

Aspen, Elk, and Fire: The Effects of Human Institutions on Ecosystem Processes

AMY HESSL

Aspen is the most widely distributed tree species in North America and the second most widely distributed tree species in the world. In the mountains of the western United States, aspen forest comprises only about 2% to 5% of total vegetative cover (Baker 1925), though at local spatial scales aspen may be absent or cover a far larger portion of the landscape. Despite its low spatial coverage at large spatial scales, aspen is one of few common hardwood species in the West, and it is increasingly recognized for the high species diversity in its stands. Aspen groves tend to harbor a rich diversity of understory plants, butterflies, and cavity-nesting birds not found in neighboring coniferous forest. Aspen also provide forage and cover for native and domestic ungulates and give us the spectacular fall vistas typical of the mountain West.

Since the 1930s, foresters and ecologists have noticed a decline in the aspen forest in parts of the intermountain West. Aspen stands in these areas are currently dominated by old age classes, with many dead and dying stems. These stands have little regeneration in the understory, which may have been invaded by coniferous trees or sagebrush. Many hypotheses seek to explain the decline of aspen, including fire suppression, climatic variability, and an overabundance of elk. Although the total disappearance of aspen in the West seems highly unlikely, given the wide distribution of the trees, the documented decline is alarming (Allen 1989, Mueggler 1989, Wirth et al. 1996, Baker et al. 1997, White et al. 1998). Given the value of aspen in western forests and the dramatic changes that have taken place in the West as a result of Euro-American settlement, we must ask, Have human activities contributed in some way to the apparent decline of aspen?

In this article I synthesize and compare current hypotheses regarding aspen decline by focusing on studies of aspen in the elk winter ranges of Rocky Mountain National Park

THE INTERACTIONS AMONG ASPEN, ELK, AND FIRE IN THE INTERMOUNTAIN WEST HIGHLIGHT IMPORTANT MISMATCHES BETWEEN ECOLOGICAL PROCESSES AND HUMAN INSTITUTIONS AND PROVIDE IMPORTANT INSIGHTS FOR THE MANAGEMENT OF NATIONAL PARKS AND OTHER PROTECTED AREAS

(RMNP), Jackson Hole (JH), and northern Yellowstone National Park (YNP) (table 1, figure 1). These three elk winter ranges, which represent some of the most intensively studied aspen forests in the West, have diverse management histories that allow broad-scale experiments for teasing apart the influence of human and biophysical drivers on ecosystem variability. And because these study areas also represent some of the larger protected areas in the continental United States, they provide the opportunity to evaluate a much broader issue: the linkages between human institutions and ecological processes in large parks and protected areas.

Amy Hessel (e-mail: ahessl@geo.wvu.edu) is a biogeographer in the Department of Geology and Geography at West Virginia University, Morgantown, WV 26506. She studies how ecological processes interact with social institutions in shaping the landscapes of the western United States. © 2002 American Institute of Biological Sciences.

Table 1. Description of the elk winter ranges in Jackson Hole and Yellowstone and Rocky Mountain National Parks.

Winter range	Size (hectares)	Elk population	Aspen cover (percentage)	Elevation (meters)	Estimated MFRI (years)
Yellowstone National Park (northern range)	140,000	~ 19,000	2	1750–2300	20–30
Jackson Hole (Gros Ventre Valley and National Elk Refuge)	80,000	~ 20,000	0.5	1800–2500	50–100
Rocky Mountain National Park (Estes Park Valley)	10,000	~ 3000	2	2378–2800	10–25

MFRI, mean fire return interval.

Source: Data were taken from studies of the Yellowstone northern range (Houston 1982, Despain 1990, Singer et al. 1994, Romme et al. 1995), Jackson elk winter range (Baker 1925, Loope and Gruell 1973), Rocky Mountain National Park elk winter range (Larkins 1997, Stohlgren et al. 1997), and the Colorado Front Range (Veblen et al. 2000).

Many explanations for the high mortality and low regeneration rates of aspen stems have been suggested, including fire suppression, elk browsing, and climatic variability (figure 2). Interestingly, many of these explanations are tied to the unique life history of aspen. Aspen are clonal plants capable of reproducing through vegetative growth (ramets). This characteristic is responsible for the large aspen stands in Colorado and Utah, some as great as 43 hectares (ha), that constitute a single individual. This life history trait is also associated with infrequent establishment from seed. The ability to reproduce vegetatively allows aspen to grow quickly, as re-

sources may be stored in underground root systems and available for rapid growth following disturbance (Jones and DeByle 1985). Aspen tend to regenerate profusely following fire (Bartos and Mueggler 1981, Brown and DeByle 1989), and the first reports of aspen decline coincided with the onset of fire suppression in many regions. In fact, some researchers have suggested that fire suppression in the 20th century may be responsible for the loss of aspen cover in some areas of the intermountain West (Loope and Gruell 1973).

Aspen provide excellent habitat and browse for many ungulate species, such as elk, deer, and cattle. In some regions of the West, ungulate populations, especially elk, have increased in recent decades, and the effect of these browsing ungulates on aspen has been noted. Scarred trees, heavily browsed aspen ramets, and high rates of ramet mortality are often found in stands sustaining heavy ungulate browsing, suggesting that ungulate browsing may be responsible for changes in some aspen populations. Ripple and Larsen (2000) have hypothesized that the loss of significant predator-prey rela-

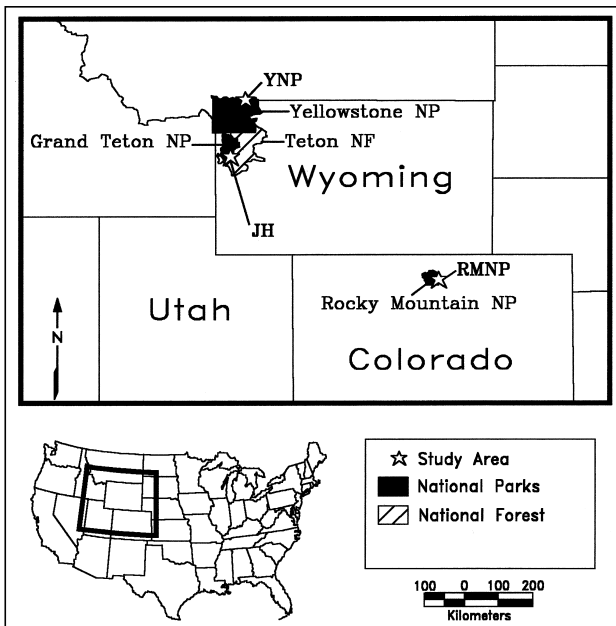


Figure 1. Map of the three study areas (stars) in the western United States. The Jackson Hole (JH) study area includes portions of Grand Teton National Park, Teton National Forest, and the National Elk Refuge. Rocky Mountain National Park (RMNP) and the Northern Range of Yellowstone National Park (YNP) are on National Park Service lands.

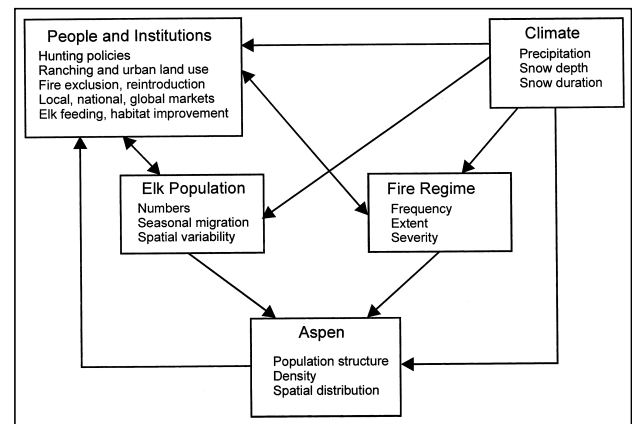


Figure 2. Conceptual model of aspen-land use dynamics in elk winter range. The top tier represents the drivers of ecosystem variability, the middle tier represents ecosystem processes, and the lowest tier represents the ecological pattern recognized and measured in the field.

tionships in the early 1900s in Yellowstone led to increased elk populations and altered elk behavior. This trophic cascade effect may have resulted in the absence of major aspen ramet recruitment since the early 1900s in Yellowstone and possibly in other parks.

Kay (1994) has argued that both predation by carnivores and hunting by Native Americans limited elk numbers before Euro-American settlement. These activities, in combination with fire use by Native Americans (Kay 1995, 1997), may have been associated with increased aspen regeneration through changes in elk populations and browsing patterns, as well as with greater opportunities for aspen ramet regeneration following frequent, low-intensity, human-ignited fires. By removing Native American land management from the aspen system, Euro-Americans may have eliminated a key factor in aspen sustainability.

On the other hand, aspen life history may explain why aspen decline could be only temporary. One benefit of clonal life history is increased longevity. Some scientists have postulated that a single clone may persist for up to 10,000 years (Barnes 1966, Mitton and Grant 1996). With such a penchant for longevity, a clone could sustain long periods without fire, and with heavy ungulate browsing and climatic variability, by maintaining itself as a dwarf shrub or in the understory of coniferous trees. According to this argument, aspen decline is temporary, part of a suite of life history traits that allow aspen to persist under unfavorable conditions (Despain 1990).

The many unknowns surrounding aspen forest dynamics have heightened the debate over the management of not only aspen but also ungulates and fire in protected areas. Among the unanswered questions regarding aspen forest ecosystems are these: How do fire and elk, and their interaction, affect aspen recruitment? Does current elk browsing affect aspen clone longevity, or can aspen persist for many centuries in the presence of heavy browsing? If aspen can persist under heavy browsing, fire suppression, or climatic variability (or all three), what mechanisms allow for its persistence? All of these uncertainties need to be clarified before management of aspen can succeed.

Ecosystems and human institutions

Though human institutions may seem unimportant in large protected areas like the Greater Yellowstone, human activities may have both direct and indirect effects on aspen dynamics and other important ecological processes. Direct effects of land use may include changes in predator populations, fire regimes, and land cover; indirect effects may include growth in elk populations in the absence of predators and, therefore, increased elk browsing on aspen. Fire suppression may have the unintended consequence of reducing opportunities for postfire reproduction (both sexual and asexual) of aspen. At the same time, abiotic influences such as climate variability affect ecological patterns and processes, making it difficult to separate human influences from the effects of biophysical drivers on ecosystem processes.

By identifying the spatial and temporal scales of human institutions and ecological processes, we can begin to identify foci for research and to address weaknesses in management (figure 3). Historically, fire and elk population dynamics have operated over large spatial and long temporal scales, generating far-reaching, pervasive impacts on regional ecosystem patterns such as aspen forest dynamics. For example, while elk natality and mortality fluctuate on an annual basis, elk migrations change over decadal timescales (Lemke et al. 1998). Similarly, an individual fire exists for a few days to a few months, but the frequency and extent of fire regimes change at decadal to centennial or millennial timescales with changing climate (Millsaugh and Whitlock 1995). Aspen forest dynamics, affected by both fire regimes and elk populations, very likely operate on annual to millennial timescales. Ramet regeneration occurs annually, stand structure changes over decades (Hessl and Graumlich 2002), and recruitment of new clones may take thousands of years (Baker 1925). In contrast, 20th-century human institutions that influence these key ecosystem processes, such as prescribed burning, regulated hunting, and even a "hands-off" management approach, have operated on small temporal and spatial scales defined by land ownership and agency policies (figure 3). For example, elk are managed by multiple agencies dealing with land areas ranging from the 100-square-kilometer (km²) National Elk Refuge to the 8900 km² Yellowstone National Park. The number of elk fed or hunted may change each year and may vary with land ownership. Similarly, prescribed fires may be planned on annual to decadal time scales, but many of them cover less than 10,000 ha. These mismatches between human institutions and ecological processes manifest

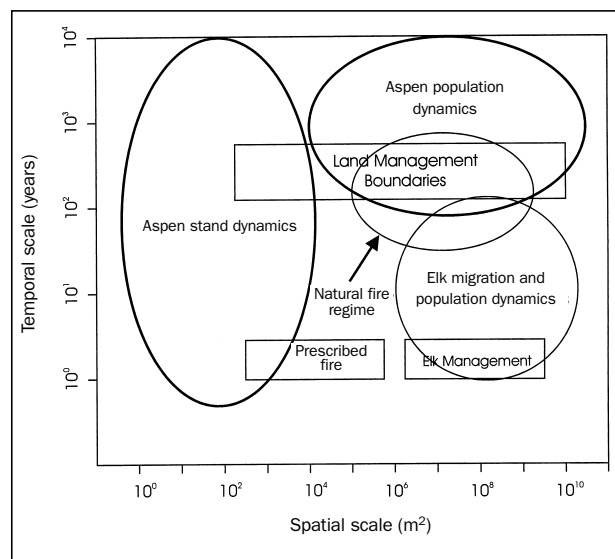


Figure 3. Spatial and temporal scales at which human institutions (boxes) and ecological processes (ellipses) operate with respect to aspen forest dynamics. The weak overlap between human institutions and ecological processes is termed a "lack of fit" (Folke et al. 1998).

themselves as ineffective management policies and ecological surprises.

Methods

To compare ecological studies of aspen in the three winter range areas, I first describe the ecological history of each winter range, including the history of aspen, fire regimes, elk populations, and land use. Next, I compare the patterns of aspen regeneration in the three study areas over the past 100 to 200 years, using previous studies of aspen stand age structures (table 2; Romme et al. 1995, Baker et al. 1997, Hessl and Graumlich 2002). Included in this analysis is a synthesis of data on drought variability, elk populations, and fire history. This synthesis allows the many variables influencing aspen ramet regeneration to be compared at a regional scale. I compare studies of recent aspen ramet regeneration inside and outside winter range areas (Suzuki et al. 1999, Barnett and Stohlgren 2001, Hessl and Graumlich 2002) and in burned and unburned sites (Romme et al. 1995, Hessl and Graumlich 2002). By reviewing this literature, I synthesize landscape-scale patterns of aspen regeneration in the context of the key variables thought to control ramet regeneration. Finally, I summarize some of the unknown factors that influence our view of recent aspen dynamics and address ways to contend with the problem of fit between human institutions and ecological processes in the context of aspen management.

Study areas

Three areas, Rocky Mountain National Park, Jackson Hole, and Yellowstone's Northern Range, have been studied extensively; together they represent a 1000 km north-south transect of aspen forest dynamics.

Rocky Mountain National Park winter range, Colorado. Aspen in the RMNP winter range occur as scattered stands within montane grassland, interspersed with forests dominated by ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*). The climate is continental, with precipitation highest in summer. Though fire history of aspen has not been studied, the fire frequency of surrounding forest types, just south of the park in the Colorado Front Range, has been investigated (Veblen et al. 2000). Fire frequency varies by elevation and with climatic variability, but mean fire return intervals between the years 1650 and 1920 range from 35 to 70 years for ponderosa pine forests in the Colorado Front Range (table 1; Veblen et al. 2000). Modern fire suppression began in 1929 and continues today, though fires may have been suppressed before 1929 by livestock grazing. Increasingly, suburban development has altered the size and composition of the winter range outside the park (Veblen and Lorenz 1991) and may have reduced the frequency with which lowland fires spread into the park.

Both elk and aspen were present before RMNP was established in 1915, though elk populations were low because elk had been nearly extirpated by market hunting for their ivory teeth ("tusks") at the turn of the 19th century (Swift

1945). Elk from the Jackson Hole herd were reintroduced to RMNP in 1913, and under protection inside the park boundaries, the elk population grew rapidly. By the 1940s, the park service began to cull the herd to stabilize the population at approximately 580 animals. Between 1944 and 1953, 1245 elk were shot (Hess 1993). Culling elk as a management technique ceased in 1962, and in 1968 the park service implemented a natural regulation policy. However, elk hunting continued just outside the park as a means to control the population. In the spring (April-May), elk currently migrate from low-elevation winter range inside and adjacent to RMNP to high-elevation parklands inside the park. In late fall (around November), the elk return to the low-elevation winter range. The effect of elk browsing on aspen was initially observed in RMNP in the 1930s (Packard 1942) and has been observed by other researchers throughout the second half of the 20th century. Managers have defined elk winter range according to elk migration routes and seasonal distributions (Bear 1989, Baker et al. 1997).

Jackson Hole winter range, Wyoming. Aspen stands in JH occur within a matrix of montane and subalpine coniferous forest composed of Douglas-fir, Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*), as well as within sagebrush (*Artemisia* spp.) grassland, forming a diffuse band of deciduous vegetation. The climate of JH, like that of RMNP, is continental, but the high in precipitation occurs in winter. Extensive fires occurred throughout JH in the mid- to late 1800s (Loope and Gruell 1973); however, it is difficult to determine whether these were unique events associated with Euro-American settlement or unusual climatic conditions, or whether they were typical for the area. According to fire scar records, between 1600 and 1900, fires occurred every 50 to 100 years in some parts of the grassland-forest boundary (Loope and Gruell 1973). Unfortunately, these records are composed of small samples and their locations are poorly documented. By the mid-20th century, fires were actively suppressed in JH, and there were no fires larger than 400 ha between 1941 and 1973 (Loope and Gruell 1973). Since the 1970s, an extensive prescribed fire program has reinstated fire in the JH winter range in Bridger-Teton National Forest, designed in part to enhance aspen regeneration.

As in RMNP, elk in JH were hunted in the 1800s for their hides and teeth, but these activities were regulated much earlier in JH, as elk hunting in Wyoming was restricted by Congress in 1871 (Sheldon 1927). Permanent settlement by ranchers began in the Jackson valley in 1883. Gradually, much of the low-elevation grassland in the valley was devoted to ranching, leaving only high-elevation areas for elk habitat. In 1897 the Teton Forest Preserve (now part of Bridger-Teton National Forest) was established, in part to provide elk winter range. Between 1909 and 1920, the Jackson valley experienced the most severe winter snow conditions of the 20th century. These heavy snows, recorded in historical documents,

Table 2. Primary data types and sources for elk winter ranges.

Primary data source	Rocky Mountain National Park	Jackson Hole	Yellowstone National Park
Static age structure	Baker et al. 1997	Hessl and Graumlich forthcoming	Romme et al. 1995
Effect of fire on sucker recruitment	NA	Hessl and Graumlich forthcoming	Romme et al. 1995
Sucker recruitment inside versus outside exclosures	Baker et al. 1997	NA	Kay 1990
Sucker recruitment inside versus outside winter range	Suzuki et al. 1999	Barnett and Stohlgren 2001, Hessl and Graumlich forthcoming	NA
Seedling regeneration	NA	NA	Romme et al. 1997
Elk population	Stevens 1980, Baker et al. 1997	Boyce 1989	Houston 1982, Romme et al. 1985, Lemke 1999
Fire regime	NA	Loope and Gruell 1973	Houston 1973
Palmer drought severity index ^a	Cook et al. 1999	Cook et al. 1999	Cook et al. 1999

NA, not available.

a. The Palmer drought severity index, derived from monthly values of temperature and precipitation, is a meteorological drought index based on water balance.

resulted in drastic mortality in the elk population (Sheldon 1927).

In 1912 the National Elk Refuge was established, and winter elk feeding began in the winter of 1912–1913. Three additional feeding grounds in the Gros Ventre Valley, Bridger-Teton National Forest, were established in 1960. Winter elk feeding at these feeding grounds continues today. In contrast to herds at RMNP and YNP, the JH elk herd is not managed according to natural regulation policies. Intensive management of elk, including regulated hunting, winter feeding, and managed herd size, currently characterizes elk management in JH. However, the JH elk herd continues to make long (> 90 km) seasonal migrations from low-elevation winter range on the National Elk Refuge and forest service lands to high-elevation summer range in Grand Teton National Park, Teton Wilderness Area, and southern YNP. Managers have defined elk winter range in the JH area according to the frequency of observations of elk in winter (Strickland 1985).

Yellowstone National Park northern range, Wyoming. Aspen forest in the northern range of YNP is characterized by small stands mixed with sagebrush grassland and Douglas-fir (Romme et al. 1995). Despite its close proximity to JH, the northern range in YNP experiences highest precipitation in summer. A fire history study in the northern range of Yellowstone noted scars on coniferous trees near aspen approximately every 50 years for the last 350 years (Houston 1973). Based on these data, Houston (1973) suggested a historical fire frequency of one fire every 20 to 30 years in aspen and surrounding forest. However, this conclusion is purely inferential, as coniferous forest fires may not burn through neighboring aspen stands, which often act as a fire-break (Fechner and Barrows 1976). Like the JH area, YNP shows evidence of extensive fires in the mid- to late 1800s (Houston 1973). Fire suppression efforts begun as early as 1886 by the US Army may have been successful in the sagebrush

steppe and grassland areas (Despain 1990) that border aspen stands. However, a “let burn” policy has been implemented in the park since 1972. Human settlement inside the park is minimal, but outside the park, livestock ranching and hunting are common and may influence the migration of animals across park boundaries.

Market hunting of elk in the 1860s and 1870s reduced YNP elk numbers dramatically, but in the late 1880s wildlife protection measures allowed elk populations to recover (Houston 1982). For the period 1880–1930, elk population size is not well described, but was likely high as a result of low hunting pressure. Between 1930 and 1968, artificial reductions shrank the population by 3000 to 6000 animals. In YNP, as in RMNP, a natural regulation policy was implemented in 1969, ending a period of artificial reductions and marking the beginning of a rise in elk populations that continued until approximately 1990 (Lemke 1999), followed by a decline to about 15,000 animals in 1999. Elk on YNP’s northern range migrate up to 128 km between their winter range in low-elevation valleys and their summer range at high elevations. Approximately one-third of the YNP northern range is located outside the park on lands in Montana, where elk may be hunted. The boundaries of the northern range in Yellowstone have been defined by the long history of elk observed in winter (Houston 1982, Lemke 1999).

Nineteenth- and twentieth-century aspen regeneration in elk winter range

I used tree-ring studies performed in the last decade from the three elk winter ranges to date aspen ramet recruitment episodes (Romme et al. 1995, Baker et al. 1997, Hessl and Graumlich 2002). Using age structures, I synthesized data on aspen recruitment by comparing major episodes of recruitment at decadal time scales with data on drought, fire history, and elk population history (table 2). In all study areas, historical aspen recruitment was measured in terms of numbers

of stems (Romme et al. 1995, Hessel and Graumlich 2002) or numbers of stands with regenerating stems (Baker et al. 1997). Because methods and sample sizes varied (table 3), I standardized recruitment between the three study areas. I identified mean levels of recruitment per decade (or sums where recruitment was measured in terms of numbers of stands) and then ranked recruitment on a scale of 0 to 4 (0 = absence of recruitment, 1 = 1% to 25% recruitment, 2 = 26% to 50% recruitment, 3 = 51% to 99% recruitment, and 4 = 100% recruitment). Elk population data were taken from a variety of sources (Stevens 1980, Houston 1982, Boyce 1989, Romme et al. 1995, Baker et al. 1997) and summarized into 10-year means to coincide with aspen recruitment values. Fire indices for JH and YNP, which represent periods of local versus extensive fires, were developed from various sources (Houston 1973, Loope and Gruell 1973). Time series of the Palmer drought severity index (PDSI) for June, July, and August were taken from Cook and colleagues' (1999) study of continental drought (grid points 36, 37, and 59). These data make up a standardized data set that allows subcontinental scale comparisons of drought over the 20th century. PDSI is a meteorological drought index based on water balance and derived from monthly values of both temperature and precipitation. High values represent cool, moist conditions, values around 0 represent normal conditions, and low values indicate hot, dry conditions. Values above 3 or below -3 indicate extremely wet or dry conditions, respectively.

The history of aspen recruitment in the three winter ranges varies but appears related to the history of fire, elk management, and climatic variability (figure 4). Major episodes of recruitment in JH and YNP during the 1870s and 1880s coincide (Romme et al. 1995, Hessel and Graumlich 2002), probably reflecting extensive fires that occurred in both areas when elk populations were extremely low because of market hunting. In YNP, aspen recruitment has essentially stopped since the end of the 19th century, but Romme and others (1995) dated only dominant trees in 15 stands, suggesting that they may have missed more recent recruitment. In contrast to YNP, JH experienced two episodes of recent recruitment (1915–1940 and 1955–1990) that appear to be related to declines in elk populations. RMNP has experienced episodic aspen regeneration since at least 1880, with greater periods of regeneration in 1907–1921, 1930–1936, 1950–1952, and 1960–1964,

but only two cohorts of aspen recruitment from 1970 to the present (Baker et al. 1997). Market hunting of elk continued well into the 20th century in RMNP, suggesting that the early periods of aspen recruitment may have been associated with low elk populations. Later episodes of recruitment coincide with periods of elk reduction carried out by the park service. The end of elk culling and the beginning of the natural regulation policy coincide with infrequent aspen recruitment since the 1970s in RMNP.

Drought variability appears to be only a weak driver of aspen regeneration in RMNP, JH, and YNP (figure 4). Early recruitment in the late 1800s coincides with a wet period in both JH and YNP, recorded by tree-ring reconstructions of PDSI (Cook et al. 1999). In YNP, recent wet periods did not produce an episode of regeneration, making it unlikely that moisture availability is the primary driver of regeneration in this region. Though periods of aspen recruitment in JH and YNP do coincide with higher PDSI values, the relative change in aspen recruitment and PDSI do not match. Despite their close proximity, the rainfall regimes of JH and YNP are dramatically different. JH experiences highest precipitation in winter, while the northern range of YNP experiences a precipitation high in summer. The summer PDSI reconstructions do not reflect these seasonal differences between the two areas, and it is unknown whether winter or summer precipitation might influence aspen recruitment patterns.

The studies described here present only static age structures (sensu Johnson et al. 1994). Aspen wood is often rotten and therefore not ideal for tree-ring dating, making it difficult to date dead trees. As a result, the role of mortality in creating the current structure of aspen stands has been largely ignored in studies of aspen age structure. However, some insight into the role of mortality in shaping age structures may be gained by observing the fate of current aspen recruitment.

A review of aspen recruitment and fire in elk winter range

As clones, aspen can store carbohydrate reserves in underground root systems, allowing rapid regrowth following disturbance. Aspen tend to sprout profusely following fire, producing a new cohort of regeneration. In YNP and JH, Romme and others (1995) and Hessel and Graumlich (2002) examined the effect of fire on current aspen recruitment in the presence

Table 3. Comparison of sample size of studies of aspen stand age structure.

Study	Number of stands	Average number of stems per stand	Total ages (years)	Classes
Baker et al. 1997	17	5–10	~ 115–230	1
Romme et al. 1995	15	5–10	~ 75–150	3
Hessel and Graumlich 2002	28	25.7	719	3

Note: The tilde (~) indicates that the actual sample size was not reported, but was inferred based on the number of stands and the number of reported samples collected at each stand. *Classes* refers to the number of elk habitat or use classes that were investigated.

of elk browsing to determine whether fire would promote aspen suckering in areas with little recent regeneration. In this section, I review the findings of this research in order to shed light on the historical aspen studies examined above.

In JH, I examined sprout density (stems < 2 meters [m] tall) 5 to 15 years after 11 prescribed fires (Hessl and Graumlich 2002). Prescribed fires varied in intensity, ranging from 10% to 95% mortality in mature trees. Sucker density for at least 5 years following fire was not significantly different in burned versus unburned stands, though variability in both groups was high. Regeneration was poor in the presence of elk browsing in all groups, suggesting that elk browsing can undo the beneficial effect of fire on aspen when elk pressure is high. However, a few burned stands inside elk winter range exhibited high densities of young aspen suckers. These stands were often located in areas of high human use, but additional study will be required to determine the exact mechanisms that allowed aspen to regenerate in the presence of high elk densities.

In YNP, Romme and others (1995) measured aspen regeneration after the large Yellowstone fires of 1988 to describe the effect of fire in the presence of high ungulate densities. They measured the ground layer of small aspen sprouts for 3 years following fire; they concluded that the range and maximum density of aspen sprouts were greater in the burned stands than in the unburned stands 2 years after fire, though, as with regeneration in JH, there was high variability in both burned and unburned stands. The range and mean in the

burned stands gradually decreased and were approaching the values of the unburned stands by the third year postfire, indicating that the fire had little long-term influence on aspen regeneration. The percentage of sprouts browsed was high everywhere, leading Romme and others (1995) to conclude that the 1988 fires would not generate large aspen stems and may have even contributed to the process of decline in aspen by killing mature trees.

Though the results of the study conducted by Romme and others (1995) suggest that the 1988 fires will not produce a flush of new aspen ramet recruitment, their study represents only one fire event and a single period of postfire climatic conditions. Future fires with different intensities, patterns, and postfire climatic conditions may have different effects on aspen recruitment. Nonetheless, managers using prescribed fire will have to account for the spatial distribution of elk and the timing of climatic conditions following fires if aspen regeneration is their objective.

Regeneration inside and outside the winter range

A few studies have examined the effect of elk browsing on aspen by comparing aspen regeneration inside and outside elk exclosures (Kay 1990, Baker et al. 1997), but these studies are limited by their small sample sizes and limited spatial extent. Landscape-scale studies that compare aspen regeneration inside and outside elk winter range measure aspen regener-

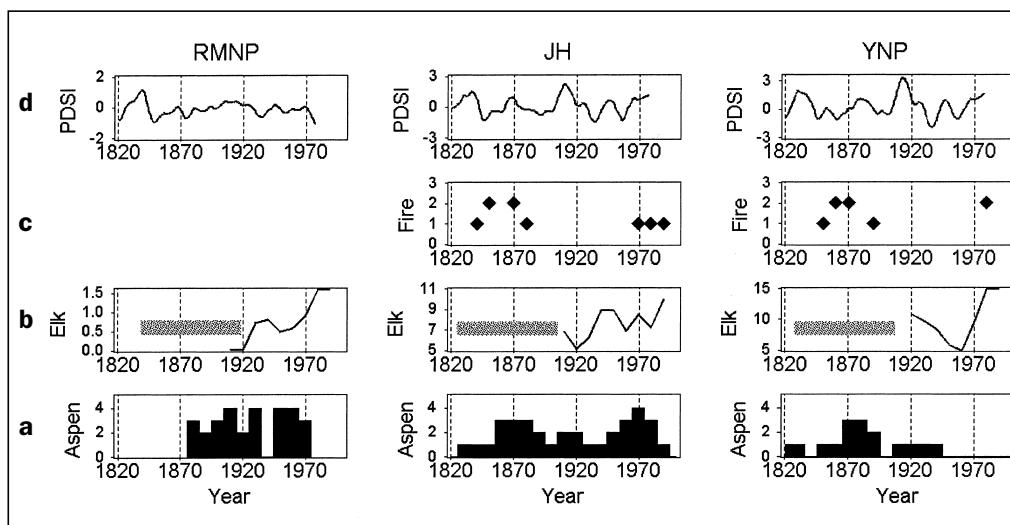


Figure 4. Comparison of aspen, elk, fire, and drought over time in RMNP (Rocky Mountain National Park), JH (Jackson Hole), and YNP (Yellowstone National Park). (a) Simplified age structure of aspen regeneration (black bars) is taken from three studies of aspen regeneration (Romme et al. 1995, Baker et al. 1997, Hessl and Graumlich forthcoming). (b) Elk represent simplified estimates of elk populations, in the thousands, compiled for RMNP, JH, and YNP (see table 2). A gray bar represents the period of market hunting. (c) Single fire events are noted with a diamond at level 1 and major fire events representing multiple large fires are noted with a diamond at level 2. Fire history data are currently unavailable for RMNP. (d) PDSI (Palmer drought severity index) reconstructions with lowess (locally weighted) smoothing (black line, 1820–1978) were generated from tree-ring chronologies taken from drought-sensitive trees located near the study areas (Cook et al. 1999).

ation across a range of sites and environmental conditions, but still compare the effects of elk browsing on regeneration at scales more appropriate to ecological processes. In this section, I review three landscape-scale studies of aspen regeneration in RMNP (Suzuki et al. 1999) and JH (Barnett and Stohlgren 2001, Hessler and Graumlich 2002). These studies allow a comparison of aspen regeneration across a gradient of elk use, from critical winter range (where elk return every year) to areas completely outside elk winter range. I also include analysis of my own data addressing calving areas, defined by wildlife managers as areas where female elk return to have offspring in the early spring. Calving areas may be located in critical winter range, winter range, or non-winter range areas, but in all of these locations, elk populations are concentrated in late winter and early spring, when aspen suckers are available.

Suzuki and others (1999) sampled aspen regeneration in winter and summer ranges inside RMNP and in winter range outside the park (on national forest land) to identify the patterns of aspen regeneration across landscape scales. Regeneration cohorts, defined as one or more stems within 2 cm diameter size classes, were counted in each stand. The authors found that between 20% and 45% of winter range stands inside RMNP had at least one regenerating cohort. Winter range on national forest land adjacent to RMNP had a higher percentage of stands with regenerating cohorts (75%), higher even than summer range in RMNP. These results demonstrate that elk impacts on aspen are strong where elk are concentrated, but they are weaker outside these high-use areas and are probably not causing a regional decline in aspen. However, because Suzuki and colleagues (1999) define a regenerating cohort as only one or more stems, it is difficult to assess how successful aspen recruitment may be in some stands with only a single regenerating stem.

We compared elk browsing on aspen ramets (< 2 m) at 30 sites located across three classes of elk range (non-winter range, winter range, and critical winter range) and two classes of elk use for calving (noncalving and calving) to determine whether elk browsing strongly affects regeneration success in JH (Hessler and Graumlich 2002). Our results show that browsing intensity is significantly lower outside the winter range. The mean height of suckers is higher outside the winter range, but not significantly different (using ANOVA [analysis of variance], $p = .155$) from the mean height in winter range or critical winter range, as all three classes are highly variable. Sucker density does not vary significantly across the three classes of elk use, indicating that elk do not prevent aspen regeneration, though browsing may limit the height of new suckers. When regeneration is compared across elk calving and noncalving areas, the results are more conclusive but demonstrate the same trends. Sucker height is significantly greater in noncalving areas than in calving areas ($p = .02$, $n = 27$), and browsing is significantly greater in calving areas than in noncalving areas ($p = .008$, $n = 27$). These results suggest that elk browsing may be concentrated where elk calve, and in these areas heavy browsing may be preventing aspen from reaching tree height.

Also working in the JH region, Barnett and Stohlgren (2001) sampled aspen ramets (< 2 m) at 68 sites in critical winter range, winter range, and non-winter range. As in our study, they observed no significant difference ($p = .25$) in aspen density across different types of winter range; however, the amount of bark browsing on regenerating stems was higher in the critical winter range compared with non-winter range and winter range sites. Barnett and Stohlgren (2001) also evaluated the relationship between elk concentration derived from elk aerial census data and aspen density and found that elk concentration was a statistically significant predictor of aspen density ($p = .005$). Their results suggest that elk habitat categories may be imperfect indicators of elk impact and that elk concentrations may indeed limit aspen regeneration in specific locations.

Definitive statements about the effect of elk densities (as indicated by elk habitat or range) on aspen recruitment are problematic, because the actual density of elk in a particular location over time is often poorly described. Elk habitat types such as winter range, critical winter range, and calving areas are defined by wildlife biologists on the basis of observed behavior of elk and on protected area boundaries; they may not be based on accurate measures of elk frequency or use. Barnett and Stohlgren (2001) make important inroads toward an accurate description of the spatial distribution of elk density.

The results of the studies discussed here suggest that heavy browsing by elk populations has had a strong influence on episodes of aspen regeneration in the past 150 years. Fire may have been an important driver of aspen regeneration before 1900, as demonstrated by the extensive regeneration in YNP and JH following the large fires of the late 1800s, but heavy elk browsing in these areas has reversed the beneficial effect of fire in recent decades. However, in the areas studied here, heavy elk browsing is limited to winter range, calving areas, and specific locations with high elk densities and does not appear to threaten aspen regeneration where elk are less common. In addition, the response of aspen to both elk browsing and fire history is highly variable and may be strongly influenced by regional climatic differences and genetic variability.

The outcome of inadequate knowledge on management practices

During the 20th century, inadequate knowledge about complex ecological systems has often led, for better or for worse, to changes in management policies. For example, the idea that fire is destructive led to a fire exclusion policy in the 20th century (Pyne 2001); the idea that elk winter range in Jackson Hole and Yellowstone was diminished by ranching led to the establishment of the National Elk Refuge, winter feeding, and predator control during the early 20th century (Sheldon 1927, Houston 1982); the idea that elk could not regulate their population in the absence of predators led to elk culling in Rocky Mountain National Park (Gysel 1959) and Yellowstone National Park (Houston 1982) during the mid-20th century; and the idea that ungulate populations are density de-

pendent led to the idea of natural regulation and the end of elk culling in national parks in the late 1960s (Houston 1982). In retrospect, we recognize that many of these management decisions were made with incomplete knowledge and were spurred by unusual events, such as the wildfires of 1910 (Pyne 2001), high elk mortality during the winter of 1919 (Sheldon 1927), and rapidly growing elk populations in the 1920s and 1930s. In addition to inadequate knowledge, management has also been shackled by the mismatch between the scales of ecological processes and human institutions. Clearly, better management depends on better knowledge of the aspects of aspen dynamics, including genetic variability and the persistence of aspen clones

Regional differences in aspen. One of the most common characteristics of recent aspen regeneration in all three study areas is the high degree of variability across elk use and recent fire history. One explanation for this high degree of variability in successful regeneration is genetic variation both within clones and across populations. Successful regeneration of aspen may be partly related to growth rate: Quickly growing suckers may escape elk browsing more effectively than suckers that grow slowly. Radial growth rates (Grant and Mitton 1979) and rates of spatial expansion (Sakai and Burris 1985) do vary between male and female clones, and there is evidence that male and female clones are spatially segregated (Grant and Mitton 1979). Growth rates also increase with heterozygosity (Mitton and Grant 1980, Jelinski 1993), and this characteristic appears spatially variable, with larger numbers of heterozygotes found in arid environments and fewer heterozygotes found in moist eastern forests (Mitton and Grant 1996). Tuskan and others (1996) suggest that aspen seedlings in YNP established after the 1988 fires are more genetically variable than the clonal stands established before the fires. However, variation within clones is still relatively high, because somatic mutations may accumulate in aspen ramets over time, increasing variability beyond what might otherwise be expected for a clonal species. Though genetic information is not yet available for the aspen populations in RMNP and JH, differences in genetic diversity of the population may account in part for highly variable responses of different clones and different populations of clones to elk browsing and post-fire regeneration. Like other aspects of aspen forest ecology, genetic variability across the entire range of aspen, and consequent variability in aspen clone responses, argues for aspen research and management conceived within the context of such variation.

Aspen persistence. In addition to variation within and between clones, there are many unknowns surrounding the ability of aspen clones to persist for long periods of time without major episodes of sexual reproduction. For example, a life span of 10,000 years for aspen clones has been posited, but no firm evidence exists to confirm this hypothesis (Jelinski and Cheliak 1992, Jelinski 1993). If clones are exceptionally long-lived, then they may have sustained heavy elk browsing

and long periods without fire in the past, and they may be able to continue to sustain themselves under current conditions. This conclusion, if borne out, would have major implications for management.

The classic explanation for aspen persistence has been regeneration following fire. Severe fires eliminate overstory coniferous forest and promote widespread aspen regeneration, resulting in even-aged stands of aspen (Jones et al. 1985). Over time, shade-tolerant conifers establish in the understory of aspen and eventually overtop the short-lived and small-statured aspen stems. When fuels adequate to support a crown fire exist, the cycle is repeated. However, though this model describes some systems in the intermountain West, other patterns of aspen stand structure are not consistent with this model. Aspen regenerate in the absence of fire (Better and Woods 1981, Hessler and Graumlich 2002), and fire does not always result in a long-term increase in aspen sucker density (as is the case when large numbers of ungulates are present) (Bartos and Mueggler 1981, Romme et al. 1995, Hessler and Graumlich 2002). Evidence from a few areas suggests that high-frequency fires may sustain multiaged stands of aspen, but this does not explain multiaged stands with no history of repeat fires. Clearly, additional research on fire and aspen is needed if aspen forests are to be sustained in areas where fire regimes have been altered by human activities.

Another key to aspen persistence may lie in the large underground root system sustained by clones. It has been proposed that aspen roots may persist in the absence of mature trees, nurtured only by transient suckers or heavily browsed "shrub" aspen (Despain 1990). However, small aspen stems tend to be functionally attached to large neighbors (Shepperd 1993), and when these root connections are severed, subordinate stems experience reduced growth (Zahner and Debyle 1965). Little evidence currently supports the idea that shrub aspen can persist in the absence of mature trees, but this hypothesis may be testable, because many stands in YNP, RMNP, and JH are experiencing high mortality of overstory trees, leaving only short, shrubby aspen stems.

A similar hypothesis for aspen persistence suggests that aspen clones may persist as co- or subdominants within coniferous forest (Abolt 1997). Following disturbance, these subdominants may recruit rapidly from root stocks, allowing clones to expand. Recent work indicates that the root mass of aspen clones invaded by conifers does not differ from the root mass of stands that are regenerating (Shepperd et al. 2001), suggesting that clone root mass may persist at least through late stages of succession. Until lately, little research has focused on the few scattered aspen stems observed in the understory of coniferous forest, but current research may improve our understanding of the frequency and longevity of these "refugial" stems. Finally, Barnett and Stohlgren (2001) have suggested that although aspen regeneration occurs as a patchy mosaic both within stands and across landscapes, these infrequent patches of regeneration are important for aspen persistence over decadal to centennial time scales. If they

are right, a few small stems might give rise to large clones, given the right environmental conditions.

Perhaps the most critical and underresearched mode of aspen persistence may be through unusual episodes of regeneration from seed. Although aspen recruitment from seed has not been well-documented in the literature, at least one major episode did occur following the Yellowstone fires of 1988 (Romme et al. 1997, Turner et al. forthcoming). However, it is unknown whether these seedlings are likely to persist in the presence of elk browsing. Questions about the timing, frequency, and importance of fire events for establishing new stands and maintaining genetic diversity remain unanswered.

Finally, all of the research explored in this synthesis was performed in locations where aspen make up only a small percentage of the vegetative cover (table 1). In some regions of the intermountain West, such as southeastern Colorado and Utah, aspen form a much larger percentage of the overstory. Few studies (Allen 1989) have addressed aspen–elk interactions in these locations where large stands may satiate herbivores. To manage aspen in a sustainable fashion, researchers and park managers must answer questions about their persistence, while recognizing that aspen's wide biogeographic range most likely means that each question has a variety of answers.

Human institutions and ecological processes. Natural regulation, the National Park Service policy for ungulate management, has been plagued with controversy since its inception. The conflict in Yellowstone's northern range, where large elk populations have had strong impacts on vegetation, has brought this controversy to the forefront of ecology (Soukup et al. 1999) and park policy (NRC 2002). Ultimately, conflict around aspen decline has generated a timely question about protected area management: Can we maintain complex ecological systems and ecological processes in the face of increasing human influence on parks and protected areas? Aspen forest dynamics, elk population dynamics, and fire regimes operate over large spatial and temporal scales, scales that often transcend land management boundaries and the life of human institutions. Approaches to the management of these large ecosystems and their attendant processes must address these questions of scale. In other words, do the scales of human institutions such as natural regulation fit the temporal and spatial scales of ecological variability (Folke et al. 1998)?

National park management policy has evolved from predator control and ungulate culling in the late 1800s through the 1960s to heavy reliance on ecological processes to regulate park resources. During the 1950s and 1960s, public outcry over ungulate reductions by park service agents led to the more publicly appealing and politically feasible alternative of natural regulation (Soukup et al. 1999). Since the late 1960s, national park management has followed the natural regulation paradigm. According to theory, ungulate populations will be self-regulating or density dependent at high densities, even in the absence of major predators, because they are limited primarily

through intraspecific competition for resources, especially winter forage, and extreme weather conditions, which influence natality and mortality. Thus, a hands-off management policy—natural regulation—was adopted.

Some critics have taken the current status of aspen in national park winter range areas as an indication that the natural regulation paradigm is inherently flawed. They argue that if vegetation is threatened by ungulate use, then ungulates must not be self-regulating at high densities. Given our incomplete state of knowledge, especially with respect to aspen persistence, it is difficult to use aspen forest dynamics to evaluate the natural regulation policy. However, natural regulation in the context of aspen, elk, and fire highlights some important mismatches between the scale of human institutions and that of ecological processes, mismatches that are likely to produce additional uncertainties for managers (figure 3).

National parks and the natural regulation paradigm are spatially and temporally constrained by distinct political boundaries, such as land ownership, but ecological processes operate at different spatial scales that transcend these boundaries (figure 3). In other words, the experimental boundaries of natural regulation have most likely been breached by far-reaching human impacts outside the parks. For example, elk that are hunted outside protected areas congregate in protected winter range, and in the case of JH are kept there by winter feeding. These heavy concentrations of elk lead to a strong impact on aspen and other vegetation. Similarly, changes in public land policy may be too slow, and rates of development outside parks too fast, relative to rates of change in biological systems. Rapid development outside parks may have consequences, as yet unidentified, for migrating animals. Fire suppression and prescribed fire have altered major ecosystem processes and dynamics such that current fire regimes may not match those required for aspen regeneration in the presence of elk browsing. Given an incomplete knowledge of aspen's ability to persist in its current environment and the apparent mismatch between human institutions and ecological processes, how should managers proceed?

To preserve and protect complex ecological systems, ecosystem management of large protected areas must consider past and present human influences on ecosystem variability and must match the scale of management to key ecological processes and drivers. Although cooperative interagency management of the Greater Yellowstone Area is one step in this direction, a specific framework for scaling management is needed. One approach may be to identify the speed and extent of key processes governing ecological dynamics and the associated management activities that affect those dynamics (figure 3). Management efforts should initially focus on identifying those processes that operate at rapid speed (such as elk migration, elk movement, and aspen ramet regeneration). Less immediate attention and precision is needed for those processes that operate at slow speeds (aspen population dynamics). These processes are still important, but managers have some flexibility in exactly when and where they occur.

Similarly, research must focus on the high-speed, far-reaching processes and evaluate the ability of species and ecosystems to resist perturbation, for example, through different modes of persistence. Even with incomplete knowledge of the ecological processes involved, prioritizing research and management decisions according to this framework may be the next step toward resolving problems of fit between human institutions and ecological processes.

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