



Interactive effects of human activities, herbivory and fire on quaking aspen (*Populus tremuloides*) age structures in western Wyoming

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Abstract

Aim Fire suppression, elk (*Cervus elaphus* Erxleben) browsing and drought have been suggested as possible explanations for low aspen (*Populus tremuloides* Michx.) ramet regeneration in elk winter range of the Greater Yellowstone Area (GYA) during the twentieth century. This study analyses the relationship between the rates of aspen regeneration, biophysical factors and human land use since 1830. This approach reveals the importance of indirect human impacts, especially through fire and elk management strategies, on forest structure.

Location This study was conducted in and around the winter range of the Jackson Hole elk herd in western Wyoming, USA. Aspen stands in this region represent the ecotone between coniferous forest and sagebrush-grassland vegetation.

Methods Age structures of aspen stands were reconstructed from tree-rings in order to determine how variation in drought, elk populations and fire occurrence may have affected aspen ramet regeneration since 1830. The effects of recent prescribed fires and elk browse on aspen regeneration were also evaluated by measuring stem height, browse intensity and age of ramets < 2 m tall in prescribed burns and in unburned areas.

Results Aspen ramet regeneration has occurred consistently but at low frequencies since 1830, with three peaks of regeneration: 1860–85, 1915–40 and 1955–90. Periods of frequent ramet regeneration coincided with low to moderate elk populations and aspen regenerated only sporadically when elk populations were high. Based on a comparison of the age structures with a tree-ring reconstruction of Palmer drought severity index (PDSI), observed PDSI and annual precipitation, drought variability appears unrelated to episodes of aspen regeneration. Recent regeneration patterns suggest that fire does not enhance the recruitment of tree-sized aspen stems in the presence of elk browse, although sample sizes were small. Since 1900, elk hunting and spatially clustered elk feeding in the study area has facilitated low but consistent regeneration of aspen ramets in the twentieth century. In contrast, extremely low ramet regeneration has been observed in national parks of the Rocky Mountains, where elk have been managed according to the ‘natural regulation’ policy (no hunting or feeding) since 1969.

Main conclusions Over time, different management strategies have altered the interactions between fire, herbivory and aspen regeneration suggesting that management history and the causes of change in management, should be explicitly included in ecological studies and future management strategies. These results also point to the value of using the spatial and temporal variation in human interactions with ecological systems as a method for understanding ecological relationships.

Keywords

Populus tremuloides, *Cervus elaphus*, climate, fire history, forest history, human impact.

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INTRODUCTION

Ecosystem processes such as fire and migrating ungulate populations operate over large spatial and temporal scales so changes in these processes have the potential to generate far-reaching, pervasive impacts on vegetation. Land-use history and management activities that affect these processes, such as predator control, fire suppression and ungulate management may directly and indirectly impact vegetation and must be included in studies of modern ecosystems (Motzkin *et al.*, 1996; Bürgi *et al.*, 2000; Foster, 2000). Although much work addressing land-use history has been conducted in the eastern and central United States, the history of human activities may also be important in understanding ecosystems in western North America. For example, in Yellowstone National Park, higher elk (*Cervus elaphus* Erxleben) populations following predator control efforts may have altered vegetation notably willow (*Salix* spp.) and quaking aspen (*Populus tremuloides* Michx.) communities through browsing (Kay, 1998; Ripple & Larsen, 2000). At the same time, climatic influences, such as drought variability, may affect vegetation on a regional scale, making it difficult to separate human influences from the effects of climate on vegetation (Veblen *et al.*, 1999). Few studies in the western United States have addressed the interacting effects of human activities and natural processes in a historical context, with notable exceptions (Bahre, 1991; Vale, 1998; Veblen *et al.*, 1999). A historical context not only reveals the importance of human activities on ecosystem pattern and process, but also enhances studies of ecological interactions through the 'experiments' created by the spatial and temporal pattern of human activities through time (Hollander, 2000). Land-use changes and ownership boundaries create landscape level manipulations that allow researchers to disentangle the many human drivers of ecosystem change from biophysical variables. These 'pseudo-experiments' are especially valuable for managing ecosystems with many interacting processes where real experimental manipulations at landscape scales would be unthinkable.

One such ecosystem is the aspen ecosystem of the Greater Yellowstone Area (GYA) where many processes including climate, fire, herbivory and predator-herbivore relationships may all affect aspen stand structure. Current patterns of aspen stand age structure have generated much debate about the relative importance of human management vs. different biophysical variables such as wolves, elk, climate and fire, in maintaining aspen ecosystems. In some areas of the Rocky Mountains, including Yellowstone National Park and Rocky Mountain National Park, aspen stands are dominated by stems in > 100 year age classes and have low rates of stem (ramet) regeneration (Gruell & Loope, 1974; Allen, 1989; Mueggler, 1989; Wirth *et al.*, 1996; Baker *et al.*, 1997; White *et al.*, 1998). Many mechanisms for the twentieth century pattern of aspen ramet regeneration in the Rocky Mountains have been suggested, including fire suppression (Gruell & Loope, 1974; Romme *et al.*, 1995), climate variability (Romme *et al.*, 1995), elimination of Native

American land-use (Kay, 1994, 1995, 1997) and predator control policies (Ripple & Larsen, 2000).

Aspen stems regenerate vigorously both sexually (genets) and vegetatively (ramets) following stand-destroying fires (Gruell & Loope, 1974; Schier & Campbell, 1978; Jones & DeByle, 1985; Romme *et al.*, 1995), suggesting that reduced fire frequency over the last century may be associated with aspen decline. However, elk browsing may inhibit and possibly prevent aspen regeneration (both ramet and genet) following fire (Olmsted, 1987; Kay, 1990, 1993; Romme *et al.*, 1995; Baker *et al.*, 1997). In Yellowstone National Park, herbivory by elk and dry climatic conditions may have prevented aspen ramet regeneration following the 1988 fires (Romme *et al.*, 1995) but these influences are difficult to separate. Kay (1994, 1995, 1997) has suggested that prior to Euro-American settlement, Native American burning practices (in combination with elk hunting) may have allowed aspen to escape heavy elk browse, although little quantitative evidence supports this view.

Ripple & Larsen (2000) hypothesize that the absence of grey wolves (*Canis lupus* Linnaeus) in Yellowstone National Park during most of the twentieth century indirectly reduced the success of aspen ramet regeneration. Wolves reduce elk numbers, modify elk movement and alter browse patterns over broad spatial scales. It follows that the absence of wolves may have led to increased browsing on aspen by elk. Top-down patterns of ecosystem regulation have been observed in other regions (Matson & Hunter, 1992; McLaren & Peterson, 1994) and may be an important influence on past aspen regeneration processes.

Many of the factors that influence aspen regeneration dynamics can be linked to patterns of human land-use history, however aspen communities have not been studied in this context. Instead, many studies (Allen, 1989; Kay, 1993, 1998; Romme *et al.*, 1995, 1997; Baker *et al.*, 1997; White *et al.*, 1998; Ripple & Larsen, 2000) have focused on protected areas and national parks. The greatest body of work has been in Yellowstone National Park where elk populations have been managed according to a 'hands off' or natural regulation policy since 1968. This management strategy assumes that density-dependent factors will limit the maximum size of ungulate populations over the long-term (Huff & Varley, 1999). As a result, the conditions in national parks may not represent aspen forest dynamics on other public lands where elk hunting and feeding were permitted during the twentieth century and fires have been, and continue to be suppressed. By comparing aspen regeneration patterns in places with different land-use histories, including differences in fire and ungulate management, it may be possible to identify which ecological and human processes have been most important in generating current age structures of aspen, both in national parks and on other public lands.

In this study we quantify the spatial and temporal variability of aspen regeneration in the Jackson region of western Wyoming, USA (Fig. 1). In contrast to most recent studies of aspen-elk interactions conducted on National Park Service lands, this study was conducted on National

Forest and National Elk Refuge lands with a long history of human land use, including intensive elk management and fire suppression. The study focuses on the following questions: (1) What is the temporal pattern of aspen ramet regeneration in the last 150 years? (2) How do climatic variability (i.e. drought), altered fire regimes (suppression and prescribed fire) and elk numbers and spatial distribution affect the observed spatial and temporal variation in aspen ramet regeneration? (3) What is the relationship (if any) between current stand age structures and the history of human land use in this study area compared with other studies of aspen in national parks?

STUDY SITE

This study was conducted in and around the winter range of the Jackson Hole elk herd on the east side of the Teton Mountains in western Wyoming (Fig. 1). The Teton Mountains are a north–south orientated massif that interrupt cyclonic activity associated with the westerlies, creating a strong rain shadow effect in the valleys just east of the range. According to climatological records from the Moran, Wyoming climate station (< 5 km northwest of the study area), mean annual precipitation is 59 cm with a winter (November–February) maximum. Mean annual temperatures are low (1.8 °C), ranging from –11.4 °C mean monthly temperature in January to 14.9 °C mean monthly temperature in July. Soils are complex and variable including inceptisols, alfisols and mollisols depending on the history of

local geomorphic activity (Teton Division Soil Survey, 1982). Vegetation is dominated by sagebrush (*Artemisia* spp.) grasslands bordered by higher elevation coniferous forest vegetation composed of lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.), Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco], Engelmann spruce (*Picea engelmannii* Parry), and subalpine fir [*Abies lasiocarpa* (Hook.) Nutt.]. Aspen stands occur at the ecotone between montane coniferous forest and sagebrush grassland, forming a diffuse band of deciduous vegetation between c. 2000 and 2550 m, with smaller stands of short stature occurring infrequently up to treeline.

Elk are the dominant wild ungulate in the Jackson valley with current herd population estimates exceeding 16,000 animals (Doug Brimeyer, Wyoming Game and Fish Department, personal communication). The Jackson herd is the second largest elk herd in the world; Yellowstone's northern herd is the largest (Boyce, 1989). Elk prefer aspen over other habitats especially in fall, winter and spring (Boyce, 1989), making aspen woodlands an important resource for elk. The Jackson Hole elk herd is composed of two major groups. One segment winters on the National Elk Refuge and one segment winters on the Bridger-Teton National Forest in the Gros Ventre watershed. In summer, both components of the herd migrate to Grand Teton National Park, Yellowstone National Park or high elevations in the Bridger-Teton National Forest (Smith & Robbins, 1994). Some animals migrate up to 100 km between winter and summer range, probably the longest migration of any of the North American elk herds (Boyce, 1989). The Jackson elk herd has been intensively managed since the early twentieth century, including regulated hunting, winter feeding (at designated 'feed grounds') and predator control (Boyce, 1989).

Fire was actively suppressed in the study area between 1940 and 1985. Prescribed fires during the 1980s and 1990s conducted by the Forest Service and Wyoming Department of Game and Fish have created a patchwork of burned and unburned aspen stands both inside and outside the elk winter range. These recent fires allowed us to evaluate the impact of fire on aspen in the presence of a range of elk impacts.

MATERIALS AND METHODS

Three categories of contemporary elk use were identified based on Wyoming Department of Game and Fish classes of elk habitat derived from annual frequency of elk observations (Doug Brimeyer, Wyoming Department of Game and Fish, personal communication). The three elk categories are: 'critical winter range' (areas where elk are observed every winter); 'winter range' (areas where elk are observed most winters) and 'non-winter range' (areas where elk are occasionally observed in winter). All aspen stands > 625 m² within the study area were identified based on maps of aspen stands generated by aerial photo interpretation (Larry Warren, Bridger-Teton National Forest, personal communication) prior to data collection. Stands smaller than 625 m² were omitted from sampling because of the difficulty of detecting them on aerial photos. Data on aspen

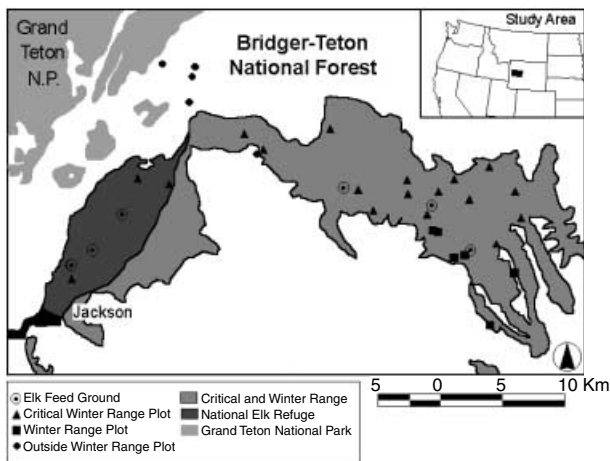


Figure 1 Map of critical winter range for the Jackson Hole elk (*Cervus elaphus* Erxleben) herd. Locations of plots are noted by triangles for those located in critical winter range, squares for those in winter range and circles for those outside winter range. Open circles with a dot indicate the locations of elk feeding grounds where elk have been fed on nearly an annual basis since 1912. The Bridger-Teton National Forest owns all lands except where denoted either private (black), Grand Teton National Park (grey), or National Elk Refuge (dark grey). Critical winter and winter range are elk habitat categories based on elk migration behaviour (see Materials and methods).

stand dynamics were collected from thirty stands selected at random from the c. 100 mapped stands, split into two categories (burned and unburned) based on management history since 1980. We randomly selected twelve stands that had been burned by recent (< 15 years old) management-ignited fires and eighteen stands that had not been burned in at least the last 40 years (Table 1). Prescribed fires occurred within the sampled stands and varied in severity. Canopy kill of mature overstory trees ranged from 5% to 95% (mean = 51.3%, SD = 36.1%). The study area was also separated into three categories of elk habitat as defined above. Stands were selected from the three categories of elk habitat and from burned and unburned aspen stands within the Gros Ventre watershed of Bridger-Teton National Forest and the National Elk Refuge (Table 1). Although we attempted to select equal numbers of stands in each category, it was difficult to locate burned stands outside the critical winter range where this management approach has not been applied frequently. Similarly, it was difficult to locate non-winter range stands that were not too distant from the original study area. Non-winter range plots were located within 5 km of the winter range boundary and have similar vegetation, elevation, slope and aspect to winter range and critical winter range plots.

Aspen distribution and stand dynamics

We constructed stand-age structures of aspen ramet regeneration similar to those constructed for other forest types (Henry & Swan, 1974; Lorimer, 1980; Duncan & Stewart, 1991). Because aspen are clonal, only the history of asexual regeneration (ramets) can be analysed using this methodology. It is currently not possible to determine the age of individual clones (genets). Therefore, references to regeneration in this paper always refer to vegetative regeneration (ramets, sprouts, or stems, not seedlings) unless noted otherwise. In each stand selected for sampling, at least forty trees (> 2 m tall) were included in one randomly located rectangular plot that was either 375 m² (six plots), 625 m² (twenty-two plots), or 1250 m² (two plots). Plot size varied according to stem density in order to include at least thirty trees > 10 cm d.b.h. in each plot. The d.b.h. of all standing trees > 2 m tall (live and dead) within each plot was measured and a random sample of twenty-five to fifty trees (live and dead) were cored twice, as close to the base as possible, to determine approximate regeneration dates. Some cores were taken up to 1 m above rotten bases, reducing the resolution of regeneration dates for these trees. Cores were processed according to standard dendrochronological techniques (Stokes & Smiley, 1968). Annual rings were counted

and cores with more than fifty rings (live and dead trees) were visually cross-dated using sequences of marker rings to improve the accuracy of estimated ramet regeneration dates (Yamaguchi, 1991). Age structures for each stand were constructed using all size classes from each plot, rather than only the dominant canopy trees (Romme *et al.*, 1995). Standing dead trees were included in this analysis but downed logs were too rotten to date and were not included.

Many cores were rotten and could not be aged because aspen in this region are often infected with fungal pathogens (Krebill, 1972). We compared the original d.b.h. distribution of all cored ramets with the d.b.h. distribution of the ramets that were included in the final age structure using a two-sample Kolmogorov–Smirnov test. We used this test to assess whether the dated sample used for age structure analysis actually represented the size structure of the sampled plots.

Although we cored each tree at least twice, only 29% of sampled trees had one or more core samples with the pith present. For trees without a pith date, we used a geometric method to estimate the number of rings required to reach the pith. We estimated the radius of the earliest ring present in each core using circles of different radii printed on clear acetate. We then estimated the remaining number of rings needed to reach the pith based on the average ring width of the earliest five rings in that core and the estimated radius of the earliest ring. Cores that required more than an estimated fifteen additional rings to reach the pith were discarded.

Villalba & Veblen (1997) recommended adjusting for coring height based on the growth curve of seedlings growing in the same conditions as the sampled trees. We did not adjust ages for coring height for several reasons. Elk have browsed nearly all suckers currently growing in the study area (see below), resulting in suppressed radial growth of suckers. Mature trees do not display the same pattern of early suppressed growth. Instead, mature trees show a pattern of rapid early growth. Therefore, the radial growth rates of current (browsed) suckers may not represent the early radial growth of mature trees because browsing intensity and its effect on ring widths has varied over time. Additionally, unbrowsed suckers (with unsuppressed radial growth) can elongate to at least 1 m year⁻¹ of growth (Romme *et al.*, 1995), making it unnecessary to adjust ages to coring height among trees that experienced little browsing by elk during the first few years of vertical growth.

Fire history

We synthesized several forms of fire history information for the study area including a study of fire scar data (Loope &

	Critical winter range	Winter range	Outside winter range	Total
Burned	8	2	2	12
Unburned	11	4	3	18
Total	19	6	5	30

Table 1 Distribution of sampled stands within three categories of elk (*Cervus elaphus* Erxleben) use and within two categories of burn history (burned = burned by prescribed fire in the last 15 years, unburned = not burned in at least 40 years)

Gruell, 1973), historical photograph analysis (Gruell, 1980a, b), informal Bridger-Teton National Forest fire history studies and recent Bridger-Teton National Forest records of prescribed fire. Because aspen tend to sucker profusely following fire, the stand origin dates can indicate past fire events especially when these dates are coupled with other independent fire history information (Romme *et al.*, 2001). We compared aspen stand origin dates with the results of earlier fire history studies by (1) recording the regeneration year of the five oldest stems in each stand, (2) identifying stands with at least three stems with synchronous (to the year) regeneration dates, (3) assigning that date as the potential stand origin date following fire and (4) comparing these dates to those of large 5-year classes based on fire scar and stand age data (not cross-dated) taken from coniferous forest surrounding aspen stands in the study area by Loope & Gruell (1973). These multiple lines of evidence were used to identify periods with extensive fires that may have been important for aspen regeneration.

Elk population dynamics

Elk population estimates between 1912 and 1997, including both temporal and spatial information, were collected from the Wyoming Game and Fish Department as well as the National Elk Refuge. The most consistent and comprehensive elk population data for the study period were collected at the National Elk Refuge, although other counts, conducted at feed grounds in the Gros Ventre Valley (1960–97) are available. Because these counts are significantly correlated with the National Refuge counts ($r = 0.5$, $P = 0.03$) but have shorter temporal depth, we conducted our analysis using the National Elk Refuge data. National Elk Refuge elk population counts are based on winter feed ground counts (1912–32) and aerial counts (1932–97) collected by the National Elk Refuge as part of its monitoring programme (Boyce, 1989). Although interannual variations in these data are primarily related to winter conditions, decadal and longer scale patterns are likely indicative of real trends independent of the sampling methods (Boyce, 1989). We supplemented elk population estimates with other historical information on elk populations and spatial distribution taken from historical accounts, including the writings of early trappers (1808–40) and government surveys (1876–98) (Delacy, 1876; Hough, 1887; Price, 1898; Irland, 1903; Mattes, 1948). Although historical accounts are often biased by the objectives of the author, a gross estimate of elk populations in the nineteenth century can be developed based on these accounts.

If elk population size does not affect aspen ramet regeneration, then we would expect aspen regeneration dates to be unassociated with elk numbers over time. We used a chi-squared goodness-of-fit test to evaluate the relationship between elk numbers and aspen regeneration between 1914 and 1994. Observed frequency of aspen ramet regeneration was summed over 5-year periods and placed in two classes (1, 0): 5-year periods in which regeneration was above the mean (1) or below the mean (0) of all 5-year

classes. Three elk classes (1, 2, 3) were defined by finding 5-year means of elk population estimates to coincide with the 5-year classes of aspen regeneration. The range of the 5-year mean values was divided into thirds and elk classes were assigned based on these thirds.

Drought

Drought may influence aspen reproductive success through moisture available for rapid growth of young suckers. Although clonal root systems allow aspen to avoid drought (Jones *et al.*, 1985), droughts of long duration may strongly affect height growth among suckers and mature trees (Stoekeler, 1960; Einspahr *et al.*, 1972; Jones *et al.*, 1985). In the foothill transition zone between sagebrush grassland and evergreen forest, aspen often occur on north-facing slopes and in the lee of snow banks, suggesting that aspen may be moisture limited in arid environments (Knight, 1994). We collected monthly precipitation data (1915–97) from the Moran climate station (National Climatic Data Center, 1998) and summer (June–August) observed Palmer drought severity index (PDSI) (Cook *et al.*, 1999; grid point no. 36). We also used an existing tree-ring (*Pseudotsuga menziesii* Franco) reconstruction of summer (June–August) PDSI (adjusted $R^2 = 0.46$, $P = 0.05$) collected in the Wind River Mountains, c. 100 km southeast of the study area (Pisarcic & Graumlich, 2002), to examine the long-term pattern of drought in the region.

We used a chi-squared goodness-of-fit test to evaluate the effect of past drought on aspen regeneration similar to the method for comparing elk and aspen. Frequency of aspen regeneration was summed in 5-year classes from 1834 to 1994. This 5-year aspen frequency was then grouped into two classes: 5-year periods where regeneration was above the mean (1) or below the mean (0) of all the 5-year classes. Instrumental PDSI values (1895–1994) were also averaged for the same 5-year periods and divided into three classes (1, 2 or 3) based on the range of values between 1895 and 1994. Observed and expected frequencies of aspen regeneration were tallied or calculated (respectively) given different moisture conditions, as defined by PDSI. If drought has little or no effect on aspen regeneration, then we expect the observed and expected frequencies of aspen regeneration to be similar.

Recent patterns of aspen regeneration

Information on recent regeneration and vigour of aspen suckers (vegetatively regenerated stems < 2 m tall) was also collected at each site using a smaller 5 × 5 m plot taken at one corner of the larger age-structure plot. Within this smaller plot each stem < 2 m tall was tallied and several estimates of elk use were recorded. Elk browsing was measured using (1) an ocular estimate of the percent of photosynthetic biomass removed by browsing, (2) height of the tallest live branch, (3) height of the tallest dead branch and (4) total number of stems (live and dead) at the base of each ramet. More than one stem per ramet indicates that the

clone had produced other stems in the past that died before reaching tree height (1.37 m). We also collected up to twenty discs from suckers in each of these smaller 5×5 m plots to estimate the age of aspen suckers.

RESULTS

Long-term patterns of aspen regeneration

A total of 1044 tree-sized aspen ramets from thirty plots (in thirty separate aspen stands) were sampled for age structure analysis. Of these stems, 774 ramets (nine to forty-five per plot) were successfully dated and 270 ramets were eliminated from the analysis because of rotten wood. More than twenty ramets were dated for twenty-two of thirty plots. Two plots were discarded from the age structure analysis because they had less than fifteen dated trees.

The d.b.h. distributions of aged stems vs. all cored stems (we cored every tree in each plot) were not significantly different (k -s statistic = 0.0376, $P = 0.5601$), indicating that the aged sample was representative of all the stems present on the plots, at least with respect to d.b.h. We also compared the number of dead stems in the original sample with the number of dead stems in the aged subsample. Of the total number of stems sampled, 32.5% were dead (338 of 1044); for the total number of stems dated, 29.1% were dead (224 of 770). This suggests that the proportion of dated samples represents (approximately) the standing dead stems present in the plots and living vs. dead trees did not bias the aged sample.

Aspen ramet regeneration at all plots with more than fifteen dated stems ($n = 28$) has occurred consistently but at low frequencies since 1830, with three peaks of

regeneration: 1860–85, 1915–40 and 1955–90 (Fig. 2). Overall 42% of the stems dated regenerated between 1839 and 1899. Thirteen plots experienced a recent period of regeneration beginning in 1960 and extending through the late 1980s. Seven plots have an intermediate regeneration period between 1910 and 1950, although this period is not as consistent between plots. Most plots with early regeneration in the 1830s continue to experience some regeneration in the late 1980s. However, five plots (of twenty-eight) have not produced any ramets > 2 m tall since 1910.

The history of ramet recruitment differs between critical winter range plots, winter range plots, and plots located outside of elk winter range (Fig. 3). Critical winter range plots comprise 54% of the total stems in the twenty-eight plots and appear to be driving the pattern of regeneration observed in Fig. 2, represented by three similar periods of regeneration. Critical winter range and winter range plots show a pulse of establishment during the 1870s and 1880s that is probably the result of fires during that period, although this pulse is weak for plots located outside the winter range (see next section). These fires may not have affected plots located outside the winter range. A recent period of recruitment in the 1990s is present in all elk classes, although this period is most accentuated in the plots located outside elk winter range where prescribed burns have generated a pulse of regeneration that has not been browsed heavily by elk. Critical winter range plots show a small pulse of regeneration during the 1920s and 1930s that is not clearly expressed in the other elk-use classes. This event may be the result of elk feeding that began in the critical winter range in 1912, reducing the effect of elk on aspen by concentrating herds near feed grounds (Fig. 1).

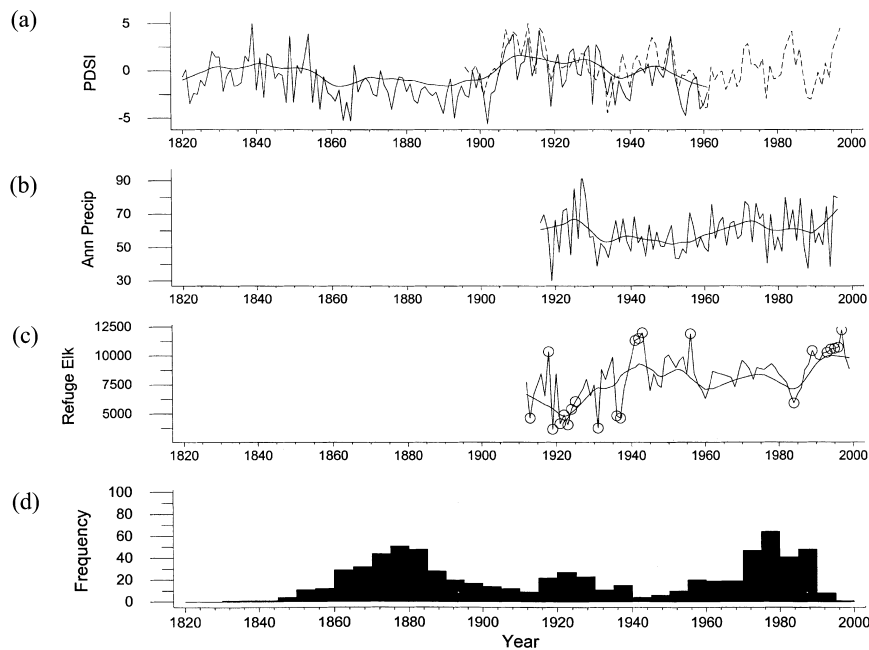


Figure 2 Raw data and loess-smoothed curves (Cleveland *et al.* 1988) with a 15-year window. (a) Tree-ring (*Pseudotsuga menziesii* Franco) reconstruction of PDSI (adjusted $R^2 = 0.46$, $P = 0.05$) from Wind River, Wyoming, 1820–1997 (Pisaric & Graumlich, 2002) (solid line) and observed PDSI (Cook *et al.*, 1999, grid point no. 36) (dashed line), (b) annual precipitation, 1915–97 and (c) estimated elk (*Cervus elaphus* Erxleben) population for the National Elk Refuge, 1912–97. Estimates of elk population highs and lows are noted with black circles (population estimate > 1 SD above or below the series mean for the period of record). The period of market hunting occurred between 1810 and 1900. (d) Combined age structure of aspen (*Populus tremuloides* Michx.) ramet regeneration frequency per 5-year period (black bars) for twenty-eight plots 1830–1997.

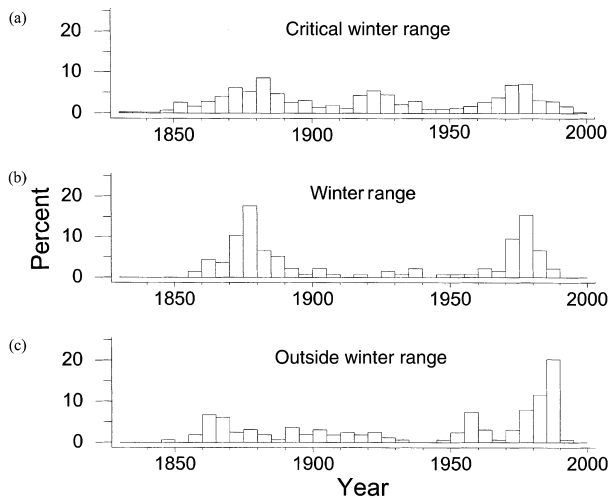


Figure 3 Combined age structure of aspen (*Populus tremuloides* Michx.) ramet regeneration present frequency for 5-year periods (white bars) for twenty-eight plots between 1830 and 1997, separated by plots located in (a) the critical winter range, (b) winter range, and (c) non-winter range of the Jackson elk herd. Sample sizes refer to the number of aspen ramets aged.

The long-term effects of elk, climate and fire

Plot age structures were pooled from the twenty-eight plots with more than fifteen dated stems to emphasize the shared variation within the study area. Ramet regeneration (stems > 2 m in height) in the last 160 years was then compared with elk population data, annual precipitation and a reconstruction of summer (June–August) PDSI from Douglas-fir (*Pseudotsuga menziesii* Franco) tree-ring chronologies (Pisaric & Graumlich, 2002) (Fig. 2). Elk population estimates were highly variable from 1912 to 1998 (Fig. 2). Periods of high aspen ramet regeneration coincided with low to moderate elk populations, and aspen regenerated only

sporadically when elk populations were high. Aspen regeneration was at its highest sustained level in the late 1800s. It has been postulated that elk populations were extremely low in the GYA during this period because of market hunting (Kay, 1990), but quantitative estimates of the elk population in Jackson area are not available for this time period. Historical records for the region indicate relatively low levels of elk between 1811 and 1860 (DeLacy, 1876; Mattes, 1948) and higher levels between 1887 and 1903 (Hough, 1887; Price, 1898; Irland, 1903). Aspen regeneration reached its lowest observed levels across all stands between 1940 and 1955 when elk population estimates were at a peak equalled only by elk estimates in the 1990s. The 1970s show short-term periods of high aspen regeneration, coinciding with elk population estimates that were less variable and remained close to or below the series mean (7748 elk) for three consecutive decades. Aspen regeneration of tree-sized stems (> 2 m) fell again beginning in 1990, coincident with high elk numbers. The chi-squared goodness-of-fit test is consistent with this interpretation (Table 2). For sixteen 5-year bins, fewer aspen regenerated during periods of high elk numbers than expected, although results were only weakly significant ($\chi^2 = 4.777$, $P = 0.092$, $n = 16$).

Aspen regeneration since 1912 appears to be unrelated to observed annual precipitation. Although high precipitation extremes, especially in the 1920s, coincide with decadal periods of aspen regeneration (Fig. 2), in general aspen regeneration does not track precipitation closely. Similarly, the chi-squared analysis of observed PDSI and aspen regeneration indicates that there is no statistical relationship between the two variables ($\chi^2 = 0.102$, $P = 0.95$, $n = 20$; Table 3). Although there may be a relationship between drought and aspen regeneration on annual time-scales, we are not able to infer this from our data because of the 5-year resolution of the aspen recruitment dates.

Long-term fire history, compiled from existing studies (Houston, 1973; Loope & Gruell, 1973), stand ages (Fig. 4) and historical photos (Gruell, 1980a), indicates that fire

Table 2 Chi-squared results for elk (*Cervus elaphus* Erxleben) and aspen (*Populus tremuloides* Michx.), 1914–94. Observed frequency of aspen ramet regeneration was summed over 5-year periods and placed in two classes: 5-year periods where regeneration was below (0) or above (1) the mean for all the 5-year classes. Numbers in parentheses represent range of ramet counts for each class. Three elk classes were defined by finding means of elk population estimates for years that coincided with the 5-year classes of aspen regeneration. The range of the 5-year means was divided into thirds and elk classes assigned based on these thirds (1, 2, 3). Numbers in parentheses represent the range of elk population estimates that fall within that class

Elk population classes (elk)	Aspen frequency classes (no. stems)		
	0 (0–22)	1 (23–69)	All
1 (4800–6815)	2	4	6
Expected	2.6	3.4	6
Standard residual	–0.4	0.3	–
2 (6816–8831)	2	5	7
Expected	3.1	3.9	7
Standard residual	–0.6	0.5	–
3 (8832–10846)	3	0	3
Expected	1.3	1.7	3
Standard residual	1.5	–1.3	–
All	7	9	16
Expected	7	9	16
Standard residual	—	–	–

$$\chi^2 = 4.777, \text{ d.f.} = 2, P\text{-value} = 0.09, n = 16.$$

PDSI classes	Aspen frequency classes (no. stems)		
	0 (0–22)	1 (23–69)	All
1 (–2.59 to –0.62)	5.0	2.0	7.0
Expected	4.9	2.1	7.0
Standard residual	0.5	–0.1	–
2 (–0.63 to –1.34)	6.0	3.0	9.0
Expected	6.3	2.7	9.0
Standard residual	–0.1	0.2	–
3 (1.35 to 3.31)	3.0	1.0	4.0
Expected	2.8	1.2	4.0
Standard residual	0.1	–0.2	–
All	14.0	6.0	20.0
Expected	14.0	6.0	20.0
Standard residual	–	–	–

$\chi^2 = 0.102$, d.f. = 2, P -value = 0.95, $n = 20$.

frequency was higher during the period between 1840 and 1879 than during the twentieth century when no fires greater than 16 ha are known to have occurred in the study area (Andy Norman, Bridger Teton National Forest, personal communication). Forty percent of the mature aspen stems (Fig. 2) and twenty-one of the twenty-nine dated cohorts (Fig. 4) regenerated during this period. However the absence of a strong pulse of regeneration outside the elk winter range during the 1830s–1890s that is present in the other elk classes (Fig. 3) suggests that this period of frequent fires may have been restricted to the winter range and critical winter range areas.

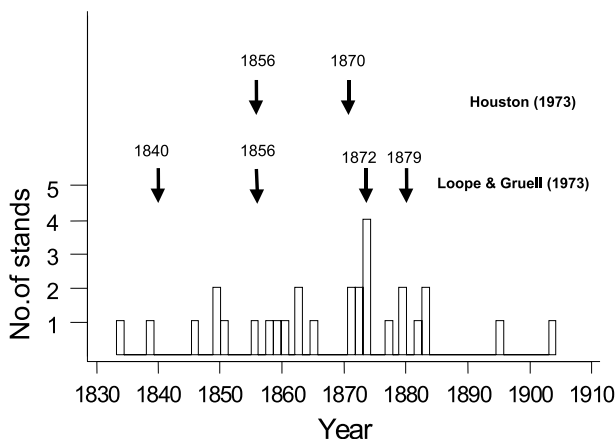


Figure 4 Frequency of aspen (*Populus tremuloides* Michx.) stand ($n = 29$) regeneration dates (bars) compared with regional fire dates (black arrows) derived from fire-scarred conifers (Houston 1973; Loope and Gruell 1973). Only large fires described by the authors (expected to be synchronous with events in aspen stands) are included.

Table 3 Chi-squared results for instrumental Palmer drought severity index (PDSI) and aspen (*Populus tremuloides* Michx.) 1899–1994. Aspen regeneration frequency was grouped into two classes (as described in the aspen and elk chi-squared analysis Table 3). PDSI was also averaged for the same 5-year periods and grouped into three equal classes (1, 2, 3) based on the range of values between 1834 and 1994. The range of values for each category is shown in parentheses

Recent patterns of aspen regeneration

Sucker density varies across all plots ranging from 0 to 62,000 stems ha^{-1} . However, twenty-eight of thirty plots have $< 21,000$ stems ha^{-1} and fourteen plots have < 5000 stems ha^{-1} (Table 4). Prescribed fires had no effect on sucker density 5–15 years following fire ($P = 0.921$; Table 4). The plot with the highest sucker density was located in the National Elk Refuge and had no history of recent fire (Bruce Smith, National Elk Refuge, personal communication). Sucker densities were lowest outside the winter range, although this relationship was not significant (Table 4).

Ocular estimates of browse percent at each plot were high (overall mean = 48%) but variable across plots, ranging from no browse evidence on any suckers (plot mean = 0%) to nearly complete browse of all suckers (plot mean = 99.8%) (Table 4). Elk browsing on aspen is variable across the three categories of elk-use, from high browsing on aspen suckers in critical winter range and winter range stands to lower browsing in areas outside the winter range ($P = 0.05$) (Table 4). With the exception of one plot, plots with average browse $< 20\%$ were either outside of the elk winter range (three plots), had evidence of old elk enclosures (two plots), or had extremely high sucker densities (two plots).

In general, sucker height was highly variable between plots (mean = 55 cm, SD = 33 cm), with eighteen of twenty-seven plots having mean sucker height between 25 and 75 cm. Plots that had been burned by prescribed fire had significantly taller suckers than plots with no history of recent fire (Table 4). Only two plots had an average sucker height > 2 SD above the mean and both of these plots were located outside the elk winter range. However, most plots (twenty-four) did not have any suckers > 150 cm tall. Plots with suckers > 150 cm tall had been burned by prescribed fire (three plots), were immediately adjacent to a road (two plots), or had steep slopes (one plot).

Table 4 Summary statistics for measures of aspen (*Populus tremuloides* Michx.) sucker vigor taken in 25 m² plots by burn class (0 = no prescribed burn, 1 = prescribed burn) and elk (*Cervus elaphus* Erxleben) use category (CWR = critical winter range, WIN = winter range, OUT = outside winter range), including: average height of live ('l') suckers (cm), SD, average height of dead ('d') suckers (cm), ocular estimate of percent of photosynthetic material removed through browse, average number of stems per ramet, average density of live suckers, average percent of suckers with no evidence of browse and total number of plots in each category. Statistically significant differences between the burned and unburned stands or between the elk use classes are noted by bold font. Three plots had no suckers and were excluded from this analysis ($n = 27$)

	Height (l)*	SD	Height (d)	SD	Browse %	SD	No. stems	SD	Density (l) ha ⁻¹	SD	% 0 browse	SD	n
Burn	0	41.1*	24.3	33.8	48.7	0.8	1.9	0.8	9755.6	14190.1	0.3	0.3	15
	1	72.6*	35.0	49.4	46.8	0.6	1.8	0.6	10270.0	13050.2	0.2	0.2	12
Elk use	CWR	48.9	26.3	52.4	54.6**	0.7	2.0	0.7	11412.6	16519.9	0.2**	0.3	17
	WIN	53.1	24.0	52.1	51.4**	0.6	1.9	0.6	9800.0	5750.8	0.1**	0.1	6
	OUT	84.3	58.6	43.2	14.1**	0.2	1.3	0.2	4640.0	3119.0	0.6**	0.4	4

* $P = 0.01$, ** $P = 0.05$.

Plots had a range of 1–3.6 branches per ramet and a mean of 1.9 branches per ramet. Plots inside winter range and critical winter range had higher numbers of branches per ramet than plots located outside, but this difference was not significant (Table 4). At one plot, a single ramet contained thirty-five branches from the base (all dead). Although this is an outlier among the sampled stands, sixteen plots had single ramets with more than five branches from the base.

Aspen suckers have regenerated over the last three decades (Fig. 5), although most (83%) of these suckers are < 100 cm tall. Mean sucker age is 5.5 years old (SD = 4.47), however, suckers can persist as short, highly branched shrubs for at least 32 years. Most suckers (88%) regenerated between 1988 and 1997 and most stems greater than 150 cm regenerated during this period, suggesting these might develop into tree-sized stems. In contrast, stems that regenerated before 1988 are shorter, with only five stems over 100 cm tall. Twenty per cent of all sampled suckers were dead, indicating that ramet mortality is high.

DISCUSSION

The role of ungulates in protected ecosystems has been controversial for many decades (Cahalane, 1943; Wright, 1999) and recent discussions of the role of elk in Yellowstone have brought this issue to the forefront of ecological literature (Olmstead, 1987; Romme *et al.*, 1995; Baker *et al.*, 1997; Suzuki *et al.*, 1999; Wright, 1999; Ripple & Larsen, 2000) and national park policy in the United States (National Academies of Science 2002). Aspen forest dynamics have been at the centre of this debate because of the suggested connection between elk browsing and aspen decline. Our study of aspen, elk, fire and drought suggests that (1) high elk populations result in increased browsing and reduced recruitment in aspen, (2) fire is linked with

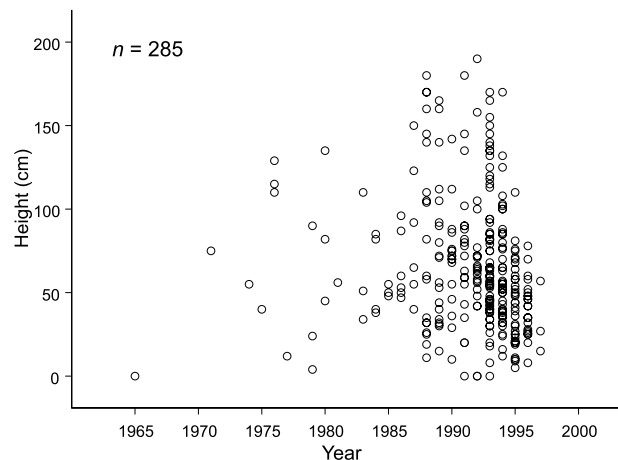


Figure 5 Plot of the height and age of aspen (*Populus tremuloides* Michx.) stems < 200 cm tall that were sampled in twenty-three plots in elk (*Cervus elaphus* Erxleben) winter range and critical winter range. The vertical line at 1997 indicates the last year that stems were sampled.

major episodes of recruitment and stand initiation, although this relationship may be uncoupled in the presence of high elk numbers, and (3) drought plays little if any role in aspen dynamics. However, our observations are both consistent and inconsistent with previous studies of aspen and elk in the western United States. We believe that three factors have led to conflicting or complex results regarding the study of aspen forest dynamics in relation to elk: (1) differing sampling strategies; (2) complex interacting drivers of ecosystem variability and (3) differing land-use histories. Although this discussion is focused on aspen forest ecosystems, many other systems have similar trophic interactions involving complex relationships between ecosystems and management making this discussion relevant to other studies of forest–ungulate interactions.

Sampling strategies

Other studies of aspen in elk winter range report little or no aspen recruitment in the late twentieth century (Romme *et al.*, 1995; Baker *et al.*, 1997; Ripple & Larsen, 2000), but have used a variety of different sampling strategies to estimate aspen ramet regeneration over time. These studies used regression relationships between d.b.h and age (Ripple & Larsen, 2000), dated dominant canopy trees only (Romme *et al.*, 1995), or dated a small sample (two to ten) of trees spread among several size classes (Baker *et al.*, 1997; Ripple & Larsen, 2000). Age and diameter are often only weakly correlated ($R^2 = 0.66$, our data) and regression relations cannot confidently yield annual or even decadal resolution data on regeneration. Including only canopy dominant trees generates age structures biased towards the older age classes and will miss recent regeneration. Dating a subsample of trees in each size class and then applying the oldest date to all trees of the same size class biases age estimates towards older trees and assumes a good relationship between size and age but can mask the presence of additional regeneration events. In this study, we used cross-dated age estimates from all trees over 2-m tall that could be dated in order to represent regeneration of aspen ramets (not cohorts) in 5-year age classes. As a result, we identified periods of aspen ramet regeneration in the twentieth century that may have been missed by other studies.

Complex interacting drivers

Previous studies of aspen regeneration dynamics have suggested that fire history, drought variability, elk browsing, aboriginal overkill of ungulates and predator eradication in the twentieth century may have played a role in creating the current pattern of aspen forest in the Rocky Mountains. Disentangling this long list of potentially interacting variables is challenging, but necessary if aspen dynamics and dynamics of other forest–ungulate systems are to be understood.

Gruell & Loope (1974) suggested that fire suppression led to a lack of aspen ramet regeneration in the area around Jackson Hole during the twentieth century. We agree that in

the absence of elk or when elk populations are low, fire is the major driver controlling aspen ramet regeneration (Fig. 4). However, when elk populations are high, browsing by elk may uncouple the relationship between fire and aspen, limiting the regeneration of tree-sized aspen ramets. In addition, unlike Gruell & Loope (1974), we observed some recent regeneration even in the absence of fire (Table 4), suggesting that fire is only partially limiting. Our results are consistent with those of Romme *et al.* (1995) who observed that aspen regenerated following the Yellowstone fires, but were heavily browsed by elk.

We found no apparent relationship between periods of aspen regeneration and drought conditions (Fig. 2 and Table 3) and agree with Ripple & Larsen (2000) and Baker *et al.* (1997) that drought does not limit aspen ramet regeneration in elk winter range. Our results are inconsistent with those of Romme *et al.* (1995) who suggested that moist periods, more suitable for aspen sucker growth (Einspahr *et al.*, 1972) are associated with aspen regeneration. However, Romme *et al.* worked with decadal-scale tree-ring width data that had an unknown correlation with observed climate data. In addition, moist conditions in the 1830s and the 1910s did not produce episodes of ramet regeneration in Yellowstone, suggesting that other factors may have been more important during these time periods (Romme *et al.*, 1995).

Kay (1994) has argued that both predation by carnivores and hunting by Native Americans limited elk numbers prior to Euro-American settlement. These activities, in combination with Native American burning (Kay, 1995, 1997) may have been associated with increased aspen regeneration through changes in elk populations, browsing patterns and increased opportunities for aspen ramet regeneration following frequent, low-intensity, human-ignited fires. Although this may have been the case in other areas of the west, there is little archaeological evidence to support this argument in the Jackson area. There are no eye-witness accounts of Natives setting fire to vegetation in Jackson Hole (Wright, 1984). In addition, the coincidence of our ramet cohort dates and large fire events recorded by conifers suggests that fires in the 1800s were probably stand-destroying (or nearly so) in aspen rather than low-intensity. Although elk may have been a major part of Native American diet elsewhere, there is little evidence to support this claim in the Jackson Area. Of more than twenty-four archaeological sites excavated in Jackson Hole, covering *c.* 8000 years of human occupation, elk bones were not recovered from any sites, although bison (*Bos bison* Linnaeus), mule deer (*Odocoileus hemionus* Rafinesque), black bear (*Ursus americanus* Pallas) and small mammals were (Wright, 1984, p. 25). In addition, surface surveys show few or no sites of human occupation on elk summer range, where humans and elk would have come into contact (Native Americans used the Jackson area only in late spring, summer and early fall). Given the archaeological evidence to date, it seems unlikely that either Native American hunting or burning had an important influence on aspen forest dynamics in Jackson Hole prior to Euro-American settlement.

Recently, several authors have argued that the eradication of native predators (especially wolves) in the Rocky

Mountains during the nineteenth and twentieth centuries had a major influence on aspen, through top-down trophic effects (Kay, 1998; White *et al.*, 1998; Ripple & Larsen, 2000). According to this argument, prior to predator control, wolf predation on elk, rather than (or in addition to) density-dependent factors, reduced the elk population and modified elk movement thereby altering elk browse on aspen. The history of predator control in Jackson is similar to that of Yellowstone National Park and other regions of the Rocky Mountains, making this explanation likely. Historical documents (Mattes, 1948; DeLacy, 1876) and quantitative analysis of historical accounts (Kay, 1990) suggest that elk sightings in the GYA (including Jackson) were relatively infrequent between 1811 and 1860, indicating that elk populations may have been lower than today, possibly because of the presence of predators. Recent migration of re-introduced wolves from Yellowstone to Jackson Hole may provide an opportunity to test this hypothesis.

Other studies of predator–herbivore interactions in terrestrial ecosystems suggest that the presence and number of predators does influence herbivore populations and may in turn affect grazing patterns and plant populations (Matson & Hunter, 1992; McLaren & Peterson, 1994). On Isle Royale, Michigan, wolves colonized the island in the 1940s, generating a new source of mortality for moose (*Alces alces* L.). Periods of suppressed balsam fir [*Abies balsamea* (L.) Mill.] tree-ring growth coincide with elevated moose densities and depressed wolf numbers, although balsam fir only comprises 59% of winter moose diet (McLaren & Peterson, 1994). In some respects, the behaviour of this system parallels that of the proposed aspen–elk–wolf interactions of the GYA. Like Isle Royale, the aspen system has three trophic levels and the taxa in each level are similar (trees, ungulates, wolves). Unlike the Isle Royale case study, however, the aspen system in the GYA is not geographically isolated, it contains other predators (bears, cougars and humans), and other ungulates (bison, moose and deer). In addition, human influence in Jackson Hole, through predator control, fire exclusion and elk management is nearly ubiquitous, although heterogeneous in time and space, making generalizations about trophic interactions difficult.

Land-use history

The two major factors affecting aspen stand age structures, elk population dynamics and fire history, are associated either directly or indirectly with changes in human land-use during the nineteenth and twentieth centuries. Market hunting of elk in the mid- to late-nineteenth century (Irland, 1903; Woodward, 1904) likely led to a reduction in elk populations and may have altered browsing patterns (Morgantini & Hudson, 1979) during this time period. Fire exclusion in the twentieth century, through both active suppression and domestic livestock grazing of fine fuels, created an almost complete absence of fire and may have reduced opportunities for aspen regeneration. Elk feeding during the twentieth century may have kept elk populations high and affected the distribution and behaviour of elk in the

study area (Sheldon, 1927; Boyce, 1989). Despite a similar history of predator control and trophic interactions, the history of aspen ramet regeneration in Jackson Hole is different from that of Yellowstone and Rocky Mountain National Parks, where, aspen stands in elk winter range are strongly dominated by old stems. This spatial and temporal variation in aspen regeneration and historical land management has several implications for how the results of this study are interpreted.

First, with the exception of a short hunting season in Grand Teton National Park, elk hunting is prohibited in all national parks. In the winter range of the Jackson Hole elk herd, composed of Forest Service and Fish and Wildlife Service lands, elk hunting has been permitted since 1943 (Wilbrecht & Robbins, 1979). In addition to reducing overall elk numbers, the presence of hunters alters the browsing activities of elk (Morgantini & Hudson, 1979). This may explain why our study reports consistent (although low) regeneration throughout the twentieth century whereas other studies of aspen ramet regeneration in national parks have reported an almost complete absence of aspen ramet regeneration since the 1960s and 1970s (Romme *et al.*, 1995; Baker *et al.*, 1997). Suzuki *et al.* (1999) observed a similar pattern of aspen regeneration in elk winter range outside vs. inside Rocky Mountain National Park. It is likely that differences in management, particularly hunting, have produced this pattern in both the Front Range of Colorado and the Jackson area.

Secondly, the Jackson Hole elk herd has been provided with supplemental feed during winter months every year but eight since 1910 (Wilbrecht & Robbins, 1979). In contrast, elk in national parks are not fed, although some animals may migrate to feed grounds outside the park. Elk tend to concentrate at these feeding stations in the winter, and this concentration of animals may reduce browsing pressure on aspen clones that are not immediately adjacent to the feeding stations, although this relationship may not be linear (Barnett & Stohlgren, 2001). One of our critical winter range stands was located within 500 m of a feeding station suggesting that this management activity may have had a strong impact on some sites in this study (Fig. 1).

CONCLUSIONS

The results of our study demonstrate the importance of comparative historical and spatial analysis (Bürgi *et al.*, 2000; Bürgi & Russell, 2001) for understanding both ecological relationships and human–environment relations. Human activities, such as the elimination of predators, fire suppression, ungulate feeding and hunting have likely reduced variability in ecosystem processes (for example, in fire-history and elk-browsing patterns), have indirectly altered aspen-regeneration patterns, and have potentially uncoupled complex relationships between wolves, elk, aspen and fire. These influences have created a landscape with a complex history of human impact that can only be understood through comparative analysis. In the Jackson area, elk populations, in the absence of predators, feed

heavily on aspen and are probably capable of preventing recruitment of tree-sized aspen stems. Recent prescribed fire in the presence of consistently high elk numbers does not produce aspen recruitment the way large fires probably did in the nineteenth century. However, elk feeding and hunting in the Jackson area may create opportunities for some aspen suckers to reach tree height by reducing elk pressure away from feed grounds. In national parks, where elk feeding and hunting have not directly influenced elk populations, studies have reported an almost complete absence of tree-sized aspen ramet recruitment since the late 1960s (Baker *et al.*, 1997; Romme *et al.*, 1997; Ripple & Larsen, 2000). Although this may in part be a result of sampling design, differing land-use histories likely play a significant role.

Identifying the connections between historical land uses and their associated ecological consequences represent the value of generating pseudo-experiments from historical human activities. By integrating history and ecology, retrospective studies explore the many factors that conditioned ecosystem structure, function and composition in the past, and suggest which of the factors may be important in the future (Foster, 2000). Small and/or unequally balanced sample sizes, difficulty in controlling for particular variables in space or time, and little quantitative data are just a few of the many shortcomings of this type of analysis. However, the historical record is a potentially rich data set of landscape level manipulations that cannot be performed on modern ecosystems but provide critical ecological information for both theory and management.

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