CONSERVATION ISSUES

Aspen in the Sierra Nevada: Regional Conservation of a Continental Species

Paul C. Rogers[1,2,4]
Wayne D. Shepperd[3]
Dale L. Bartos[2]

[1] College of Natural Resources
Utah State University
Logan, UT 84322

[2] USDA Forest Service
Rocky Mountain Research Station
860 North 1200 East
Logan, UT 84321

[3] USDA Forest Service
Rocky Mountain Research Station
2150 Centre Ave., Building A
Fort Collins, CO 80526

[4] Corresponding author:
progers@fs.fed.us; 435-755-3572

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ABSTRACT: Quaking aspen (*Populus tremuloides* Michx.), a common species in North America, is a minor species in the Sierra Nevada of California. However, the limited coverage of aspen in this area appears to carry a disproportionate biodiversity load: numerous species are dependent on the unique components of aspen forests for habitat. Land managers in the region believe the species is declining due to fire suppression policies of the past century. Recent research from other regions shows mixed results when assessing the extent of decline. This review focuses on the crossroads between human and natural history to describe a broader picture of aspen ecology in the Sierra Nevada. The method used here combines a review of the ecological literature with historical synthesis. A central conclusion is that the current "decline" in aspen must be placed in the context of an unusual regeneration pulse brought on by intensive Euro-American resource extraction activities of the late 19th century. We address unique features of the Sierra aspen population, the interface of climate change and human-caused disturbance, and conservation strategies for restoration of an aspen community more closely aligned with contemporary climate-disturbance cycles. Conservation recommendations include reintroduction of mixed-severity natural fires and complimentary wildlife, such as top predators, where practical, plus allowance for local flexibility where deviations are appropriate based on ecology and social concerns.

Index terms: biodiversity, climate, disturbance, fire, history, *Populus tremuloides*

INTRODUCTION

In evergreen-dominated forests of montane western North America, aspen (*Populus tremuloides* Michx.) provide aesthetic and ecological diversity beyond their relatively minor coverage on the landscape. Some have suggested aspen as a "keystone" species, endorsing its elevated role in supporting entire ecosystems (Manley et al. 2000; Campbell and Bartos 2001). In the Sierra Nevada, aspen are often associated with increased moisture, rich soils, and lush undergrowth compared to adjacent conifer forests. Small aspen stands may act as oases for wildlife and diverse plants requiring moist habitat. There is evidence, however, suggesting that contemporary aspen coverage, along with landscape-level linkages, have been altered considerably during historical times.

Our goal is to explore historical changes and place them in an ecological context. The following questions provide a framework for this exploration: (1) Does the small amount of aspen today provide clues of past forest communities?; (2) What effect have humans had on the current extent of these forests in the Sierra Nevada?; (3) Can we conserve a species that, although common continentally, may be threatened regionally?; and (4) How much intervention is appropriate given the present state of aspen and intensive human use of these mountains? We will address these subjects, primarily through a review of contemporary aspen literature and historic records. Historical disturbance ecology and the Sierra Nevada's dynamic climate over past centuries provide unifying themes for this work.

The intensity of human use, both contemporary and historical, as well as the very limited coverage of aspen on the landscape, distinguishes the Sierra Nevada from other large regions of aspen presence. Regional conservation for a species at its geographic margin, as well as one pushed to its limits by human intrusions, is a daunting undertaking. However, we believe this unique situation may provide the ideal laboratory for adaptive management practices, as well as continental lessons in aspen conservation.

REVIEW OF LITERATURE

Aspen Range and Ecology

Quaking aspen is the most widespread tree species in North American. Aspen are found to the north in the Arctic Circle and south into Mexico. The species grows from the Atlantic coast to the Pacific, occurring in most United States regions and all Canadian provinces (Preston 1976). In addition to its environmental adaptability, aspen is known universally as a colonizer of recently disturbed sites. As a seral species, aspen is relatively short-lived (< 150 years) in most environments, although exceptions occur throughout the West in some persistent stands (Mueggler 1985).

Mueggler (1988) classified "stable" aspen types throughout the Interior West, and Barry (1971) found some small stands persisting in the Sierra Nevada. In the western U.S., however, many feel that lack of a "historic level" of disturbance (primarily fire, but also grazing and climate influences) is pushing the species toward decline (Brown 1995; Bartos and Campbell 1998; Gallant et al. 2003; Di Orio et al. 2005). In the Sierra Nevada proper, most aspen stands are associated with riparian and meadow environs, although other physiographic aspen habitat may be found regionally (Shepperd et al. 2006). This review specifically examines aspen in the Sierra Nevada ecoregion section (Bailey et al. 1994) as shown in Figure 1.

Perhaps the most important feature of aspen ecology is that the species reproduces primarily by asexual root sprouting. All stems (ramets) originating from a parent root system form genetically identical aspen stands (clones). What the casual observer sees as aspen "trees" are really individual ramets arising from the parent root system. Over time, many of the original root connections are severed as ramets develop their own root systems to support nutrient uptake (Shepperd and Smith 1993). This reproductive strategy allows aspen to establish quickly in disturbed environs, sustain collective clonal health by resource sharing, and persist as a distinct biological unit for millennia (Mitton and Grant 1996; Romme et al. 1997). Counting aspen tree rings will give ramet age, not the age of the overall clone. Estimates of maximum clone ages range from 1000 to over a million years (Barnes 1975). Some researchers believe that DNA sequencing will eventually be used to date somatic mutations, and thereby allow more accurate estimates of aspen clone ages (Karen Mock, Utah State University geneticist, pers. comm.). Similarly, future correlation of genetic and climatic records may reveal key ecological processes in the extended life histories of aspen clones.

Aspen's clonal habit enables estimates of past stand and landscape extent based on current species distribution, stand structure, and tree health (Rogers 2002). To achieve this, it is important to understand the principal ecological factors that shape aspen forests. Aspen reproduce prolifically, grow relatively fast in full sunlight, and die out through various mechanisms brought on by increasing succession of competing conifers (Jones and Schier 1985). Although individual ramets can live beyond 200 years, aspen stands are generally short-lived and succumb to decay and succession between 80-120 years of age (Baker 1925; Hinds 1985; Rogers 2002).

For example, assume there is a single aspen stem among a forest of conifer species. When that ramet originated from a larger clone after a historic disturbance (e.g., crown-replacing fire), we may assume it is a remnant of a forest once dominated by clonal cohorts. By aging this single aspen, we can calculate the time since the disturbance. From that time, an originally pure aspen stand slowly succeeded over the following century, or so, to a cover of more common shade-tolerant conifers such as red fir (*Abies magnifica* A. Murr.) or white fir (*Abies concolor* Lindl. ex Hildebrand.). While this presents a typical scenario, there is the possibility that a lone aspen now on the landscape may have originated as a "second generation" ramet in a small gap of mature pure aspen. In either case, this stem would have originated prior to subsequent conifer shading and thus, at the very least, represents the approximate date of conifer invasion (aging cohort conifers should will confirm this). The likelihood of this stem being of seed origin is remote, given the rarity of these events due to very strict seedbed requirements (Barnes 1966; McDonough 1979; Romme et al. 1997). We are unaware of any published accounts of seedling establishment in the Sierra Nevada, though we assume that these events have occurred under specific circumstances (McDonough 1979; Quinn and Wu 2001).

Though aspen clones reproduce exceptionally well following fire, other disturbances will result in similar fecundity. Much of the high elevation western landscape is lined with vertical avalanche paths filled with juvenile aspen stems. Unlike the more brittle wood of maturing conifers, aspen stems can withstand seasonal bending from snow in addition to their ability to quickly colonize slide zones (Potter 1969; Veblen et al. 1994). However, aspen that establish in avalanche paths often remain stunted for years before being severed by larger slides. Severe wind events, landslides, or forest pathogens may also clear the way for new aspen stands. Human actions, such as tree felling, land clearing, road building, and prescribed burning may result in new aspen sprouts. Human activities that stimulate aspen regeneration may also lead to high disease rates from infection of logging-related wounds on remaining trees. For example, a study in Colorado showed a 19% increase in tree mortality 5-7 years after cutting (Walters et al. 1982).

If successful aspen regeneration is the goal, management actions should be preceded by a thorough understanding of species ecology, local disturbance regimes, and historical human impacts (Rogers 1996; Landres et al. 1999; Franklin et al. 2002; Rogers 2002).

Historical Disturbance Ecology

There is a rich history of the environmental impacts from European settlement in California's Sierra Nevada (Jackson et al. 1982; Strong 1984; Palmer 1992; Beesley 1996; Cermak 2005). Assessing impacts on the limited cover of aspen forests in the region has not been attempted. Thus, our objective is to trace the pre-settlement, Euro-American settlement, and modern era patterns of disturbance focusing on aspen forests. Without direct evidence of aspen change over this period, a great deal of this analysis relies on inference based in known ecological reaction to disturbance events. Prior to historical examination, a look at long-term climate of the Sierra Nevada will provide an environmental context for estimating 'range of natural variability' (Landres et al. 1999).

Climatic Context

Climate has a profound effect on disturbance cycles. Research using tree ring patterns, sediment and ice cores, and longer geologic records have produced several examples of high climatic variability at century- to millennial-scales (Bjorse and

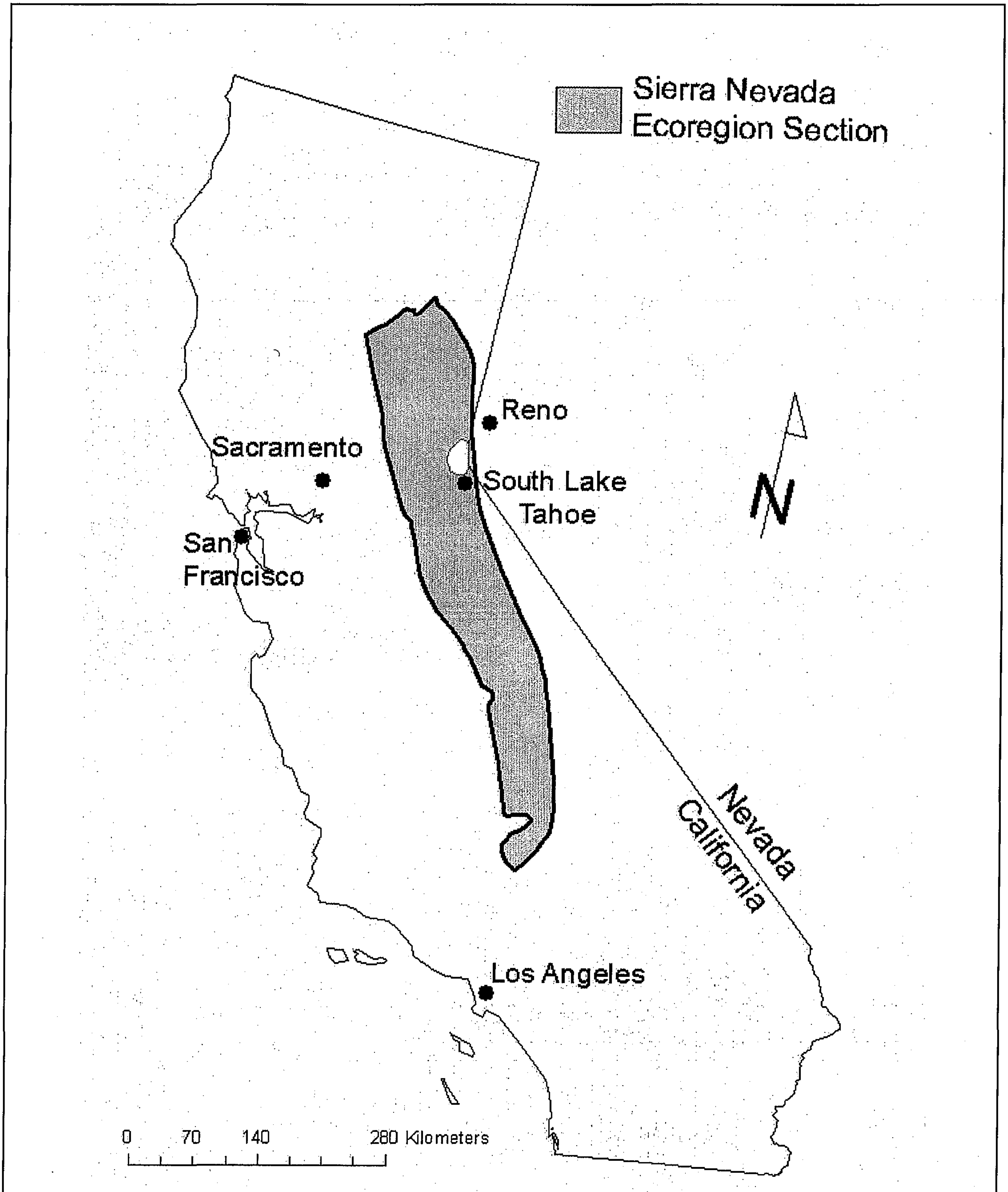

Figure 1: The Sierra Nevada ecoregion is shown in relation to the state of California.

Bradshaw 1998; Whitlock and Knox 2002; Pierce et al. 2004).

In the Sierra Nevada, Millar and Woolfenden (1999a) used tree rings and meadow sediment cores to document three distinct climatic periods of note: the Medieval Warm, the Little Ice Age, and the modern era. A warm dry Medieval Warm Period (900-1350) was followed by the cool and moist Little Ice Age (1450-1900). During the Medieval Warm Period, frequent mixed severity fires (ground fires with irregular crowning) were more common – favoring a more regular aspen regeneration in a patchy mosaic. Millar and Woolfenden (1999a) further note an active period of volcanic vent eruptions between 1350-1450, which likely led to increased fire starts from a source not often considered. In contrast, the Little Ice Age exhibited infrequent, but more severe, crown fires in montane forests (Millar and Woolfenden 1999a) which favors large-extent establishment by colonizers (Pierce et al. 2004). The former strategy is favorable to aspen maintenance on a decadal scale, while the latter promotes larger pulses of aspen renewal (and expansion?) over centuries. As an aside, the Little Ice Age coincides with a period ("pre-settlement") assumed to be the pristine ideal of natural systems minimally influenced by humans. Though human impacts were certainly less, reconstructed vegetation patterns from this era should be expected to compare poorly with today's landscapes because climates were so different. Finally, the modern era has been warmer and moister (Millar et al. 2004). Relatively wet periods over the past 600 years favored the growth of red and white fir rangewide – hence the proliferation of red fir and the notable legacy of 400-600 year old fir in the subalpine zone (Millar and Woolfenden 1999b). Concurrent with fir's dominance, a longer and more severe fire regime has become the norm.

Pre-settlement

Anthropological evidence shows that Native Americans have likely lived in the Sierra Nevada for the past 10,000 years with a population estimated to be about 90,000-100,000 prior to European settlement (Parker 2002). Authors have differed in their assessment of levels of impact by aboriginal societies (Denevan 1992; Anderson and Moratto 1996; Vale 1998, 2002). An exhaustive synthesis (Parker 2002) of demographics, physical environment, lightning strikes, climate patterns, tree ring records, and anthropological land uses concludes that aboriginal populations modified landscapes intensively near permanent settlements, but effectively left most of the range to natural disturbance and succession. A recent pre-settlement fire history near Lake Tahoe pinpoints most fire starts (90%) to climatic conditions common in the period from 1650-1850. Late summer weather, including dry conditions during La Ni a years and peak lightning strikes, appear sufficient to account for the number and seasonality of pre-settlement fire regimes (Taylor and Beaty 2005).

The limited impacts of aboriginal Americans on native flora were further reduced by dramatic human population declines near the end of the pre-settlement era (1780-1850). In advance of European settlement, disease reduced Native populations by up to 80% (Beesley 1996).

This transition from Native American to Euro-American impacts was based not only on great changes in population, but on the scale and intensity of landscape utilization. Natives exploited the mountain range at a subsistence level; settlers extracted resources and converted land at an industrial level. Cermak (2005, p.11) echoes this sentiment in relation to burning:

> While some Native American fires were no doubt set for various purposes, other fires were probably caused by Native American carelessness.... At any rate, Native American burning had little effect upon California's forests compared to the repeated, widespread burning of forests and brushlands practiced by miners, lumbermen, stockmen, settlers and others during the last half of the nineteenth century.

Euro-American Settlement

The mid-19th century gold rush bought prospectors and settlers into California's high country in large numbers (Beesley 1996). Initial settlement was followed by successive waves of resource extraction-driven development, which contributed to land clearing and opportunistic expansion of aspen forests. The new course set by Euro-Americans upon settlement in the Sierra Nevada is best characterized by intensive use and abuse of natural resources, beginning with mining and followed by small-scale water diversion for mining, logging, grazing, and eventually large-scale water diversion and dam building for agriculture, hydroelectric, and urban use (Figure 2). Activities often overlapped. For example, hydraulic mining diverted streams to "mine" gold-bearing sediments along major Sierra tributaries. Palmer (1992, p.138) estimates use in just northern Sierra watersheds as being 136 million liters of water in a 24 hour period – some three times the use of urban San Francisco during that era. These operations, spread throughout the range – but more commonly on the west slope – completely cleared adjacent hillsides of vegetation and sent millions of tons of sediment downstream.

Logging had an enormous impact on the central Sierra Nevada. In the Lake Tahoe Basin, logging to support the Comstock mining district in Nevada nearly denuded the Carson range (east of Lake Tahoe), and impacted all forests surrounding the lake to some degree (Strong 1984). Historic photos from this period show barren hillsides behind logging decks stacked high with locally harvested timber (Strong 1984, p.27). Near Truckee, huge volumes of logs were extracted to supply mines, construct giant V-shaped flumes for transporting logs, and for the Union Pacific rail line. Beesley (1996) estimated that 300 million board feet (707,000 m^3) of timber were harvested to construct snow sheds for the railroad and an additional 20 million board feet (47,194 m^3) per year to maintain the sheds. In Comstock mining efforts an additional 70 million board feet (165,181 m^3) a year, for about 10 years, were consumed in flume construction, mine ties, fuel wood, home building, and construction of a narrow-gauge rail line from Virginia City to Spooner Summit and eventually Lake Tahoe itself. This rail line allowed massive

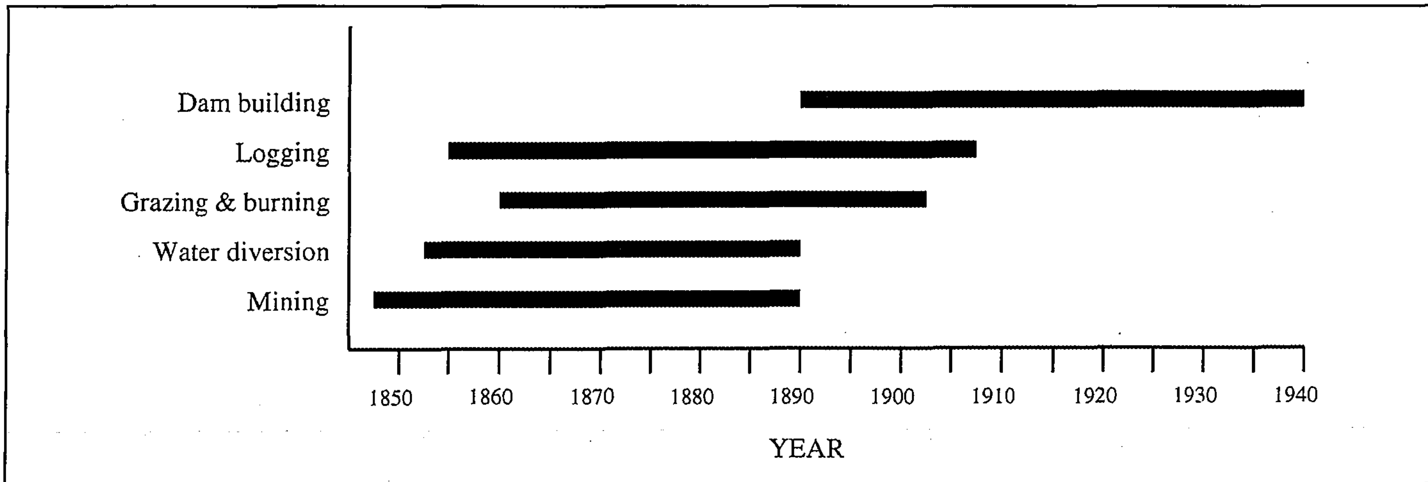

Figure 2: Bars on the chart represent years of greatest impact from associated activities. Activities continued after the periods shown here, but at greatly reduced levels. The activities often occurred in conjunction with one another. For example, water diversion complimented mining and logging supported both mining and water diversion (Sources: Beesley 1996; Jackson et al. 1982).

exploitation of lumber, which was towed by boom from various points across the lake (Strong 1984; Beesley 1996). Strong (1984, p.31-32) further explains that accepted logging practices often involved post-harvest burning – which contributed to large fires in 1889, 1898, 1902, and 1903 – and resulted in expanses of brush fields in the following decades. In 1900, government agent George Sudworth made an extensive survey of the Stanislaus Forest Reserve on the west slope of the Sierra Nevada. He encountered small mills in the headwaters of each major, and many minor, west slope drainages, and found evidence that mills had moved several times after exhausting the entire supply of lumber within a 4.0-4.8 km radius (Sudworth 1900, p.513).

Though mining and logging activities were widespread during the late 19th century, they probably affected less total land than grazing. Sheep (*Ovis* spp.) were the dominant livestock in the 19th century, though some cattle (*Bos* spp.) grazing did occur. During the "sheep boom" (1870-1890), there were no restrictions on the number of sheep or the timing and movement of herds. Although accurate estimates of sheep use during this period are not available, Beesley (1996, p.7) says that they numbered in "the millions" and Cermak (2005, p.13) estimated 7 million statewide, a substantial portion of which likely used the prime high elevation rangeland. Although forage and trampling by sheep can devastate overused meadows, both meadow and forest alike were affected by the common and widespread practice of burning pasturage upon exiting the mountains to stimulate future forage. Numerous authors detailed these uncontrolled burning practices (Sudworth 1900; Leiberg 1902; Jackson et al. 1982; Beesley 1996; Kinney 1996; Cermak 2005), though one quote stands out from a P.Y. Lewis (Barrett 1935, p.23): "We started setting fires and continued setting them until we reached the foothills. We burned everything that would burn."

In sum, the various land clearing activities stimulated aspen sprouting and removed competition for sunlight. As we will see, a very different regulatory climate followed, helping to ensure aspen's initial success through the early part of the 20th century.

Modern Era

The modern era is characterized by implementation of much needed regulation of forestlands in the Sierras. After documentation of natural resource abuse by the likes of Sudworth (1900), Leiberg (1902), and preservationists such as John Muir (1982), the age of scientific land management began to take hold; grazing would be limited and monitored to some degree, logging would be planned and inspected, and mining and water use would be closely regulated – all, theoretically, with the backing of proven science and resource enumeration. In hindsight, this approach was fraught with scientific weakness and personnel shortages for implementing nascent management practices, but esprit de corps often carried the day in the newfound agencies. How the Forest Service in California's newly formed "Region 5" tackled the fire issue is a prime example of regulation, and likely the birth of 'command and control' management (Holling and Meffe 1996) as a reaction to the laissez faire settlement era.

After the big fires of the 1890s and early 1900s, forest managers began discussing fire suppression as a means of controlling the situation. Meanwhile, established forest use practices of the day included intentionally setting fires. In 1910, however, extreme fire conditions in the northern Rockies (Pyne 2001) brought the national debate – fire suppression versus "light burning" – to the forefront (Hoxie 1910). Stuart Bevier Show, a California forester, played a national role in advancing fire suppression policy in the U.S. Forest Service (Show and Kotok 1930). Zealous fire suppression was quickly adopted by other federal and state agencies. This policy, coupled with heavy burning and timber extraction of the previous era, is likely a key factor in the development of contemporary aspen forests.

The legacy of early 20th century scientific forestry was the firm establishment of practices designed to bring both nature and resource extraction into alignment with management objectives. Hence, fire would be suppressed with military fervor; rivers would be controlled with dams and diversions; forests would be "managed" for highest yields through a menu of cutting techniques to reduce dead trees, small trees, infested trees, and high tree density; and game animals would be regulated by elimination of large predators and optimization of species' populations. Academics kept pace by expanding natural resource coursework in range science, wildlife management, engineering, silviculture, entomology, pathology, and forest economics. Though all of these developing disciplines contributed needed understanding to land management practices, their core mission was to quantify forest inputs and outputs for commercial benefit and regulation. In the Sierras, the economic engine driving forest management was timber harvest – specifically, high value, fast growing conifer species. Secondarily, forage for livestock and wild ungulates were considered forest "products" to be favored in management plans. Aspen was considered a lesser tree species, which interfered with resource goals.

Around mid-century, the tide began to shift from control of nature to understanding, and eventually working with, natural processes. "Multiple Use" meant that agencies were transforming from single use missions, such as cutting timber or grazing livestock, to a variety of "outputs" such as recreation, wildlife, or water uses. Even with this makeover, dominant uses continued to drive management actions. On the heels of multiple use management came increased legal requirements of the 1970s meant to bolster protection for multiple resources. This transformation from a production mode, primed by California's rapid population growth, to a stewardship mode was not easy – and remnants of command and control management are with us still (Beesley 1996). However, the evolution of resource management continues as well, with greater acceptance of disturbance-based management practices today (Rogers 1996).

The modern era, especially in response to settlement practices, had a great impact on the Sierra Nevada landscape. In particular, aspen extent was certainly curtailed by the combined effects of fire suppression, management favoring conifers, and grazing of aspen sprouts by livestock and unfettered wild ungulates. To an unknown degree, a relatively moist 20th century (Millar et al. 2004) aided managers in successfully implementing fire suppression. Recently a spate of warmer and dryer years has lead to more intense fire activity. It may be that the temporary false confidence of a moist 20th century has fueled management strategies (i.e., fire suppression, intense logging, grazing, and wildlife use) that are unsustainable for a period of changing environmental conditions.

DISCUSSION

Aspen in the Sierra Nevada: a Unique Resource

Regardless of historic actions by humans, quaking aspen has probably never been a wide-ranging species in the Sierra Nevada. However, Potter (1998), basing his work on dendrochronology of aspen and associated conifers, suggests that aspen was more abundant than its current extent and that fire suppression and grazing have helped reduce aspen cover over the past 150 years. Further, we believe that several decades of intense grazing accompanied by annual burning (Cermak 2005) of montane communities (Strong 1984) promoted a pulse of aspen establishment when these practices were curtailed, circa 1900. A similar argument could be made for logging practices of that era, which favored post-harvest "brush" burning (Hoxie 1910; Cermak 2005) leaving large areas open to aspen colonization. Today the aspen forest type makes up less than 1% of the Sierra Nevada's forested lands (Bruce Hiserote, Pacific Northwest Research Station, USDA Forest Service, pers. comm.). In contrast, forests in the Interior West states of Utah and Colorado contain 9 and 16 % aspen types, respectively (Rogers et al. 1998; Keyes et al. 2001).

Not only is aspen cover limited in California, but its domain is limited by comparison to Rocky Mountain habitat. Potter (1998, pp. 65-80) describes two "potential natural plant communities" of aspen cover for the Sierra Nevada. Both of these community types are adjacent to relatively moist riparian or meadow settings, with deep soils, low slope angles, and composed of stands less than five acres in size (Potter 1998). Though larger aspen stands exist, average stand sizes are smaller and diversity of community types fewer than Interior West aspen conditions (Mueggler 1988; Potter 1998). Greater aspen type diversity in other western mountain locations is likely related to their ability to flourish away from streams. In terms of stand size, some authors have speculated that there is a direct relationship between stand size and age of aspen clones (Kemperman and Barnes 1976). Smaller stands in the eastern United States are more conducive to occasional seedling establishment, whereas larger western clones rarely establish from seed, thus facilitating very old clones of great size (Kemperman and Barnes 1976; Mitton and Grant 1996). A perplexing condition of Sierra Nevada aspen stands is that they appear to take on general characteristics of both eastern and western North American aspen: relatively arid Sierra stands appear more similar to eastern forests in terms of stand size and more like Interior West forests in relation to predominant clonal reproduction (Strain 1964; Barry 1971). It may simply be that the small extent of individual stands, as well as regional cover, is a product of marginal aspen habitat combined with recent climate patterns and anthropogenic practices that favor conifer dominance.

The limited cover of aspen forest may be misleading in terms of its role in providing critical biodiversity to the Sierra Nevada. Plant diversity is commonly higher in aspen stands than surrounding conifer vegetation types (Mueggler 1985). Moreover, Sierra aspen is important as forage and lodge material for beaver (*Castor Canadensis* Kuhl.), which subsequently affects local water tables, stream dynamics, use by aquatic and terrestrial wildlife, and water availability for riparian-dependent plants. Avian species richness is also strongly related to preferences for aspen communities generally (Griffis-Kyle and Beier 2003), as well as in the Sierra Nevada specifically (Richardson and Heath 2004). Cavity nesting birds are attracted to mature aspen stands because they are often susceptible to a variety of stem decays beyond 60-80 years of age (Rogers 2002), making aspen excellent candidates for cavity creation by red-naped sapsuckers (*Sphyrapicus nuchalis* Baird) and secondary nesters (Dobkin et al. 1995). Aspen is also known for exceptionally soft wood and thin bark, further facilitating cavity nesting, even in healthy ramets.

Interactions between wildlife and vegetation, in this case aspen regeneration and development, may be crucial to maintenance or alteration of successional trajectories. Impacts of the cascading effects of human manipulations of wildlife populations are increasingly common in the literature (Noss et al. 1999; Ripple et al. 2001; Ripple and Beschta 2005). A unique aspect of Sierra Nevada aspen environments is the lack of elk (*Cervus elaphus* L.), considered a primary factor responsible for failure of aspen reproduction elsewhere (Kay 1990; Baker et al. 1997; Matson 2000). Though less research has been done on the effects of deer (*Odocoileus* spp.) browsing on aspen, it may be that deer, or deer in combination with domestic cattle, are fulfilling a similar role as elk elsewhere (Loft et al. 1993). In either case, a missing element in Sierra disturbance and regeneration cycles may be the lack of large predators to keep ungulates from over browsing new aspen shoots. After large fires, new seedlings established in Yellowstone National Park were browsed less by elk, especially at sites with limited predator visibility such as gullies, following wolf (*Canis lupus*) reintroduction (Ripple et al. 2001). In the Sierra, however, browsing takes place unhindered by carnivorous threat, making successful aspen regeneration difficult. The combined effects of reduced fire on the heels of intense late-19th century disturbance and the elimination of historic trophic impacts on vegetation have left a natural system greatly altered by humans. Efforts at righting these large-scale ecological impacts should involve reintroduction of natural processes, native carnivores, and core areas for these elements to thrive. Some, but not all, of these efforts may involve management practices that emulate natural processes in an adaptive manner (Rogers 1996) and avoid 'command and control' approaches (Holling and Meffe 1996).

Climate Change and Human Impacts

Investigations into historic vegetation conditions and disturbance regimes often focus on estimations of natural variability (Landres et al., 1999). Generally, greater success has been garnered in reconstructing past processes rather than historic forest structures (Stephenson 1999); thus it is prudent to focus conservation efforts on understanding of appropriate disturbance regimes based on climate patterns if we are to successfully restore the 'range of natural variability.' Recent research in the Sierra Nevada region shows that climate has fluctuated during the Holocene (Woolfenden 1996) as well as over the last millennium (Stine 1996; Millar et al. 2004).

Coincident with a departing Little Ice Age and an advancing warm moist period was the onslaught of settlement activities discussed earlier. This transition period, roughly 1850-1900, was characterized by fluctuations of dry and moist conditions culminating in a drought in the 1890s (Woolfenden 1996; Millar et al. 2004). In this region, frequent fires, likely a combination of grazing-related burning and drought conditions, proliferated into the early 20th century (Beaty and Taylor 2001). Late season, high severity, burns proliferated in upper montane forests, although they caution that topography added additional complication to local fire-vegetation patterns. Drought years occurred in the Lassen National Forest region in 1864, 1883, and 1889 (Beaty and Taylor 2001). Cycles of wet years promoting quick understory growth followed immediately by dry periods encourage intense forest burning (Beaty and Taylor 2001). This pattern favored increased aspen regeneration as Potter (1998, p.67) notes: "In general, the ages of the current aspen component in many stands corresponds relatively well with the end of intensive grazing pressures in the late 1800's and the institution of fire suppression policies in the early 1900's." Though subsequent fire suppression in the 20th century limited the spread of fires, a generally wetter modern era (Millar et al. 2004) complimented that practice. The net effect of the last 150 years has been climate pattern and human intervention combining to promote a regeneration pulse followed by a cessation of new aspen establishment under a regime of unusually limited burning.

Many speculate that we are now on the brink of another climatic shift – one that will bring warmer and dryer patterns to western mountainous regions (Overpeck et al. 1990; Dale et al. 2001; McKenzie et al. 2004). A prudent course toward 'natural range of variability' for aspen under this scenario may be to emulate disturbance patterns and processes of the Medieval Warm Period, rather than those found during the Little Ice Age. A warm/dry climate facilitating increased frequency of mixed severity fires may be more favorable to aspen expansion, or at least greater aspen renewal paired with conifer culling. This stands in marked contrast to policies, practices, and climate that favored shade tolerant species other than aspen (Di Orio et al. 2005; Shepperd et al. 2006).

Conservation Strategies for Regionally Limited Aspen

Small pockets of aspen have remained in the Sierra Nevada landscape despite large-scale human intervention favoring other species. Aspen have persisted in this landscape for millenniums (Strain 1964); but due to the short-lived nature of individual ramets, we do not have a clear picture of the extent of aspen through time. However, it is evident that past climates, such as the Medieval Warm Period (Millar and Woolfenden 1999a; Pierce et al. 2004), favored frequent fires that likely promoted regular pulses of aspen regeneration. It is less clear how surface fire regimes affect aspen regeneration, but we know frequent ground fires promote persistence of fire resistant species at lower elevations (Skinner and Chang 1996; Taylor and Beaty 2005). In the red fir zone, where most aspen are found (Potter 1998), a mixed fire regime seems to be characteristic: where litter is heavy, fire frequency is increased, and where there are considerable granite outcrops, fire is less frequent (Skinner and Chang 1996). However, 20th century fire suppression and moist conditions limited the spread of ground fires and their possible transition to crown fires.

In the 21st century, there is evidence of an aspen community that has declined precipitously (Di Orio et al. 2005). However, widespread human impacts during the settlement period led to extensive stand initiation. Additionally, subsequent management went to the other extreme by putting out fires, thus limiting new stand development. So, does the current "decline" in aspen signal a community in peril or is it a century-long reduction from an over-abundance instigated by invasive human practices? Stine (1996) suggests that conservation actions today should not try to recreate vegetation prior to Euro-American contact, but efforts should focus on emulating processes that correct an ecological course toward that which would have occurred minus large-scale human intervention. Following this approach, we suggest three guidelines for an aspen conservation strategy in the Sierra Nevada.

First, to design a conservation strategy for maintaining aspen on the landscape, we should move beyond debates of stand extent and composition to a strategy of realigning communities based on reinstitution of natural processes (Costanza et al. 1993; Holling and Meffe 1996; Rogers 1996). Stephenson (1999) echoes the importance of "keystone processes," specifically fire in Sierra sequoia (*Sequoiadendron giganteum*) groves, as being essential to restoration of forest structure (as opposed to mechanically restoring structure prior to process).

The 'natural range of variability' in aspen is highly climate and disturbance dependent. During cool and wet periods, aspen naturally declines, but its highly adaptive nature allows it to persist under many landscape conditions, albeit at periodic low-levels-in-waiting for disturbance (Strain 1964; Jones 1985; Lieffers et al. 2001). As conditions warm and dry, we might expect increased mixed severity or crown fires because of recent prolonged fire-free periods (Swetnam 1993) and expansion of aspen stands. Therefore, adoption of disturbance-based forest management practices that emulate natural processes rather than combat them (Rogers 1996) and being cognizant of climate conditions may hold the greatest promise for restoring aspen. In truth, contemporary management has yet to come to grips with allowing unfettered mixed severity and crown fire disturbance – an integral component of many high elevation ecosystems, including aspen forests. Alternative management actions, like targeted logging prescriptions, may allow site-specific options (e.g., near developed areas) for increasing aspen cover. However, these mechanical solutions may introduce other ecological issues such as long-term nutrient loss, aspen stem decay (Walters et al. 1982), and political, legal, and philosophical considerations. With many of these issues in mind, Shepperd et al. (2006) review silvicultural options to address a variety of aspen situations – both near developed areas and in the greater forest matrix.

Second, a mutually beneficial strategy for plants and animals is important for healthy aspen. Climate and disturbance are important, but they mainly address the stand initiation portion of aspen conservation. Maintenance of stand variability, and a complimentary strategy of biotic diversity, is dependent on restoration of trophic interactions. Specifically, a conservation approach, which favors reduction and movement of wild herbivores by reintroduction of carnivores, and domestic livestock through reduction and strategic rotation, will promote aspen regeneration after disturbance. Large reserves and a series of linked smaller reserves will be essential to retaining home ranges for carnivores that prey on wild ungulates. Reintroduction of predator-prey dynamics in combination with limited livestock use will restore a host of ecosystem functions in areas primarily influenced by natural processes, such as wilderness and other reserves (Baker 1992; Noss et al. 1999). Realizing the difficulty of adopting this strategy in a highly developed region such as the Sierra Nevada is not sufficient reason for rejecting implementation of incremental conservation strategies toward this end.

Third, these broad suggestions are contingent on local system knowledge and, therefore, should be adjusted appropriately to meet conservation objectives. It may not be possible to restore crown or even mixed severity fire regimes at some locations. In these areas, mechanical thinning or clearing of brush may be necessary to avoid political or social conflict (Shepperd et al. 2006). By conducting restorative activities incrementally, or during safe burn windows, some of these potential conflicts may be avoided. Essentially, we are advocating a "buffer" and "core" approach here – realizing the developed nature of the Sierra Nevada and acknowledging both natural and political variability in the system (Gunderson et al. 1995). After all local considerations, if restoration toward 'natural range of variability' is the goal, land managers should maintain a focus on emulating, as near as practical, forest processes that aspen have thrived under for millennia.

CONCLUSION

A scant forest cover of aspen today can tell us much about the past. Most contemporary stands are small in size and moderately-to-heavily invaded by conifers. We know that greater time between fires – such as has occurred in the Sierras of the past century – allows succession to advance, favoring conifers. People have also had a great effect on the extent of existing aspen. The heavy impact of the settlement era promoted unusual regeneration. Human disruption of aspen life cycles has left an appearance of a contemporary decline, although viewing this situation with a broader lens reveals a more complex picture potentially out of sync with climatic trends. If we adjust our focus toward a process-based conservation strategy, rather than a structure- or composition-based approach, we may have more success in reaching our ultimate goal. That goal, we believe, should be one of restoring a semblance of aspen cover that would have been present in the 21st century had we not intervened so heavily in the past.

A central tenant of this paper has been to advance a conservation approach germane to a unique Sierra Nevada aspen community. Understanding that community is contingent on a rich blend of social and ecological interplay, it is indicative that this interaction acknowledges spatial and temporal variability. In the past, anthropogenic heavy-handedness, based on limited ecological knowledge, has wrought lasting impacts. Attempts to overpower inevitable natural processes with structure-based management techniques designed to restore specific conditions may merely succeed in delaying, and possibly intensifying, inevitable disturbances (Holling and Meffe 1996). In this paper, we are not evoking a "greater" or "higher" knowledge, so much as advocating a "wider net" of understanding and use of adaptive practices. A key element of this strategy is restoration of climate-based natural processes, over mechanical intervention, where possible. In practice, local options will involve compromises in proximity to developed areas. In sum, process-based conservation is dependent on the widest understanding of physical factors, such as climate, disturbance, and species-related ecology, as well as an appreciation of the contemporary and historical social context.

Aspen is unlikely to be geographically abundant in the Sierra Nevada landscape even under optimistic scenarios. In its limited extent, however, this species plays a disproportionate role in regional plant and animal diversity. Conservation strategies aimed at reestablishing ecological processes will likely benefit the regionally limited aspen community, as well as biodiversity within the greater Sierra Nevada ecosystem.

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Paul C. Rogers is currently a Ph.D. candidate at Utah State University, Department of Wildland Resources. He earned his B.S. degree in Geography from Utah State University and his M.S. degree in Geography from the University of Wisconsin – Madison. Paul worked for the USDA Forest Service, Rocky Mountain Research Station for 16 years and is volunteering for that institution currently.

Wayne D. Shepperd is a recently-retired Research Silviculturalist for the USDA Forest Service, Rocky Mountain Research Station. He has a B.S. degree in Outdoor Recreation and an M.S. and a Ph.D. in Silviculture from Colorado State University. He has published numerous scientific papers on aspen ecology and management during his 37-year career with Forest Service Research.

Dale Bartos is a Research Ecologist and Project Leader with the USDA Forest Service, Rocky Mountain Research Station. He is also an Adjunct Assistant Professor at the Department of Wildland Resources, Utah State University.

LITERATURE CITED

Anderson, M.K., and M.J. Moratto. 1996. Native American land-use practices and ecological impacts. Pp. 187-206 *in* SNEP Science Team and special consultants, eds., Volume II: Assessments and scientific basis for management options, Sierra Nevada Ecosystem Project: final report to Congress. University of California, Davis, Centers for Water and Wildland Resources, Davis.

Bailey, R.G., P.E. Avers, T. King, and H.W. McNab. 1994. Ecoregions and subregions of the United States [map]. U.S. Department of the Interior, Geological Survey, Washington, D.C.

Baker, F.S. 1925. Aspen in the central Rocky Mountain region. U.S. Department of Agriculture. Washington, D.C.

Baker, W.L. 1992. The landscape ecology of large disturbances in the design and management of nature reserves. Landscape Ecology 7:181-194.

Baker, W.L., J.A. Munroe, and A.E. Hessl. 1997. The effects of elk on aspen in the winter range in Rocky Mountain National Park. Ecography 20:155-165.

Barnes, B.V. 1966. The clonal growth habit of American aspens. Ecology 47:439-447.

Barnes, B.V. 1975. Phenotypic variation of trembling aspen in western North America. Forest Science 21:319-328.

Barrett, L.A. 1935. A record of forest and field fires in California from the days of the early explorers to the creation of the Forest Service. U.S. Department of Agriculture, Forest Service, Pacific Southwest Region, San Francisco, Calif.

Barry, W.J. 1971. The ecology of *Populus tremuloides*, a monograph Approach. University of California, Davis.

Bartos, D.L., and R.B. Campbell, Jr. 1998. Decline of quaking aspen in the Interior West--examples from Utah. Rangelands 20:17-24.

Beaty, M.R., and A.H. Taylor. 2001. Spatial and temporal variation of fire regimes in a mixed conifer forest landscape, Southern Cascades, California, USA. Journal of Biogeography 28:955-966.

Beesley, D. 1996. Reconstructing the landscape: an environmental history, 1820-1960. Pp. 3-24 *in* SNEP Science Team and special consultants, eds., Volume II: Assessments and scientific basis for management options, Sierra Nevada Ecosystem Project: final report to Congress. University of California, Davis, Centers for Water and Wildland Resources, Davis.

Bjorse, G., and R. Bradshaw. 1998. 2000 years of forest dynamics in southern Sweden: suggestions for forest management. Forest Ecology and Management 104:15-26.

Brown, M. 1995. Aspen decline in the inland Northwest: a review of some relevant literature. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station (Portland, Ore.) and the Smithsonian Institution (Washington, D.C.).

Campbell, R.B., and D.L. Bartos. 2001. Aspen ecosystems: objectives for sustaining biodiversity. Pp. 299-307 *in* W.D. Shepperd, D. Binkley, D.L. Bartos, T.J. Stohlgren, and L.G. Eskew, eds., Sustaining aspen in western landscapes: symposium proceedings. RMRS-P-18, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. Fort Collins, Colo.

Cermak, R.W. 2005. Fire in the forest: a history of forest fire control on the National Forests in California, 1898-1956. R5-FR-003, U.S.

Department of Agriculture, Forest Service, Pacific Southwest Region, Albany, Calif.

Costanza, R.L., C.F. Wainger, and K. Maler. 1993. Modeling complex ecological economic systems. BioScience 43:545-555.

Dale, V.H., L.A. Joyce, S. McNulty, R.P. Neilson, M.P. Ayres, M.D. Flannigan, P.J. Hanson, L.C. Irland, A.E. Lugo, C.J. Peterson, D. Simberloff, F.J. Swanson, B.J. Stocks, and B.M. Wotton. 2001. Climate change and forest disturbances. BioScience 51:723-734.

Denevan, W.M. 1992. The pristine myth: the landscape of the Americas in 1492. Annals of the Association of American Geographers 82:369-385.

Di Orio, A.P., R. Callas, and R.J. Schaefer. 2005. Forty-eight year decline and fragmentation of aspen (*Populus tremuloides*) in the South Warner Mountains of California. Forest Ecology and Management 206:307-313.

Dobkin, D.S., A.C. Rich, J.A. Pretare, and W.H. Pyle. 1995. Nest-site relationships among cavity-nesting birds of riparian and snowpocket aspen woodlands in the northwestern Great Basin. Condor 97:694-707.

Franklin, J.F., T.A. Spies, R. Van Pelt, A.B. Carey, D.A. Thornburgh, D.R. Berg, D.B. Lindenmayer, M.E. Harmon, W.S. Keeton, D.C. Shaw, K. Bible, and J. Chen. 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. Forest Ecology and Management 155:399-423.

Gallant, A. L., A.J. Hansen, J.S. Councilman, D.K. Monte, and D.W. Betz. 2003. Vegetation dynamics under fire exclusion and logging in a Rocky Mountain watershed, 1856-1996. Ecological Applications 13:385-403.

Griffis-Kyle, K.L., and P. Beier. 2003. Small isolated aspen stands enrich bird communities in southwestern ponderosa pine forests. Biological Conservation 110:375-385.

Gunderson, L.H., C.S. Holling, and S.S. Light. 1995. Barriers and Bridges to the Renewal of Ecosystems and Institutions. Columbia University Press, New York.

Hinds, T.E. 1985. Diseases. Pp. 87-106 *in* N.V. DeByle and R.P. Winoker, eds., Aspen: ecology and management in the United States. GTR-RM-119, U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo.

Holling, C.S., and G.K. Meffe. 1996. Command and control and the pathology of natural resource management. Conservation Biology 10:328-337.

Hoxie, G.L. 1910. How fire helps forestry. Sunset 25:145-151.

Jackson, T.W., R. Herbert, and S. Wee. 1982. History of the Tahoe National Forest: 1840-1940. U.S. Department of Agriculture, Forest Service, Tahoe National Forest, Nevada City, Calif.

Jones, J.R. 1985. Distribution. Pp. 9-10 *in* N.V. DeByle and R.P. Winokur, eds., Aspen: ecology and management in the western United States. GTR-RM-119, U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo.

Jones, J. R., and G.A. Schier. 1985. Growth. Pp. 19-24 *in* N.V. DeByle and R.P. Winokur, eds., Aspen: ecology and management in the western United States. RM-GTR-119, U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo.

Kay, C.E. 1990. Yellowstone's northern elk herd: a critical evaluation of the "natural regulation paradigm." Ph.D. diss., Utah State University, Logan.

Kemperman, J.A., and B.V. Barnes. 1976. Clone size in American aspens. Canadian Journal of Botany 54:2603-2607.

Keyes, C., P. Rogers, L. LaMadeleine, and D. Atkins. 2001. Utah Forest Health Report: a baseline assessment 1999/2001. State of Utah, Department of Natural Resources, Division of Forestry, Fire and State Lands, Salt Lake City.

Kinney, W. 1996. Conditions of rangelands before 1905. Pp. 31-46 *in* SNEP Science Team and special consultants, eds., Volume II: Assessments and scientific basis for management options, Sierra Nevada Ecosystem Project: final report to Congress. University of California, Davis, Centers for Water and Wildland Resources, Davis.

Landres, P.B., P. Morgan, and F.J. Swanson. 1999. Overview of the use of natural variability concepts in managing ecological systems. Ecological Applications 9:1179-1188.

Leiberg, J.B. 1902. Forest conditions of the northern Sierra Nevada, California. Paper 8, U.S. Geologic Survey, Washington, D.C.

Lieffers, V.J., S.M. Landhausser, and E.H. Hogg. 2001. Is the wide distribution of aspen a result of its stress tolerance? Pp. 311-323 *in* W.D. Shepperd, D. Binkley, D.L. Bartos, T.J. Stohlgren, and L.G. Eskew, eds., Sustaining aspen in western landscapes: symposium proceedings. RMRS-P-18, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, Colo.

Loft, E.R., J.G. Kie, and J.W. Menke. 1993. Grazing in the Sierra Nevada: home range and space use patterns of mule deer as influenced by cattle. California Fish and Game 79:145-166.

Manley, P.N., J.A.A. Fites-Kaufman. M.G. Barbour, M.D. Schlesinger, and D.M. Rizzo. 2000. Biological integrity. Pp. 403-600 *in* D.D. Murphy and C.M. Knopp, eds., Lake Tahoe watershed assessment: Volume I. PSW-GTR-175, U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, Calif.

Matson, N.P. 2000. Biodiversity and its management on the National Elk Refuge, Wyoming. Yale Forestry & Environmental Studies Bulletin 104:101-138.

McDonough, W.T. 1979. Quaking aspen--seed germination and early seedling growth. RP-INT-234, U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. Ogden, Utah.

McKenzie, D., Z. Gedalof, D.L. Peterson, and P. Mote. 2004. Climate change, wildfire, and conservation. Conservation Biology 18:890-902.

Millar, C.I., R.D. Westfall, D.L. Delany, J.C. King, and L.J. Graumlich. 2004. Response of subalpine conifers in the Sierra Nevada, California, U.S.A., to 20th-century warming and decadal variability. Arctic, Antarctic, and Alpine Research 36:181-200.

Millar, C.I., and W.B. Woolfenden. 1999a. The role of climate change in interpreting historical variability. Ecological Applications 9:1207-1216.

Millar, C.I., and W.B. Woolfenden. 1999b. Sierra Nevada Forests: where did they come from? Where are they going? What does it mean? Pp. 206-236 *in* R.E. McCabe and S.E. Loos, eds., Transactions of the 64th North American Wildland and Natural Resources Conference, 1999 March 26-30, Burlingame, California Wildlife Management Institute, Washington, D.C.

Mitton, J.B., and M.C. Grant. 1996. Genetic variation and the natural history of quaking aspen. Bioscience 46:25-31.

Mueggler, W. F. 1985. Vegetation associations. Pp. 45-55 *in* N.V. DeByle and R.P. Winoker, eds., Aspen: ecology and management in the United States. RM-GTR-119, U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo.

Mueggler, W.F. 1988. Aspen community types of the Intermountain Region. GTR-INT-250, U.S. Department of Agriculture, Forest Service, Intermountain Research Station. Ogden, Utah.

Muir, J. 1982. The Wilderness World of John Muir. Houghton Mifflin, Boston, Mass.

Noss, R. F., E. Dinerstein, B. Gilbert, M. Gilpin, B.J. Mille, J. Terborgh, and S. Trombulak. 1999. Pp. 99-128 *in* M.E. Soulé and J. Terborgh, eds., Continental Conservation: Scientific Foundations of Regional Reserve. Networks Island Press, Washington, D.C.

Overpeck, J.T., D. Rind, and R. Goldberg. 1990. Climate-induced changes in forest disturbance. Nature 343:51-53.

Palmer, K. 1992. Vulcan's footprint on the forest: the mining in industry and California's National Forests, 1850-1950. Pp. 136-153 *in* H. Steen, ed., The origins of the National Forests: a centennial symposium. Forest History Society, Durham, N.C.

Parker, A.J. 2002. Fire in Sierra Nevada forests: evaluating the ecological impact of burning by Native Americans. Pp. 233-267 *in* T.R. Vale, ed., Fire, Native Peoples, and the Natural Landscape. Island Press, Washington, D.C.

Pierce, J.L., G.A. Meyer, and A.J.T. Jull. 2004. Fire-induced erosion and millennial-scale climate change in northern ponderosa pine forests. Nature 432:87-90.

Potter, D.A. 1998. Forested communities of the upper montane in the central and southern Sierra Nevada. PSW-GTR-169, U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station. Albany, Calif.

Potter, N.J. 1969. Tree-Ring Dating of Snow Avalanche Tracks and the Geomorphic Activity of Avalanches, Northern Absoroka Mountains, Wyoming. Geological Society of America, Special Paper 123:141-165.

Preston, R.J. 1976. North American Trees. Iowa State University Press, Ames.

Pyne, S.J. 2001. The big blowup. Pp. 34-45 *in* A. True, ed., Wildfire: a Reader. Island Press, Washington, D.C.

Quinn, R.D., and L. Wu. 2001. Quaking aspen reproduce from seed after wildfire in the mountains of Southeastern Arizona. Pp. 369-376 *in* W.D. Shepperd, D. Binkley, D.L. Bartos, T.J. Stohlgren, and L.G. Eskew, eds., Sustaining aspen in western landscapes: symposium proceedings, Grand Junction, Colorado, USA. RMRS-P-18, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, Colo.

Richardson, T.W., and S.K. Heath. 2004. Effects of conifers on aspen-breeding bird communities in the Sierra Nevada. Transactions of the Western Section of the Wildlife Society 40:68-81.

Ripple, W.J., and R.L. Beschta. 2005. Linking wolves and plants: Aldo Leopold on trophic cascades. BioScience 55:613-621.

Ripple, W.J., E.J. Larsen, R.A. Renkin, and D.W. Smith. 2001. Trophic cascades among wolves, elk and aspen on Yellowstone National Park's northern range. Biological Conservation 102:227-234.

Rogers, P., M. Schomaker, W. McLain, and S. Johnson. 1998. Colorado forest health report 1992-95: a baseline assessment. Colorado State Forest Service and U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station and Rocky Mountain Region, Fort Collins, Colo.

Rogers, P. 2002. Using Forest Health Monitoring to assess aspen forest cover change in the southern Rockies ecoregion. Forest Ecology and Management 155:223-236.

Rogers, P.C. 1996. Disturbance ecology and forest management: a review of the literature. INT-GTR-336, U.S. Department of Agriculture, Forest Service, Intermountain Research Station. Ogden, Utah.

Romme, W.H., M.G. Turner, R.H. Gardner, W.W. Hargrove, G.A. Tuskan, D.G. Despain, and R.A. Renkin. 1997. A rare episode of sexual reproduction in aspen (*Populus tremuloides* Michx.) following the 1988 Yellowstone fires. Natural Areas Journal 17:17-25.

Shepperd, W., P.C. Rogers, D. Burton, and D. Bartos. 2006. Ecology, biodiversity, management, and restoration of aspen in the Sierra Nevada. RMRS-GTR-178, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. Fort Collins, Colo.

Shepperd, W.D., and F.W. Smith. 1993. The role of near-surface lateral roots in the life cycle of aspen in the central Rocky Mountains. Forest Ecology and Management 61:157-170.

Show, S.B., and E.L. Kotok. 1930. The determination of hour control for adequate fire protection in the major cover types of the California pine region. Technical Bulletin 209, U.S. Department of Agriculture, Forest Service, Washington, D.C.

Skinner, C.N., and C. Chang. 1996. Fire regimes, past and present. Pp. 1041-1070 *in* SNEP Science Team and special consultants, eds., *Volume* II: Assessments and scientific basis for management options, Sierra Nevada Ecosystem Project: final report to Congress. University of California, Davis, Centers for Water and Wildland Resources, Davis.

Stephenson, N.L. 1999. Reference conditions for giant sequoia forest restoration: structure, process, and precision. Ecological Applications 9:1253-1265.

Stine, S. 1996. Climate, 1650-1850. Pp. 25-30 *in* SNEP Science Team and special consultants, eds., Volume II: Assessments and scientific basis for management options, Sierra Nevada Ecosystem Project: final report to Congress. University of California, Davis, Centers for Water and Wildland Resources, Davis.

Strain, B.R. 1964. Physiological and Morphological Variability of Quaking Aspen Clones. University of California, Los Angeles.

Strong, D.H. 1984. Tahoe, an Environmental History. University of Nebraska Press, Lincoln.

Sudworth, G.B. 1900. Stanislaus and Lake Tahoe forest reserves, California, and adjacent territory. Government Printing Office, Washington, D.C.

Swetnam, T.W. 1993. Fire history and climate change in giant sequoia groves. Science 262:885-889.

Taylor, A.H., and R.M. Beaty. 2005. Climatic influences on fire regimes in the northern Sierra Nevada mountains, Lake Tahoe Basin, Nevada, USA. Journal of Biogeography 32:425-438.

Vale, T.R. 1998. The myth of the humanized landscape: an example from Yosemite National Park. Natural Areas Journal 18:231-236.

Vale, T.R. 2002. Fire, Native Peoples, and the Natural Landscape. Island Press, Washington, D.C.

Veblen, T.T., K.S. Hadley, E.M. Nel, T. Kitzberger, M. Reid, and R. Villalba. 1994. Disturbance regime and disturbance interactions in a Rocky Mountain subalpine forest. Journal of Ecology 82:125-135.

Walters, J.W., T.E. Hinds, D.W. Johnson, and J. Beatty. 1982. Effects of partial cutting on diseases, mortality, and regeneration of Rocky Mountain aspen stands. RM-RP-240, U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo.

Whitlock, C., and M.A. Knox. 2002. Prehistoric burning in the Pacific Northwest: human versus climatic influences. Pp. 195-231 *in* T.R. Vale, ed., Fire, Native Peoples, and the Natural Landscape. Island Press, Washington, D.C.

Woolfenden, W. B. 1996. Quaternary vegetation history. Pp. 47-70 *in* SNEP Science Team and special consultants, eds., Volume II: Assessments and scientific basis for management options, Sierra Nevada Ecosystem Project: final report to Congress. University of California, Davis, Centers for Water and Wildland Resources, Davis.