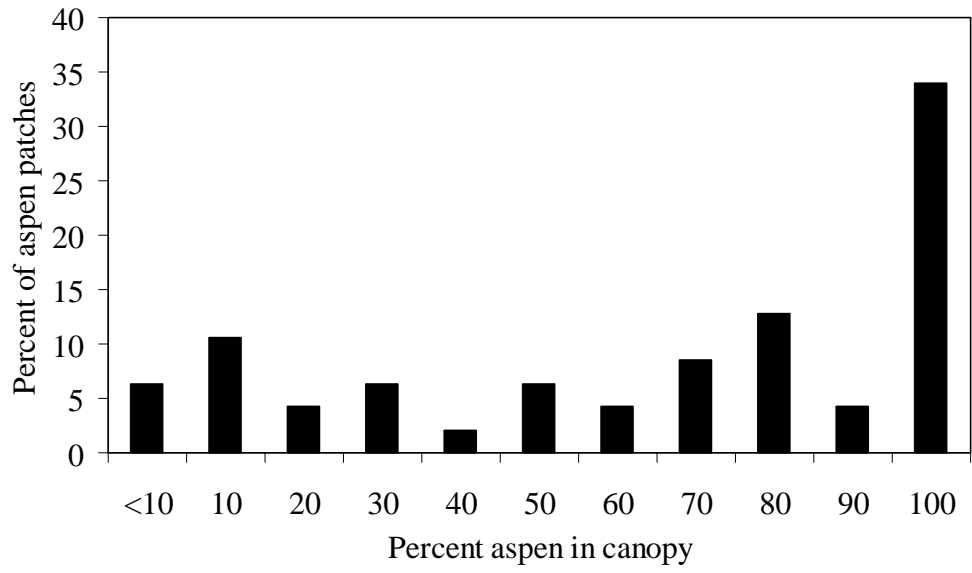


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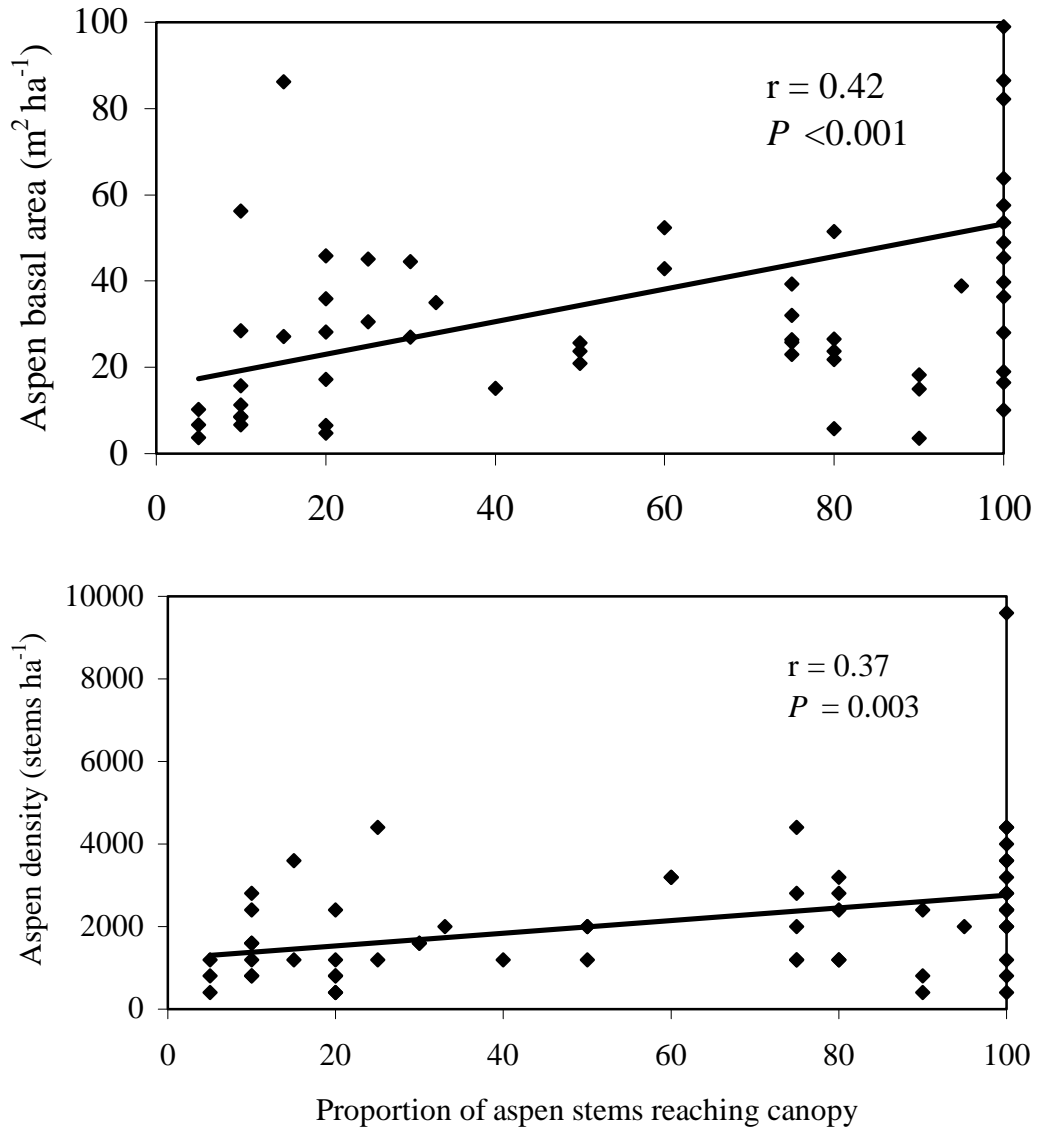


Figure 8

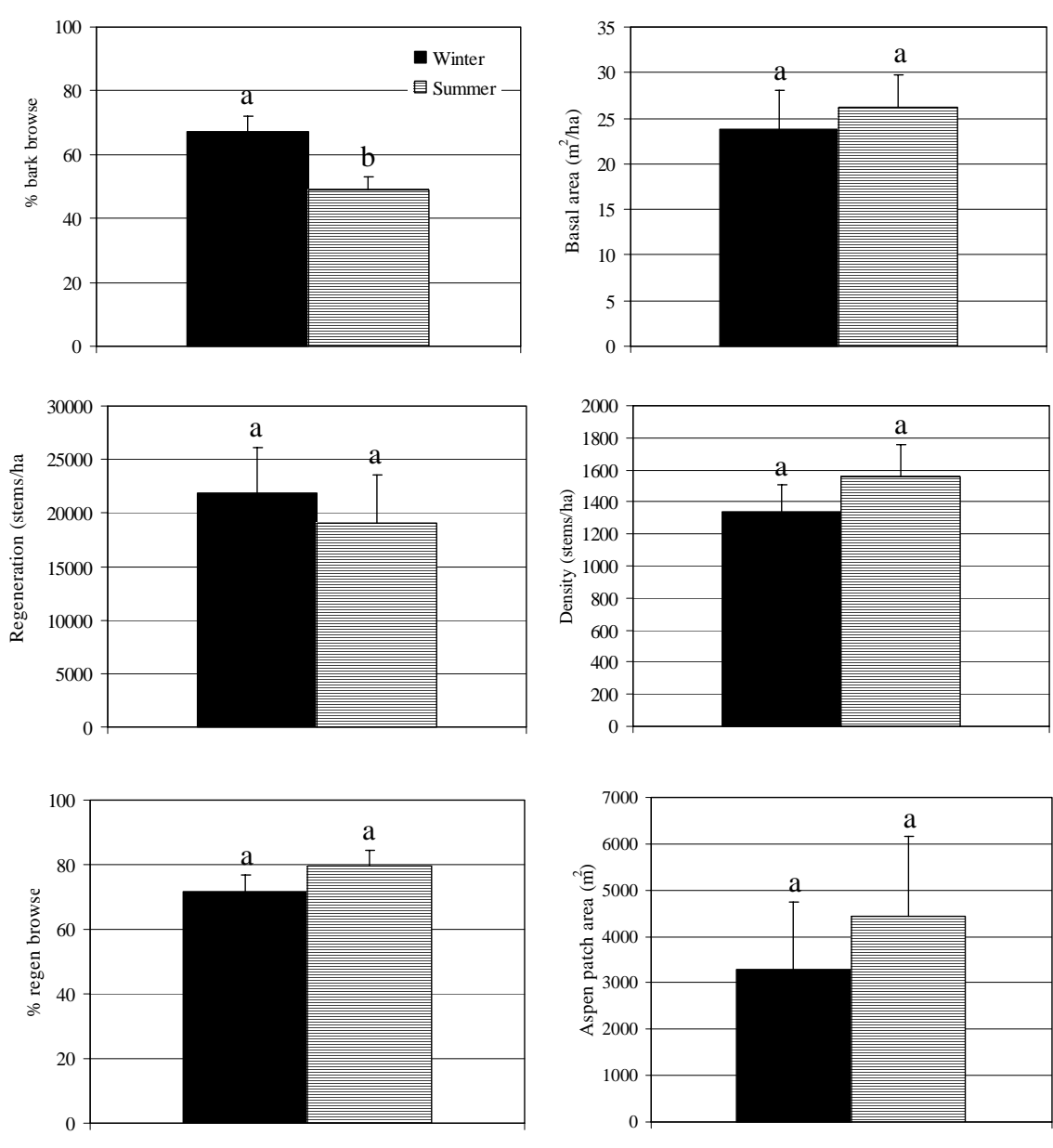


Figure 9

