Age distribution of aspen in Rocky Mountain National Park, USA

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Abstract

The age structure of aspen in Rocky Mountain National Park was characterized to determine if the number of aspen established in recent decades was substantially lower than would be expected from long-term trends. At lower elevations on the eastside of the Park, aspen density averaged 1250 trees/km², compared with 550 trees/km² at higher elevations and on the westside. Most aspen in the Park were relatively young, with trees less than 80 years old accounting for 90% of aspen trees and 50% of aspen basal area. The number of trees in each decadal age class increased exponentially from 1855 through 1965, with no decade showing significantly higher or lower aspen numbers than expected from the long-term trend. The number of aspen dating to 1975–1995 at lower elevations on the eastside fell 80–95% below the level expected from the long-term trend. No decline was evident in the rest of the Park. A variety of factors influences the rates of aspen mortality and recruitment, including major disturbances, climate patterns, conifer in-growth, and browsing. Severe browsing by elk appears to be the main factor accounting for low aspen numbers at low elevations on the eastside.

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1. Introduction

The forests of the Rocky Mountains are dominated by conifer species, with the notable exception of aspen (*Populus tremuloides* Michx.; Peet, 2000). Aspen forests contribute disproportionately to the diversity of plant and animal species in these landscapes, frequently containing twice the number of species per unit area as found in conifer forests (DeByle, 1985; Turchi et al., 1995; Stohlgren et al., 1997, 1999; Chong et al., 2001).

The establishment of new aspen stands in the central Rocky Mountains generally follows major disturbances, particularly forest fires, with new stems sprouting from surviving root systems and with rare establishment of new seedlings. The development of new stands then depends on a host of factors, particularly the level of browsing by wildlife and livestock, and the extent of conifer establishment and competition. A reduction in landscape coverage of aspen could result from a reduction in stand-replacing fires, as well as increases in browsing or conifer competition. All of these factors have operated throughout the long-term history of forests in the Rocky Mountains, but their influence on aspen stands may have changed in the 20th century as a result of fewer major fires, and increased browsing that may have resulted from extirpation of predators and introduction of exotic livestock.

Changes in the extent of aspen in Rocky Mountain National Park would have major implications for plant and animal species, as well as for tourism and overall goals of ecosystem protection. Does the Park still have the amount of aspen that would have been typical prior to the mid-19th century? Previous studies have documented low recruitment of new stems in portions of the Park with very high elk browsing (Olmsted, 1979, 1997; Baker et al., 1997), but higher recruitment across the rest of the Park. For example, only 20% of aspen stands in heavily browsed, low elevation areas of the Park contained stems younger than 30-year-old, compared with about 75% of aspen stands at higher elevations and in the surrounding national forest land (Suzuki et al., 1999). An aspen stand with a young cohort of stems may still have fewer stems than would develop in the absence of unusually intense browsing.

We were particularly interested in determining whether a doubling of elk population (Lubow et al., 2002) following adoption of a predation-free “natural regulation policy” in the 1960s led to a substantial decline in numbers of young...
aspen trees. Controlled experiments with browsing exclosures have clearly demonstrated that wildlife can reduce aspen regeneration, and we know that most aspen stands have not successfully regenerated since the 1960s in areas with the highest elk use (Suzuki et al., 1999). However, a longer-term context is needed to know if recent patterns in aspen recruitment are unusual relative to long-term trends, or if periodic increases and decreases in aspen recruitment have been common in the past. Perhaps aspen recruitment was exceptionally high in the late 1800s and early 1900s, and a reduction in recruitment in the late 20th century might reflect a long-term legacy of an earlier pattern. Alternatively, aspen recruitment at a landscape scale might be fairly consistent, with little influence of historic changes in land use or legacies of previous recruitment success.

We determined the age structure of aspen stems across the Park, allowing us to evaluate whether any cohort was represented by substantially more or fewer stems than would be expected based on the long-term pattern. A period showing higher-than-expected numbers of aspen might indicate a period of high fire or low elk populations, whereas periods with fewer-than-expected aspen might indicate few fires, high elk populations, or extensive conifer in-growth (Kaye et al., 2003, 2005). If aspen recruitment was consistent across the decades prior to the 1960s, then the unique event of the very high elk populations may be driving unique changes in aspen numbers.

2. Methods

The study area was the entire Rocky Mountain National Park from the lowest elevations (2500 m) to the upper elevation range of aspen (3200 m; Kaye et al., 2003). Average annual minimum and maximum temperatures at low elevation near Estes Park, Colorado (105°30’W, 40°24’N) at 2400 m elevation are −1.5 and 14.0 °C. Growing season (May–October) temperatures average 4.0–21.0 °C, with an average of 370 mm year−1 precipitation (http://cdo.ncdc.noaa.gov/). Forests at low elevations are typically dominated by ponderosa pine (Pinus ponderosa Doug. ex Laws.), shifting with increasing elevation to mixed conifer (ponderosa pine, Douglas-fir) (Pseudotsuga menziesii (Mirb.) Franco), lodgepole pine (Pinus contorta Dougl.) to Engelmann spruce (Picea engelmannii Parry ex Engelm) and subalpine fir (Abies lasiocarpa Hook. Nutt.) forests. Aspen trees occur throughout this elevation range, with greatest numbers at middle elevations (near 2800–3000 m; Kaye et al., 2003).

Based on previous work, we expected aspen age structure might differ between the low-elevation (<2800 m) winter range of elk on the eastside of the Park and the rest of the Park. A 1 km × 1 km grid was established for the entire Park, and 150 grid points were chosen at random for sampling (Fig. 1). Eight of these chosen grid points fell in the low-elevation, eastside area that provides winter range for large numbers of elk. An additional 49 grid points were chosen at random from a 0.5 km × 0.5 km grid within the low-elevation, eastside area, giving total sample sizes of 57 for low-elevation, eastside, and 142 for the rest of the Park. Most of these random plots had no aspen stems, so the number of plots containing at least one prism-counted aspen was 22 for the low-elevation eastside and 24 for the rest of the Park.

Each chosen grid point was visited; if no aspen were present in the vicinity, no measurements were taken. If at least some aspen were present, a plot was established with a series of 12 prism points in a triangle (at 50-m intervals; Fig. 2). Aspen stems were tallied with a 1.15 m2/ha basal area factor prism, and each aspen was cored to determine age at 1.4 m height. Our focus was on the date when aspen stems would begin to exceed the major browsing height by elk. The basal area of conifers was also tallied in each plot, with a 4.59 m2/ha basal area factor prism. Ages of conifers were not examined. Tree core dates were determined by standard dendrochronology techniques; about 2/3 of the cores could be cross-dated with confidence, and cross-dating ages were usually within 3 years of ring-count ages. We expect that aspen ages are accurate to within 0–3 years.

Typical prism cruises estimate tree size distributions by dividing the basal area factor of the prism by the basal area of each tree, and averaging across prism sample points. We converted this diameter distribution to an estimated age distribution by assuming each tree’s age represented a cohort (of the calculated number) of trees of the same age (Binkley et al., 2006). For example, a 25-cm tree counted with a 1.15 m2/ha factor prism would have a basal area of 490 cm2, and represent 23.4 trees of that size. If the age of the tree were 133 years, we would include 23.4 trees with an age of 133 years in the tally. The number of trees were summed across the entire area (low-elevation, eastside or the rest of the Park), and divided by the number of prism points to estimate the number of aspen trees in each 10-year age class. The number of stems in each decadal cohort was the product of 20–70 known core ages, extrapolated via the prism’s basal area factor.

We fit a linear trend to the logarithm of aspen numbers per decade from 1860 to 1960 (including years from 1855 to 1964). Any decade (including the three decades after the calibration period) that deviated from the line by more than two standard errors was defined as unusual.

The value of this prism-based approach to estimating age structure of the aspen population may be limited by two major assumptions. The processes leading to the death and recruitment of aspen stems would need to be generally consistent over the time period examined, as would be expected in a classic balanced, uneven-aged forest. If patterns of tree mortality and recruitment varied too greatly across decades, then patterns across many decades would be too noisy to detect decades with unusual numbers of aspen stems. The prism-based approach to determining the number of trees in each age class assumes that tree ages are sufficiently related to tree diameter to produce a reasonable representation of the age distribution across the landscape. Each of these factors could prevent detection of a real deviation in the overall trend in stem numbers and age classes. However, these potential problems would not lead to any false identification of unusual periods.
3. Results and discussion

The density of aspen in Rocky Mountain National Park averaged about 1250 stems/km² for the low-elevation eastside, and 550 stems/km² for the rest of the Park (below 3200 m); these estimates include locations where the prism cruise detected no aspens. Sample plots that included at least one aspen stem (among the 12 prism points) averaged 2.5 m²/ha of aspen basal area and 19.4 m²/ha basal area of conifers. Lodgepole pine trees accounted for about 64% of the conifer basal area, followed by about 20% each for Englemann spruce and for subalpine fir, with minor amounts of Douglas-fir, ponderosa pine, and limber pine. Aspen basal area declined weakly with increasing conifer basal area ($P = 0.02$, $r^2 = 0.13$).

Some aspen stems could not be aged because of heartrot. About 90% of trees less than 10 cm at 1.4 m were datable, compared with 70% for larger diameter classes. A total of 651 trees were aged, and the oldest tree encountered dated to 1689 (with an estimated pith date of 1685, for an age of 321 years at 1.4 m; P. Brown, Rocky Mountain Tree Ring Laboratory, personal communication), which we believe is the oldest reported age for an aspen tree. The next oldest tree was 205 years old, and 10 trees fell between 150 and 165 years.

Fig. 1. Random plot locations, sampled from a 1 km × 1 km grid across Rocky Mountain National Park, supplemented by additional plots from a 0.5 × 0.5 km grid in the low-elevation eastside of the Park.

Fig. 2. Twelve prism points were established at each plot, at 50-m intervals in a regular triangle. All 12 prism points were averaged to provide a single estimate for each plot.
Aspen ages correlated moderately well with diameter (Fig. 3), with a standard error of the estimate of 23 years. The distribution of aspen stem sizes showed an exponential increase with successive decades (Fig. 4), as expected for a balanced, uneven age forest.

The prism approach identified trees to be cored based on the proportion of size classes comprising the total basal area of aspen. The smallest trees (<5 cm dbh) comprised a very low proportion of aspen basal area, and were represented by 44 sampled trees (6% of aged cores). The majority of sampled aspen were between 5 and 30 cm (86% of aged cores), with 8% of aged cores >30 cm. If we had determined age structure from cores taken from trees in fixed-area plots, our sample would have been comprised about equally of trees less than 5 cm and trees between 5 cm and 30 cm, with fewer than 0.05% of the cores coming from trees >30 cm.

The period from 1975 to 1995 at low elevation on the eastside had 80–95% fewer aspen than would be expected based on the trend from 1855 through 1965 (Fig. 5). This finding is consistent with the low proportion of regenerating aspen stands (since the late 1960s) found by Baker et al. (1997) and Suzuki et al. (1999) for this portion of the Park. Across the rest of the Park, no decades had significantly fewer than expected aspens, and 1965–1975 had more aspen than expected. Suzuki et al. (1999) also found that most aspen stands contained young stems outside the low-elevation eastside of the Park, consistent with the density of young stems in our sampling.

A recent report noted that most aspen trees in Colorado are over 120 years old (Colorado Forest Health Advisory Board, 2005), but only about 1% of aspen in Rocky Mountain National Park were older than 120 years (accounting for 10% of aspen basal area, Fig. 6). About 90% of the trees, and 50% of basal area, were 80 years old and younger. Recent inventories of stand ages of aspen in Colorado showed that about 6% of aspen stands in Colorado are older than 120 years, half were over 75 years, and just 20% were younger than 50 years (data from

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Fig. 3. Relationship between tree diameter and age for 647 trees, omitting two trees older than 200 years and trees larger than 50 cm.

Fig. 4. Across the whole Park, the number of aspen per km² (bars) declined exponentially with increasing tree size ($r^2 = 0.78$); undatable trees ranged from about 15% of trees between 5 and 15 cm, rising to about 30% for larger trees. The sample of dated aspen cores had the greatest representation from the 5 to 30 cm diameter classes, with relative few dates for trees smaller or larger.

Fig. 5. Logarithm of number of aspen stems per km² by age class for the two portions of Rocky Mountain National Park. Lines show the long-term trend from 1855 through 1965 (low-elevation, eastside: log aspen = $-31.432 + 0.018 \times$ decade, $r^2 = 0.85$, $P < 0.0001$; rest of Park: log aspen = $-21.668 + 0.013 \times$ decade, $r^2 = 0.76$, $P < 0.001$). Gray bars indicate aspen densities within two standard errors of the estimate from the long-term trend; solid bars are more than two standard errors above, and open bars are more than two standard errors below the trend.

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USDA Forest Service Forest Inventory and Analysis; M.T. Thompson, personal communication March, 2007). The aspen forests of Rocky Mountain National Park have greater proportions of younger stems, indicating either younger stands or a tendency in the statewide inventory data to represent older stems disproportionately to stem numbers.

Some decades may have differed substantially from the long-term trend of expected aspen densities, without being detected with confidence by our sampling approach. For example, the number of aspen stems dating to 1985–1995 in the higher elevation and westside portions of the Park fell about 45% below the long-term expectation, but this deviation was only one standard error below the trend line. The precision of our ability to determine anomalous periods depends on both the decade-to-decade variation among typical decades, and the imprecision added by variation in the relationship between stem size (and probability of inclusion in the prism points) and tree age.

Prior to 1900, stand-replacing fires had a return interval on the order of 300 years across much of Rocky Mountain National Park (Sibold et al., 2006; Buechling and Baker, 2004). Fires were less extensive in the 20th century, as a result of climate conditions and active fire suppression (Buechling and Baker, 2004). The current age distribution of aspen in the Park does not show any marked legacy of a changed fire regime. This contrasts strongly with the Kaibab Plateau in northern Arizona, where introduction of livestock eliminated the frequent surface fire regime (Fulé et al., 2003) and led to 10-fold increases in aspen numbers (Binkley et al., 2006). Surface fires were probably much less frequent in the elevation range of aspen in Rocky Mountain National Park than on the Kaibab Plateau, and any change in fire regimes in the late 19th century had too little effect on aspen to be detected by our survey.

The population of elk varied dramatically in the Park in the 19th and 20th century. No records are available on elk population in the 19th century, but the elk were extirpated by the end of the century. Browsing impacts on aspen recruitment and survival may have remained high even as elk populations declined, as a result of domestic livestock. In the early 20th century, elk were reintroduced and livestock were removed, with unknown impacts on aspen. The elk population was managed with active killing in the mid-20th century, before the policy of natural regulation (in the absence of major predators) was adopted in the late 1960s. The age structure of aspen in the Park indicates that the interacting effects of fires, elk population changes, and livestock grazing had more-or-less consistent effects on aspen from 1855 to 1965. Some periods of high or low recruitment and survival may have occurred during some decades, but these effects were not large enough to leave a large legacy in the current age structure. The post-1975 decrease in aspen numbers in the low-elevation, eastside portion of the Park appears to be unprecedented in past the 140 years.

About two-thirds of all aspen stems occur within a matrix of conifer stands rather than in pure aspen stands (Kaye et al., 2003). Aspen regeneration is very low in stands with more than 10 m²/ha of conifer basal area (Kaye et al., 2005). The basal area of conifers has likely increased across the Park in recent decades, but any increase would not likely be more pronounced in the low-elevation, eastside portion of the Park.

The lack of a significant change in aspen numbers in recent decades in the higher elevation and westside portions of the Park supports the idea that high impacts of elk browsing have been more important in reducing aspen numbers than climate conditions, fire incidence, or conifer in-growth (Kaye et al., 2005). Restoring the numbers of young aspen that would be characteristic of the low-elevation, eastside of the Park will likely require substantial reductions in elk browsing impacts on aspen shoots, either by reduced elk numbers or altered patterns of landscape use (cf. Ripple and Beschta, 2004).

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