

THESIS

FIRE HISTORY AND SEROTINY IN THE ROCKY MOUNTAINS  
OF COLORADO

Submitted by

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WE HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER OUR SUPERVISION BY CARISSA F. AOKI ENTITLED FIRE HISTORY AND SEROTINY IN THE ROCKY MOUNTAINS OF COLORADO BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE.

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## ABSTRACT OF THESIS

### FIRE HISTORY AND SEROTINY IN THE ROCKY MOUNTAINS OF COLORADO

Fire is a natural part of forested ecosystems in Colorado, playing an essential role in regenerating and maintaining forests. I studied two aspects of fire: historical fire regime in mixed-conifer forests, and serotiny in lodgepole pine.

I. During the 1990s and early 2000s, fire management in the western United States was often based on lessons learned from fire regime studies in ponderosa pine ecosystems in the Southwestern states. As managers sought to apply these policies to an ever-broader range of forest types, it became clear that different forest types were characterized by different fire regimes and thus required further research as well as new management strategies. Mixed-conifer forests have been particularly hard to quantify in terms of their historical fire regimes. My study aimed to understand the historical range of variability (HRV) in a mesic mixed-conifer forest in southwestern Colorado. Banded Peak Ranch, located in the San Juan Mountains of Colorado, provided a unique setting in which to study the historical fire regime of this forest type in the southern Rocky Mountains. I used a combination of stand age structure, species composition, and fire scar data, collected at two different spatial scales on 40 plots, in both logged and

unlogged stands. At both scales, I found a combination of mixed- and high-severity fire regimes. The spatial distribution of fire severity appears to have been patchy, with mixed- and high-severity stands lying in close proximity to one another. Species composition and age structure varied widely among both the high- and mixed- severity stands, suggesting that a variety of future disturbance regime trajectories might be expected.

II. Regeneration in Rocky Mountain lodgepole pine (*Pinus contorta* var. *latifolia*) is characterized by two methods of reproduction: serotinous cones, which open and release their seeds only under heat from fire; and non-serotinous cones, which open and release their seeds with cone maturity. Stands with a high proportion of serotinous cones can thus regenerate strongly following stand-replacing fire. I used data from across Rocky Mountain National Park (ROMO) to quantify the distribution of serotiny on the landscape and to try to understand the key abiotic variables controlling serotiny. I found that serotiny varied from 0-97% per stand, with an average across the landscape of 58%. Because my data did not correlate strongly with any single variable, I used regression tree analysis to explore the combined effects of abiotic variables on serotiny. Elevation, aspect, and topographic convergence index (a measure of local moisture) were the key variables in the resulting regression tree, and higher serotiny was correlated with the range of each variable that is more conducive to fire—lower, more west-facing, drier. Previous research has shown that serotiny is affected by stand-replacing fire, but not by low-severity fire. In an environment such as the lodgepole pine forests of ROMO, where stand-replacing fire is the predominant fire regime, serotiny is highly related to the environmental variables that generally contribute to fire occurrence.

III. Serotinous cones remain on living trees for many years, holding within them the canopy seed bank for regeneration after fire. After large-scale mortality caused by mountain pine beetle (*Dendroctonus ponderosae*), however, the seeds in serotinous cones may remain on the dead trees for a number of years. I tested seeds from living and beetle-killed serotinous stands to determine whether they remain viable after tree death, and whether germination rates were affected by cone age. There was no significant difference between germination success rates from the living stand vs. the dead stand. While there was a significant relationship between cone age and germination success, cones that were 21-25 yrs still had >30% germination rates. I conclude that post-beetle regeneration likely will not be limited by viable seed availability in stands with serotinous cone-bearing trees.

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## **Foreword**

Researchers interested in fire may be housed in many different departments—examples include ecology, forestry, geography, and botany. Each of these has its own particular approach to asking questions about fire, but what they have in common is an interest in disturbance, or put another way, in the effects of fire's interaction with the biota on a landscape. This broad umbrella of inquiry can relate seemingly disparate lines of questioning into common ones.

The two main parts of this thesis—a mixed-conifer fire history study in southwestern Colorado and a lodgepole pine serotiny study in Rocky Mountain National Park—were conceived and funded entirely separately from one another. One was a dendrochronological study aimed at understanding the pre-Euro-American settlement fire regime in the mesic mixed-conifer forest type, and the other investigated serotiny, a reproductive trait of Rocky Mountain lodgepole pine that researchers believe is largely driven by fire. (Chapters two and three are part of the same project.) These studies represent two different forest types, in geographically different parts of the state of Colorado, with quite different central questions. However, I found that the knowledge I gained about fire regimes from the mixed-conifer study greatly enhanced my ability to conduct the serotiny study. Fire, of course, occurs at a landscape-scale, and whether one studies its effects directly, as in fire history, or indirectly, as in serotiny, a similar set of knowledge informs both studies. Furthermore, the quantitative methods I learned while

pursuing the serotiny study were substantially different from those used in dendrochronological work, thus expanding the analytical toolbox I will have available for future projects.

It is part of graduate student life that one's funding may not be consistent, and the resulting thesis or dissertation may seem more like a many-headed hydra than like a coherent, linear progression of scholarly inquiry. But I would argue that the diversity of experience gained from disparate projects can only enhance one's educational process and future scientific pursuits. Many graduate students in the natural resource sciences, myself included, come to the field from other careers, or having taken time off between undergraduate college and graduate school. I have occasionally wondered whether the fact that many graduate programs require a student to sign up with a specific advisor and project might not restrict the creative thinking and intellectual growth of those students. Allowing seemingly quite different topics to be covered in a thesis or dissertation permits these students to explore the possibilities of different lines of inquiry, while still allowing them to finish school within a reasonable time frame.

A modified version of chapter one was printed and submitted to the owners and managers of Banded Peak Ranch, and was edited by Bill Romme and Peter Brown. Chapter three—in a form very similar to the chapter in this thesis—has already been submitted for publication consideration, and was edited by Bill Romme and Monique Rocca.

## **Chapter 1: Fire Regime of a Mixed-Conifer Forest in Southwestern Colorado**

### INTRODUCTION

In the western United States, fire history studies in low-elevation ponderosa pine (*Pinus ponderosa*) forests have been contrasted with those from high-elevation subalpine forests, demonstrating the wide range of fire regime characteristics between the two forest types (Schoennagel et al. 2004; Veblen 2003). A network of fire history studies now exists throughout the West, extending from southern British Columbia to northern Mexico (Kitzberger et al. 2007). This research includes a strong body of work in both the montane ponderosa pine forest type and the high-elevation subalpine forest type, but studies in the mixed-conifer are rare. Indeed, even a simple definition of what constitutes the “mixed-conifer” forest has been elusive. Dieterich (1983) pointed out that “mixed-conifer” includes a wide variety of forest types, ranging from mixed-conifer-pinegrass ecosystems in Oregon, to sequoia-mixed-conifer forests in the Sierra Nevada, to ponderosa pine-white fir forests in Crater Lake National Park. Within Colorado’s San Juan Mountains, Romme et al. (2009) distinguished between “warm-dry” mixed-conifer forests, and “cool-moist” or “mesic” mixed-conifer forests, which differ from one another in elevation, aspect, major species, disturbance regime, and stand structure. “Cool-moist” and “mesic” are often used interchangeably. I will hereafter use the term “mesic,” as this term is commonly used in most vegetation classifications.

For fire management purposes, each type of mixed-conifer forest must be characterized within its own climatic, vegetative and geographic context. Banded Peak Ranch, located in southwestern Colorado, provides a unique setting in which to study the historical fire regime of mesic mixed-conifer forests in southwestern Colorado. The ranch's location in the eastern San Juan Mountains, on the western slope of the Continental Divide, marks it as one of the coolest and wettest sites in this mountain range (PRISM Climate Group). Both warm-dry and mesic mixed-conifer forests are found on the ranch, but mesic mixed-conifer forests are by far the more extensive. Research has been conducted on the fire ecology of warm-dry mixed-conifer forests in the San Juan Mountains, but the mesic mixed-conifer forests have received little study. Existing fire history studies in the immediate area are Brown and Wu (2005), Grissino-Mayer et al. (2004), and Wu (1999). While two of these studies included a mixed-conifer component (all were focused on forests where ponderosa pine was either a sole dominant or a principal overstory species), less attention was given to the "mesic" end of the mixed-conifer spectrum. Studies of mixed-conifer forests nearby, but not directly in the San Juans, include Margolis et al. (2007) and Touchan et al. (1996).

In higher elevations of the San Juans, mesic mixed-conifer forests occur between elevations of approximately 2200 and 3100 m. Tree species may include Douglas-fir (*Pseudotsuga menziesii*), Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), white fir (*Abies concolor*), and quaking aspen (*Populus tremuloides*). Blue spruce (*Picea pungens*) and southwestern white pine (*Pinus strobiformis*) also occur in some stands. Ponderosa pine (*Pinus ponderosa*) may be present in small numbers, but

this species is more typically associated with warm-dry mixed-conifer forests (Romme et al. 2009).

Following unusually severe fire seasons throughout the western United States in 2000 and 2002, land managers and policy makers began implementing a series of fire policies aimed primarily at fuels reduction (Franklin and Agee 2003; Stephens and Ruth 2005; Veblen 2003). Based on the idea of using fire's "historical range of variability" (HRV) for management decision-making, these policies were predicated on the assumption that 20th century fire suppression caused an unnatural build-up of fuels in many fire-dependant ecosystems, leading to the extremely large and severe fires of recent decades. These decisions, however, resulted from the coincidence of the need for science on which to base policy, with the fact that many of the initial fire regime studies in the west were carried out in ponderosa pine ecosystems. In recent years, studies in other forest types have diversified our knowledge of fire regimes, and increased our understanding of how management might respond differently in these forest types. As a result, HRV has become a more complicated concept when used for management decision-making. With careful application, however, HRV remains a valuable concept for managers and researchers alike (Keane et al. 2009; Keeley et al. 2009).

To explore the HRV of the mesic mixed-conifer forests in my study, I used a fire regime definition focused on fire severity, such as that outlined by Brown (2000). In this definition, potential fire regime classifications focus primarily on the effects of fire on the overstory vegetation. At one end of the spectrum, a low-severity fire regime implies little or no overstory mortality, while at the other end, a high-severity, or stand-replacing, regime implies extensive overstory mortality. Between these two definitions lies the less-

easily quantified “mixed-severity” fire regime, in which fine-scale patches of high- and low-severity fire are found in close proximity. Many workers have contributed to our understanding of the two ends of this spectrum, with studies showing that montane ponderosa pine forests are often outside their low-severity HRV (e.g., Covington and Moore 1994; Fulé et al. 1997), while subalpine forests often lie well within their high-severity HRV (e.g., Romme 1982; Sibold et al. 2006). These opposing outcomes are attributed to the effect of Euro-American settlement of the western U.S. in the late 19<sup>th</sup> century, and the institution of fire suppression policies throughout the country in the early 20<sup>th</sup> century, both of which have contributed to the departure of montane forest types from HRV.

In this context, the objectives of my study were 1) to determine the fire regime of the Banded Peak Ranch mesic mixed-conifer forests prior to human influence caused by Euro-American settlement; and 2) to ascertain in what ways this forest type is within or outside of its HRV and to formulate management recommendations based on this information. To accomplish these goals, I collected field data on the ranch in the summer of 2007 with an eye toward answering the following questions:

How frequent were past fires, what was the spatial extent and distribution of low-severity fire relative to that of stand-replacing fire, and how, if at all, has this changed through time?

How does the mesic mixed-conifer fire regime present at the Ranch fit with what is known of fire regimes in lower elevation ponderosa pine forests and higher-elevation spruce-fir forests? Is there a basis for defining a “mixed-severity” fire regime in mesic mixed-conifer forests based on this information?

## METHODS

### *Study area*

Banded Peak Ranch, Catspaw Ranch, and Navajo Headwaters Ranch (three separate but contiguous properties, hereafter referred to collectively as “Banded Peak Ranch”) are located in the eastern San Juan Mountains in southwestern Colorado, southeast of Pagosa Springs, Colorado (Figure 1). With its eastern boundary on the Continental Divide, the ranch area comprises approximately 22,250 hectares (55,000 acres). The Navajo River runs down the center of the property, with its headwaters found in the upper third of the ranch. The eastern property line follows the Continental Divide, and federal land borders the property on three sides: San Juan National Forest to the west, South San Juan Wilderness to the north, and Rio Grande National Forest to the east. The nearest available climate instrumental data to compare to the mixed-conifer elevations on the ranch are from Wolf Creek Pass (3243 m, 1957-2005) and Pagosa Springs (2209 m, 1906-1998), each located approximately 35 km from the study area. The elevation gradient between the two sites approximates the elevation gradient on the ranch. Average annual precipitation was 1152 mm and 513 mm, respectively; average maximum January temperatures were -1.0°C and 3.3°C, and average maximum July temperatures were 18.8°C and 28.4°C. Relative to other locations in the San Juan Mountains, Banded Peak Ranch is on average cooler and wetter. Figure 2 uses PRISM modeled climatic data (PRISM Climate Group) to compare recent temperature and precipitation data among three locations in the San Juan Mountains.

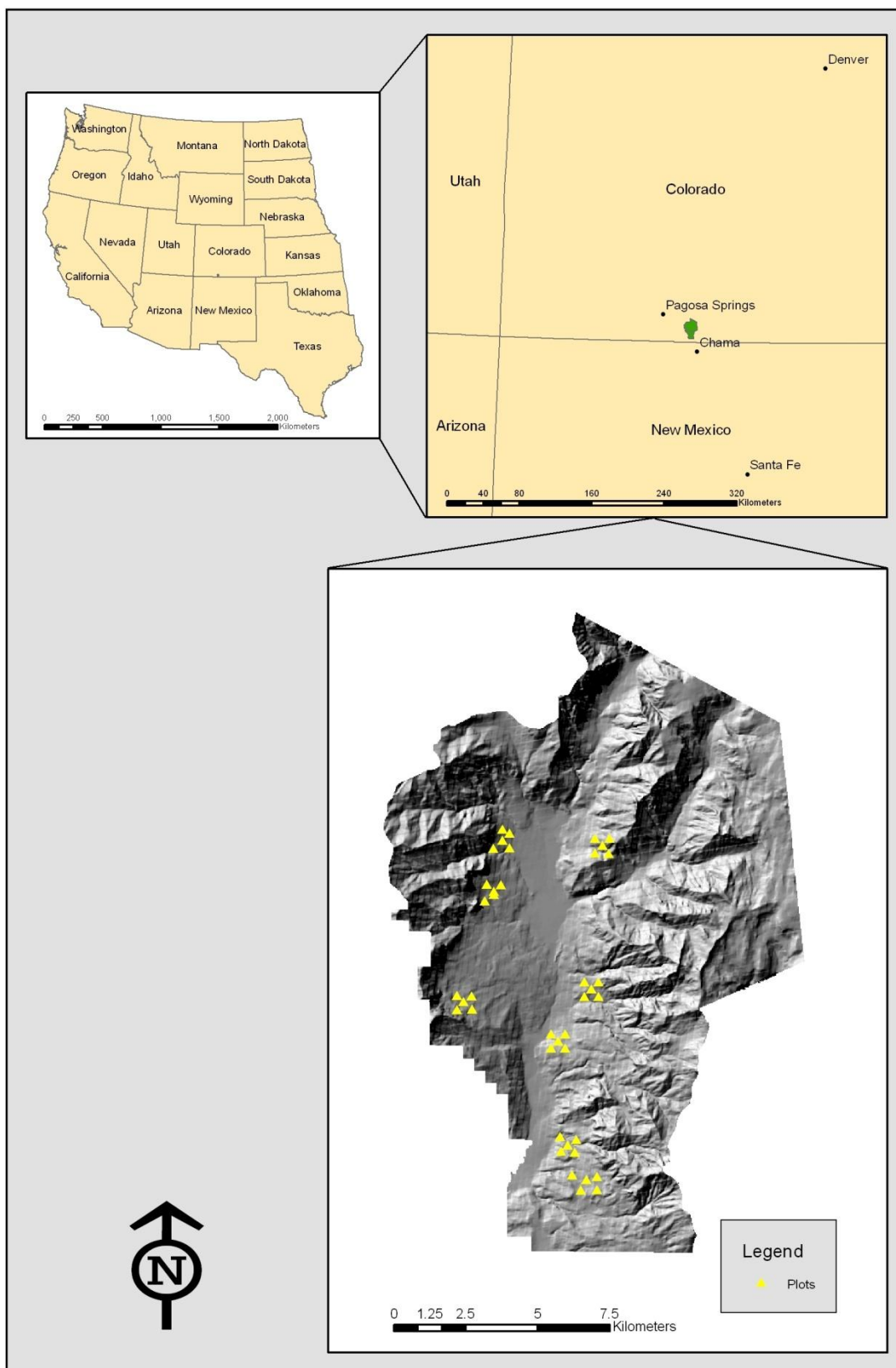


Figure 1. Map showing Banded Peak Ranch location and plots



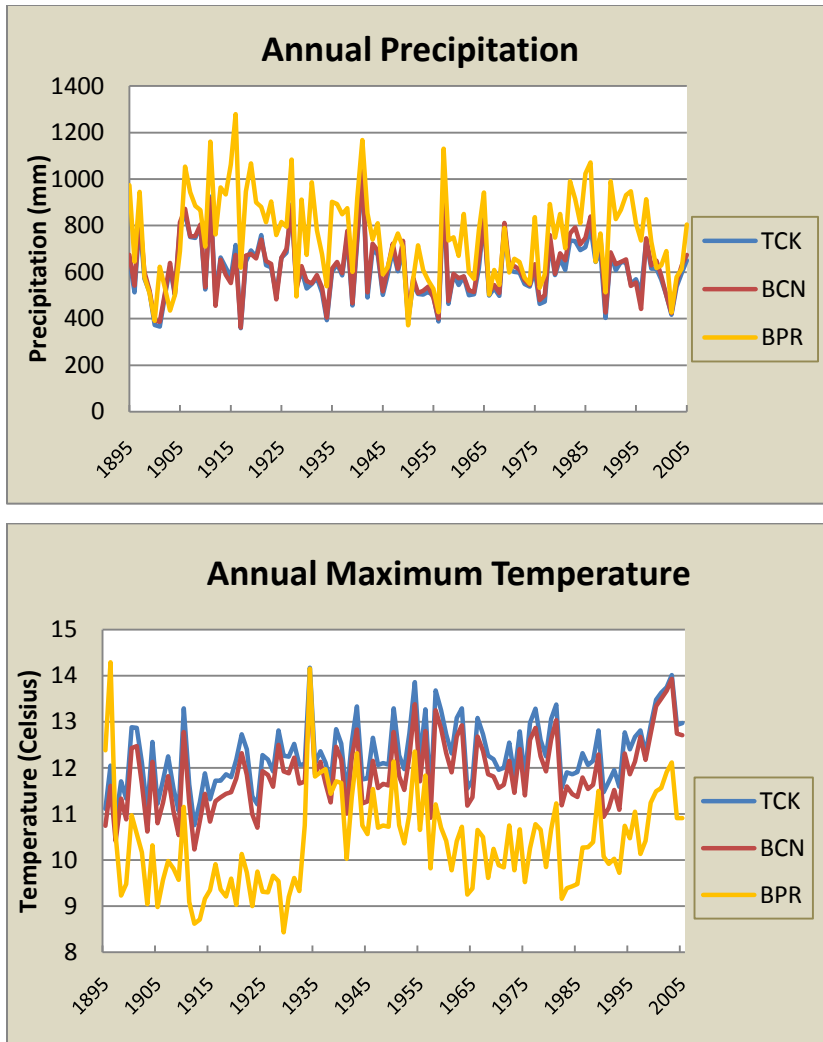


Figure 2. Annual precipitation and maximum temperature at three sites in the San Juan Mountains. All are at comparable elevation and all support mixed-conifer forests. Taylor Creek (TCK) and Burnette Canyon (BCN) are located at the west end of the range near Dolores, Colorado. Banded Peak Ranch (BPR) has been noticeably wetter and cooler than the sites to the west.

### *Sampling methods*

The main objectives of my field sampling were to collect both fire-scar and age structure data. Low-severity fires often leave injuries (fire scars) on trees without killing them, thus providing a very good record of past low-severity fire history. In other forests where fires are less frequent and of higher severity, trees are often killed outright, and little or no scar evidence remains. In these forests, age structure analyses are often the

only way to obtain fire history information. If the oldest trees in a stand are younger than the known life expectancy of the dominant tree species, or if most of the trees in a stand appear to be about the same age, this suggests a stand-replacing fire at some time in the past. The use of fire scar data in conjunction with stand age structures provides a more complete picture of the fire regimes that occurred in mixed-conifer forests on Banded Peak Ranch.

Fieldwork took place in the summer of 2007. Using the USGS digital elevation map for the ranch, I selected areas that were between 2500 and 3100 meters (8200 and 10,200 feet), to focus on the elevations where the mesic mixed-conifer type is known to occur. Hawth's Tools software (Beyer 2004) was used to randomly select eight site locations within this elevation range. These were stratified within the administrative boundaries of the three ranch areas, so that two sites were located on Navajo Headwaters, two on Catspaw, and four on Banded Peak Ranch.

I placed a grid of five plots at each site, using the site location as the center plot and placing the other four plots in a 500 m square box around the center plot. This resulted in 40 plots total across the ranch (Table 1). At each plot, I used an *n*-tree distance sampling method (Jonsson et al. 1992; Lessard et al. 2002) to select the 30 trees (living or dead) nearest to plot center. Only trees  $\geq 20$  cm in diameter at breast height (DBH) were sampled, to maximize the possibility of obtaining samples from the pre-Euro-American settlement period. Core samples were collected using a power increment borer, and a chainsaw was used to collect wedge samples from snags, downed logs, and stumps. For each sample, collected information included: species; diameter at breast height (DBH); diameter at sampling height (DSH; 10 cm or ~6 in above ground level);

Site	Plot	UTM-E	UTM-N	Elevation	Aspect	Slope
Dolomite Lake	1	347053	4108224	2842	45	10
Dolomite Lake	2	347567	4108205	2802	55	17
Dolomite Lake	3	347285	4108006	2840	230	0
Dolomite Lake	4	347057	4107720	2923	55	60
Dolomite Lake	5	347570	4107738	2841	310	5
Bull Elk Pond	1	350313	4106882	2488	290	40
Bull Elk Pond	2	350813	4106882	2577	273	5
Bull Elk Pond	3	350563	4106632	2580	265	55
Bull Elk Pond	4	350313	4106382	2583	310	10
Bull Elk Pond	5	350813	4106382	2638	215	25
Little Muddy	1	350640	4103322	2521	275	45
Little Muddy	2	351200	4103205	2673	280	30
Little Muddy	3	350893	4103027	2599	305	25
Little Muddy	4	350669	4102812	2628	343	35
Little Muddy	5	351149	4102767	2637	0	35
Bear Creek	1	351052	4101977	2688	230	40
Bear Creek	2	351917	4101937	2824	255	30
Bear Creek	3	351549	410816	2779	255	37
Bear Creek	4	351352	4101457	2739	250	43
Bear Creek	5	351920	4101481	2854	0	10
Elephant Head	2	348583	4112054	2676	100	20
Elephant Head	3	348333	4111832	2699	190	20
Elephant Head	4	348021	4111503	2724	100	30
Elephant Head	5	348333	4117332	2364	20	60
Big Muddy	1	351474	4108688	2658	19	25
Big Muddy	2	351974	4108688	2728	245	30
Big Muddy	3	351724	4108438	2694	flat	0
Big Muddy	4	351474	4108188	2622	230	30
Big Muddy	5	351974	4108188	2654	180	10
Johnson Mtn	1	351851	4113672	2831	270	20
Johnson Mtn	2	352351	4113672	2894	15	35
Johnson Mtn	3	352101	4113422	2850	285	40
Johnson Mtn	4	351851	4113172	2768	0	90
Johnson Mtn	5	352320	4113155	2909	250	40
Beaver Creek	1	348625	4113999	2679	55	10
Beaver Creek	2	348875	4113849	2620	80	4
Beaver Creek	3	348625	4113599	2654	120	15
Beaver Creek	4	348322	4113331	2693	150	10
Beaver Creek	5	348875	4113349	2606	130	30

Table 1. Site (column 1) and plot (column 2) locations in UTM coordinates (NAD 1983 Zone 13N), including elevation, slope and aspect of each plot.

whether the sample was living, stump, or log; location relative to plot center (distance and azimuth); and remnant condition (bark still present, sapwood present, or eroded). In cases where a stump was too deteriorated for collection, its presence and location were noted, along with DSH and, if possible, species.

Core samples were collected from living trees at 10 cm above ground level to minimize missed rings between ground (germination) and coring heights. Fire-scar data were obtained by taking partial cross sections from living trees (a common dendrochronological method which allows the tree to live following sampling) and full cross sections from remnants, i.e., snags, downed logs, and stumps.

Fire scars were sampled thoroughly within each plot, and additional samples were collected from a wider radius as we moved from plot to plot within a study site. Previous “high-grade” logging (i.e., selective removal of the largest merchantable trees) at a number of my plot locations made some of the sample collection difficult, since stumps were often too eroded for sampling.

In the lab, all samples were surfaced with successively finer grits of sandpaper to enable viewing under a microscope, then visually crossdated using standard dendrochronological methods (Stokes and Smiley 1968). When a sample did not reach pith, a geometric “pith estimator” was used to estimate the number of years between the innermost dateable ring and the pith date. Samples that did not easily crossdate visually were further analyzed by measuring the tree ring widths using a sliding stage measurement system, then applying program COFECHA (Holmes 1983) to the ring widths to facilitate crossdating. Due to Banded Peak Ranch’s cool, wet location, many samples proved unusable due to advanced deterioration of the wood. For example, out of

834 conifer age structure samples collected in the eight sites, 555 were dateable to a specific age, and 578 were at least partially dateable (i.e., the center of the sample was rotten or otherwise undateable, but the remainder was still useful). Including aspen, 1208 samples were collected in the eight sites.

### *Fire severity determination*

The 40 plots included a wide range of variation in terms of slope, aspect, and elevation, as well as in current species composition. Some sites had been logged, others not, with some sites including both logged and unlogged plots. In microcosm, our study sites represented a fairly common condition of mixed conifer forests both in Colorado and elsewhere in the western United States—the heterogeneity of these forests has long confounded efforts to understand their historical fire regimes. Analyzing age structure, in particular, becomes something of a challenge in determining even a single component of historical fire regime, in this case, fire severity.

The problem is that fire scars tend to occur primarily in *low* severity fire regimes, in which fire injures—but does not kill—the trees in the stand. For fire regimes that tend to kill entire stands of trees, often few or no fire scars are left behind. In these cases, stand age structure provides the next most informative proxy in helping us understand historical fire regimes. If the entire stand was killed in a past fire, evidence of that event will present itself in the form of a stand age structure in which all of the living trees established more recently than the fire that killed the trees in the previous stand. Depending on the life history of the species, these post-fire individuals may have established promptly after the fire and thus all may be of about the same age today

(typical of aspen), or they may have established more-or-less continuously since the fire (typical of white fir).

Another part of the difficulty with trying to glean historical information about stand-replacing fires is that the fire will generally have removed any previous record of fire in that stand—standing dead trees and downed logs may have been left by the last fire, but once a few decades or more have passed, these remnants will be well on their way to complete decomposition. With fire scars, a single stand may contain many scars from many different fires, from which one may calculate an “average” interval between fires. Using stand age structure, however, can only tell us about the most recent stand-replacing fire—we must assume that the time-since-last-fire indicates something about the fire interval, but we do not have multiple examples to strengthen this assumption.

In their 2003 study of mixed severity fire in Grand Canyon National Park, Fulé and others described their method for distinguishing “fire-initiated” from “non-fire-initiated” plots as follows: “When the oldest tree or trees were the fire-resistant species PIPO [Ponderosa pine] and PSME [Douglas-fir], the plot was classified as non-fire-initiated. When the oldest trees were the fire-susceptible species POTR [aspen], PIEN [spruce], or ABLA [subalpine fir], the plot was classified as fire-initiated. ABCO [white fir] was considered intermediate in fire resistance and old-ABCO plots were classified as non-fire-initiated when accompanied by uneven-aged PIPO or PSME, and as fire-initiated when accompanied by approximately equal-aged POTR.” These criteria assume a “high severity” regime in the “fire-initiated” plots. In their results, however, they found such confounding factors as more than one aspen cohort on the same plot, or aspen cohorts in plots together with older fire-resistant conifer—either case would indicate that

stand-replacing fire may have taken place in part of the plot, but not in another part of the plot. Heyerdahl and others (in press) used a “severity table” to help identify their plots, including factors such as fire scar presence or absence, relative recruitment dates of different cohorts, etc. Hessburg et al. (2007) created a dichotomous key for the same purpose. Because I found that my samples did not fit exactly within any of these systems, I used my data to design my own system for Banded Peak Ranch, based on the table idea.

Determining fire severity using age data often requires qualitative assessments, in spite of the quantitative nature of the data. Different kinds of evidence play greater or lesser roles from plot to plot, and rarely does a single plot fall into a clear categorization as either “high” or “mixed” severity. In addition to different evidence types being present in different plots, my severity designation was complicated by the difficulties we found in sample collection and processing (e.g., trees that were rotten in the center and so could not be dated, stumps that were too rotten to be collected, trees that were too large for my increment borer, etc.). For example, a plot containing five aspen might include just one dateable aspen, making it difficult to say anything about an aspen “cohort” in that plot. Or aspen might be the “oldest” dated sample in a plot, but one of the other conifer samples that could not be dated may have been even older.

## RESULTS

### *Fire scar data*

I did not find many fire scars, suggesting that the “low-severity/high-frequency” fire regime type is not widespread in mixed conifer forest on the ranch. Low-severity fire

regimes generally leave behind numerous fire scars, often multiple scars on a single tree. Such trees may date back several hundred years. In my sampling, however, I found few samples of this type. In addition, half the dateable fire scar samples contained only one fire scar (as opposed to multiple scars), suggesting that fires were either relatively infrequent and generally of a high enough severity to kill, rather than scar, most of the trees in each stand (the scarred trees were the rare exception).

Notably, the year 1879 appeared as a fire date on 8 of the twenty dateable fire scar samples. 1879 has been documented as a major fire year in many other studies in the region near Banded Peak Ranch, as well as across the west. Some of the regional studies that have found widespread fire in 1879 include: Grissino-Mayer and others (2004) and Wu (1999) in the San Juan Mountains, Margolis and others in the southern Sangre de Cristo Mountains (2007), and Touchan and others in the Jemez Mountains (1996). Examples from other locations in the West include: Grand Canyon National Park (Fulé et al. 2003), Rincon Mountains, Arizona (Baisan and Swetnam 1990), Rocky Mountain National Park (Sibold et al. 2006), White River National Forest (Sudworth 1899), and Animas Mountains, New Mexico (Baisan and Swetnam 1995).

I found an 1879 date on trees in four of the eight sites (sites 1, 2, 3, and 6), though not at all plots in each of those sites (remembering that there are five plots per site). It is likely that these fire-scarred trees were the result of surface burning that occurred adjacent to patches of stand-replacing fire. Four of the 8 1879-scarred trees had been scarred more than once during their lifetime, suggesting that a low-severity/high-frequency regime was operating in that stand, or that a mix of low-severity and high-severity fires characterized the area. But with a relative lack of fire scars, these data



alone could not answer these questions about fire severity in 1879. For more information on the relative severity of the burned patches in the 1879 fire, I turned to the aspen age structure data (see next section).

In addition to the 1879 fire, I found two other fire scar dates that matched those found in other regional fire history studies: 1748 (Brown and Wu 2005; Grissino-Mayer et al. 2004; Margolis et al. 2007), and 1861 (Brown and Wu 2005)<sup>1</sup>.

Also of note in the fire-scar data was a surprisingly large number of single fire scars throughout the 20<sup>th</sup> century that dated to a variety of different years, with no one year being duplicated in any other sample. In all likelihood, these represent scars that a) were actually caused by something other than fire, e.g., by lightning or by another tree falling along the trunk and scraping off the bark; or b) were caused by small fires that went out before spreading and before causing any significant change in stand structure. I made every effort not to collect samples that were obviously scarred from something other than fire (such as a skid or fell scar) or a single lightning strike that did not affect adjoining trees, but again, since many of the trees had been cut during high grading, it was often difficult to discern these details. Assuming that at least some percentage of these scars was caused by fire, it seems clear that small, non-spreading fires may have occasionally occurred in some areas of the ranch. While sampling, I observed the frequent occurrence of lightning-scarred trees that did not appear to be related to nearby patches of fire, further supporting this conclusion. Moreover, in several wilderness areas across the West, where fires have been allowed to burn without interference, it has been

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<sup>1</sup> After the random sampling was complete, I had the opportunity to sample an area that had just been logged the month before. I did not include the site in my data, as it was not randomly selected. However, I found two more fire dates that correlated with surrounding studies: 1806 (Brown and Wu 2005) and 1851 (Brown and Wu 2005; Grissino-Mayer et al. 2004; Margolis et al. 2007; Touchan et al. 1996).

observed that most of the cumulative area burned in a decade is accounted for by only a few large fires, and that the majority of fires extinguish naturally before burning any substantial amount of area. This pattern results from the fact that ignition often occurs at times when fuels are too wet to carry fire. Small patches may burn but these fires go out before becoming extensive. Extensive fires generally occur in mid- to higher-elevation forests only in those rare years when ignition combines with extreme weather conditions (wind, high temperatures, low relative humidities) to result in very continuous, extremely dry fuels.

A standard suite of fire history statistics (e.g., mean fire interval) is usually computed for ponderosa pine forests where fire scars are abundant. However, because we found so little evidence of spreading, low-severity fires, it was not possible to compute these kinds of statistics for the mesic mixed-conifer forests of Banded Peak Ranch.

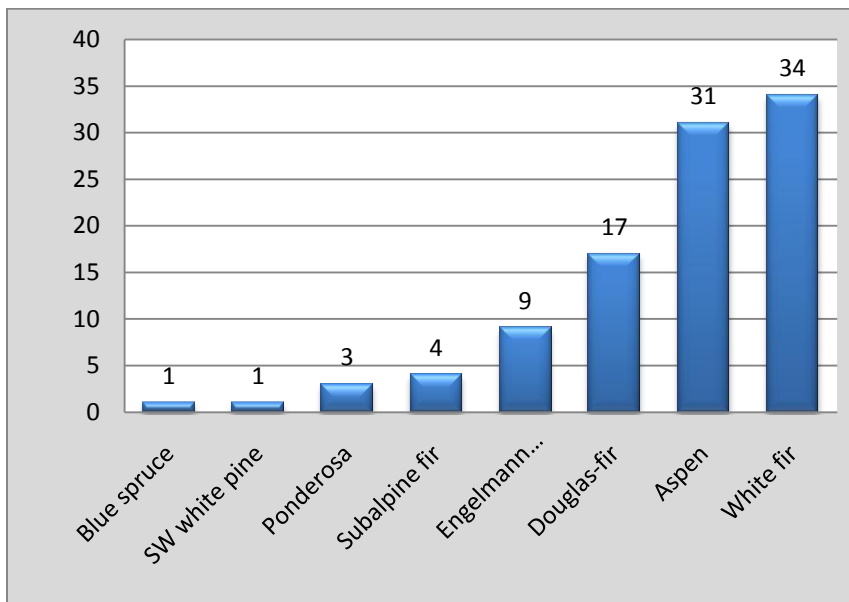


Figure 4. Percentages of tree species across all sampling sites.

*Species composition, aspen establishment dates, general age structure*

Overall, the paucity of ponderosa pine across all of my plots indicates that the majority of the mixed-conifer forest on the ranch is of the “mesic” variety (Figure 4). Ponderosa pine comprised just 3% of the overall species composition. By contrast, white fir and aspen comprised 34 and 31% of the total, respectively. (For a complete summary of species composition by individual sites, see Appendix A.)

With the prevalence of aspen on the landscape, I looked first at their recruitment patterns in my attempt to characterize past fire severity. Because aspen regenerate by suckering, and are often the first to colonize a site post-fire, the presence of even-aged aspen cohorts can provide easily recognizable data on stand-replacing fire (Baker 1925;

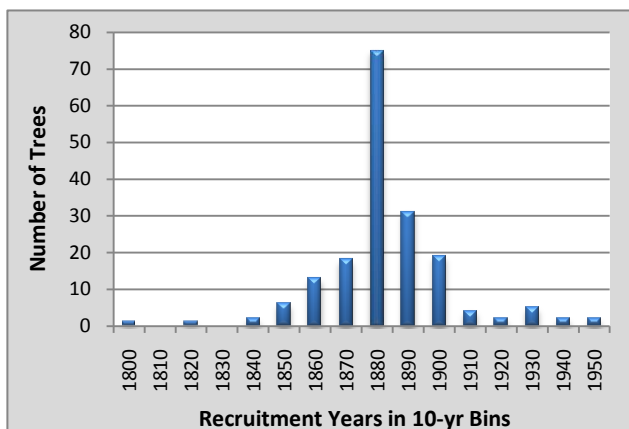


Figure 5. Aspen recruitment across all study sites.

Jones and DeByle 1985; Margolis et al. 2007). My initial evaluation found a notable spike in recruitment in the decade of the 1880s (Figure 5). These data support my findings in the fire-scar sampling that the 1879 fire burned in many locations across the ranch. The presence of even-aged aspen also indicates that many, if not most, of these patches burned at a high-severity, i.e., they were stand-replacing fires.

I also found that the 1880s aspen recruitment was not equally distributed across the ranch. It appears that while the 1879 fire spread widely on the eastern half of the

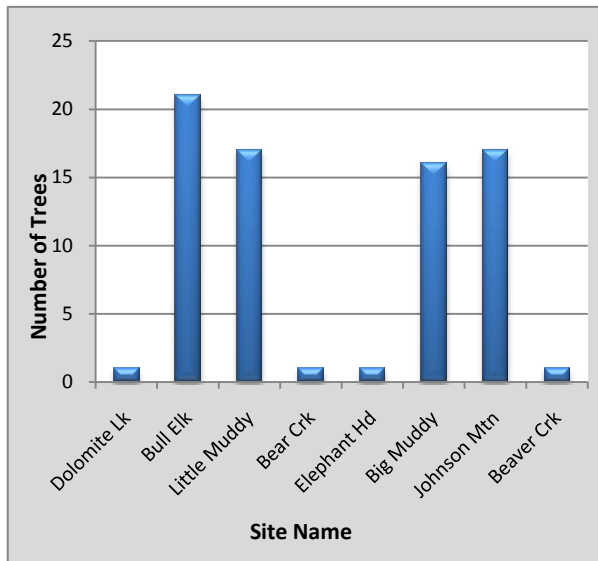


Figure 6: Aspen recruitment during the 1880s decade, by site name.

ranch and burned severely in many places, the western side was relatively unaffected. In Figure 6, we can see that sites at Bull Elk Pond, Little Muddy, and Big Muddy (located on the eastern side of the valley) all included significant aspen recruitment during the 1880s, as opposed to sites at Dolomite Lake, Bear Creek, Elephant Head, and Beaver Creek (mostly on the west side), which did not.

As for the overall age structure regardless of species, extensive tree recruitment began in the mid- to late-nineteenth century, and continued into the early 20th century (Figure 7). In other words, the majority of sampled trees were less than 150 years old. The increase in recruitment during the late 19th and early 20th centuries has been documented throughout the Southwest, and has been—at least in lower-elevation ponderosa pine forests—attributed in part to an increase in moisture during this period (e.g., Savage and others 1996). The highlight of this period was a pulse of ponderosa

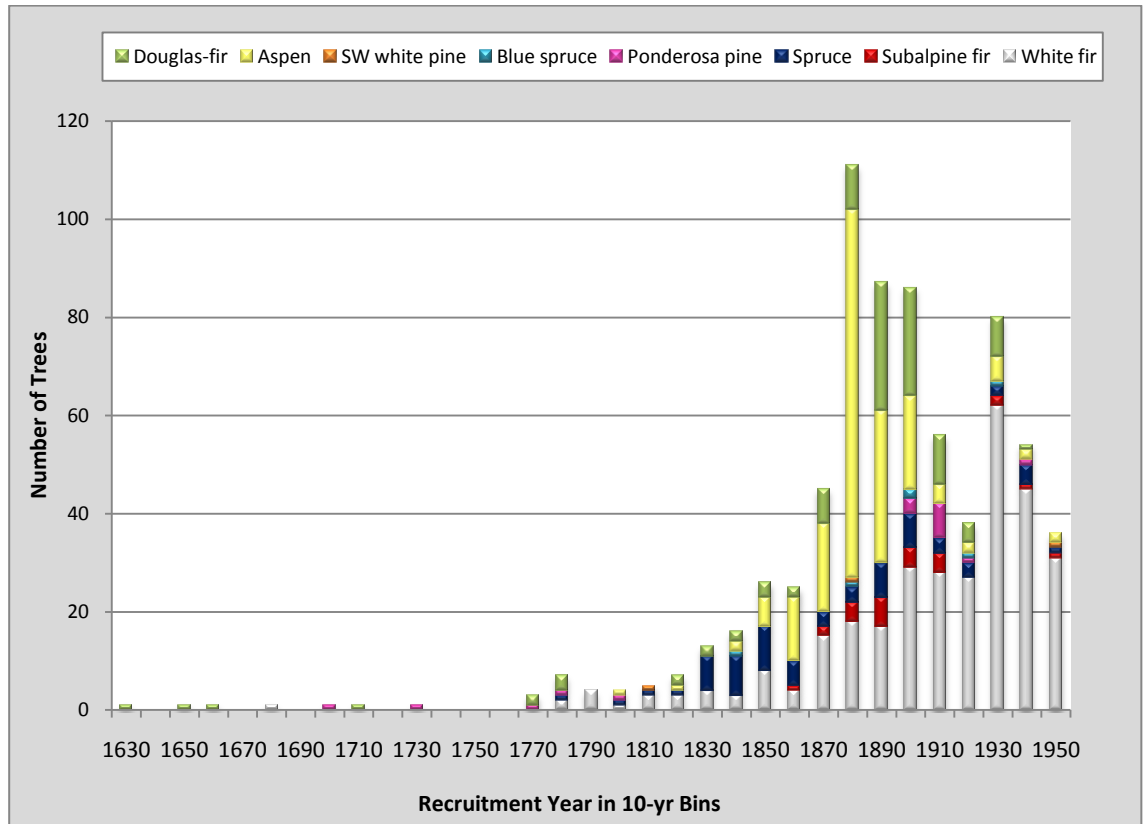


Figure 7: Tree recruitment years for all sampled trees.

pine regeneration apparent in age data from throughout the Southwest centered on the year 1919. The region around Banded Peak Ranch experienced a similar wet period as documented by both Palmer Drought Severity Indices (a measure of how dry the region was in any given year: Cook and others, 2004) and in modeled reconstructions of precipitation (PRISM Group, 2004). From these two datasets, points located near Banded Peak indicate above average moisture during the first three to four decades of the 20th century (Figure 8), which corresponds quite strongly to the peak in tree recruitment across all species. The late 20th century was another wet period in the Southwest (Figure 8). A similar pulse of tree recruitment may have occurred during this recent wet period,

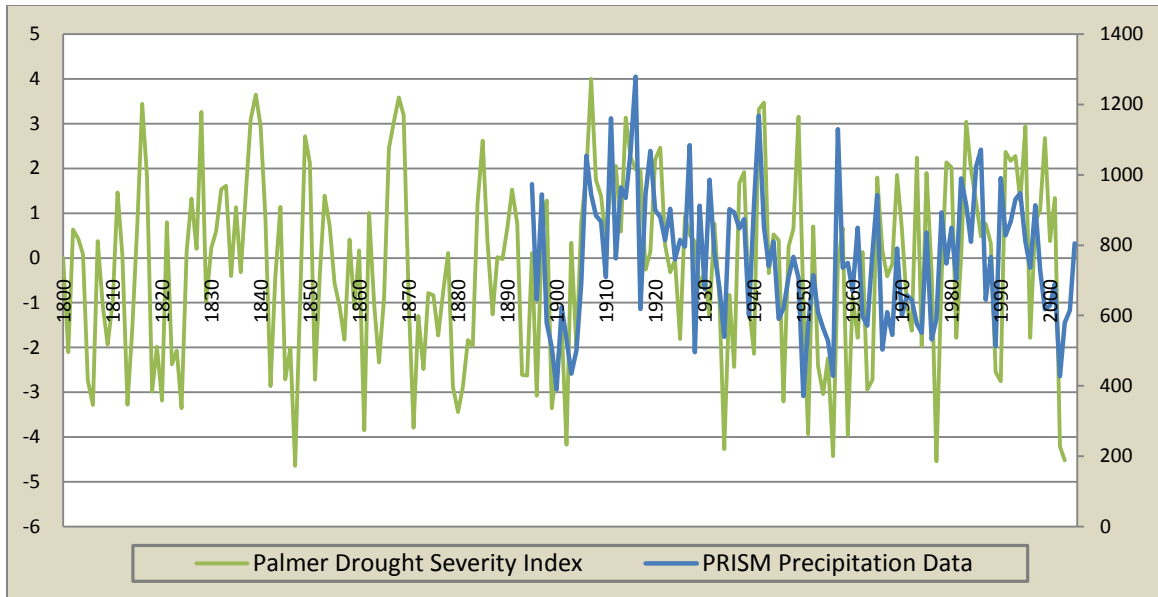


Figure 8. Climate history on Banded Peak Ranch. Left Y axis represents departure from the mean for the Palmer Drought Severity Index (i.e., positive numbers indicate relatively wet conditions; negative numbers indicate relatively dry); right Y axis represents annual precipitation in mm, based on PRISM data (a model derived from instrumental records collected at weather stations in the region). Note the wet period in the early 20<sup>th</sup> century when many of the trees now present on the ranch became established. Data sources: Cook and others 2004, PRISM 2008.

but this recent pulse would not be detected by my sampling method which intentionally emphasized sampling older trees. The relative lack of trees dating to earlier periods can be attributed in part to mortality from extensive late 19th century fires (see below), but 20th century logging undoubtedly also played a role (as mentioned above, many of the stumps remaining in my plots could not be sampled due to decay). Douglas-fir, white fir and ponderosa pine can all live to ages upward of 300 years, so the lack of trees dating back before 1850 indicates a disturbance such as logging or fire that took out many or most of the older trees<sup>2</sup>.

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<sup>2</sup> Since my sampling was not specifically targeted toward logged vs. unlogged areas, a different sampling design would be required to understand the change in overstory caused specifically by logging.

### Fire severity classification

Using the sampled data, I devised a list of evidence types that support the interpretation of either “high” or “mixed” severity, or a third category, “not fire initiated or >250 year fire interval” (Table 2). These latter stands did not contain any evidence of

Evidence of High Severity	Evidence of Non-Fire (NFI) or Fire Interval >250yrs
<p>A. Oldest tree in plot is POTR</p> <p>B. Plot contains one and only one even-aged aspen cohort (<math>\geq 5</math> trees recruited within a 10 year span), and all conifer recruitment post-dates it.</p> <p>C. Plot contains one even-aged conifer cohort per species (<math>\geq 5</math> trees of a single species recruited within a 20 year span, total span of recruitment not &gt;100 yrs); if in a plot containing POTR, conifer cohort post-dates it</p> <p>D. Truncated age structure (i.e., no trees recruited prior to X date, with that date being less than the known life span of the conifer species in the plot); only applies in unlogged plots</p>	<p>a. Presence of conifer &gt;250 years old</p> <p>b. PSME or PIPO oldest tree in plot (make note if logged)</p> <p>c. Continual recruitment within a species (over &gt;100 years, where no clear cohort is otherwise present), i.e., uneven-age</p> <p>d. Presence of stumps or undated samples <math>\geq 100</math> cm DSH</p>
Evidence of Mixed Severity	
<p>1. Presence of 1 or more fire scars in plot<sup>3</sup></p> <p>1a. Presence of 1 or more fire scars near plot</p> <p>2. One even-aged aspen cohort; conifer recruitment pre-dates it</p> <p>3. One even-aged aspen cohort; one or more aspen individuals date to earlier period</p> <p>4. One even-aged conifer cohort; one or more individuals date to earlier period</p>	<div style="border: 1px solid black; padding: 5px;"> <p>POTR = <i>Populus tremuloides</i> (aspen)</p> <p>PSME = <i>Pseudotsuga menziesii</i> (Douglas-fir)</p> <p>PIPO = <i>Pinus ponderosa</i> (ponderosa pine)</p> <p>DSH = diameter at sampling height</p> </div>

Table 2. Fire severity classification system.

<sup>3</sup> I distinguish between “in plot” and “near plot” because our other evidence types are strongly tied to exact “in plot” characteristics. The majority of my fire scar samples were found “near plot,” but should not be considered as strongly when determining fire severity “in plot.”

having been affected by fire within the last 250 years—but I have no way of knowing whether fire may have been present prior to that date. Thus the lack of fire evidence tells us that the plot either was not fire initiated, OR that the fire interval is so long that no evidence remains of any past fire. This does not preclude the possibility of, for example, a 275 or 300 year fire interval. In some cases, a subjective decision needed to be made in regard to whether or not samples that could not be dated (due to logging or rot or both) would have changed the interpretation of the data. It was not possible to devise consistent “rules” for these decisions. Generally, cohorts that were trending toward an even-aged condition led me to assume that the remaining samples were in the same age group, particularly if samples were of similar DBH (diameter at breast height) or DSH (diameter at sampling height). In cases where samples that could not be dated might have changed the decision, I looked at the DBH or DSH of the undated samples to see how they might relate to the dated samples. For each plot, I then listed which evidence types applied and made a final determination of fire severity. In most cases, plots contained evidence from just one of these evidence groups, but in cases where there was conflicting evidence, I looked more closely at the individual samples to try to determine which kind of evidence should take precedence over the others. (See Appendix A for the detailed forest structure used determine fire severity.)

### *Fire severity results*

Table 3 summarizes my conclusions about each plot, as well as the overall percentage of plots that contained mixed- vs. high-severity regimes. Overall, I found that 45% of my plots were historically high-severity, 25% were mixed-severity, 25% were not



fire-initiated (or time since last fire was so long that no fire evidence remained), and 5% were not determinable (Figure 9). All but one of the high-severity plots was located on the eastern side of the valley. (See Appendix B for a map of the plots with severity designations noted.) Two of the eastern sites, Johnson Mountain and Bull Elk Pond, were 100% high-severity, but while all the plots in the Bull Elk Pond site appear to date from the 1879 fires (i.e., all the aspen post-date 1879), the Johnson Mountain plots do not appear to have all burned in the same year (i.e., one plot burned at high-severity in 1879, but this fire did not occupy the entire *site*—other plots burned at high-severity in earlier years). Taken together with the other three eastern sites (1, 2 and 4 high-severity plots per site), I can infer that these high-severity fires varied in their size/extent, not surprising given the heterogeneous topography of the valley.

## DISCUSSION AND MANAGEMENT RECOMMENDATIONS

Many previous fire regime studies, particularly in ponderosa pine forest types, focused primarily on structurally-centered restoration practices in their management recommendations. In other words, dendroecological methods were used to ascertain the historical density, age structure, and species composition of the stands in question, and management techniques were geared toward achieving those historical standards. Various combinations of mechanical thinning and prescribed fire were then used by managers to meet these goals. Since that time, ecologists and managers have increasingly come to recognize that changing climate conditions dictate a more flexible restoration strategy, one based more on process than on structure (e.g., Falk 2006, Harris and others 2006, Millar and others 2007). More theoretical approaches include

reconceptualizing ecosystems in economic terms, and quantifying ecosystem “goods and services” and the processes that yield them (Harris and others 2006, de Groot and others 2002). In all cases, those interested in “process-centered restoration” (Falk 2006) recognize that many facets of future climate change are unknowable in the present, and thus require a management viewpoint that can adapt to changing conditions. The word “toolbox” often emerges in these papers, implying that priorities and goals will change over time, and that a variety of approaches will be implemented to achieve them. All of this points toward a management strategy based less on defined “targets” and “outcomes,” one wherein “success” may be less well-defined. The integration of science and management is a complex task, with the means and ends of each often coming into conflict. Below I discuss my results and management recommendations in that context.

### *Fire regime*

I found that the pre-European settlement fire regime of the mesic mixed-conifer forest on Banded Peak Ranch was much closer to its subalpine counterpart than to the montane ponderosa forest type. Fire scar evidence was scant, suggesting a relative lack of low-severity fire, while aspen and other age structure data support the widespread occurrence of stand-replacing fire. As for the length of time between these fires, an average number is difficult to pinpoint, since stand-replacing fires eradicate the evidence of fire in that location previously. Some of my plots may have experienced relatively short intervals such as that between the 1851 and 1879 fires. Some may have experienced very long intervals, as in the plots where no fire evidence remains.

How large were the high-severity patches in these historical fires? The data that I collected are not sufficient to answer this question definitively, but I can make some preliminary interpretations. Recall that each site consists of a central plot plus four additional plots arranged to form a square that is 500 m on a side. Because all five plots in the Bull Elk Pond site burned at high severity in 1879, I can infer that this patch of high-severity fire was approximately the size of the site, i.e., 500 m x 500 m, for an area of 250,000 m<sup>2</sup> (= 25 ha = 60 acres). The actual size of the patch might be larger or smaller than 25 ha, since the fire may have continued burning at high severity for a considerable distance outside the area of my site or it may have burned at lower severity in places within the interior of the site. Nevertheless, only this one of my eight randomly located sites had evidence of high severity fire in the same year in all five plots; all of the other sites recorded a mix of high severity, mixed severity, and non-fire initiated stands among the five plots, or a mix of high-severity fire in different years. This pattern suggests that high severity patches as large as an entire site, i.e., on the order of 25 ha or larger, were the exception rather than the rule; most patches apparently were smaller. I emphasize that this analysis is tentative, however. A new study with a different kind of sampling design would be needed to more rigorously document the the patch structure of historical fires. In forests with historical stand-replacing fires, the size of these fires, not their severity, will be the key to understanding their relationship to their HRV, and management steps that should or should not be taken in that context.

As Banded Peak Ranch managers have already learned, low-severity prescribed burns are very effective in reducing fuel loads and fire hazard in ponderosa pine forests, but are less effective in mesic mixed-conifer forests because the fuel structure is so

different in the two forest types. It is difficult to get low-severity fires to spread in the deep but compact fine fuels of a white fir stand, and once started, it often is difficult to keep the fire from spreading out of control into the canopy. In the mesic mixed-conifer forest, then, it may make sense to shift the focus from reintroducing fire (i.e., prescribed low-severity fire), to mechanically creating fire breaks within known larger patches of heavy small diameter fuel loading where the spread of a wildfire can be stopped or slowed. Eventually it may be feasible to safely ignite prescribed crown fires, which in small patches could be a very effective method for creating fuel breaks in mesic mixed-conifer forests. When safe methods for prescribed high-severity fire are confirmed, and all regulatory hurdles have been met, the possibility of reintroducing more extensive fire into mesic mixed-conifer forests can be revisited. At that point, if appropriate fuel breaks already have been created by mechanical means, the risk of “larger-than-usual” high-severity fire will be greatly reduced and some or many lightning-ignited fires may be allowed to burn without interference.

In addition to zones of high-severity fire, I also found evidence of mixed-severity fire, where patches of high- and low-severity fire have intermingled, or where more than one age cohort exists within a single plot. This suggests that although forests with stand-replacing fire regimes are generally not recommended for low-severity prescribed fire, there may be some stands where such prescription burns may be appropriate. In the Little Muddy plot, for example, the location happened to fall on an apparent boundary between dry and mesic mixed-conifer, the former having a much larger ponderosa pine component. Within my plots, white fir still dominated, but fire-scarred stumps indicated that at least some of the plots may previously have contained more pine, as well as a

larger component of historical low-severity fire. Restoration of low-severity fire through prescribed burning may thus not be inappropriate here.

#### *Historical range of variability (HRV)*

Over the ranch as a whole, the exclusion of fire over the last century has undoubtedly created patches that are outside their HRV (notably in the warm-dry mixed-conifer forests), but the ranch also includes large areas that are still within HRV (notably the spruce-fir forests at the highest elevations). What about the mesic mixed-conifer forests? Two elements of this question can be addressed as follows. First, regarding intervals between large fires, I note that no widespread fire has occurred since 1879, although another large fire is almost certain to occur eventually during some future year when the appropriate drought, wind conditions, and ignition coincide. However, I do not know if or just how far outside HRV the current fire interval may be, because the only previous large fire for which I have much information is the last one in 1879. I know that earlier fires occurred, but I do not know if those fires were as extensive as the 1879 fire. Thus, intervals between 1879-type fires may have been quite long even before the fire exclusion period. Secondly, regarding fire severity, if the next large fire is partially stand-replacing, this fact by itself will not indicate an ecosystem outside its HRV, because I know that the 1879 fire was stand-replacing in many places. What will be important in the next fire will be the proportion of that burned area that is stand-replacing. If most or nearly all of the area burned in the next large fire is stand-replacing, then it will be a very different kind of a fire than occurred in 1879, but if the next fire burns in a heterogeneous manner with intermingling patches of high and low severity

burning, then this will indicate that fire severity is still within HRV. In any event, a continued exclusion of high and mixed-severity fire from the landscape may begin to move more and more of the landscape outside of its HRV because of what will probably be a lengthier fire-free interval than anything in the past.

From a management perspective, it is important to remember that in forests where high-severity fire is *within* HRV, these fires will not “devastate” the landscape. It might be useful here to consider the relatively slow recovery of places where a *high*-severity fire burned in a historically *low*-severity location (such as Colorado’s recent Hayman Fire) versus the relatively swift recovery of places where a *high*-severity fire burned in a historically *high*-severity location (such as the Yellowstone fires). In the latter example, a so-called “catastrophic” series of wildfires produced robust post-fire regeneration—a mosaic of heterogeneous plant communities across what many feared would become a homogeneous moonscape of devastation (Turner and others 2003). This rapid regeneration is due to the adaptations to fire that the varying species have, such as sprouting ability in the case of aspen, or winged seeds in the case of some conifers. As documented above, I believe that significant portions of the mesic mixed-conifer landscape on Banded Peak Ranch burned at high-severity in the past, with another significant portion burning at “mixed” severity (where the severity is still “high” but is “mixed” with patches of no burning or low-severity burning). I can expect, then, that at least some portion of the landscape is will regenerate following high-severity fire.

The most important factors affecting regeneration after high-severity fire are patch size of burned areas (i.e., what is the greatest distance to the nearest surviving source of new seeds?) and the life history strategies of the tree species in question (i.e.,

can they re-sprout from surviving roots, and if not, what kinds of seeds do the trees produce, how are they dispersed, and how likely are they to germinate in post-fire conditions?). With regard to patch sizes, my study found that even in the extensive 1879 fires, the sizes of individual burned patches varied greatly on the landscape. Some were larger than my 25 ha (60 acre) study sites, while others were smaller than a single 30-tree plot within a site. The number of plots showing evidence of mixed severity within a single plot also confirms my view that patches of low severity and high-severity fire are sometimes closely intermingled, and that intervals between successive high-severity fires at a point on the ground may vary widely. While my study could not reconstruct every square meter of the burn pattern across the forest, we can reference the findings in the modern-day Yellowstone fires, where researchers have found that most locations with high-severity burn patches (even in those very extensive fires) were within 50 - 200 m (165-650 feet) of a low-severity or even unburned patch (Turner et al. 2003). Banded Peak Ranch contains more rugged topography than Yellowstone, so I can hypothesize that the opportunity for an even more heterogeneous burn pattern might exist here. In other words, the probability of a mosaic pattern of burning on Banded Peak Ranch, even under high-severity conditions, is likely quite high. This would ensure that burned areas would have a good chance of being close enough to unburned or lightly burned patches to receive seeds from surviving trees.

With regard to the second factor affecting post-fire regeneration—the life history strategies of the trees—many of the mesic mixed-conifer species have reproductive strategies that are well-adapted to surviving high-severity fire. Unlike ponderosa pine seeds, which are relatively large, and subject to being eaten by insects, birds, and small

mammals even before they reach the ground, many of the mixed-conifer species (such as Engelmann spruce, subalpine fir, and white fir) have lighter, winged seeds that are wind-dispersed. These seeds can be carried from unburned areas to burned areas more readily than the heavier seeds of ponderosa pine, perhaps explaining in part why ponderosa pine forests often regenerate more slowly after high-severity fire. My study showed that while aspen and white fir dominate over the landscape as a whole, species composition on a plot to plot basis is quite mixed (see Appendix A). This mix of trees at a fine scale may provide a more varied seed source than the overall species composition might otherwise suggest.

One species of concern, however, is Douglas-fir. Because of previous logging activity on the Ranch, large Douglas-fir trees are now relatively scarce in much of the mesic mixed-conifer forest, and some of those that do remain are surrounded by a dense grove of small white fir that could carry a fire into the crowns of the large Douglas-fir. It might be feasible and appropriate to survey the locations of healthy, large Douglas-fir trees (and other conifer species) that could serve as seed sources after the next fire, and remove any white fir that are found to be crowding around them. This kind of mechanical thinning would not be emulating a “natural” process, because it would be “natural” for these large trees to be killed in a fire, but protecting the remaining seed trees would help to compensate for the “unnatural” loss of these trees to 20<sup>th</sup> century logging.

## CONCLUSION

My study found that both high- and mixed-severity fire occurred naturally on the landscape, and that the patch sizes of burning were quite heterogeneous. The main



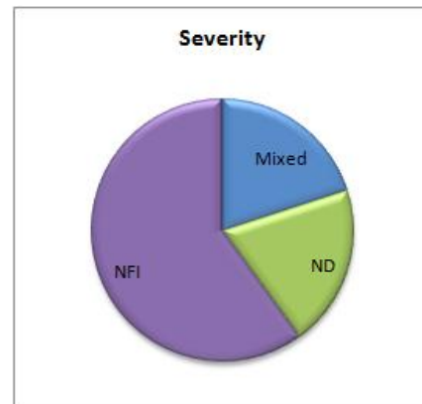
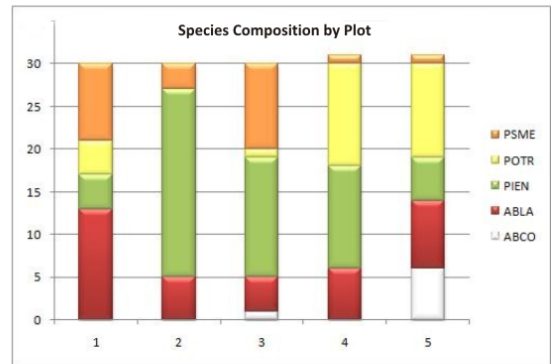
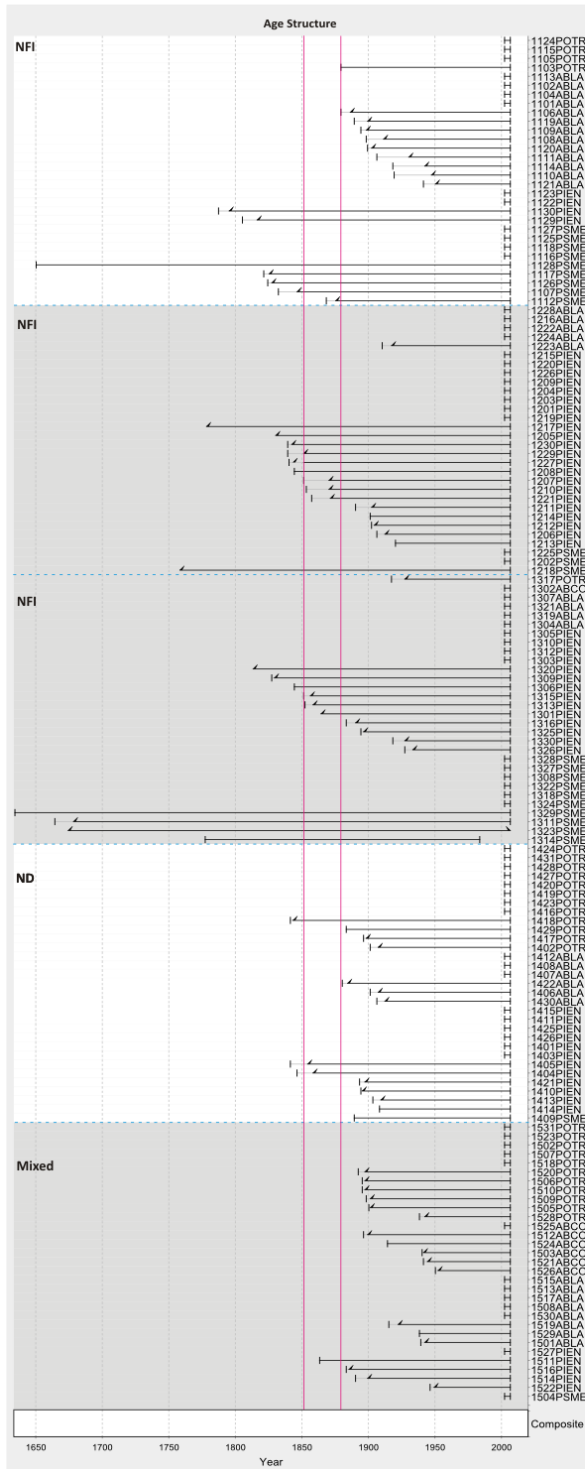
concern from a present-day management perspective, then, is whether a high-severity fire today might be larger in *extent* than under historical conditions, not whether a high-severity fire will burn in a formerly low severity location. Further research is needed to determine the outcomes for biodiversity and general ecosystem function in the case of *larger* than usual high-severity fires, as opposed to fires that are more *severe* than usual. 1879 was a large fire year throughout the southwestern United States, and Banded Peak Ranch certainly experienced areas of both high and low-severity burning in that year. However, even in this widespread fire year, some, if not most, of the western portion of the ranch appeared to escape burning, and patches of fire on the eastern side apparently were not continuous. I expect that a future large fire will burn in a manner generally similar to that of the 1879 fire, even though specific locations of burning will differ. Thus, even if some portions of the landscape are outside of HRV (i.e., have unnaturally high fuel loads and are more susceptible to a climate that may be warmer and drier than in the past), the complex topography and heterogenous vegetation patterns of the ranch will likely prohibit a valley-wide conflagration. Based on the information I have at present, efforts to mitigate future fire severity in areas remote from ranch infrastructure do not appear necessary. However, fuel reduction to create defensible space around buildings and other vulnerable infrastructure should be a high priority, because another extensive and likely severe fire like the one in 1879 will almost certainly occur at some point in the future.

As I noted in the introduction, the term “mixed-conifer” may refer to a much broader range of forest types than the adjacent forest types we call “montane ponderosa pine” or “subalpine spruce-fir.” Even within the relatively short distance encompassing

the Rocky Mountains in Colorado, the species composition in so-called “mixed-conifer” can vary widely. For example, white fir only occurs in southern Colorado, while lodgepole pine occurs only in the northern portion of the state. As such, any discussion concerning fire regimes in mixed-conifer forests, or management practices therein, should be careful not to extrapolate from one kind of “mixed-conifer” forest to another. The mesic mixed-conifer in the San Juan Mountains may bear a greater resemblance to its subalpine neighbor, with top-down effects such as climate serving as the primary driver of fire occurrence, but management decisions in specific locations will still need to consider the bottom-up drivers such as topography and microclimate that can lead to the heterogeneity of “mixed-conifer” that we see on the ground.

APPENDIX A. DETAILED FOREST STRUCTURE AND SPECIES COMPOSITION DATA

## Dolomite Lake



### LEGEND

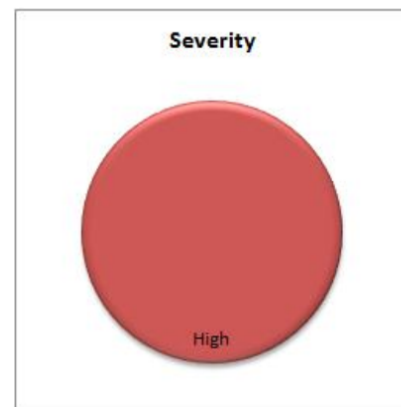
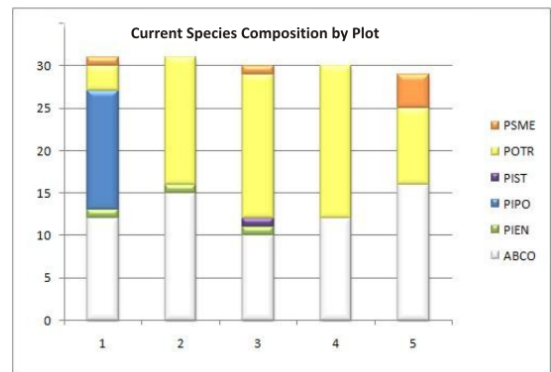
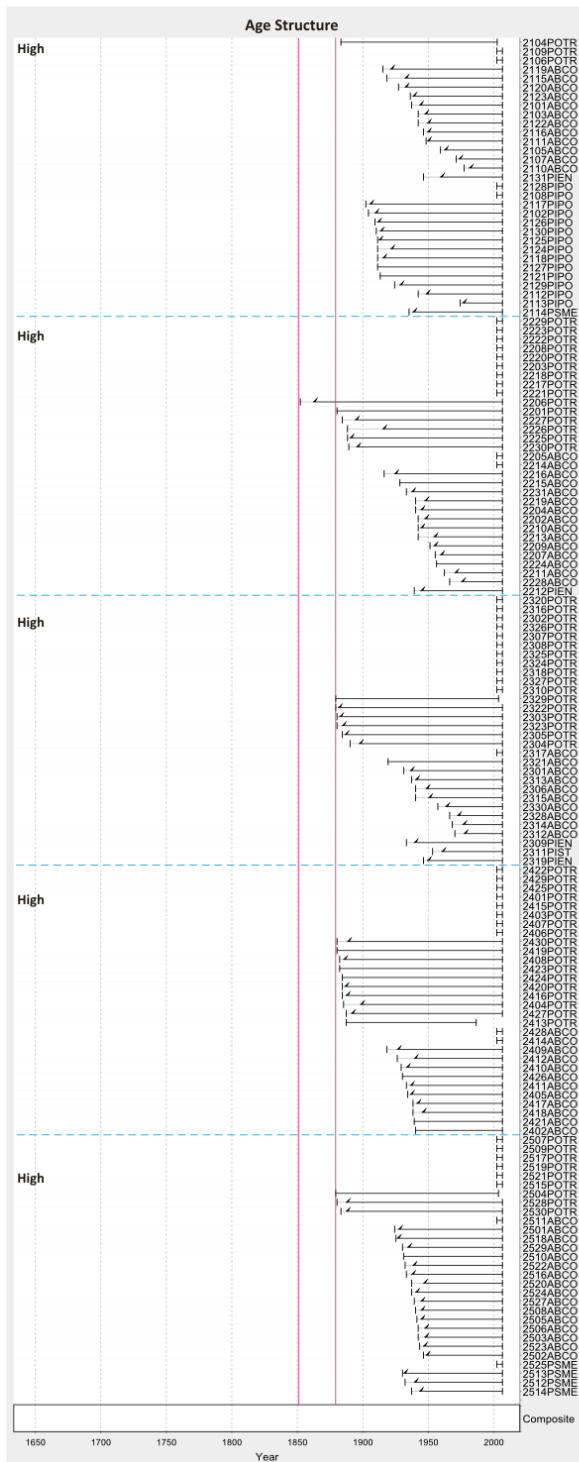
ABCO = white fir (*Abies concolor*)  
 ABLA = subalpine fir (*Abies lasiocarpa*)  
 PIEN = Engelmann spruce (*Picea engelmannii*)  
 PIPO = Ponderosa pine (*Pinus ponderosa*)  
 PIPU = blue spruce (*Picea pungens*)  
 PIST = Southwestern white pine (*Pinus strobiformis*)  
 POAM = narrowleaf cottonwood (*Populus angustifolia*)  
 POTR = quaking aspen (*Populus tremuloides*)  
 PSME = Douglas-fir (*Pseudotsuga menziesii*)

Pink lines represent the major western fire years of 1851 and 1879.

H = undateable

estimated inner date  
 pith date outer date  
 = logged

# Bull Elk Pond



## LEGEND

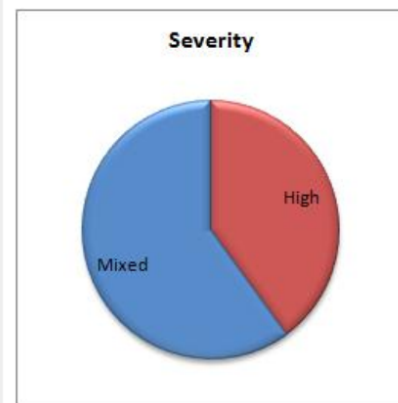
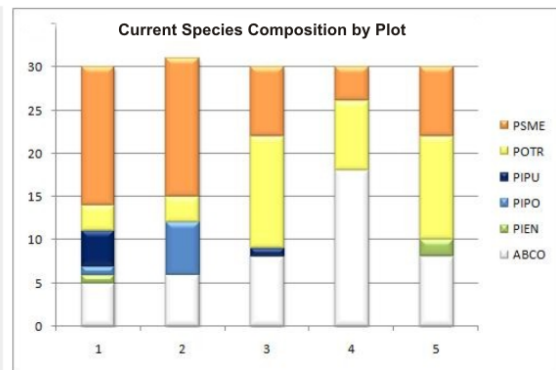
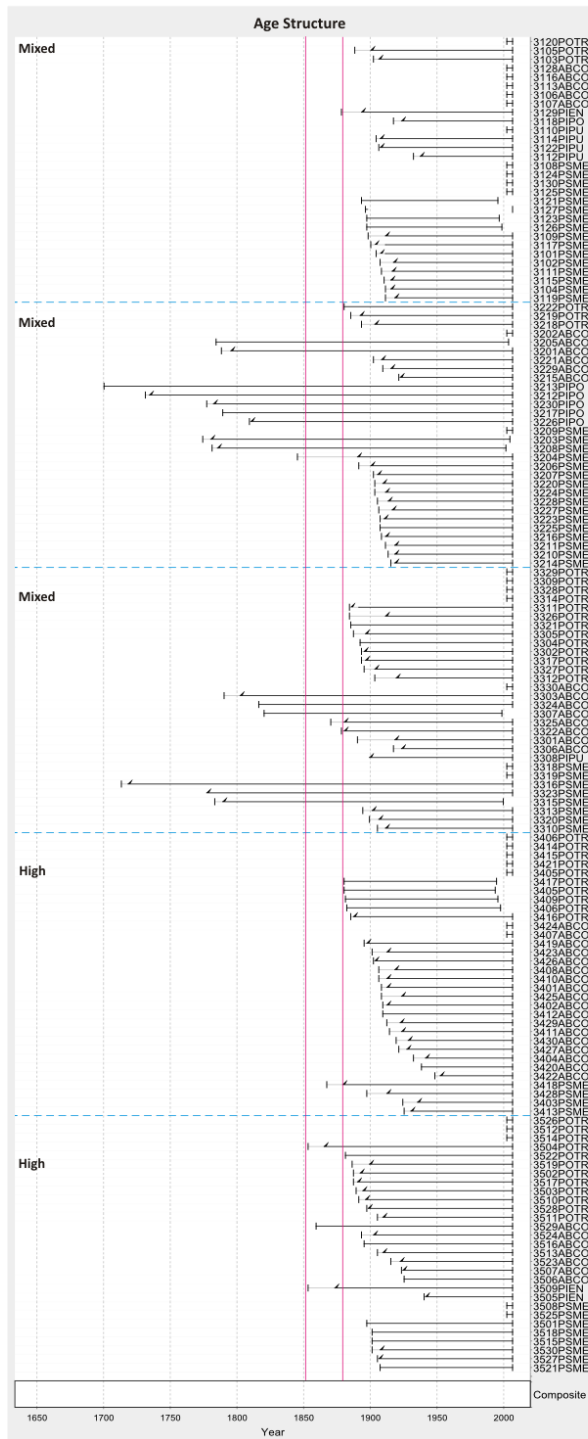
ABCO = white fir (*Abies concolor*)  
 ABLA = subalpine fir (*Abies lasiocarpa*)  
 PIEN = Engelmann spruce (*Picea engelmannii*)  
 PIPO = Ponderosa pine (*Pinus ponderosa*)  
 PIPU = blue spruce (*Picea pungens*)  
 PIST = Southwestern white pine (*Pinus strobiformis*)  
 POAM = narrowleaf cottonwood (*Populus angustifolia*)  
 POTR = quaking aspen (*Populus tremuloides*)  
 PSME = Douglas-fir (*Pseudotsuga menziesii*)

Pink lines represent the major western fire years of 1851 and 1879.

H = undateable

estimated inner date  
 pith date outer date  
 = logged

## Little Muddy



### LEGEND

ABCO = white fir (*Abies concolor*)  
 ABLA = subalpine fir (*Abies lasiocarpa*)  
 PIEN = Engelmann spruce (*Picea engelmannii*)  
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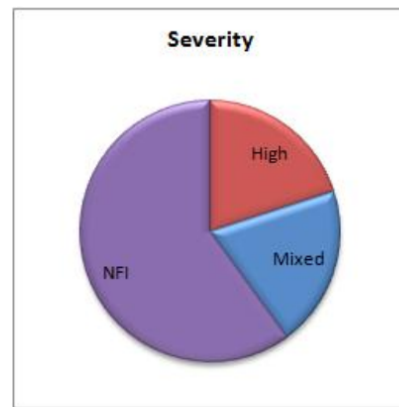
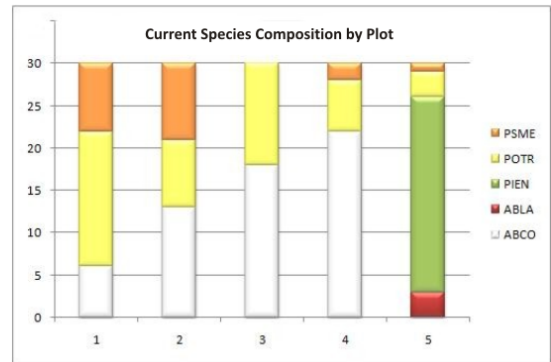
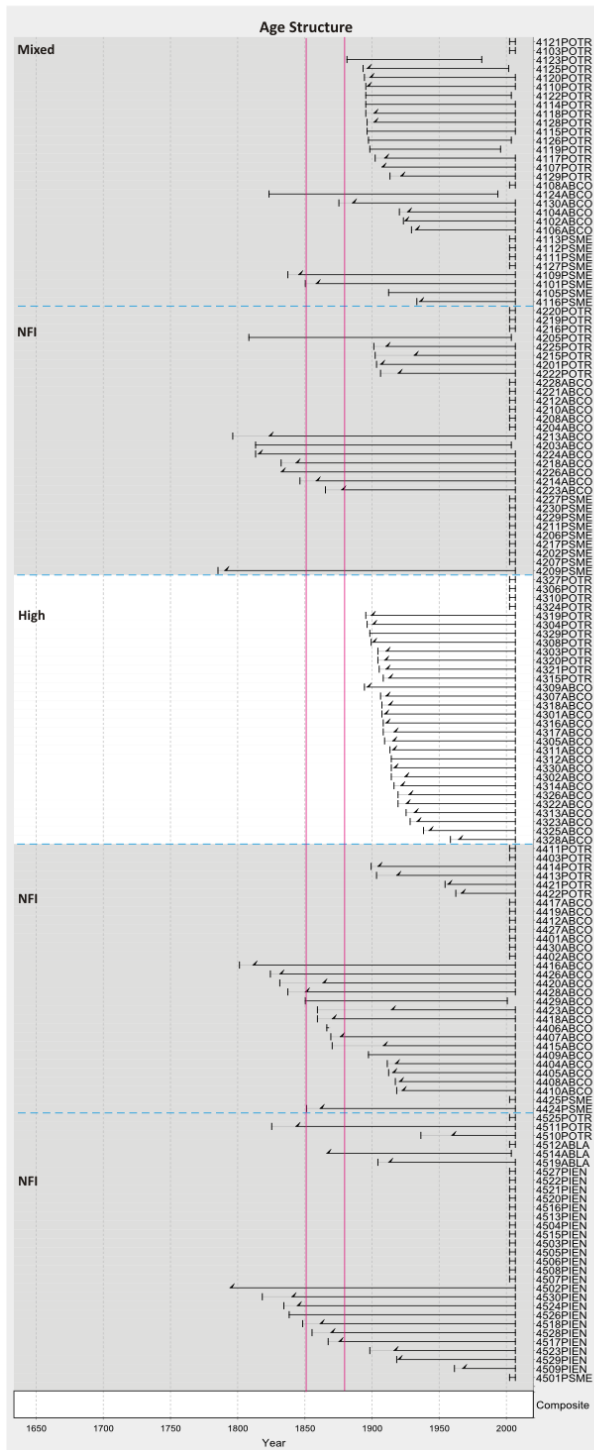
Pink lines represent the major western fire years of 1851 and 1879.

H = undateable

The diagram shows a horizontal line representing a tree segment. From left to right, it is divided into three parts: a small shaded triangle labeled 'inner date', a larger unshaded triangle labeled 'estimated', and a final section labeled 'outer date'. A vertical line at the far left is labeled 'pith date'.

☐ = logged

# Bear Creek



## LEGEND

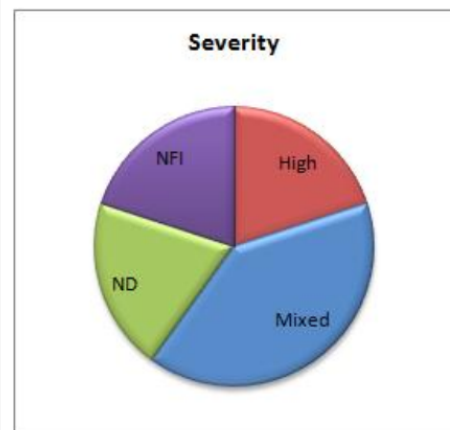
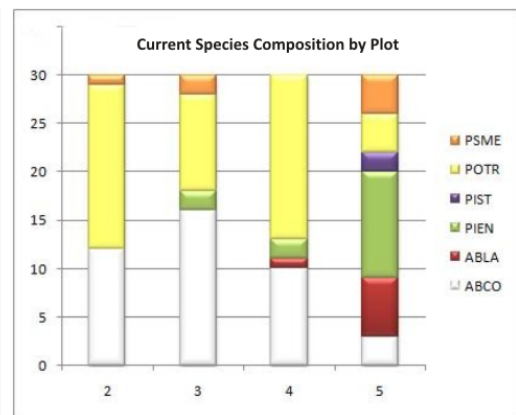
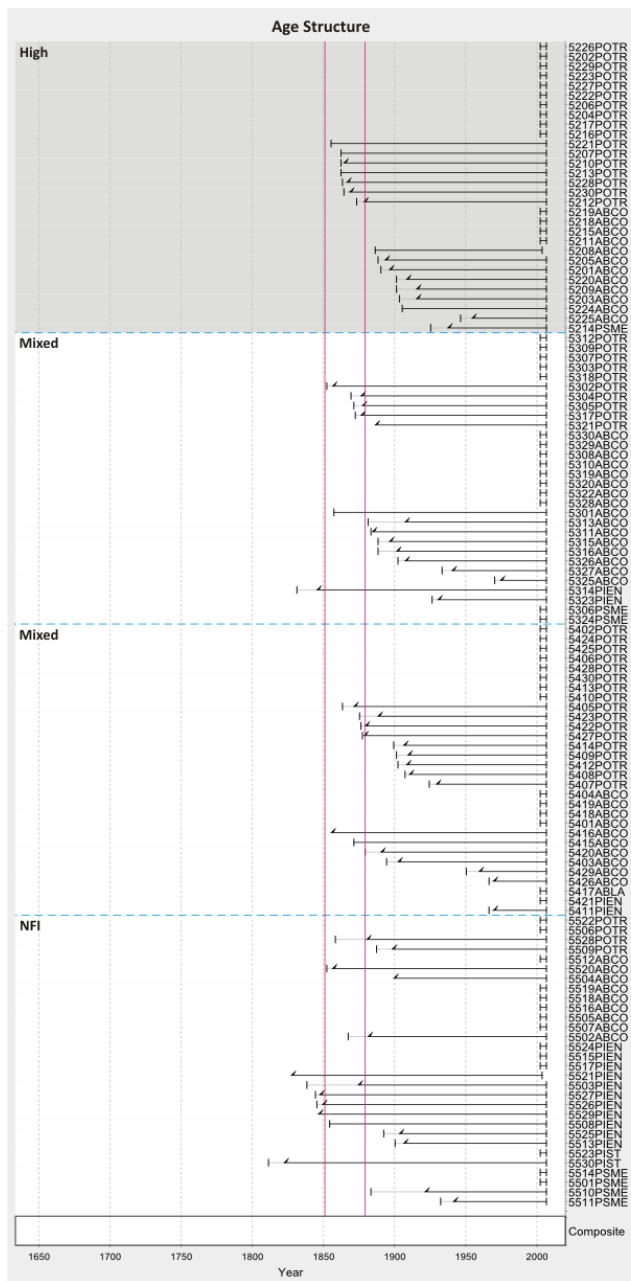
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Pink lines represent the major western fire years of 1851 and 1879.

H = undateable

estimated inner date  
 pith date outer date  
 = logged

# Elephant Head



## LEGEND

ABCO = white fir (*Abies concolor*)  
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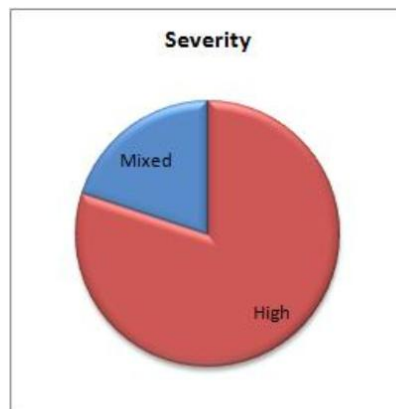
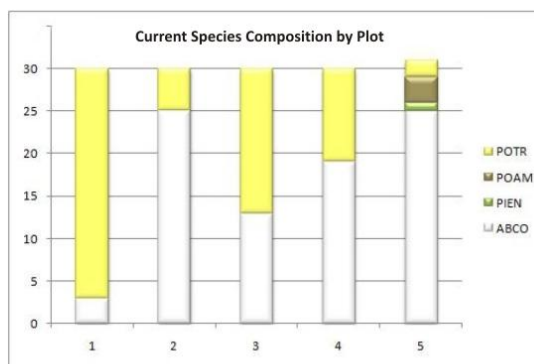
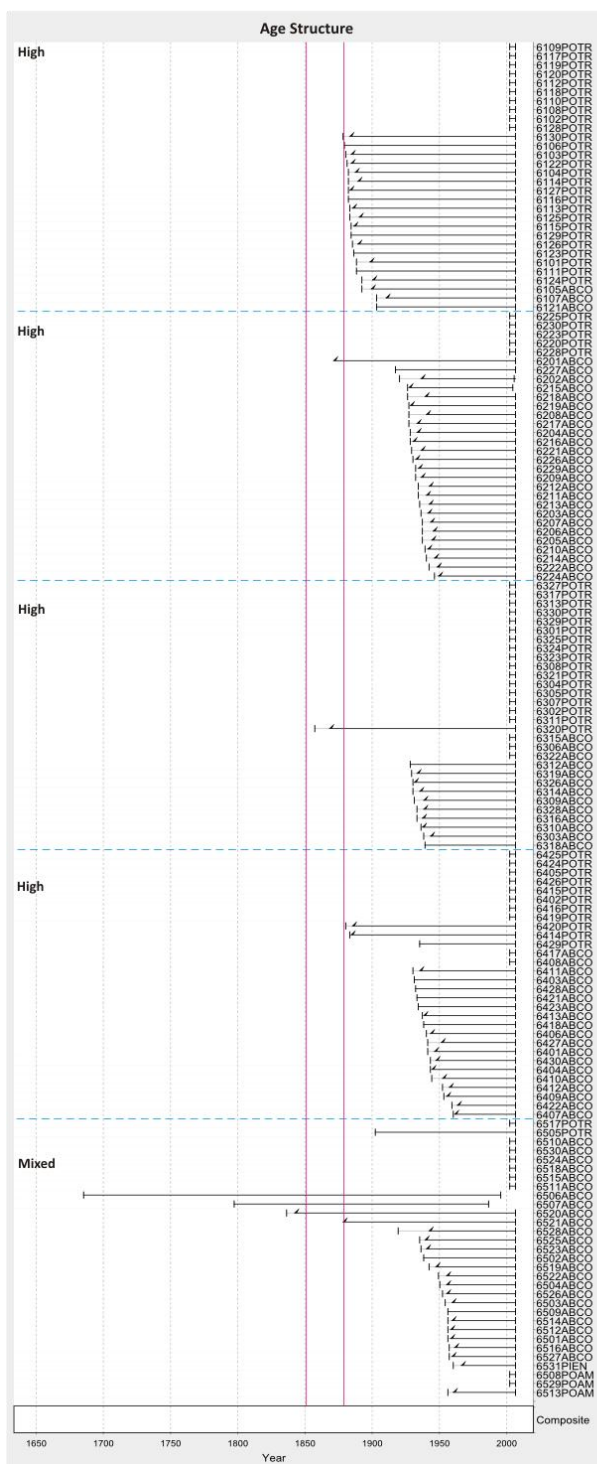
Pink lines represent the major western fire years of 1851 and 1879.

H = undateable

estimated inner date  
 pith date outer date  
 = logged



## Big Muddy



### LEGEND

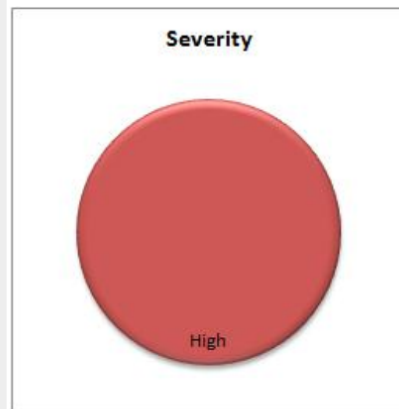
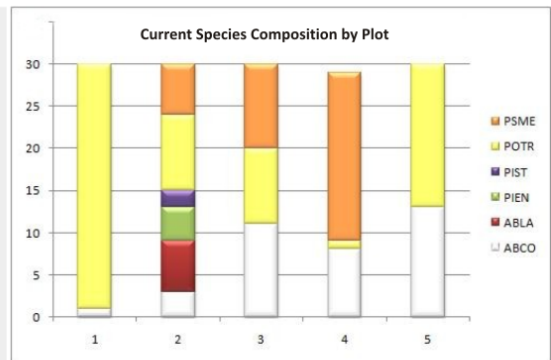
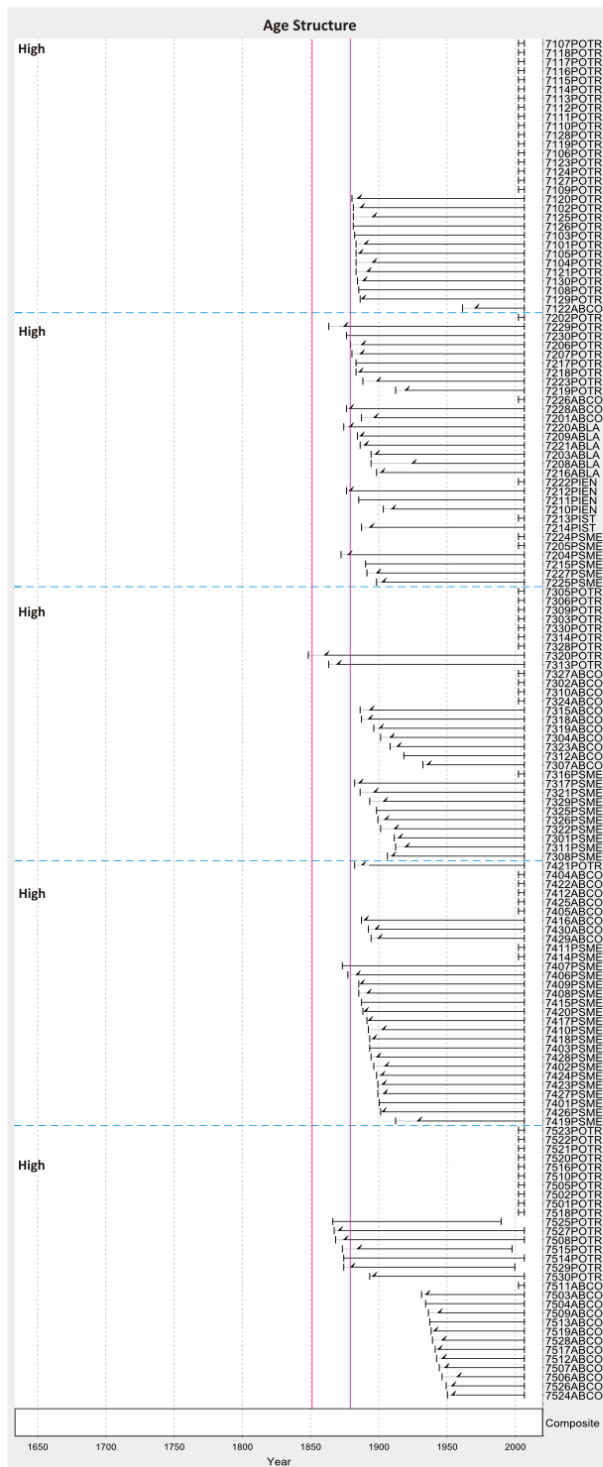
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 PSME = Douglas-fir (*Pseudotsuga menziesii*)

Pink lines represent the major western fire years of 1851 and 1879.

H = undateable

The diagram shows a horizontal line representing a tree-ring segment. From left to right, it is divided into four sections: a small section labeled 'estimated', a section labeled 'inner date' with a black wedge at its left boundary, a large section labeled 'outer date', and a small section at the far right labeled 'pith date'. Below the line, a grey box contains the text '= logged'.

# Johnson Mountain



## LEGEND

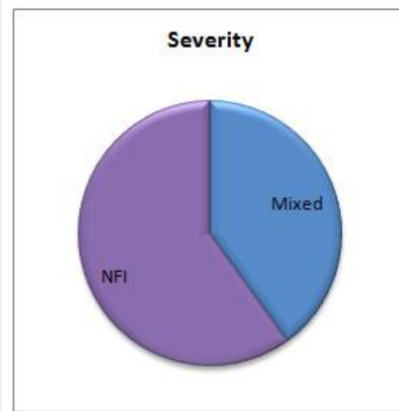
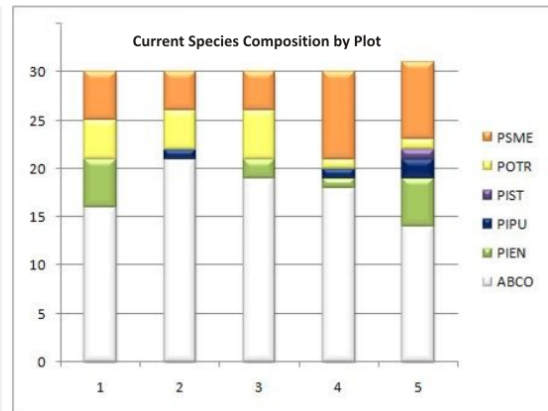
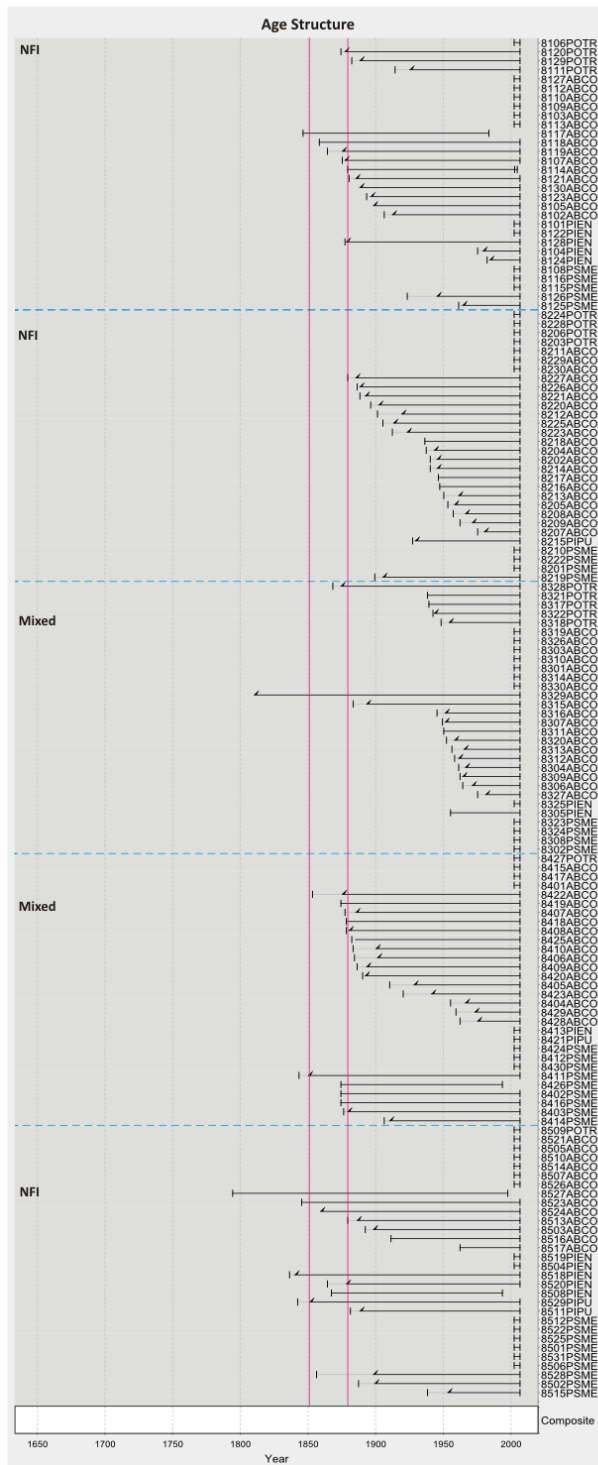
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 PSME = Douglas-fir (*Pseudotsuga menziesii*)

Pink lines represent the major western fire years of 1851 and 1879.

H = undateable

estimated inner date  
 pith date outer date  
 = logged

# Beaver Creek



## LEGEND

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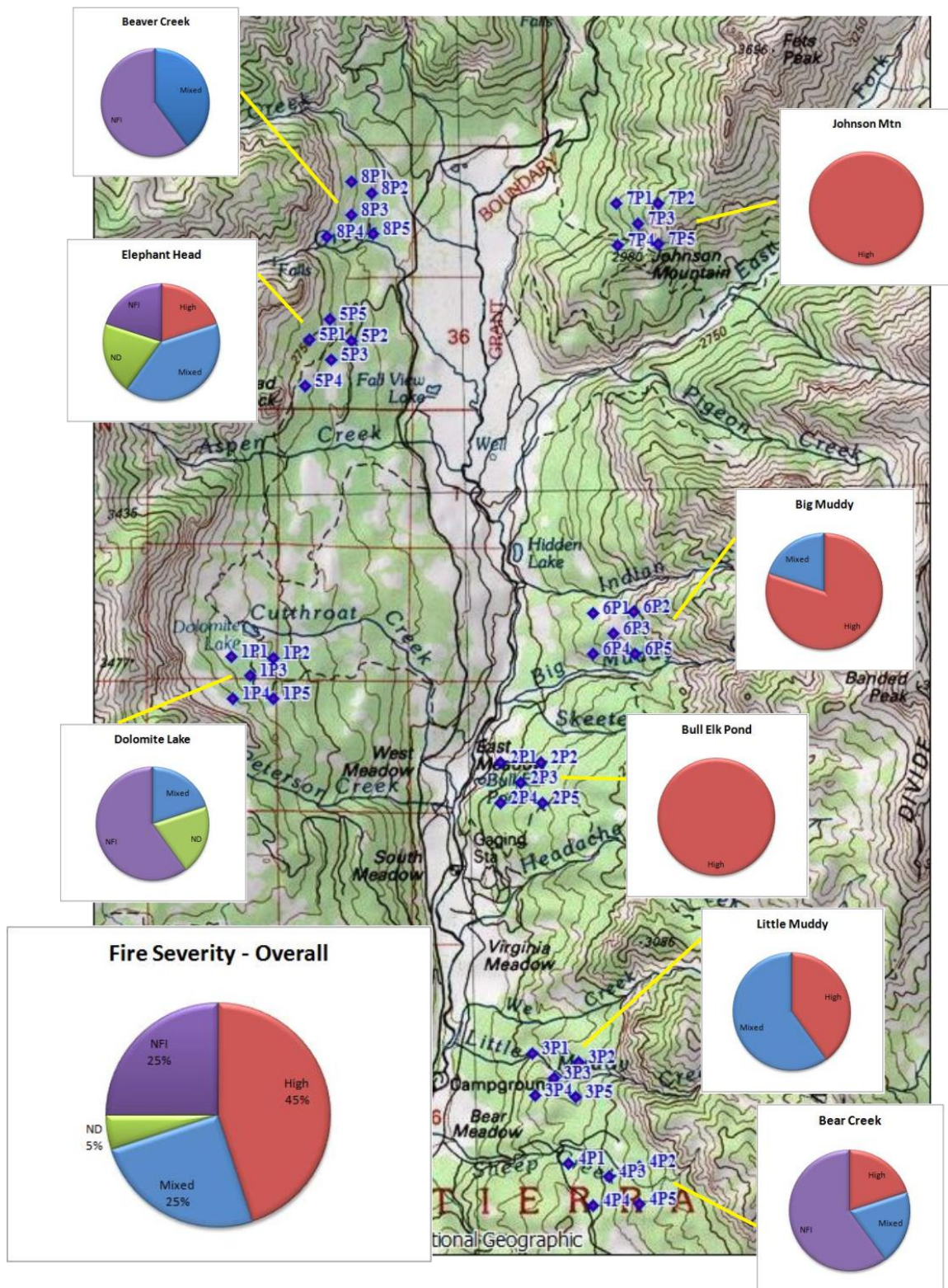
Pink lines represent the major western fire years of 1851 and 1879.

H = undateable

estimated inner date  
 pith date outer date  
 = logged

## APPENDIX B: FIRE SEVERITY MAP





## **Chapter 2: Lodgepole pine serotiny in Rocky Mountain National Park**

### INTRODUCTION

Lodgepole pine (*Pinus contorta*) is a two-needled pine occurring in four geographically distinct varieties across North America (Lotan and Critchfield 1990). The dominant varieties are coastal pine, *Pinus contorta* var. *murrayana*, and Rocky Mountain lodgepole pine, *Pinus contorta* var. *latifolia*. The latter are distinguished by the occurrence of serotinous cones, which require high heat to open and disperse their seeds (e.g., Clements 1910; Johnson and Gutsell 1993; Knapp and Anderson 1980). These cones protect their seeds during the primary heating event of a fire, releasing them afterwards so that they can provide the next generation of seedlings. Individuals of this variety, however, do not display the serotinous trait uniformly--both serotinous and non-serotinous cones are produced within any given stand, and sometimes even on a single tree. Research has shown that the occurrence of serotiny within stands affected by fire can have a tremendous impact on post-fire regeneration (Schoennagel et al. 2003; Tinker et al. 1994; Turner et al. 1997).

The relationship between serotiny and fire has long been known, having been documented in the early 20<sup>th</sup> century by Tower (1909), Clements (1910) and Mills (1915), among others. That fire is typically required to open serotinous cones is well-established, but the relationship between various fire regime parameters and the percent occurrence of serotiny among individuals and among stands has been more difficult to

explain. The three measures of fire regime that can be measured on a historical basis and thus related to serotiny are fire severity, fire frequency, and, in higher elevation systems, time since last stand-replacing fire (stand age)<sup>4</sup>. Abiotic factors that influence the occurrence of fire, such as elevation, aspect, and local moisture may therefore also have a significant relationship to the occurrence of serotiny on a landscape. Indeed, in the absence of detailed fire history data, the latter often serve as more easily-measured proxies for fire.

Rocky Mountain National Park (ROMO) offers an ideal location to study serotiny in inland lodgepole pine. The steep eastern side of the park contrasts with the more gentle western side, and the Continental Divide provides two different moisture regimes, with orographic uplift enhancing winter precipitation on the wetter west side, against the drier east side's rain shadow. The lodgepole pine community in the park thus represents a broad range of conditions under which this species can be found in the Rocky Mountains, but a broad-scale study of serotiny in the park has never been conducted. My study had two aims: 1) to describe the occurrence of serotiny in ROMO; and 2) to characterize the abiotic variables that influence the expression of serotiny on the landscape.

## METHODS

### *Study Location*

Established in 1915, Rocky Mountain National Park lies approximately 90 km northwest of Denver, Colorado, and comprises approximately 107,600 hectares in the

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<sup>4</sup> Note that the latter should not be confused with fire frequency in high elevation forests.

Front Range (Figure 1). The Continental Divide bisects the park from north to south. Forest types within the park range from montane ponderosa pine to subalpine spruce-fir. Lodgepole pine occurs extensively throughout the park, in the intermediate elevations between the montane and the subalpine, from approximately 2300 to 3500 m. Precipitation varies from the east to the west sides of the park, with an average annual precipitation of 500 mm at Grand Lake (west), and 390 mm at Estes Park (east)<sup>5</sup>.

## METHODS

### *Field Sampling*

Prior to conducting my sampling, I needed to devise a method to evaluate the serotiny status of a given tree. Previous research in Yellowstone National Park had identified morphological characteristics of individual cones, which could be used in the identification of a cone as “serotinous” or “non-serotinous” (Tinker et al. 1994). However, my field observations led me to believe that the lodgepole pine in ROMO did not have the same morphological characteristics. I therefore devised a dichotomous key which I used to identify trees as either serotinous, non-serotinous, or of mixed serotiny (see Appendix A). While serotinous cones generally open with the heat from fire, a small percentage of serotinous cones may in fact open over time even in the absence of fire, making it difficult to simply use “open” versus “closed” to determine the serotiny of cones on a tree. A recent mountain pine beetle (*Dendroctonus ponderosae*) outbreak had caused extensive mortality in many of the stands that I sampled; many serotinous cones were beginning to open in response to warmer conditions, thus accentuating this potential

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<sup>5</sup> Data at <http://ccc.atmos.colostate.edu/dataaccess.php>.



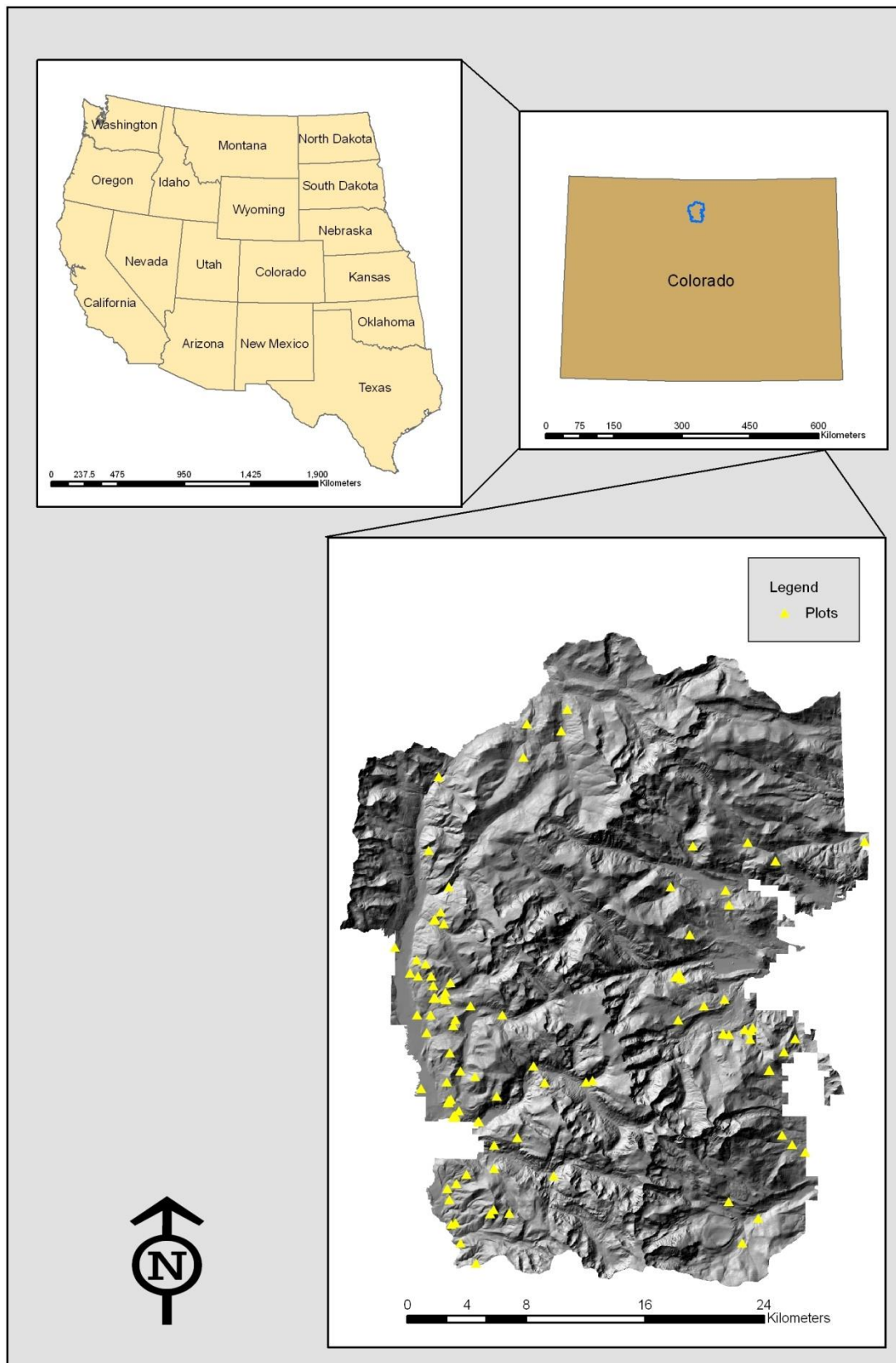


Figure 1. Map of Rocky Mountain National Park location and plots.

problem. I wanted to be certain that I did not misidentify an open serotinous cone as a non-serotinous one, and vice versa. Of the trees with “open” cones, my key distinguishes between trees that contain a majority of serotinous cones, some of which may be open; trees that contain a mix of serotinous and non-serotinous cones; and trees that contain only non-serotinous cones. In the field, I used binoculars to observe the cones on the trees.

Using the park’s vegetation maps, potential sampling locations were selected from all areas within the park containing lodgepole pine. Sampling points were generated on the landscape using a spatially balanced randomization method (Theobald et al. 2007). At each point, I laid out a cluster of three plots, each of which was 20 m x 20 m. The first plot had its southeast corner at the randomly generated point. The second plot was placed at a random azimuth to the first, 60 m from the original point. The third plot was placed at 90 degrees in a clockwise direction from the second point, 90 m from the original point. At each plot, I recorded the elevation, aspect, and slope, then conducted a complete census of the trees greater than 1.4 m in height. In a few exceptional cases, where a plot was particularly dense, a partial section of the plot was censused, then multiplied to obtain total numbers for the plot. For each tree, I recorded its species, diameter at breast height, whether it was living or dead, and serotiny status. The number of mixed serotiny trees was very small, and as a result, these were merged with the trees counted as serotinous. In some cases, trees did not have cones, or they were not visible from the ground. In these cases, I marked the serotiny as indeterminate. Only trees for which I could determine the serotiny were included in my total

calculations. To determine the approximate age of each stand, I used an increment borer to obtain a core sample from three trees in or near the plot. Trees were sampled at 10 cm height to minimize the number of missed years between ground level and coring height. The cores were later mounted and sanded, and the rings counted. In addition to the data collected in the field, I also used data contributed by Jason Sibold. Sampling methods are described in Sibold et al. (2007). Aspect was re-sampled according to the method below, and additional topographic variables were calculated in the same manner for both datasets.

#### *Additional topographic variables*

Initial data exploration indicated that the occurrence of serotiny on the landscape might be influenced by environmental variables beyond the slope, aspect, and elevation I collected as part of my original field sampling. I added three additional variables to the dataset, all calculated from the 10 m DEM obtained from the USGS seamless website. The first was solar radiation, calculated for an estimated “fire season length,” beginning with the spring equinox and ending with the fall equinox. Next I calculated the topographic convergence index (TCI), a measure of moisture at a point on the landscape, calculated from its upslope contributing area (Beven and Kirkby 1979). Both solar radiation and TCI were calculated in ArcGIS 9.2 (ESRI 2009). Finally, to calculate a measure of landscape roughness, I obtained assistance from David Coblenz of Los Alamos National Laboratory. He generated roughness data using the eigenvector ratio method (Guth 1999; McKean and Roering 2004) running in the program MicroDEM. The value was calculated in windows of increasing size, and as these converged at 600 m,

I used the values obtained from this window size in my analysis. Finally, in addition to supplementing the dataset with these new variables, I also replaced the aspect value collected in the field with a smoothed value calculated in a 5 x 5 neighborhood block from a 30 m DEM of the park. Aspect values collected in the field reflect only the aspect within the 20 x 20 m plot, and do not reflect the broader-scale aspect that may actually influence the response variable in question. Because aspect values are circular, the new aspect values were further transformed into two variables, northness and eastness, each of which ranges from -1 to 1. Northness was calculated as  $\cos(\text{aspect})$  and eastness as  $\sin(\text{aspect})$ .

### *Statistical Analysis*

The serotiny data for each cluster was recorded as a proportion. Investigating multiple independent variables that may affect a binomial response variable is often done by multiple logistic regression. My attempts to utilize logistic regression, however, were hampered by resulting overdispersion. I turned instead to regression tree analysis, from a family of methods sometimes referred to as CART (classification and regression trees). Analyses were accomplished in the “rpart” package in the software R (R Development Core Team 2009). CART methods have been in practice for over twenty years (Breiman 1984), but have only come into use by ecologists in the past decade (De'ath and Fabricius 2000; McCune and Grace 2002).

## RESULTS

### *Descriptive statistics*

As Clements observed a century ago, “Individual trees in the same stand show the most extreme differences in cone opening” (1910). Across the park, serotiny varied from 0 to 97% (Table 1), with a mean of 58%. Notably, serotiny was higher on the west side than the east side, with a median value of 69% on the west side and 52% on the east side. Serotiny also varied more widely on the east side, with a standard deviation of 32% versus 18% on the west side.

### *Regression tree analysis*

Summary statistics for the independent variables are shown in Table 2. The regression tree analysis narrowed the list of variables to just three: elevation, eastness, and topographic convergence index (TCI) (Figure 2). Both elevation and TCI were utilized more than once in subsequent splits. Higher serotiny was associated with lower elevations, lower eastness (i.e., more west-facing), and lower TCI (i.e., less wet topography). The analysis rejected the variables of slope, stand age, solar radiation, and topographic roughness.

## DISCUSSION

Although researchers in lodgepole pine have known about the relationship between fire and serotiny for over a century, the exact nature of that relationship has proved complex and difficult to explore. The mere occurrence of the trait appears to vary

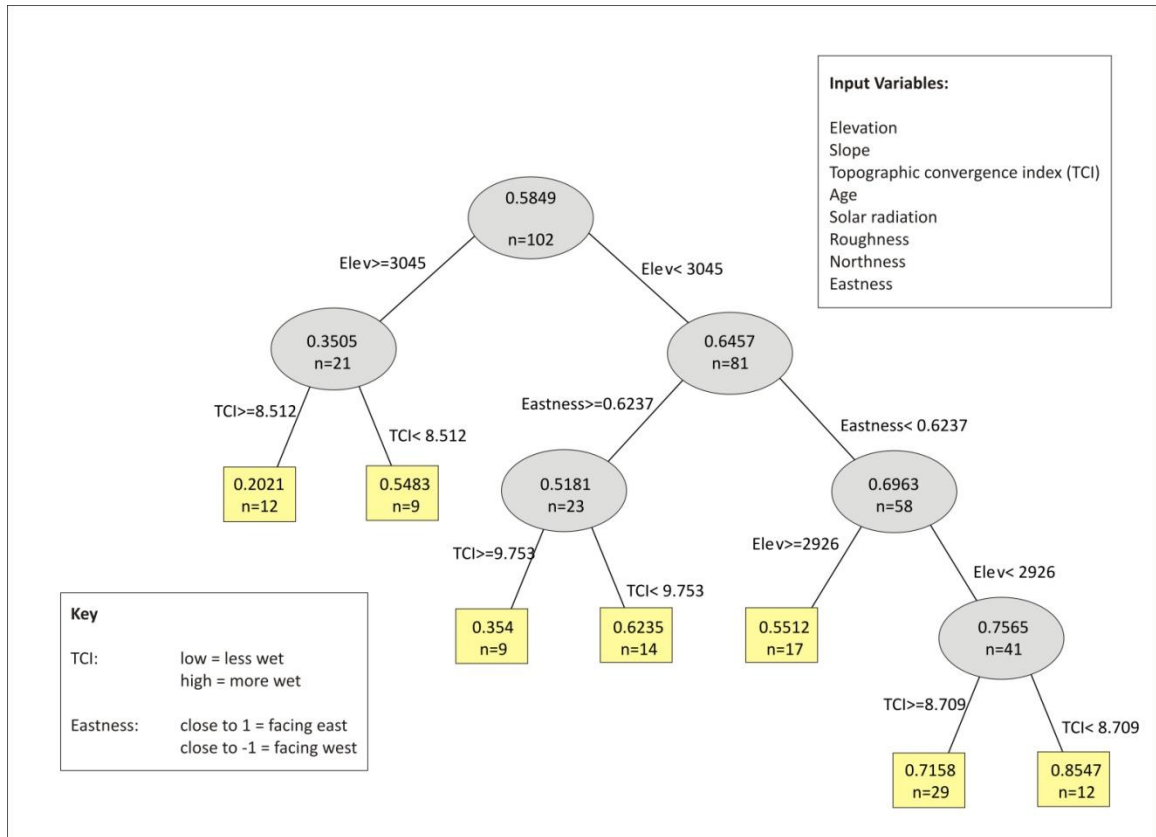


Figure 2. Regression tree output for the response variable proportion serotinus.

widely from one location to another. With a median serotiny level of 64% over 102 plots, I found higher levels of serotiny overall than had been found in previous research in Yellowstone National Park (Schoennagel et al. 2003; Tinker et al. 1994) and in Montana (Muir and Lotan 1985). In other words, “high serotiny” in one location may mean something different than “high serotiny” in another location. We can, however, draw some general conclusions from prior research to date.

Previous workers have demonstrated a relationship between serotiny and elevation (Schoennagel et al. 2003; Tinker et al. 1994), with lower percent serotiny at high elevations. Since lower elevations, which tend to be drier, generally have a higher occurrence of fire, this suggests a relationship between serotiny and “more fire.” We

should not, however, conflate this with a relationship with “fire frequency.” Muir and Lotan (1985) showed that high serotiny was related to stand-replacing fire, but not to lower severity fires. Gauthier et al. (1996) obtained similar results in jack pine, a serotinous species in Canada that sometimes hybridizes with lodgepole pine (Lotan and Critchfield 1990). When we refer to “fire frequency” and serotiny, we should be careful to distinguish between the frequencies of high-severity fire regimes versus the frequencies of low-severity ones. I will return to this issue below.

Schoennagel et al. (2003) additionally showed an interaction between age and elevation, with all high elevation stands having low serotiny, while stands at lower elevations varied quadratically with age—the very youngest and very oldest stands had low serotiny, while the “middle-aged” stands had the highest levels of serotiny. This supports the earlier work of Mason (1915) and Crossley (1956), who both documented a lack of serotiny in young stands, even one that had established following a recent (17 years previous) severe burn. These results suggest that a physiological component also plays a role in serotiny—that trees do not begin expressing serotiny until they are older. The age of this “switch” is still open for debate.

My results showed that elevation, aspect (expressed as “eastness”), and local moisture had the greatest effect on percent serotiny. The regression tree allows us to see the relationship between these variables, and even allows some variables to branch more than once. Based on the results, topographic position (elevation or aspect) appears to have the primary influence, followed secondarily by local moisture. Because these environmental variables parallel those that give rise to fire, the results support the idea that a propensity for a particular landscape toward fire generally leads to a propensity for

higher serotiny. I should note, however, that lodgepole pine in ROMO is largely a stand-replacing fire system, and these results reflect that. When we say that topographic situations that give rise to more fire also give rise to more serotiny, we should not extrapolate this to the complete range of fire frequencies, which includes high-frequency, low-severity regimes that are not stand-replacing. Some low-severity fire has been shown to occur within lodgepole pine in ROMO (Sibold et al. 2007; Sibold et al. 2006), with attendant short fire return intervals, or high frequencies. As the two studies cited above indicate, low-severity fire seems not to affect future serotiny at the stand level. Therefore in ROMO, where lodgepole pine at lower elevations may contain a low-severity fire regime component similar to that of ponderosa pine, we should not assume that serotiny will similarly be correlated with higher fire frequencies, when the frequency parameter has been measured for low-severity fire.

James Lotan (1976) once said, “There is considerable pay-off in trying to relate cone serotiny to fire history. If cone serotiny could be linked to fire history, then [it] would serve as a biometric gage or index to fire history.” My findings showed that serotiny can indeed be related to fire history, but that we must be careful about which components of fire history we apply on a given landscape. Here, abiotic variables conducive to fire contribute to higher serotiny, but only in cases where fire is measured for stand-replacing regimes. In measures of low-severity fire, where the same abiotic variables contribute to even more frequent fire, the relationship no longer holds. It is also important to remember the physiological component, wherein young stands, regardless of fire history, tend to be non-serotinous.



## CONCLUSION

I found that the serotinous trait is widely distributed across Rocky Mountain National Park, and that the main contributing variables to its distribution are the topographic variables related to fire—lower elevation, lower moisture, and sunnier aspects. Rocky Mountain lodgepole pine has evolved to survive under a wide variety of environmental conditions—non-serotinous cones disseminate their wind-borne seeds between fire events, and serotinous cones release their seeds en masse in the event of a stand-replacing fire. The serotinous trait itself also exhibits wide variability, and in ROMO, appears to occur with great frequency so that even stands with what we might call “low serotiny” within the bounds of this study may actually still contain a substantial component of serotinous trees. In terms of the current and future health of ROMO’s lodgepole pine forests, the canopy seed bank is therefore well-intact, and well-adapted to future scenarios including both fire and non-fire. 20<sup>th</sup> century fire suppression is not likely to have had a significant effect on these systems, which normally experience long fire-free intervals of over a century in length.

Going forward, however, the forest will need fire at some point to regenerate and to maintain its current resilience according to its present evolutionary path. In addition, the outcome of the current mountain pine beetle (*Dendroctonus ponderosae*) outbreak is hard to predict. Serotinous stands regenerate so well following fire due to the bare mineral soil left behind by the fire. Even if the serotinous cones on the many standing beetle-killed trees do open in the absence of fire, the substrate may not be conducive to regenerative success. In this scenario, if stand-replacing fire does not occur in the near

future, the chances of success in establishing within an existing understory (and in a few decades, among a large amount of blowdown) may be equal for serotinous and non-serotinous trees, thus breaking—at least temporarily—the cycle of fire-selected serotiny.

## TABLES

	East	West	Total
Mean	47	64	58
Median	52	69	64
Std. dev.	32	18	25
Range	0 – 97	14 – 91	0 – 97

Table 1. Summary statistics for serotiny values (%) on the east and west sides of the park.

	<i>Elevation</i>	<i>Eastness</i>	<i>Northness</i>	<i>Slope</i>	<i>TCI</i>	<i>Solar Radiation</i>
Mean	2871	-0.15	-0.31	16	9.31	1185172
Median	2860	-0.42	-0.48	17	9.05	1203135
Std Dev	183	0.75	0.56	9	1.61	79114
Range	2540 - 3311	-1 - 1	-1 - .87	1 - 40	6.87 - 15.73	879739 - 1286210

Table 2. Summary statistics for the independent variables used in the regression tree analysis.

APPENDIX A: FIELD KEY FOR IDENTIFICATION OF LODGEPOLE PINE TREE TYPES IN  
ROCKY MOUNTAIN NATIONAL PARK

1. Tree alive – 2
1. Tree dead – 4
2. Of cones  $\geq 3$  yrs old,  $< 25\%$  are closed – **living non-serotinous tree**
2. Of cones  $\geq 3$  yrs old,  $> 25\%$  are closed – 3
3. Of cones  $\geq 3$  yrs old, 25-75% are closed – **living mixed serotiny tree**
3. Of cones  $\geq 3$  yrs old,  $> 75\%$  are closed – **living serotinous tree**
4.  $\geq 95\%$  of cones are closed (figure a)– **dead serotinous tree not releasing seeds**
4.  $< 95\%$  of cones are closed – 5
5. Cones open uniformly throughout the crown (figure b)– **dead non-serotinous tree**
5. Cones not open uniformly throughout the crown – 6
6. All open cones open only at the tip, opening asymmetrically (figure c) – **dead serotinous tree releasing seeds**
6. Not as above
7. Open cones of two types: some open only symmetrically/fully (figure b), some open only at the tip, opening asymmetrically (figure c)– **dead mixed serotiny tree releasing seeds**
7. Open cones of only one type: open fully and symmetrically (figure b); all other cones closed with serotinous shape – **dead mixed serotiny tree not releasing seeds**



a) cones on dead serotinous tree, not releasing seeds



b) cone on dead non-serotinous tree (note symmetrical shape and fully open)



c) cones on dead serotinous tree, releasing seeds (note asymmetrical opening, primarily at the tip)

### **Chapter 3: Lodgepole Pine Seed Viability Following Tree Death from Mountain Pine Beetle Attack in Colorado**

#### **INTRODUCTION**

The mountain pine beetle (*Dendroctonus ponderosae*) has recently reached epidemic population levels in the United States and Canada (Raffa et al. 2008). In Colorado, the State Forest Service estimates that over 600,000 ha have been affected during the current outbreak, a scale unprecedented in recorded history. Lodgepole pine (*Pinus contorta* var. *latifolia*), the tree most affected in the outbreak, usually regenerates in large numbers following stand-replacing fire. An important regeneration mechanism is the production of serotinous cones, which remain closed until stimulated by the heat of a fire to open and release their seeds (Clements 1910; Tower 1909). Lodgepole pine vary greatly in the proportion of serotinous and non-serotinous cones (Schoennagel et al. 2003), but many of the stands affected by the current outbreak in Colorado are composed of predominantly serotinous trees. A recent survey of lodgepole pine stands on the west side of Rocky Mountain National Park found a mean serotiny per stand of 64% (see previous chapter). In the absence of fire, large numbers of beetle-killed trees will remain on the landscape, with their seeds still tightly held within the cones. What will this mean for the future regeneration of these stands across the landscape?

Unlike a fire, in which seeds are released by heat in a single event, a large-scale mortality event caused by beetles will result in a slower release of the seeds. The cones

will open over a number of years, either through radiant heat in the canopy or by absorbing heat near the ground as limbs break off and fall (Lotan 1964; Tower 1909). A key question, then, is whether or not seeds held in serotinous cones remain viable for years after the tree has died. Early studies indicated that in some instances, seeds could survive a number of years on a dead tree, or even separated from the tree (Mills 1915; Sargent 1880; Tower 1909). Mirov (1946) showed that lodgepole pine seeds kept in cold storage for over nine years still maintained high germination rates. However a controlled experiment utilizing seeds remaining in the canopy of standing dead trees has not yet been done. Will stands dominated by serotinous lodgepole pine have the viable seed needed for regeneration over the years following the beetle outbreak?

To test this question, I conducted an experiment using serotinous trees from the current beetle outbreak in Rocky Mountain National Park, Colorado, comparing viability in serotinous cone seeds between living trees and trees killed in the current outbreak, as well as between cones located on younger vs. older portions of branches. Knowing whether seed viability declines over time in dead trees will help us to understand the future regeneration possibilities for these stands with extensive overstory mortality.

Before I began my study, I also needed to determine an effective method of determining cone age from sampled branches. Previous studies requiring cone aging used bud scale scars or branch whorls to determine age (e.g., Benkman et al. 2003; Hellum and Barker 1981). However, bud scale scars are often not visible beyond the initial years of a stem's growth, and branch whorl morphology on old trees is often highly variable. Most morphological studies of pine stem growth and its relation to cone growth (e.g., Franklin and Callaham 1970; 1914; Van Den Berg and Lanner 1971) have been

conducted on young stems, making it difficult to know whether it was reasonable to count one year for each whorl of branches or cones in older stems or branches. These previous studies describe lodgepole pine as a multi-nodal species, which can produce more than one whorl of branches or cones per year. No study has yet documented how to use these whorls for aging once the stem or branch has matured.

I addressed three questions: 1) Can branch and cone whorls be used to reliably age cones? 2) Does viability of seeds of a given age differ between live trees and trees dead at least 3 years after beetle attack? 3) Does seed viability differ in older vs. younger serotinous cones?

#### STUDY AREA AND METHODS

Two sites were selected on the western side of Rocky Mountain National Park (ROMO), where the current outbreak is underway. To collect samples from trees that had been dead for the longest period of time, I selected a lower-elevation site near ROMO's western entrance, Harbison Meadows Picnic Area (2661 m, uneven ages ranging from approximately 180 to 280 y). Within the first year following an attack, the dead tree's needles turn red. These needles subsequently drop off, with nearly 100% needle loss occurring between 2 and 3 years post-attack (British Columbia Ministry of Forests 1995). Nearly all the overstory trees at Harbison Meadows had been killed by beetles, and most had lost all their needles, so the seeds on these trees have been on dead branches for at least 3 years, possibly longer. I selected Timber Lake Trailhead (2716 m, even-aged stand of approximately 110 y), also on the west side of ROMO, as the site for sampling living trees. A few trees in this area showed evidence of beetle attack, but most appeared healthy. Ten representative canopy trees were felled by chainsaw at each



location, for a total of 20 trees. Individual branches were then harvested from the upper third of each individual. The harvested limbs were stored in a cool, dry basement for approximately 5 months.

My first task was to determine the ages of the cones along the branches (my methodological question 1). To do this, we cut apart several samples, and finely sanded cross-sections taken from between branch or cone whorls (Fig. 1). The annual rings in these cross-sections were then counted under a dissecting scope to determine the age of the nearest adjacent cone. I made detailed observations of the relationship between whorl

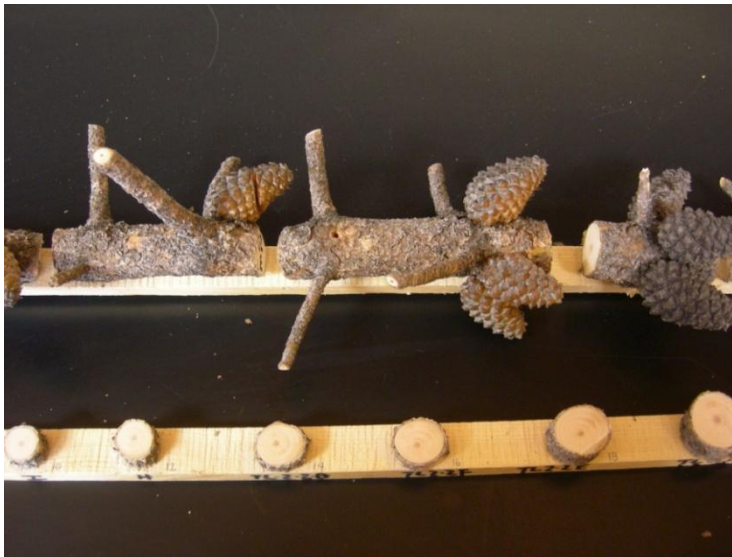


Figure 1. Branch fragment shown (above) with mounted and sanded cross-sections (below). In this example, the fragment was sectioned every two whorls.

morphology and the age of the branch at that point, to determine whether the whorls provided accurate aging for the cones themselves.

Once I was confident in my ability to correctly identify the number of years per whorl (see Results below), I removed the cones and placed them in five-year age bins ranging from 5 to 25 y. (To ensure proper dating on each individual sample, a cross-

section was taken and ring-counted from the cut end of all samples, and if the branch's tip was missing, a cross-section was also taken and counted from the top end, thus assuring proper cone aging between the two ends.) I then heated the cones for 24 hours in an oven at 60°C, an average temperature to completely open serotinous cones without inhibiting their germination response through overheating (Clements 1910; Johnson and Gutsell 1993; Knapp and Anderson 1980; Perry and Lotan 1977). Seeds that were clearly empty were removed, and the remainder were de-winged and divided into lots of up to fifty seeds per age bin per tree. The seeds were prechilled at 3°C for 5 wk (Tanaka 1984). Each lot was placed in a petri dish containing two filter paper circles, then dusted with the fungicide Captan (50 percent), and wetted with 5 ml of water (Abouguendia and Redmann 1979). The dishes were covered and placed in a germinator with alternating light and temperature (27°C for 8 h in the light, 20°C for 16 h in the dark (Knapp and Anderson 1980; Tanaka 1984). The filter paper was re-wetted as needed throughout the experiment. Seeds with the radicle protruding at least 1mm were considered germinated.

Germination percentages were compared using logistic regression, with tree status (living/dead) and age bins as predictor variables. Analysis was performed using R statistical software (R Development Core Team 2009). The lowest age bin (0-5 y) was eliminated due to the large number of missing branch tips from the dead trees whose crowns tended to shatter upon hitting the ground.

## RESULTS

*Question 1: Cone ages and branch morphology.*—I identified two distinct morphologies, one in which the branches stemmed upward at an acute angle to the main

stem, and did indeed represent one year per whorl, and a second one in which the branches stemmed in multiple directions from the branch, sometimes appearing to represent two whorls. These rings also represented just a single year, though they often could appear to represent two (Fig. 2).

The two morphologies were distinct enough from one another that it was almost always possible to distinguish them on the branch and assign ages correctly.



Figure 2. Two examples of “double whorls” representing one year each. In the photo on the right, years are marked with arrows

*Question 2: Seed viability in dead vs. living trees.*—Seeds from the dead trees germinated at an average rate of 53%, compared with 58% from the living trees (Fig. 3a). This difference was not statistically significant ( $P = .64$ ).

*Question 3: Younger vs. older cones.*—Average germination rates from both sampling sites declined significantly with age ( $P < .0001$ , Fig. 3b.), however the average germination rate over both sites was  $>30\%$  even for the oldest age bin.

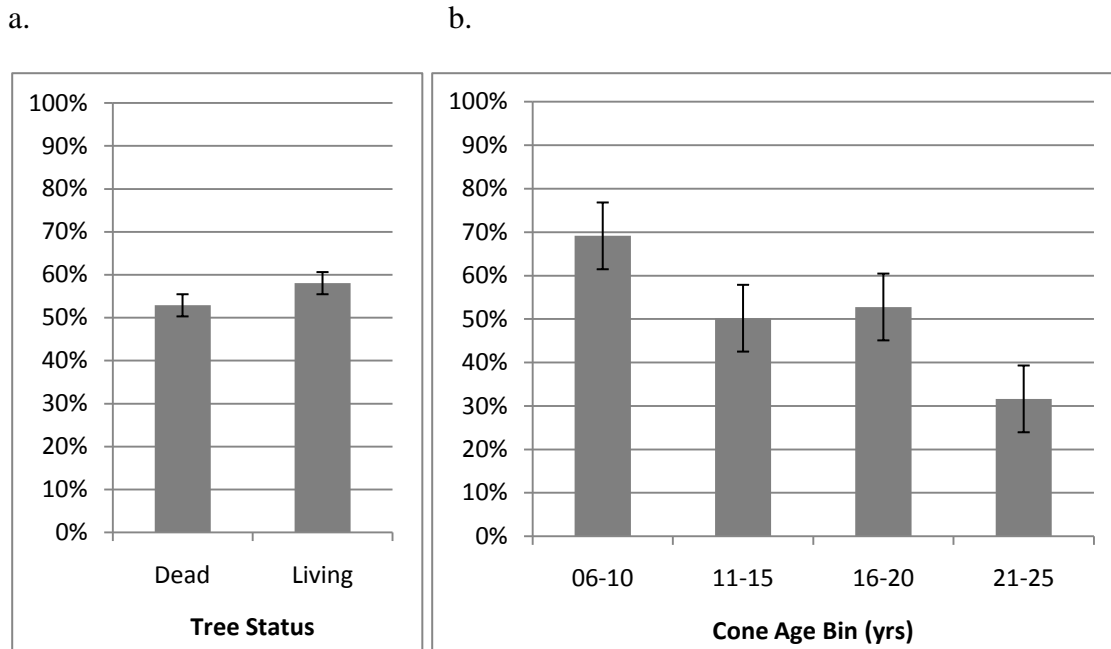


Figure 3. Comparison of average percent germination. a) dead trees vs. living trees; b) cone age bins in years

## DISCUSSION

Landowners and the public see many hectares of dead trees across the landscape, and they worry that these stands may not regenerate. Previous studies of extensive mountain pine beetle mortality have shown that lodgepole pine stand structure can change substantially following beetle outbreaks (e.g., Roe and Amman 1970; Sibold et al. 2007). Moderate outbreaks where advance regeneration is present may lead to the successional dominance of other species such as Douglas-fir (*Pseudotsuga menziesii*) or subalpine fir (*Abies lasiocarpa*), while severe outbreaks in single-story stands may lead to dominance by grasses which subsequently suppress lodgepole pine regeneration (Amman 1977; Stone and Wolfe 1996). However, previous studies have not addressed successional questions related to stand serotiny and canopy seed viability following beetle-induced tree mortality. While non-serotinous cones release their seeds as the

cones mature, leaving little seed bank for regeneration following an outbreak, serotinous cones have the potential to hold a canopy seed bank from which beetle-killed stands may regenerate. Many of the beetle-killed stands in ROMO contain a high percentage of serotinous trees. Their cones will begin to open following tree death, particularly from ground heat as the branches fall; only a few days near the soil surface are required to break the cone's resin bonds (Lotan 1964; Tower 1909). My experiment showed that these standing dead serotinous trees do hold many viable seeds, even after the beetle epidemic has moved on and most of the overstory has died. Even cones that had been on the tree for up to 25 y prior to tree death contained many viable seeds. Thus, stands with a high percentage of serotinous trees may follow a different post-beetle regeneration trajectory than non-serotinous stands.

Other variables, such as quality of seed beds, competition with herbaceous and shrub species, and seed predation, may result in poor regeneration. However, my results suggest that post-beetle regeneration likely will not be limited by viable seed availability in stands with serotinous cone-bearing trees.

## References

- Abouguendia Z.M. and Redmann R.E. 1979. Germination and early seedling growth of four conifers on acidic and alkaline substrates. *Forest Science* 25: 358-360.
- Amman G.D. 1977. The role of the mountain pine beetle in lodgepole pine ecosystems: Impact on succession. *In* Mattson W. J. (ed.), *The role of arthropods in forest ecosystems*, pp. 3-18. Springer-Verlag, New York.
- Baisan C.H. and Swetnam T.W. 1990. Fire history on a desert mountain range: Rincon Mountain Wilderness, Arizona, USA. *Canadian Journal of Forest Research* 20: 1559-1569.
- Baisan C.H. and Swetnam T.W. 1995. Historical fire occurrence in remote mountains of southwestern New Mexico and northern Mexico. *In* Brown J. K., Mutch R. W., Spoon C. W. and Wakimoto R. H. (eds.), *Proceedings of the symposium on fire in wilderness and park management (30 March - 1 April 1993, Missoula, MT)*, pp. 153-156. U.S. Department of Agriculture, Forest Service General Technical Report INT-GTR-320, Intermountain Forest and Range Experiment Station, Ogden, Utah.
- Baker F.S. 1925. Aspen in the central Rocky Mountain region. U.S. Department of Agriculture, Bulletin 1291, Washington, D.C., 47 p.
- Benkman C.W., Parchman T.L., Favis A. and Siepielski A.M. 2003. Reciprocal Selection Causes a Coevolutionary Arms Race between Crossbills and Lodgepole Pine. *The American Naturalist* 162: 182-194.
- Beven K.J. and Kirkby M.J. 1979. A Physically Based, Variable Contributing Area Model of Basin Hydrology. *Hydrological Sciences Bulletin* 24.
- Breiman L. 1984. *Classification and regression trees*. Wadsworth International Group, Belmont, Calif.
- British Columbia Ministry of Forests 1995. *Bark Beetle Management Guidebook*. Forest Practices Branch, Victoria, B.C.

- Brown J.K. 2000. Introduction and fire regimes. *In* Brown J. K. and Smith J. K. (eds.), Wildland fire in ecosystems: effects of fire on flora. Gen. Tech. Rep. RMRS-GTR-42-vol. 2. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 257 p.
- Brown P.M. and Wu R. 2005. Climate and disturbance forcing of episodic tree recruitment in a southwestern ponderosa pine landscape. *Ecology* 86: 3030-3038.
- Clements F.E. 1910. The life history of lodgepole burn forests. U.S. Department of Agriculture, Forest Service, Washington, D.C.
- Covington W.W. and Moore M.M. 1994. Southwestern Ponderosa Forest Structure: Changes since Euro-American settlement. *Journal of Forestry* 92: 39-47.
- Crossley D.I. 1956. Fruiting habits of lodgepole pine. Canada Department of Northern Affairs and National Resources, Forestry Branch, Forest Resources Division Technical Note 35.
- De'ath G. and Fabricius K.E. 2000. Classification and Regression Trees: A Powerful Yet Simple Technique for Ecological Data Analysis. *Ecology* 81: 3178-3192.
- ESRI 2009. ArcGIS version 9.2. Redlands, California.
- Franklin E.C. and Callaham R.Z. 1970. Multinodality, branching, and forking in lodgepole pine (*Pinus contorta* var. *murrayana* Englem.). *Silvae Genetica* 19: 180-184.
- Franklin J.F. and Agee J.K. 2003. Forging a Science-Based National Forest Fire Policy. *Issues in Science & Technology* 20: 59-66.
- Fulé P.Z., Covington W.W. and Moore M.M. 1997. Determining reference conditions for ecosystem management of southwestern ponderosa pine forests. *Ecological Applications* 7: 895-908.
- Fulé P.Z., Crouse J.E., Heinlein T.A., Moore M.M., Covington W.W. and Verkamp G. 2003. Mixed-severity fire regime in a high-elevation forest of Grand Canyon, Arizona, USA. *Landscape Ecology* 18: 465-486.
- Gauthier S., Bergeron Y. and Simon J.-P. 1996. Effects of Fire Regime on the Serotiny Level of Jack Pine. *The Journal of Ecology* 84: 539-548.
- Grissino-Mayer H.D., Romme W.H., Lisa Floyd M. and Hanna D.D. 2004. Climatic and human influences on fire regimes of the southern San Juan Mountains, Colorado, USA. *Ecology* 85: 1708-1724.

- Guth P.L. 1999. Quantifying and visualizing terrain fabric from digital elevation models. *In* 27th Applied Imagery Pattern Recognition (AIPR) Workshop, sponsored by the SPIE (The International Society for Optical Engineering). Vol. 3584.
- Hellum A.K. and Barker N.A. 1981. The relationship of lodgepole pine cone age and seed extractability. *Forest Science* 27: 62-70.
- Hessburg P.F., Salter R.B. and James K.M. 2007. Re-examining fire severity relations in pre-management era mixed conifer forests: inferences from landscape patterns of forest structure. *Landscape Ecology* 22: 5-24.
- Holmes R. 1983. Computer assisted quality control in tree-ring dating and measurement. *Tree-Ring Bulletin* 44: 69-75.
- Johnson E.A. and Gutsell S.L. 1993. Heat budget and fire behaviour associated with the opening of serotinous cones in two *Pinus* species. *Journal of Vegetation Science* 4: 745-750.
- Jones J.R. and DeByle N.V. 1985. Ecology: Fire. *In* DeByle N. V. and Winokur R. P. (eds.), *Aspen: Ecology and management in the western United States*. USDA Forest Service General Technical Report RM-119, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO, 283 p.
- Jonsson B., Holm S. and Kallur H. 1992. A forest inventory method based on density-adapted circular plot size. *Scandinavian Journal of Forest Research (Sweden)*.
- Keane R.E., Hessburg P.F., Landres P.B. and Swanson F.J. 2009. The use of historical range and variability (HRV) in landscape management. *Forest Ecology and Management* 258: 1025-1037.
- Keeley J.E., Aplet G.H., Christensen N.L., Conard S.G., Johnson E.A., Omi P.N., Peterson D.L. and Swetnam T.W. 2009. Ecological foundations for fire management in North American forest and shrubland ecosystems. Gen. Tech. Rep. PNW-GTR-779. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 92 p.
- Kitzberger T., Brown P.M., Heyerdahl E.K., Swetnam T.W. and Veblen T.T. 2007. Contingent Pacific-Atlantic Ocean influence on multicentury wildfire synchrony over western North America. *Proceedings of the National Academy of Sciences* 104: 543-548.
- Knapp A.K. and Anderson J.E. 1980. Effect of Heat on Germination of Seeds from Serotinous Lodgepole Pine Cones. *American Midland Naturalist* 104: 370-372.



- Lessard V.C., Drummer T.D. and Reed D.D. 2002. Precision of density estimates from fixed-radius plots compared to N-tree distance sampling. *Forest Science* 48: 1-6.
- Lotan J.E. 1964. Regeneration of lodgepole pine: a study of slash disposal and cone opening. Research Note INT-16. USDA Forest Service, Intermountain Forest and Range Experiment Station, Ogden, UT.
- Lotan J.E. 1976. Cone serotiny-fire relationships in lodgepole pine. *In* Montana Tall Timbers Fire Ecology Conference and Fire Management Symposium, pp. 267-278. Tall Timbers Research Station, Tallahassee, Florida.
- Lotan J.E. and Critchfield W.B. 1990. Lodgepole pine. *In* Burns R. M. and Honkala B. H. (eds.), *Silvics of North America: Volume 1. Conifers*. Agricultural Handbook 654, U.S. Department of Agriculture, Washington, D.C.
- Margolis E.Q., Swetnam T.W. and Allen C.D. 2007. A stand-replacing fire history in upper montane forests of the southern Rocky Mountains. *Canadian Journal of Forest Research* 37: 2227-2241.
- Mason D.T. 1915. The life history of lodgepole pine in the Rocky Mountains. US Department of Agriculture Bulletin 154.
- McCune B.M. and Grace J.B. 2002. Analysis of Ecological Communities. MjM Software Design, Gleneden Beach, OR.
- McKean J. and Roering J. 2004. Objective landslide detection and surface morphology mapping using high-resolution airborne laser altimetry. *Geomorphology* 57: 331-351.
- Mills E.A. 1915. *The Rocky Mountain Wonderland*. Houghton Mifflin, Boston.
- Mirov N.T. 1946. Viability of pine seed after prolonged cold storage. *Journal of Forestry* 44: 193-195.
- Muir P.S. and Lotan J.E. 1985. Disturbance history and serotiny of *Pinus contorta* in western Montana. *Ecology* 66: 1658-1668.
- Perry D.A. and Lotan J.E. 1977. Opening temperatures in serotinous cones of lodgepole pine. Research Note INT-228. USDA Forest Service, Intermountain Forest and Range Experiment Station, Ogden, UT.
- PRISM Climate Group. Oregon State University, <http://www.prism.oregonstate.edu>, created 16 Feb 2008.
- R Development Core Team 2009. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

- Raffa K.F., Aukema B.H., Bentz B.J., Carroll A.L., Hicke J.A., Turner M.G. and Romme W.H. 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. *BioScience* 58: 501-517.
- Roe A.L. and Amman G.D. 1970. The mountain pine beetle in lodgepole pine forests., Research Paper INT-71. USDA Forest Service, Intermountain Forest and Range Experiment Station, Ogden, UT.
- Romme W.H. 1982. Fire and Landscape Diversity in Subalpine Forests of Yellowstone National Park. *Ecological Monographs* 52: 199-221.
- Romme W.H., Floyd M.L., Hanna D., Redders J.S., McGarigal K. and Crist M. 2009. Landscape condition analysis for the south-central highlands section, southwestern Colorado and northwestern New Mexico. Unpubl. Report to the USDA For. Serv. San Juan National Forest. Durango, CO, USA.
- Sargent C.S. 1880. Vitality of the seeds of *Pinus contorta*. *Botanical Gazette* 5: 54.
- Schoennagel T., Turner M.G. and Romme W.H. 2003. The influence of fire interval and serotiny on postfire lodgepole pine density in Yellowstone National Park. *Ecology* 84: 2967-2978.
- Schoennagel T., Veblen T.T. and Romme W.H. 2004. The Interaction of Fire, Fuels, and Climate across Rocky Mountain Forests. *BioScience* 54: 661-676.
- Shaw G.R. 1914. The genus *Pinus*. Riverside Press, Cambridge.
- Sibold J.S., Veblen T.T., Chipko K., Lawson L., Mathis E. and Scott J. 2007. Influences of secondary disturbances on lodgepole pine stand development in Rocky Mountain National Park. *Ecological Applications* 17: 1638-1655.
- Sibold J.S., Veblen T.T. and González M.E. 2006. Spatial and temporal variation in historic fire regimes in subalpine forests across the Colorado Front Range in Rocky Mountain National Park, Colorado, USA. *Journal of Biogeography* 33: 631-647.
- Stephens S.L. and Ruth L.W. 2005. Federal forest-fire policy in the United States. *Ecological Applications* 15: 532-542.
- Stokes M.A. and Smiley T.L. 1968. An introduction to tree-ring dating. University of Chicago Press, Chicago.
- Stone W.E. and Wolfe M.L. 1996. Response of understory vegetation to variable tree mortality following a mountain pine beetle epidemic in lodgepole pine stands in northern Utah. *Plant Ecology* 122: 1-12.

- Sudworth G.B. 1899. White River Plateau Timber Land Reserve. Twentieth annual report of the United States Geological Survey, Part V. Forest reserves., pp. 117-179. United States Government Printing Office, Washington, D.C.
- Tanaka Y. 1984. Assuring seed quality for seedling production: cone collection and seed processing, testing, storage and stratification. *In* Duryea M. L. and Landis T. D. (eds.), *Forest Nursery Manual: Production of Bareroot Seedlings*, pp. 27-39. Martinus Nijhoff/Dr W. Junk Publishers, for Forest Research Laboratory, Oregon State University, Corvallis, The Hague/Boston/Lancaster.
- Theobald D., Stevens D., White D., Urquhart N., Olsen A. and Norman J. 2007. Using GIS to Generate Spatially Balanced Random Survey Designs for Natural Resource Applications. *Environmental Management* 40: 134-146.
- Tinker D.B., Romme W.H., Hargrove W.W., Gardner R.H. and Turner M.G. 1994. Landscape-scale heterogeneity in lodgepole pine serotiny. *Canadian journal of forest research(Print)* 24: 897-903.
- Touchan R., Allen C.D. and Swetnam T.W. 1996. Fire history and climatic patterns in ponderosa pine and mixed-conifer forests of the Jemez Mountains, northern New Mexico.
- Tower G.E. 1909. A study of the reproductive characteristics of lodgepole pine. *Proceedings of the Society of American Foresters* 4: 84-106.
- Turner M.G., Romme W.H., Gardner R.H. and Hargrove W.W. 1997. Effects of fire size and pattern on early succession in Yellowstone National Park. *Ecological Monographs* 67: 411-433.
- Turner M.G., Romme W.H. and Tinker D.B. 2003. Surprises and lessons from the 1988 Yellowstone fires. *Frontiers in Ecology and the Environment* 1: 351-358.
- Van Den Berg D.A. and Lanner R.M. 1971. Bud Development in Lodgepole Pine. *Forest Science* 17: 479-486.
- Veblen T.T. 2003. Key issues in fire regime research for fuels management and ecological restoration. *In* *Fire, fuel treatments and ecological restoration: conference proceedings; 16–18 April, 2002*, pp. 259-276. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO.
- Wu R. 1999. Fire history and forest structure in the mixed conifer forests of southwest Colorado. Master's Thesis, Colorado State University: Fort Collins.