

# Aspen's Ecological Role in the West

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**Abstract**—Aspen exhibits a variety of ecological roles. In southern Colorado, the 1880 landscape mosaic contained a range of stand ages, of which half were >70 years old and half were younger. Pure aspen stands in southern Colorado are widespread and may result from previous short fire intervals that eliminated local conifer seed sources. Aspen regeneration in northern Yellowstone Park is controlled by ungulate browsing pressure and fire, so it has been limited since 1920. However, an episode of aspen seedling establishment occurred after the 1988 fires. We urgently need additional detailed, local case studies of aspen ecology to inform management decisions.

## Introduction

As the most widely distributed tree species in North America (Fowells 1985), quaking aspen (*Populus tremuloides*) exists within a great diversity of ecological settings and exhibits a similar diversity of ecological roles. Generalizations about aspen's ecological role are therefore difficult—and potentially dangerous. Nevertheless, several key questions about aspen ecology need to be answered to help guide our decisions about sustainable aspen management today and in the future.

In this paper we address three basic questions about the ecological role of aspen in the Rocky Mountain West. For each question, we offer more than one answer, based on several case studies that reflect the wide range of ecological settings in which aspen occurs. One important outcome of this comparative analysis is the recognition that we urgently need additional detailed, local case studies of aspen ecology. The questions are:

1. What was the range of variability that existed prior to EuroAmerican settlement in the late 1800s, with respect to aspen disturbance regimes and landscape patch dynamics?
2. What are the major factors, biotic and abiotic, that control aspen successional dynamics and responses to disturbance?
3. Do aspen's life history traits and reproductive mechanisms provide adequate resilience to impending climatic and environmental changes?

## Question 1: Pre-1900 Aspen Disturbance Regimes and Landscape Patch Dynamics

Aspen disturbance regimes and landscape patch dynamics have been highly variable in both time and space. We illustrate this range of variability by examining two very different case studies. The first comes from the southern Rocky Mountains, in the western San Juan National Forest. Here aspen is the dominant cover type, creating the landscape matrix over thousands of hectares. In this area fire clearly was a major disturbance agent in the past, but ungulate

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browsing apparently was of minimal importance. The second case study is from the northern Rocky Mountains, specifically the winter ungulate range of Yellowstone National Park. Aspen stands in this area exist as relatively small patches within a matrix of other vegetation types, and both fire and ungulate browsing have been important components of the disturbance regime.

### ***Aspen Fire History and Patch Dynamics in the San Juan National Forest***

Aspen forest is a dominant cover type over extensive areas at middle elevations in the western San Juan National Forest, where individual patches of aspen forest may cover hundreds of hectares (Jones and Schier 1985; Romme et al. 1992). The most important agent of disturbance in aspen forests of the southern Rocky Mountains before 1900 was fire, although other natural disturbances were locally important including windthrow, fungal diseases, tent caterpillars and other insects, snow damage, hail, lightning, and sunscald (Jones and DeByle 1985a; Jones et al. 1985; Romme et al. 1999; Veblen 2000).

Jones and DeByle (1985b:77) observed that "... almost all even-aged aspen stands in the West appear to be the result of severe fire, whether or not the aspen type is climax on the site." Yet despite this widespread recognition of the importance of past fire in aspen forests, we have little specific information on aspen fire history in the southern Rockies. Baker (1925) studied fire scars in Ephraim Canyon in central Utah and concluded that light fires had occurred every seven to 10 years within the general region of his study area (actual extent of the study area not specified). Meineke (1929) determined that fires had occurred in every decade of the nineteenth century at the Great Basin Range Experiment Station in the Wasatch Range, Utah, but that the only severe fire was in 1867. Harniss and Harper (1982) found that the conifers were older in subalpine fir-aspen stands at higher elevations than in white fir-aspen stands at lower elevations. They suggested that this may reflect longer fire intervals at the higher elevations, but their study provided no estimates of actual fire intervals in the aspen zone. To obtain more detailed and quantitative estimates of past fire intervals and landscape dynamics within the aspen forest type, we studied fire history in an aspen-dominated landscape on the western flanks of the La Plata Mountains in the San Juan National Forest.

#### ***Methods***

Reconstructing fire history is more difficult in aspen forests than in some other forest types, because aspen are easily killed by fire and few fire-scarred trees can be found with which to date past fires. Therefore, we used a less precise method of determining fire history that was based on the statistical distribution of current stand ages, i.e., the time since the last lethal fire (Johnson and Gutsell 1994). To develop this method, we began by sampling five aspen stands in 1995 within the Lime Creek burn, an area near Silverton, Colorado, where an extensive fire in 1879 was documented by written records. In two aspen stands, we removed an increment core from every stem within a circular plot at a height of about 1 meter. The cores were glued to slotted boards, air dried, sanded, and stained. The number of annual rings was counted under 20-power magnification using a dissecting microscope. Additional years were added to the estimate of stem age for cores that had missed the center of the tree, based on the radius of curvature of the innermost rings, and three years were added to the age of each stem as an estimate of the time required to grow to coring height.

The age structure of aspen stems in the 1879 Lime Creek burn was constructed from all readable cores in the two stands (about 20% of the sampled increment cores were rotten, lacking centers, or otherwise unreadable). The post-fire aspen that which resprouted after the documented 1879 burn was clearly detectable in the current age structure of the stands (figure 1). Nearly 60% of the aspen trees in our sample had established between 1880 and 1890, even though many individuals of younger age classes were present due to continued recruitment of stems into the canopy for several decades following the fire. The Lime Creek data also revealed that very few aspen trees had survived the fire in 1879, as would be expected in such a fire-sensitive species. Next, we collected increment cores only from 15–20 of the largest and oldest appearing stems in three additional stands within the Lime Creek burn area. The age structure of these stands similarly contained a prominent cohort of stems that had established within a decade after 1879, plus numerous younger stems from the 1890s–1910s (data not shown). From this preliminary analysis of current age structure in stands of known fire history, we determined that in subsequent analyses of stands with unknown fire history, we could assume that the oldest cohort of 2+ living aspen stems dating to a single decade in any stand today represents the initial postfire cohort.

**Landscape-scale fire history**

Once we had verified that postfire aspen cohorts could still be detected in aspen stands that burned >100 years ago, we determined fire history in a 76 km<sup>2</sup> area of unknown fire history at an elevation of 2,650–3,310 m in the western portion of the San Juan National Forest (Romme et al. 1999). A 1 km<sup>2</sup> grid was overlaid on the 7.5-minute topographic quadrangles for the study area based upon the UTM 1,000 m grid tics. A sample point was randomly chosen within each 1 km<sup>2</sup> grid cell such that each unit of the total study area had an equal probability of being sampled (Johnson and Gutsell 1994). The sampling sites identified on the map then were located in the field. If the sampling point appeared to have been logged, we randomly selected another point within the 1 km grid cell. At each point we collected an increment core at breast height from the 20 largest sound aspen trees. Cores were glued to boards, sanded, stained, and dated as described above.

We then summarized the ages of dominant aspen stems in each of the 76 sampled stands, and estimated the decade in which the most recent lethal fire



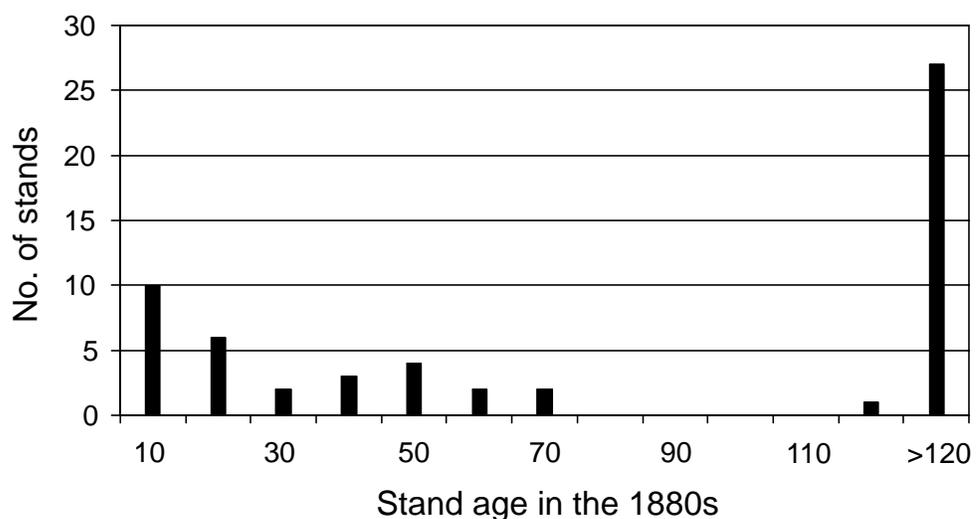
**Figure 1**—Age structure in 1995 of all aspen stems >5 cm d.b.h. within two aspen stands known to have originated after a lethal fire in 1879, Lime Creek burn, San Juan National Forest, Colorado.

had occurred. The oldest postfire cohort detected was from the 1760s, and we found cohorts in other stands representing fires in every decade from the 1810s through 1870s (figure 2). Twenty-seven stands did not contain any set of 2+ trees established within the same decade that was old enough to represent a postfire cohort, but these stands did contain individual old aspen trees (>150 yr). In these stands, we assumed that the stand had originated long ago and that most or all of the original postfire cohort had died through natural causes such as disease. We could not assign a precise age to these stands but called their date of origin “pre-1760s” since the oldest recognizable postfire cohort was from the 1760s. Some of these stands may have originated more recently than the 1760s and had simply lost their postfire cohort, but we think that most actually did date from before the early 1800s because of their all-aged, all-sized canopy structure. Another 19 stands contained no apparent postfire cohort but no old trees either; time since fire in these stands could not be determined and they were listed as “unknown” and deleted from the statistical analysis. See Romme et al. (1999) for additional details of sampling and determining stand ages.

### ***Fire History and the Landscape Mosaic During the Reference Period***

Table 1 summarizes the number of aspen stands that became established in each decade from the 1870s to the 1760s, as well as the number of old stands of uncertain origin date (“pre-1760s”). None of the stands that we sampled had originated later than 1880, apparently because no extensive fires occurred in our study area after this time. However, small fires have occurred elsewhere in the San Juan Mountains during the 20<sup>th</sup> century, and small patches of younger aspen stands can be found in those areas. Extensive fires occurred in our study area in the 1870s and 1860s. Fewer stands date from the early to mid 1800s, either because there were fewer or less extensive fires during that time, or because evidence of these early fires has been destroyed by the fires of the later 1800s. Approximately 45% of the sampled stands appeared to have last burned at some time prior to the early 1800s (“pre-1760s” in table 1).

What kind of a landscape mosaic existed in the aspen zone prior to the grazing, logging, and fire control efforts of the 20<sup>th</sup> century? Figure 2 summarizes the distribution of stand ages as they must have existed in the mid-1880s. These ages were determined by subtracting the decade of stand origin (table 1) from 1880. For example, the 10 stands that originated in the 1870s (table 1) would have been about 10 years old in the mid-1880s (figure 2). We determined in this way



**Figure 2**—Distribution of stand ages in the 1880s within a 77-km<sup>2</sup> study area within the San Juan National Forest, Colorado, estimated by subtracting the decade of stand origin (table 1) from 1880.

**Table 1**—Number of stands within a 77-km<sup>2</sup> study area in the western San Juan National Forest, Colorado, that established after lethal fires in each decade since the 1760s.

Decade of last fire	Number of sampled aspen stands
1870s	10
1860s	6
1850s	2
1840s	3
1830s	4
1820s	2
1810s	2
1800s	0
1790s	0
1780s	0
1770s	0
1760s	1
Pre-1760s	27
Unknown	19
Total	76
Total, exc. unknown	57

that the median stand age in the 1880s was about 70 years. This means that about half of the stands in the landscape were >70 years old and half were <70 years old. If half of the landscape had burned within the previous 70 years, then it would require about twice this length of time, or 140 years, for an area equal to the entire landscape to burn. Thus, our best estimate of the fire rotation period in an aspen-dominated landscape during the period of indigenous settlement is about 140 years.

We conclude from this analysis that within this aspen dominated landscape during the period from the mid-1700s to the late 1800s, approximately half of the aspen forest consisted of relatively young stands developing after fires within the preceding 70 years, and that half of the stands had escaped fire for more than about 70 years. Fires occurred somewhere within the 76 km<sup>2</sup> study area nearly every decade, but it required more than a century for an area equal to the entire study area to be burned. Some stands probably were re-burned at relatively short intervals (<70 years), but many others persisted for more than a century without burning.

### **Caveats**

Three important weakness of this fire history study should be acknowledged. First, we cannot say in which exact years fires occurred, because dating fires from postfire age cohorts is inherently less precise than dendrochronological dating based on fire-scarred trees. However, because fire scars are so rare in aspen forests, the decade-level precision that we achieved is probably about the best that can be done in aspen-dominated landscapes of the southern Rocky Mountains. A second weakness of our method is that it cannot distinguish between two or more fires within the same decade, nor can it depict actual sizes or shapes of patches created by individual fires. Finally, it is important to note that we probably detected only the relatively large fires that occurred in the past. Many smaller fires undoubtedly occurred in places between the locations of our sample points and were not detected. This may not be a serious error from the standpoint of interpreting past fire effects, however, because a few large fires

probably were responsible for most of the burned area; this is the case today in boreal forest and several other types of fire-dominated landscapes (Johnson 1992; Moritz 1997; Romme et al. 1998).

It is also important to recognize that we have created a “snapshot” of the structure of the aspen forest mosaic at a single time at the very end of the period preceding extensive EuroAmerican land use changes, viz., the 1880s. We do not know just how representative this particular decade was of the period of several centuries before the 20<sup>th</sup> century. The landscape mosaic in 1880 probably was similar in its broad features to earlier mosaics, but there must have been fluctuations over time. Thus, in earlier periods, the median stand age probably was greater or less than the 70 years that we determined for the mid 1880s. Note, for example, the period in the late 1700s and early 1800s, a time when apparently few aspen stands were regenerated by fire in our study area (table 1). This was a period of reduced fire activity throughout the Southwest (Swetnam and Betancourt 1998; Swetnam et al. 1999), when the age structure of aspen forest mosaics in many areas probably shifted toward a predominance of older stands. In contrast, the middle and late 1800s was a time of greater fire frequency throughout the Southwest, when the aspen landscape mosaic may have been dominated by younger stands. Therefore, in evaluating today's age structures and developing desired future conditions, the 70-year median stand age that we determined for the 1880s should be viewed only as an approximate characterization of the conditions during the pre-1900 reference period.

Finally, we note that our study area in the western San Juan Mountains is located on a broad expanse of gently sloping terrain, with little topographic complexity and therefore few barriers to extensive fire spread under dry windy conditions. In other parts of the Rocky Mountains, where the terrain is more rugged or dissected, pre-1880 fire intervals probably were longer and the 1880 landscape structure probably contained a higher proportion of older stands than is depicted in figure 2.

### ***Comparison of current conditions***

Patch clearcutting now has replaced fire as the dominant disturbance agent in our study area (Crouch 1983; Shepperd 1993). However, the landscape mosaic still resembles the pre-1900 mosaic in its broad features, and overall, aspen appears to be thriving. Important practical questions remain about the optimal size and shape of logging units, and about differences between postfire and post-logging habitats (e.g., snags and coarse woody debris; Romme et al. 2000). However, aspen shows no serious decline and is in no danger of disappearing from this ecosystem (cf. Kay 1997).

In portions of the southern Rocky Mountains where no logging is allowed, the distribution of aspen stand ages is gradually shifting toward a preponderance of older age classes (Mueggler 1989). From an ecological standpoint, this is probably not a cause for concern, at least not in many areas (cf. Johnson 1994). Note in the age structure data from the Lime Creek burn (figure 1) that canopy stems are continuing to regenerate in most old stands, even after the original postfire cohort has largely disappeared. Nor is there evidence of replacement by conifers in many aspen stands of the San Juan Mountains (see below). Old aspen stems, especially those with decay, are extremely important for wildlife (DeByle 1985), and we see no obvious signs of diminished ecosystem function (e.g., gross productivity, decomposition, biodiversity) as these aspen stands age. Fire frequency likely will increase in the next century because of global warming (Graham et al. 1990), regardless of current management policies, and many old stands will be lost to wildfire. Therefore, rather than regarding late-successional

aspen stands as a problem that needs to be fixed by returning them to younger states via logging or prescribed burning, we suggest that late-successional stands be regarded as valuable components of aesthetics and biodiversity, and worthy of preservation.

This case study may be representative of other areas on the western slope of Colorado and perhaps also portions of Utah and northern New Mexico, where aspen dominates mid-elevation portions of the landscape and fire was the principal agent of disturbance prior to EuroAmerican settlement.

### ***Aspen, Elk, and Fire in Northern Yellowstone National Park***

Only about 2% of the 140,000-ha ungulate winter range in northern Yellowstone National Park is classified as an aspen cover type (Hessl 2000). Aspen stands are mostly small, discrete patches within a landscape dominated by sagebrush (*Artemisia tridentata*) steppe and conifer forests of Douglas-fir (*Pseudotsuga menziesii*) or lodgepole pine (*Pinus contorta* var. *latifolia*). Aspen is largely restricted to a narrow elevation zone near the forest/steppe ecotone (Despain 1990).

Unlike the situation in southern Colorado, where stands have usually regenerated prolifically after disturbance, the extent and density of aspen stands in northern Yellowstone have clearly decreased during the 20<sup>th</sup> century (Wagner et al. 1995; Kay 1997; White et al. 1998). The current aspen decline is due largely to chronic heavy elk browsing. However, reconstructions of aspen age structures reveal that aspen overstory regeneration in northern Yellowstone may have been episodic even before the ecological changes that began with park establishment and EuroAmerican settlement of adjacent lands in the late 1800s. Most of the mature aspen found today in northern Yellowstone became established between 1871 and 1920 (Ripple and Larsen, in press[a]). A reanalysis of Warren's (1926) aspen data set indicates that aspen overstories were successfully regenerating, at least in places, from the 1750s through 1920s (Ripple and Larsen in press[a]). However, canopy regeneration may have been less widespread before 1870 than it was afterward, e.g., some photographs from the late 1800s show mostly sapling aspen stands apparently resprouting after recent fire. The late 1800s was a unique period in the ecological history of this area, when a combination of low elk numbers, recent fires followed by fire suppression, wolves, and moist weather allowed aspen stems to grow into large size classes over most of the ungulate winter range (Romme et al. 1995). This unique combination of conditions has not recurred since the early 20<sup>th</sup> century, and no significant aspen tree regeneration has occurred since that time (Ripple and Larsen, in press[a]). It is even possible that mature aspen were more abundant in the early 20<sup>th</sup> century, following the unique conditions of the late 1800s, than at any time in the previous century or centuries. As Singer et al. (1998) emphasize, the northern Yellowstone ungulate range must be viewed as a nonequilibrium system that exhibits wide variation in response to variability in climate and herbivore pressures (more on this below).

## **Question 2: Controls on Aspen Succession and Responses to Disturbance**

Aspen stands may exhibit a variety of successional trajectories following disturbance. These trajectories are determined by local climate, soils, browsing

pressures, and seed sources. Also, as we suggest below, contingent historical events that occurred before the most recent disturbance may have a powerful influence on successional dynamics. We examine two case studies that illustrate responses to two very different kinds of disturbance regimes, local histories, and successional responses. The first study is from the San Juan National Forest, Colorado, where past fires were followed almost always by aspen regeneration, but with highly variable densities of associated conifer species. The second study is from northern Yellowstone National Park, where the success of postfire aspen regeneration is strongly influenced by ungulate browsing pressure.

### ***Seral Versus Stable Aspen Forests in the San Juan National Forest, Colorado***

Aspen may be found in pure stands, without any other tree species, or as a seral species in stands going through succession toward eventual domination by conifers. The conifers that gradually replace aspen in seral stands of the southern Rocky Mountains usually are Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) at higher elevations, white fir (*Abies concolor*) and Douglas-fir at middle elevations, and ponderosa pine (*Pinus ponderosa*) at the lowest elevations. There is some controversy regarding the successional status of pure aspen stands. Some investigators argue that such stands really are not “climax,” but have been disturbed in the past and conifer replacement simply occurs over very long time periods (centuries or millennia). Other investigators suggest that pure aspen stands do in fact represent a stable vegetation type, independent of disturbance.

Regardless of the long-term successional status of pure aspen stands, it probably makes sense to regard them as a stable vegetation type within the intermediate time scales that managers have to deal with (Fetherolf 1917; Baker 1925; Langenheim 1962; Morgan 1969; Severson and Thilenius 1976; Mueggler 1985). For the remainder of this paper, we refer to pure aspen stands having little or no conifer component as “stable aspen.” We refer to aspen stands having enough conifers to dominate the stand once the current aspen canopy has died as “successional aspen.”

Stable aspen stands have an uneven age structure and lack conifers (Mueggler 1976, 1989; Betters and Woods 1981). They tend to be associated with certain combinations of elevation, topography, and substrate, but the patterns of association are weak. Baker (1925) reported that “heavy-soiled flats” are not favorable for conifers and support primarily aspen, whereas rocky soils favor conifers. Pfister (unpublished dissertation, cited in Mueggler 1976) reported that stable aspen stands were common at lower elevations, but that higher-elevation aspen stands tended to be seral to conifers. Similarly, K. T. Harper (personal communication, cited in Mueggler 1985) has observed that stable aspen communities are commonly found at mid-elevations and on southerly exposures, but that successional aspen communities predominate at higher elevations and on northerly exposures. Soils under stable aspen stands usually are richer than soils under a mix of aspen and conifers, but this may be a result of aspen dominance rather than a cause (Parker and Parker 1983; Cryer and Murray 1992). To better understand the environmental controls on aspen forest succession, we studied successional versus stable aspen stands in the San Juan National Forest, Colorado.

### ***Methods***

We located 65 mature aspen stands in a study area centered on the fire history study area described above, but also including some surrounding lands in the

western portion of the San Juan National Forest. The stands were selected from topographic maps and field observations to represent the full range of elevation, substrate, topographic conditions, and conifer densities found in this portion of the San Juan Mountains. In each stand (about 1 ha in extent) we measured conifer density in a belt transect placed through the center of the stand, collected 10 increment cores from dominant canopy aspen trees, measured soil pH and hue at five points along the central transect, and recorded elevation, substrate, slope aspect, slope position, and steepness. After computing conifer densities in all stands, we defined stable stands as those having <200 conifer stems/ha and successional stands as those having 200 or more conifer stems/ha. In fact, most of the stands classified as stable had no conifers at all, but the broader definition was necessary to provide adequate sample sizes for chi-square analyses.

### Results

The observed frequency of stable stands was significantly greater than expected at elevations below 8,000 feet, and was less than expected above 8,000 feet (chi-square test,  $P = 0.02$ , table 2). Thus, stable aspen stands in the western San Juan Mountains tend to be associated with lower elevations, consistent with other observations (cited in Mueggler 1976), although successional stands also are common at lower elevations. Aspen stands at higher elevations tend to be successional, although we found some stable stands at all elevations up to 10,500 feet.

Stable aspen stands also were significantly ( $P < 0.05$ ) associated with shale substrates rather than sandstones or igneous rocks, consistent with Baker (1925), but the pattern in our San Juan National Forest study area was weak and probably not ecologically meaningful (data not shown). Chi-square tests revealed no significant patterns in frequency of stable versus successional aspen stands with respect to soil hue, soil pH, aspect, slope position, or slope steepness. There was a significant association between stable versus successional aspen stands and stand age, i.e., older stands tended to be successional and younger stands tended to be stable (data not shown). However, older stands also were significantly associated with higher elevations and younger stands with lower elevations, so elevation appears to be the most important underlying variable associated with aspen successional patterns in this area.

### Interpretation

These results suggest that the occurrence of stable versus successional aspen forests in the western San Juan National Forest is explained not by deterministic climatic or topographic gradients, but by local historical contingencies. Many of the stable aspen stands are located adjacent to a zone of ponderosa pine that

**Table 2**—Frequency of stable aspen stands (<200 conifers/ha) in relation to elevation in the western San Juan National Forest, Colorado. The pattern is significantly different from the null model (chi-square = 10.27, 3 degrees of freedom,  $P = 0.0164$ ,  $n = 65$ ).

Elevation	Observed	Expected
<i>feet</i>		
6,000–7,000	21	15
7,001–8,000	16	10
8,001–9,000	21	29
9,001–10,500	7	11

covers an extensive plateau area just to the west and at lower elevations than the aspen zone. Median fire intervals before 1880 in the ponderosa pine zone were five to 15 years (Romme et al. 1999), because of frequent summer dry periods and highly flammable litter. Fires that were ignited in the ponderosa pine zone probably often spread into the adjacent aspen forests. The resulting fire intervals in the low-elevation aspen forests probably were longer than in the pine forests, because of the low flammability of aspen fuels, but were shorter than the time required for conifer seedlings to reach reproductive age. Consequently, conifer seed sources were locally eliminated in many stands. However, the aspen responded to frequent fire by resprouting from the roots, thus maintaining its local dominance.

In contrast, median fire intervals in aspen forests at the higher elevations, remote from the ponderosa pine zone, were substantially longer than in aspen at lower elevations. For example, median fire intervals prior to 1900 were >150 years in spruce-fir forests of the San Juan Mountains (Romme et al. 1999). Hence, conifer seed sources persisted at the higher elevations, and most aspen stands remained successional. Baker (1925) similarly suggested that recurrent fires (at about a 50-year rotation) may help maintain pure aspen forests by eliminating conifer seedlings and saplings. Thus, we hypothesize that many stable aspen stands in the southern Rocky Mountains and perhaps elsewhere, especially those at lower elevations, developed primarily in response to very short fire intervals in the past. These stands now persist without conifer invasion even in the absence of fire, because local conifer seed sources have been eliminated.

### ***Effects of Fire and Ungulate Browsing on Aspen in Yellowstone National Park***

The large fires of 1988 burned nearly a quarter of the northern Yellowstone winter range. However, even though the fires stimulated abundant sucker production in most of the burned aspen stands, almost none of those suckers are growing into new canopy stems today (Romme et al. 1995; Kay 1997). Why is aspen responding to this recent disturbance by fire in a fundamentally different manner than it did a century ago? The principal reason appears to be chronic heavy browsing by elk. The browsing is clearly preventing the aspen sprouts from growing taller than about 0.5 m and also may be gradually reducing the density and overall vigor of the sprouts and of the underlying aspen root system (White et al. 1998). Whereas fire formerly stimulated aspen tree regeneration in this region, current heavy browsing pressure has “uncoupled” the beneficial effect of recent fires on aspen (Hessl 2000). The warmer and drier climatic conditions of the 20<sup>th</sup> century also may have stressed the aspen and made them less resilient to browsing (Coughenour and Singer 1991).

We suggest that Yellowstone's northern winter range is representative of other areas in the West where aspen has always been a somewhat marginal species, because of suboptimal climate and soils coupled with heavy ungulate browsing pressures. A similar 20<sup>th</sup> century decline in aspen has been documented on elk winter ranges in Rocky Mountain National Park, Colorado (Olmsted 1979; Baker et al. 1997), in the Jackson valley, Wyoming (Krebill 1972; Bartos et al. 1991; Hessl 2000), and in Banff, Jasper, Yoho, and Kootenay National Parks in Canada (White et al. 1998). Aspen probably is most vulnerable to decline in this kind of ecological setting—in response not only to chronic heavy browsing, but also to drought and changes in the fire regime.

However, it is premature to predict a certain loss of aspen even in these landscapes where it is most vulnerable to decline. In the same national parks listed above, but outside the ungulate winter ranges, and in places like southwestern Colorado where climate and soils apparently are optimal for aspen, there is little or no evidence of aspen decline (Suzuki et al. 1999; Romme et al. 1999). Even within the elk winter range of the Jackson valley, Wyoming, Hessl (2000) found some stands that were regenerating adequately after prescribed fires, perhaps because of unique genetic characteristics or other subtle factors not immediately obvious. Moreover, aspen clones can persist for a very long time, even when subjected to intense browsing or competition from conifers (Despain 1990; Peterson and Peterson 1992). White et al. (1998) observed in Jasper National Park that aspen began to regenerate again after wolves were reestablished in the 1970s. With the recent reintroduction of wolves in Yellowstone, it is possible that predation pressure will reduce elk densities and modify elk foraging behavior in such a way that aspen will be able to escape browsing pressure and regenerate in portions of the northern range where no significant regeneration has occurred in the last 80 years (Ripple and Larsen, in press[a]). Ripple and Larsen (in press[b]) also report that “jackstraw piles” of fallen conifers killed by the 1988 fires provided aspen sprouts with at least partial protection from elk browsing in northern Yellowstone National Park.

### **Question 3: Aspen Life History Traits, Reproductive Mechanisms, and Resilience**

As a long-lived clonal species that reproduces primarily via vegetative sprouting, aspen responds very effectively to local disturbances that fall within the recent historic range of variation in disturbance kind and severity. Thus, in the San Juan Mountains study area, fire poses no serious threat to the long-term persistence of extensive aspen stands, even if fire frequency increases in the next century in response to global climate change. Similarly, aspen in the San Juan Mountains should be able to withstand reasonable logging and grazing programs, especially if those programs are designed to mimic the disturbance regime of the pre-1900 period as much as possible (Romme et al. 2000).

The situation is less clear in northern Yellowstone, where current browsing intensity may exceed historic levels—not with respect to acute browsing intensity (which must have been occasionally intense at many times in the past) but possibly with respect to the chronic heavy browsing pressure now occurring. Nevertheless, aspen's long genet life span, extensive root systems, and ability to produce new stems asexually have enabled it to persist throughout a century of heavy browsing pressure and may maintain the species well into the next century even under the current disturbance regime (Despain 1990).

However, asexual reproduction via root sprouting is not enough. To be able to cope with broad-scale climate change or habitat alterations that exceed the range of variation experienced during the last several centuries, aspen must be able to maintain genetic diversity through sexual reproduction and to produce new genetic individuals through seedling establishment (Eriksson 1992; Mitton and Grant 1996). Climate simulations under doubled-CO<sub>2</sub> scenarios suggest that climatically suitable geographic ranges for many species will shift substantially during the next century, and that conditions within species' ranges may be altered (Romme and Turner 1991; Bartlein et al. 1997). Moreover, most individual aspen genets that we see on the landscape today may have established

during cooler climates in the past, e.g., during the Little Ice Age or even in the early Holocene (Baker 1925; Cottam 1954; Barnes 1966; Tuskan et al. 1996), and hence may not be genetically well equipped to cope with the warmer climates and other environmental changes expected in the next century.

Aspen seedlings have been notoriously rare in the West throughout the 20<sup>th</sup> century, but genetic studies within mature populations indicate that occasional seedling establishment has occurred during previous centuries (Jelinski and Cheliak 1992). The most recent episode of sexual reproduction in aspen occurred following the 1988 Yellowstone fires (Kay 1993; Romme et al. 1997). The 1988 fires burned about 300,000 ha in and around Yellowstone National Park and were the largest fires in this region in the last 300 years (Romme and Despain 1989). Extensive surveys conducted in 1993 revealed that aspen seedlings were restricted to burned areas and varied greatly in local density, with maximum densities of >300 stems/ha (Romme et al. 1997). Notably, aspen seedlings were abundant in many areas well outside the pre-1988 distribution of aspen, as well as within the pre-1988 distribution. What does this unexpected response to the extensive fires of 1988 indicate about aspen's resilience to the environmental changes expected in the next century? We address this broad question by posing three smaller questions:

### ***Why Did Extensive Aspen Seedling Establishment Occur After the 1988 Fires?***

Establishment of new aspen genets in the West apparently has been infrequent and episodic (Jelinski and Cheliak 1992), principally because aspen seedlings are extremely intolerant of desiccation or competition (Moss 1938; McDonough 1979). A rare "window of opportunity" for seedling establishment occurred after 1988, due to a combination of unusually moist and cool weather in early summer, the occurrence of extensive bare substrate where competition from other plants was greatly reduced, and prolific seed production by mature aspen individuals that survived the fires. For instance, May precipitation in Yellowstone National Park was 139–197% of average in 1989–1991, and total plant cover in burned forests was 2–53% of cover in unburned forests (Romme et al. 1997).

The next century is likely to bring more extensive fires (Graham et al. 1990), which could mean more episodes of aspen seedling establishment if the concurrent weather conditions are cool and moist. However, if the fires of the next century are associated with drought and high temperatures, then aspen may be unable to establish new genets, and increased fire activity instead may lead to local extirpation of some old clones without establishment of new genets—especially in areas of chronic heavy ungulate browsing or other stresses on aspen.

### ***What Are the Patterns of Genetic Diversity in the Aspen Seedlings?***

Seedling populations sampled in 1993 exhibited greater overall genetic diversity than adult populations sampled on Yellowstone's northern range (Tuskan et al. 1996). However, as of 1997, there were no strong spatial patterns in the genetic structure of seedling populations across the Yellowstone Plateau (Stevens et al. 1999). This suggests that intense selection pressures have not yet occurred in the seedling populations, i.e., that we still see a more-or-less random distribution of genetic composition across the landscape reflecting vagaries of seed source and seed dispersal. Stevens et al. (1999) hypothesize that selective

mortality will occur over the next few decades, and that local genetic diversity in seedling populations will decrease as one or a few genotypes come to dominate individual sites.

It seems logical that this infusion of new individuals with unique genetic recombinations into the aspen populations of the Greater Yellowstone area will enhance the species' ability to survive or even thrive in the face of impending climatic and environmental changes. However, we are in only the earliest stages of what will be a long-term population process. The rare episode of aspen seedling establishment that occurred after the 1988 Yellowstone fires provides a unique opportunity to document the establishment of new aspen individuals and genetic structure in a natural setting.

### ***What Will Be the Long-Term Ecological Role of the New Aspen Genets?***

Based on the resampling of permanent plots from 1996–1998, aspen seedling densities are decreasing across most of the Yellowstone Plateau (M.G. Turner and W. H. Romme, in preparation). Causes of mortality appear to include heavy browsing by elk as well as locally adverse microclimate and soils conditions. Over much of Yellowstone National Park, many or even most of the new aspen individuals that appeared after 1988 seem destined to disappear over the next few decades, leaving no lasting ecological legacy.

However, some of the new aspen genets are thriving and appear likely to become well established and to persist indefinitely. For example, in one study area in west-central Yellowstone National Park, aspen genets that germinated in 1989 were >1 m tall in 1999 and had a single dominant stem. These individuals were growing in a dense tangle of fallen pine stems killed by the 1988 fires, which probably protected the aspen seedlings from excessive elk browsing. Thus, even though most of the aspen seedlings that established soon after the 1988 fires may perish, enough may survive to increase overall genetic diversity of the species and to establish new genets in new locations. Tuskan et al. (1996) suggest that episodes of new aspen genet establishment may typically exhibit just such a pattern of initially high seedling densities, followed by extensive mortality with survival of a few individuals that are best adapted to local conditions and which go on to produce clonal structures. Additional seedling establishment events of this kind in the future may be crucial to long-term survival of aspen in the Yellowstone region if climate change in the next century shifts the elevational zones of tolerance for plant species (Romme and Turner 1991; Bartlein et al. 1997) and if continued browsing pressure combined with drought and other stresses causes local extirpation of some old aspen clones.

## **Conclusions and Management Implications**

1. Aspen plays a variety of roles in western landscapes, depending on the ecological context. We urgently need more detailed, local case studies of aspen ecology, disturbance regimes, responses to disturbance, landscape patch dynamics, and genetic and population structure to further illustrate its different roles and to provide a reliable basis for making useful generalizations. For example, our understanding of the very different pre-1900 disturbance regimes in aspen forests of the San Juan National Forest and northern Yellowstone National Park helps to explain the very different responses to recent disturbance that have been observed in the two systems.

2. Long-term persistence of aspen may be threatened, especially in the face of broad-scale global change, in settings like Yellowstone's northern range, where (a) aspen stands have always been patchy and restricted to limited portions of the landscape, probably due in part to locally marginal climate and soils conditions, and (b) ungulate browsing is intense, concentrated, and chronic.

3. Long-term persistence of aspen probably is not threatened, even in the face of global change, in settings like the San Juan National Forest where (a) aspen stands are extensive and cover a wide range of elevations and topographic positions, probably due in part to locally favorable climate and soils conditions, (b) fire was the principal disturbance agent in the past, and (c) ungulate use is relatively light or widely dispersed.

4. In settings like the San Juan National Forest, conifer invasion of aspen stands is a natural successional process that has always occurred in some stands during long fire-free intervals, and there have always been some long fire-free intervals. For example, the paucity of fire in the 20<sup>th</sup> century somewhat resembles the reduced fire activity of the late 1700s and early 1800s in the Southwest. The relatively high proportion of old aspen stands that we see in some unlogged landscapes today probably is not far outside the historic range of variability in landscape patch structure.

5. Old aspen stands in the southern Rockies, with or without conifer invasion, are extremely valuable for wildlife and aesthetics and show no obvious decline in ecosystem function. Because the next century is likely to bring increased fire frequency, similar to what occurred in the late 1800s or even exceeding the fire frequency of that period, old aspen stands probably will become less abundant in the future—regardless of current management decisions.

6. Although aspen reproduces primarily via asexual root sprouting, it also periodically produces new genetic individuals via sexual reproduction and seedling establishment. Seedling establishment is associated with large-scale disturbances (e.g., fire) that coincide with cool moist climatic conditions. The resulting genetic recombination and establishment of new individuals in new geographic locations may enhance aspen's ability to tolerate the broad-scale climate and habitat changes anticipated in the next century.

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