Aspen age structure in the northern Yellowstone ecosystem: USA

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Abstract

Age-structure analysis of aspen (*Populus tremuloides*) was conducted on Rocky Mountain elk (*Cervus elaphus*) winter range in the northern Yellowstone area by collecting increment cores from aspen trees in Yellowstone National Park, the Gallatin National Forest, and the Sunlight/Crandall area of the Shoshone National Forest. Our goal was to compare aspen age structure for elk winter range in the park with age structures developed for elk winter range in the national forests. We collected increment cores from aspen in three diameter size classes and three aspen habitat types (xeric, mesic, and scree). A special effort was made to collect increment cores from the relatively rare scree habitat type, since scree forms a ''natural exclosure'' where browsing pressure on aspen is reduced. The age structure of aspen in Yellowstone was significantly different from the age structures of aspen in either of the national forest areas ($P < 0.001$). The Gallatin and Sunlight/Crandall age structures were not significantly different ($P = 0.288$). Only 6% of aspen stands in Yellowstone contained stems that originated from 1920 to 1989, while 87 and 84% of the stands in the Gallatin and Sunlight/Crandall areas, respectively, contained stems from that period. Within Yellowstone, the age structure of aspen in the scree habitat type differed significantly from the mesic and xeric sites that were available for browsing ($P < 0.001$). Aspen stems originating after 1920 dominated the scree stands, while trees originating between 1870 and 1920 dominated the non-scree stands. Aspen stands have successfully recruited new stems into their overstories in all habitat types from 1880 to 1989 in elk winter range on national forest areas surrounding the park. Within the park, aspen stands recruited new overstory stems between 1860 and 1929 in all habitat types. Since 1930, Yellowstone aspen have recruited overstory stems mostly in scree habitat type stands and other areas of reduced browsing pressure. We concluded that changes in ungulate browsing patterns due to differences in predation risk best explain the spatial and temporal pattern observed.

1. Introduction

Since the 1920s, researchers on the northern winter range of Rocky Mountain elk (*Cervus elaphus*) in Yellowstone National Park have documented the failure of existing aspen (*Populus tremuloides*) clones to regenerate replacement overstory stems (Warren, 1926; Rush, 1932; Grimm, 1939; Barmore, 1965; Kay, 1990; Romme et al., 1995; Houston, 1982; Meagher and Houston, 1998). The decline of overstory aspen is of concern because it is a unique and important species in the park and throughout the greater Yellowstone ecosystem, which includes portions of the states of Idaho, Montana, and Wyoming in the western USA.

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Aspen is one of the few upland deciduous tree species present in the ecosystem, and it ranks among the highest cover types for aboveground net primary productivity in the area (Hansen et al., 2000). Aspen forests are important for biodiversity; they support a greater variety of plant associations, as well as greater bird species richness and total abundance, than do the surrounding conifer forests (Winternitz, 1980; Turchi et al., 1995; Dieni and Anderson, 1997).

Aspen reproduces principally by vegetative means, where ramets develop from clones thought to be thousands of years old (Barnes, 1966; Mitton and Grant, 1996). Successful aspen reproduction from seed is infrequent, so the maintenance of these existing, self-regenerating clones is critical to the continued presence of aspen in Yellowstone National Park and in other western landscapes (Barnes, 1966; Jelinski and Cheliak, 1992; Mitton and Grant, 1996).

The northern range is located in the valleys of the Yellowstone, Lamar, and Gardiner Rivers. The boundary designation for Yellowstone National Park splits the northern elk winter range in two, with a portion of it inside the park and a portion of it outside, in what is now a mixture of private land and the Gallatin National Forest. On the northern range in Yellowstone National Park, there has been much debate over the possible reasons why aspen has failed to regenerate its overstory throughout most of the 20th century. Even so, researchers agree that there has been little aspen overstory recruitment in Yellowstone National Park since 1920, and that the areal coverage of overstory aspen has declined. Houston (1982) estimated a decline of 40–60% in the park's aspen canopy coverage during the 20th century. Kay and Wagner (1996) estimated the loss at 95% since 1872, when Yellowstone National Park was established.

From the early- to mid-1900s, scientists attributed the decline of aspen to overbrowsing by ungulates, especially elk (Skinner, 1928; Rush, 1932; Grimm, 1939; Barmore, 1965). Since the 1970s, however, several alternative hypotheses have been proposed. These include the lengthening of the interval between fires (Houston, 1973; Singer et al., 1998), a trend toward a warmer, drier climatic regime (Meagher and Houston, 1998; Singer et al., 1998), the removal of native American environmental influences, including the deliberate setting of fires and overexploitation of elk populations (Kay, 1994, 1998), and the

alteration of trophic cascades relationships among predators, elk, and aspen (Ripple and Larsen, 2000; Larsen and Ripple, 2001; Ripple et al., 2001). Some authors have proposed that an interaction of several factors may best explain the failure of aspen to regenerate overstory stems during the 20th century (Romme et al., 1995; Meagher and Houston, 1998; Yellowstone National Park, 1997).

In a comprehensive study of aspen on Yellowstone National Park's northern range, Ripple and Larsen (2000) concluded that the current aspen overstory originated primarily between 1860 and 1930, with essentially no overstory regeneration since then on sites available to ungulate browsing. Romme et al. (1995) developed the only other published aspen age structure for the northern range in Yellowstone National Park, sampling only canopy-dominant trees and concluding that the current cohort of large aspen stems originated mostly in the 1870s and 1880s. Warren (1926) collected 31 aspen increment cores from a restricted geographic area (near the park's Camp Roosevelt) in 1921–1922, dating their origin to the 1870s and 1880s. However, his objective in collecting these cores was to establish an age-diameter growth relationship, not to provide a comprehensive age-structure analysis of aspen on the northern range. Increment cores have also been used to develop aspen stand age structures in the southern portion of the greater Yellowstone ecosystem (Krebill, 1972; Gruell and Loope, 1974; Hessl, 2000).

Most of the aspen research on the northern range has focused on conditions within Yellowstone; the status of aspen on the northern range in the Gallatin National Forest has not been as intensively studied. Kay (1990) conducted a limited aspen age-structure comparison between Yellowstone National Park and the Eagle Creek area of the Gallatin, and found younger aspen stems in the national forest than in the park. St. John (1995) conducted a study of ungulate impacts on aspen on the Gallatin's portion of the northern range, concluding that current levels of ungulate (cattle and elk) use have resulted in the deterioration of aspen clones.

East of Yellowstone, aspen occur in the Sunlight/Crandall elk wintering area of the Shoshone National Forest. Although there are no published studies dedicated to the status of aspen in the Sunlight/Crandall area, Hyde and Beetle (1964) noted that aspen ramets

in this area were heavily browsed and overstory stems had been high-lined by elk during the early 1960s. Internal Forest Service documents also indicate that several Sunlight/Crandall area aspen stands had been cut or burned in 1980–1981, in an attempt to stimulate ramet production in decadent aspen stands (King, personal communication, 1999).

Yellowstone National Park was established in 1872 as the world's first national park. From 1872 to 1886, great reductions in wildlife populations occurred throughout the Yellowstone area during the "market-hunting era", when large animals were shots for their hides and their carcasses poisoned to eliminate predators such as the gray wolf (*Canis lupus*) (Schullery and Whittlesey, 1992). In terms of its effect on aspen, the market-hunting era is thought to have reduced browsing pressure enough to allow a large cohort of aspen overstory stems to be established on the elk's northern range (Romme et al., 1995; Meagher and Houston, 1998). Elk and other wildlife populations gradually increased, however, as the market-hunting era closed. Yellowstone park management and land-use practices increasingly diverged from non-park areas over time. Hunting was banned within the park in 1883, but remained legal outside park boundaries, including a late-season hunt conducted during the month of January (Haines, 1977). Domestic livestock grazing practices also diverged inside and outside of park boundaries. Limited stock grazing was allowed within the borders of Yellowstone National Park during the early years after establishment, but discontinued over time (Haines, 1977). Outside park boundaries, stock grazing became the dominant use for rangelands (Rush, 1932). In the late 1800s, the federal government began to set aside certain areas outside Yellowstone National Park as "forest reserves", which were also available for grazing. Shoshone National Forest was established east of the park in 1891, becoming the first national forest in the United States. To the north of Yellowstone Park, the Gallatin National Forest was established in 1899. By 1926, as the need for additional elk winter range was recognized, remaining federal lands on the northern range in the Gallatin National Forest were withdrawn from further human settlement and cattle grazing was reduced (Rush, 1932). During the second-half of the 20th century, additional lands in the Gallatin National Forest have been removed from

cattle grazing and are now managed as elk winter range (Lemke et al., 1998).

The goal of this study was to use aspen increment cores to develop and compare aspen age structures for elk winter ranges inside and outside of Yellowstone National Park. The specific objectives of this study were to determine whether there were significant differences in aspen age structure between the portion of the northern range that lies in Yellowstone National Park and that of the Gallatin National Forest, and between the park's northern range and the elk winter range in the Sunlight/Crandall areas of the Shoshone National Forest. We also sought to interpret any differences in aspen age structures in terms of ecological and/or anthropogenic processes.

2. Study areas

We selected two areas of elk winter range in close proximity to Yellowstone National Park's northern range and compared their aspen age structures with those from within the park. These two areas were the northern range in the Gallatin National Forest and the Sunlight/Crandall elk winter range in the Shoshone National Forest (Fig. 1). The northern range is the wintering area for the largest elk herd in the greater Yellowstone ecosystem. The landscape consists of steppe, with islands of Douglas fir (*Pseudotsuga menziesii*) and aspen intermixed, and with more continuous conifer forests of Douglas fir, Engelmann spruce (*Picea engelmannii*), and Lodgepole pine (*Pinus contorta*) above 2000 m. The northern range occupies an area of approximately 153,000 ha, with approximately 65% within Yellowstone National Park and 35% outside the park in a mixture of private and Gallatin National Forest lands (Lemke et al., 1998). Livestock grazing allotments occur on some portions of the Gallatin National Forest considered in this study. Private lands within the National Forest boundaries were not included.

The portion of the Shoshone National Forest included in this study was the Sunlight and Crandall Creek basins, both of which are tributaries of the Clarks Fork of the Yellowstone River. The boundaries of the Sunlight/Crandall study area correspond to the critical elk winter range boundary established by the Wyoming Department of Game and Fish. Private lands
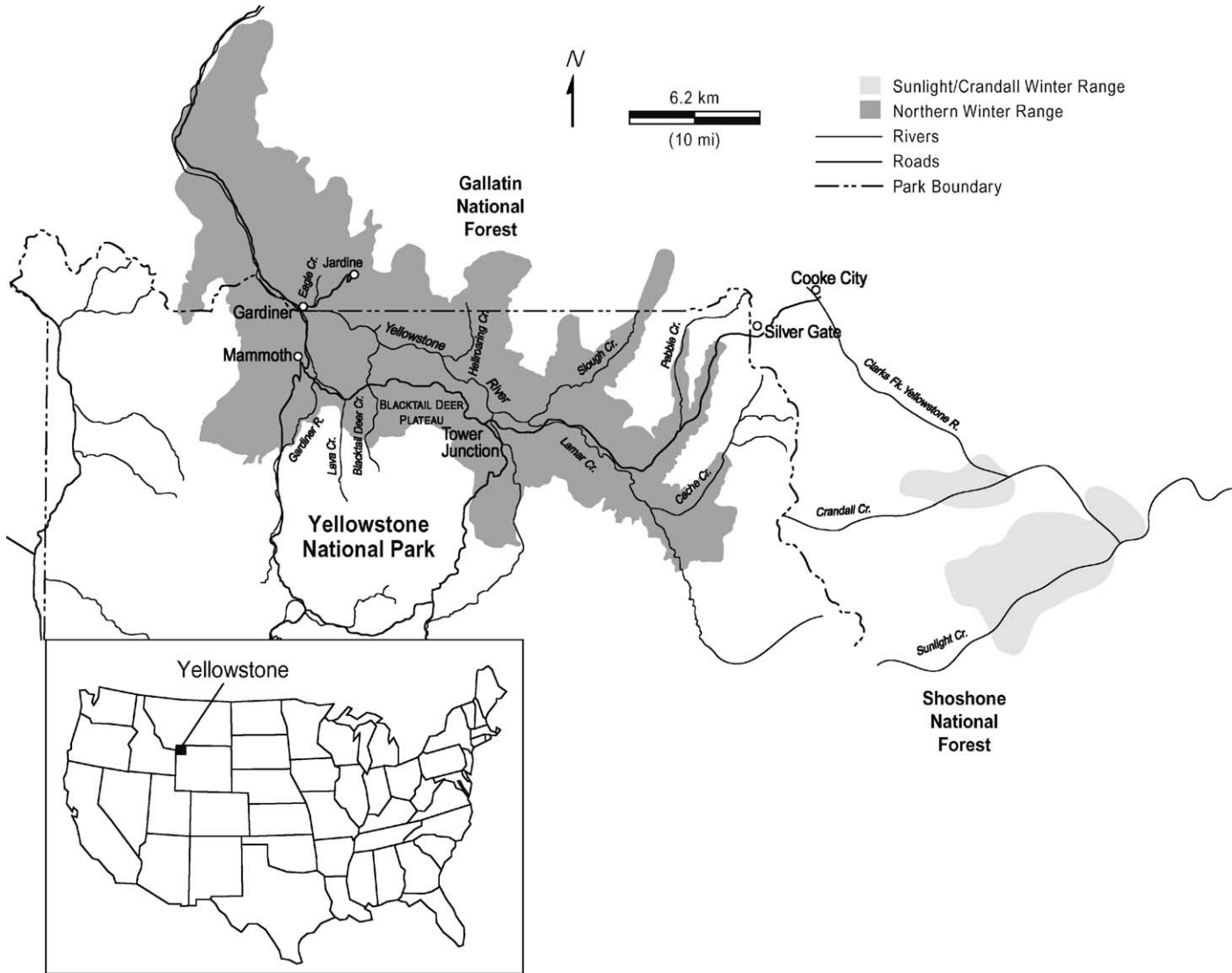
Fig. 1. Study area map showing the elk winter ranges considered in this study. Yellowstone National Park and the Gallatin National Forest each administer a portion of the northern range. The Sunlight/Crandall elk winter range is east of the park and is part of the Shoshone National Forest.

were eliminated from consideration, but livestock grazing allotments exist on portions of the national forest land. Aspen occurs in small patches within a steppe matrix in this area, similar to its landscape pattern on the northern range.

The climate of the study area is characterized by cold winters and short, cool summers. Aspen occur in areas of the western US that receive at least 38 cm of precipitation annually (Jones and DeByle, 1985) and the northern Yellowstone area is near this lower limit. On the park portion of the northern range, Mammoth Hot Springs averages 39 cm per year, while Tower (elevation = 1910 m) averages 43 cm per year (Western Regional Climate Center, 2000). Aspen stands on the Gallatin's portion of the northern range are within the same elevational range as are those in the park, and receive comparable amounts of precipitation, since precipitation is strongly correlated with elevation in this mountainous region (Dirks and Martner, 1982). At the Crandall Creek weather station (elevation = 1968 m), annual precipitation averages 37 cm (Western Regional Climate Center, 2000).

3. Methods

In Yellowstone National Park and the Sunlight/ Crandall basins, a set of color infrared (CIR) aerial photographs was used to inventory existing aspen stands and select a random sample. These photographs were taken in September 1988 at a scale of 1:24,000. CIR photography was used because of the simplicity with which aspen (white crowns in the late fall CIR photographs) could be differentiated from conifers (red crowns in CIR). All aerial photograph interpretation was done with a scanning stereoscope, and sufficient detail was present in the CIR photographs to discern individual aspen crowns in poorly stocked stands. A 1.0 cm × 1.5 cm (240 m × 360 m ground dimensions) rectangular grid was placed on each aerial photograph, and each cell was identified as either containing or not containing aspen. The sample was then stratified to include only those grid cells containing aspen. From the stratified sample, a random selection was made of 100 grid cells in Yellowstone National Park and 55 cells from the Sunlight/ Crandall basins. These cells comprised of the sample for collecting the increment cores.

The 1988 CIR flight did not provide complete coverage in the Gallatin portion of the northern range. Therefore, a 1995 set of 1:24,000 scale natural-color aerial photographs was used to inventory aspen in the Gallatin. Grids were placed over the aerial photographs and an aspen inventory was conducted using the same methods as described for Yellowstone National Park and the Sunlight/Crandall basins. A random sample of 75 cells containing aspen was chosen from the Gallatin National Forest inventory.

In the field, aspen increment cores were collected in one randomly selected aspen stand lying within each chosen grid cell. To capture the range of aspen ages within the stands, we attempted to obtain two cores from each of three diameter-at-breast-height (DBH) classes: 5–9, 10–19, and >20 cm DBH. We cored a maximum of nine trees in each stand, since cores cannot be collected from many large diameter aspen due to heart rots. Cores were drilled at a height of 1 m above the ground, and the calculated ages were not adjusted for coring height. The elevation, aspect, and slope were recorded for each sampled stand.

After drying, the cores were mounted on wooden trays and the annual growth rings were counted using a dissecting microscope and standard dendrochronological procedures (Stokes and Smiley, 1968). We determined the aspen ages by counting the growth rings of each increment core twice and taking the mean. A blind recount was then conducted on cores from the park to derive an error estimate. The recount resulted in a mean difference of 4.1 years (S.E. = 0.53, $n = 91$) between estimated ages. We collected two increment cores from several trees ($n = 14$) to derive another estimate of accuracy for our aspen ages. The mean age difference between these pairs of cores taken from the same tree was 3.6 years (S.E. = 0.24). Cross dating was attempted, but was not successful due to the complacency in the ring widths. The distributions of aspen ages were skewed, so we used the Kruskal–Wallis (KW) test to compare median ages and the Kolmogorov–Smirnov (KS) test to determine whether the age distributions differed among the three study areas (Ramsey and Schafer, 1997).

To further assess the temporal pattern of aspen origination dates, we calculated the percentage of stands containing stems that originated in four time periods, reflecting different eras in the history of the Yellowstone area. The pre-1870 period represents the

era before the establishment of Yellowstone National Park. The 1870–1899 era encompassed the market-hunting era and the early years of the park. From 1900 to 1919, ungulate populations were completely protected, while significant predator eradication efforts were undertaken. The period from 1920 to 1998 represents the current era of low levels of aspen overstory recruitment on the park's northern range. To assess the influence of site on overstory recruitment, we calculated the percentage of stands in each habitat type that contained aspen stems originating in each of the four time periods.

Three generalized habitat types were used to describe possible differences in aspen growth due to site quality (Despain, 1990; St. John, 1995). The habitat types were delineated by understory vegetation, site wetness, and topography in the following manner.

1. Xeric sites

   The understory of these aspen stands included grasses, such as Idaho fescue (*Festuca idahoensis*), bluebunch wheatgrass (*Agropyron spicatum*), bearded wheatgrass (*Agropyron caninum*), and the forb yarrow (*Achillea millefolium*). These stands often included or were surrounded by big sagebrush (*Artemisia tridentata*). The soils of this habitat type were derived from andesite and sedimentary tills and were generally dry.

2. Mesic sites

   This aspen habitat type contained sites with moist to saturated soil conditions, including mid-slope benches, riparian areas, and wet meadows. A mixture of grasses and tall forbs characterized this habitat type. Timothy (*Phleum pratense*) was a dominant grass type in the understory of these stands, with Idaho fescue and bearded wheatgrass also present. Forbs included yarrow and goldenrod (*Solidago missouriensis*). Aspen stands in wet meadows and riparian areas also included various types of sedges (*Carex* spp.) mixed with timothy and forbs.

3. Scree stands

   An aspen community growing on scree slopes characterized these sites. The understory was typified by sparse vegetation and thin soils in a rock substrate (St. John, 1995). Xeric conditions predominated in scree aspen stands.

In addition to our random sample, we collected increment cores in all aspen stands of the scree habitat type that were encountered during the course of the field work in Yellowstone National Park. These scree stands are a relatively rare habitat type and were valuable for comparative purposes, since the scree forms a "natural exclosure" where ungulate browsing levels were typically low. The KS test was used to determine whether the distribution of aspen ages in Yellowstone National Park was different in the scree habitat type than in the non-scree mesic and xeric habitat type stands.

Climatic variation was inferred from two dendroclimate indices prepared by Stockton (1973). For the northern range in both Yellowstone National Park and the Gallatin, the Gardiner dendroclimate index was used (Stockton, 1973). For the Sunlight/Crandall area, the Dead Indian Hill dendroclimate index was used (Stockton, 1973). Poisson log regression (Ramsey and Schafer, 1997) was used to analyze the relationship between 5-year averages for the dendroclimatic indices (independent variable) and aspen origination dates (dependent variable). The purpose of this analysis was to test whether climatic fluctuations (as measured by the dendroclimate indices) were related to the incidence of aspen origination. Five-year averages were developed from the dendroclimate indices and regressed against the sum total of aspen originating during these same 5-year periods. The regression was conducted separately for each of the three areas. Precipitation data from Mammoth Hot Springs and Tower within the park were also compared with aspen origination dates using Poisson log regression.

4. Results

Of the 210 aspen stands sampled, 180 stands yielded increment cores that could have origin dates assigned to them. Of the 30 stands in which usable cores could not be obtained, 27 were in Yellowstone National Park, and three were in the Sunlight/Crandall basins. In total, 598 increment cores were successfully dated. Ripple and Larsen (2000) published the results from the portion of the northern range in Yellowstone National Park, where 98 cores were dated from 57 aspen stands. In the Gallatin National Forest, 273 cores were dated from 63 stands and in the Sunlight/Crandall basins, 189 cores

were dated from 51 aspen stands. An additional 38 increment cores were obtained from nine scree habitat type stands in Yellowstone Park.

The aspen age structures (in 10-year periods) derived from the increment cores are shown in Fig. 2. The age distribution of aspen (non-scree habitat types) on the park's northern range is shown in Fig. 2a. Ninety-five percent of the cores collected in Yellowstone National Park originated before 1920; the peak 10-year period of aspen stem origination was from 1880 to 1889. The temporal pattern of aspen origination was more continuous on the Gallatin's portion of the northern range, with aspen origination dates in every 10-year period from 1860 to 1989 (Fig. 2b). The Sunlight/Crandall basins also exhibited a continuous pattern of aspen origination, with stems originating during every 10-year period between 1880 and 1989 (Fig. 2c). We did not collect increment cores for any trees <5 cm DBH, so the period 1990–1998 was not represented in our graphs.

The mean and median ages of aspen stems in the three areas are compared in Table 1. The median aspen age was significantly higher in Yellowstone than in the Gallatin or Sunlight (KW $P < 0.001$) areas. The median ages were not different when comparing the Gallatin and Sunlight/Crandall study areas (KW $P = 0.788$). The distribution of aspen ages in the park was also significantly different from either of the national forest areas (KS $P < 0.001$). However, the age distributions in the Gallatin and Sunlight/Crandall areas were not significantly different (KS $P = 0.288$).

Table 1
A comparison of aspen ages on selected elk winter ranges in the northern portion of the greater Yellowstone ecosystem

Study area	n	Mean aspen age	S.E. aspen age	Median aspen age
Yellowstone	98	106.1	3.0	107.0
Gallatin	273	64.3	1.8	66.5
Sunlight/Crandall	187	64.4	2.2	64.3

We also analyzed aspen stem origination at the stand level over four time periods (pre-1870, 1870–1899, 1900–1919, 1920–1998). The percentage of stands with stems originating in these periods is shown in Table 2. When comparing stands in the park to those in the national forests, we found the largest differences in the period from 1920 to 1998. In Yellowstone, only 6% of aspen stands contained stems originating between 1920 and 1998, while the percentages in the Gallatin and Sunlight/Crandall areas were 87 and 84%, respectively (Table 2). We also stratified our samples by habitat type to analyze whether mesic or xeric type stands differed in their ability to produce overstory stems. At the stand level, we did not find a consistent pattern of aspen overstory recruitment success based on habitat type.

Within Yellowstone, we collected 38 increment cores from nine scree habitat type aspen stands. The age distributions of these aspen are given in Fig. 2d. The KS test was used to compare the age

Table 2
The percentage of aspen stands with stems originating in four time periods from 1870 to 1989

Study area	Aspen stands sampled	n	Percentage of aspen stands with stems originating by period			
			Pre-1870	1870–1899	1900–1919	1920–1998
Yellowstone	All	57	13	83	38	6
Gallatin	All	63	5	51	32	87
Sunlight/Crandall	All	51	2	27	39	84
Yellowstone	Mesic habitat type	29	11	79	36	4
	Xeric habitat type	25	16	88	40	8
Gallatin	Mesic habitat type	34	0	50	21	88
	Xeric habitat type	29	10	52	45	86
Sunlight/Crandall	Mesic habitat type	29	0	41	48	72
	Xeric habitat type	22	5	9	27	100

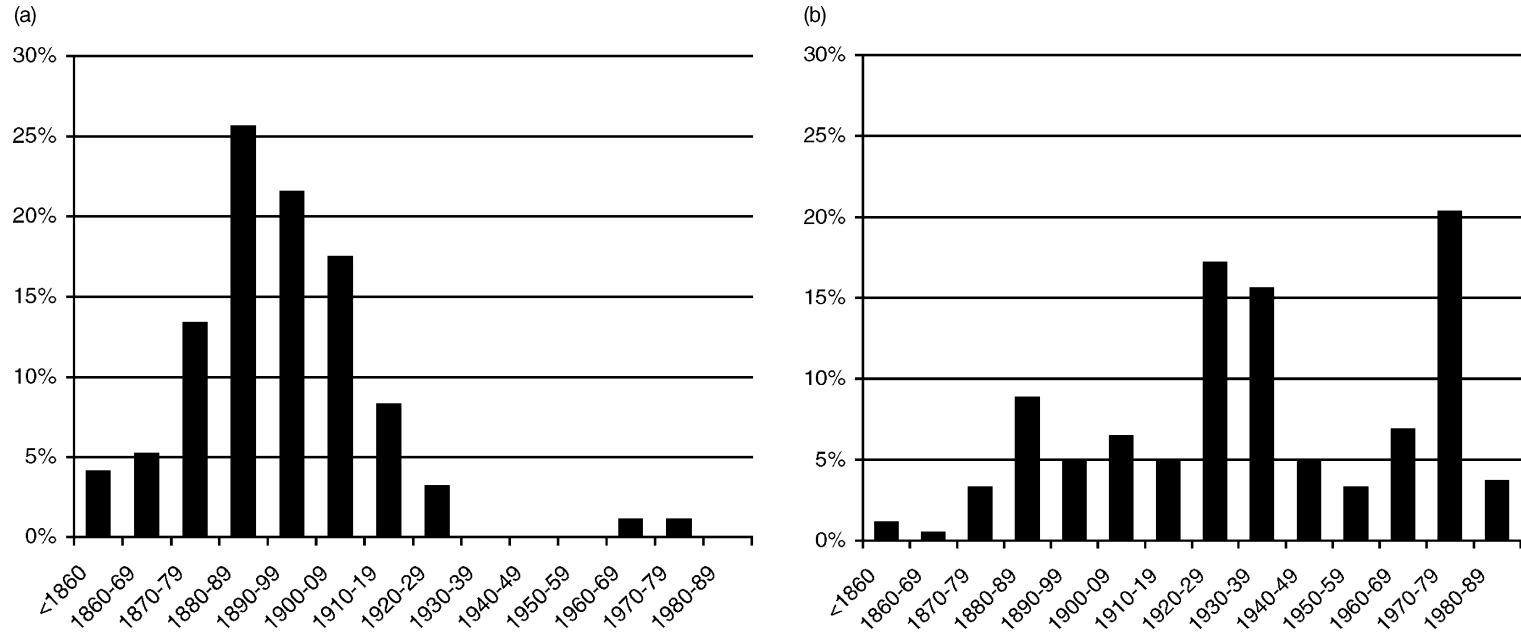Since aspen stands may have multiple age classes, the percentages add up to more than 100%.

(a)

(b)

Fig. 2. The percentage of 1998 aspen overstory stems established during 10-year periods on elk winter range in (a) Yellowstone National Park non-scree habitat type aspen stands ($n = 98$, from 57 stands); (b) the Gallatin National Forest ($n = 273$, from 63 stands); (c) the Sunlight/Crandall area of the Shoshone National Forest ($n = 189$, from 51 stands); and (d) the scree habitat type in Yellowstone National Park ($n = 38$, from 9 stands).
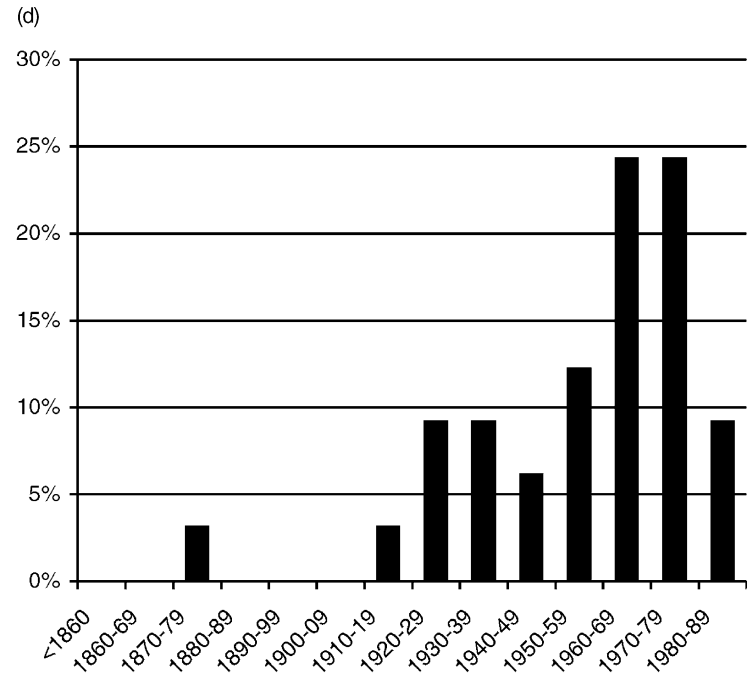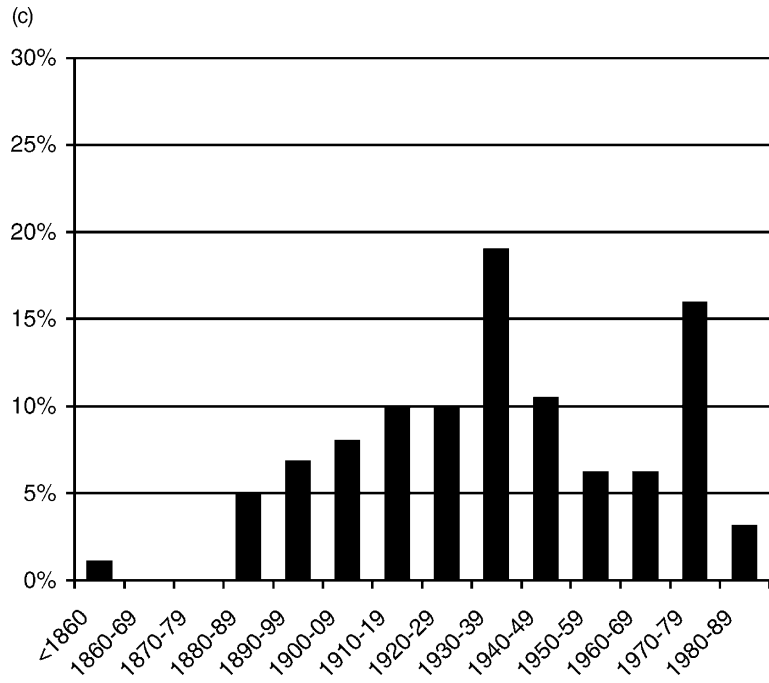
(c)

(d)

Fig. 2. (*Continued*).

distributions of scree aspen stands with non-scree xeric and mesic stands in the park. The age distributions of the aspen in the scree stands differed significantly from those of the non-scree stands, with the age distributions in the scree stands containing trees that originated mostly after 1920 ($P < 0.001$).

Using Poisson log regression, we found no significant relationship between aspen origination and climatic fluctuations, as measured by the dendroclimate indices (Yellowstone, $P = 0.369$; Gallatin, $P = 0.400$; Sunlight/Crandall, $P = 0.195$). Poisson log regression was also used to test the relationship between 5-year averages of precipitation and aspen origination on the northern range. We did not find a significant relationship between precipitation fluctuations and aspen origination on the northern range, either in Yellowstone or in the Gallatin ($P > 0.512$).

5. Discussion

Aspen stands outside Yellowstone National Park differed in several important respects from those inside. Aspen in the Gallatin and the Sunlight/Crandall basins exhibited a more continuous pattern of overstory recruitment than did those in Yellowstone, especially for the period of 1920–1989 (Fig. 2). In the Gallatin and Sunlight/Crandall areas, we documented aspen overstory recruitment success during every 10-year period from 1880 to 1989. In contrast, aspen overstory recruitment essentially ceased on the Yellowstone portion of the northern range after the 1920s, except in scree habitat types (Fig. 2d) and other areas protected from ungulate browsing such as fenced exclosures. In Yellowstone, only 6% of the randomly selected stands contained overstory stems that originated between 1920 and 1989; in the Gallatin the percentage was 87%, and in the Sunlight/Crandall basins it was 84% (Table 2). Suzuki et al. (1998) found a similar pattern in Rocky Mountain National Park, Colorado, and in the surrounding Roosevelt National Forest. They studied aspen stands on elk winter range inside and outside of park boundaries and concluded that higher percentages of aspen stands were regenerating in the National Forest than in Rocky Mountain Park.

Using 5-year averages, we did not find a significant relationship between precipitation levels in the park

(measured at Mammoth Hot Springs) and aspen origination dates on the northern range. Similarly, there was not a significant relationship between the dendroclimate indices and aspen origination dates on any of the elk winter range areas we considered. In the Gros Ventre Valley south of Yellowstone National Park, Hessl (2000) also concluded that there appeared to be only a weak relationship between aspen origination and a local (Uhl Hill) dendroclimate index. Baker et al. (1997) concluded that the temporal pattern of aspen origination corresponded weakly, or not at all, with climatic and hydrologic variables in a study conducted on elk winter range in Colorado's Rocky Mountain National Park.

Aspen can tolerate severe cold, but may not tolerate arid or semiarid conditions well (Jones et al., 1985); thus, trends toward a more arid climate have been proposed as an explanation for aspen decline on the northern range (Houston, 1982; Yellowstone National Park, 1997; Singer et al., 1998). At the stand level, the spatial pattern we observed was not consistent with a lack of moisture being a significant variable in predicting aspen overstory recruitment success. If moisture stress were affecting aspen recruitment, we would expect that mesic sites such as riparian areas or wet meadows would produce greater numbers of overstory stems over time. In Yellowstone National Park, we observed the opposite, where the greatest recruitment success occurred in the scree habitat type, which are xeric sites with thin, rocky soils (Fig. 2a and d). On the national forest areas surrounding the park, we found that aspen successfully recruited overstory stems on both mesic and xeric habitat types (Table 2). Based on our observations, we conclude that habitat type and the climatic variation expressed in the dendroclimate indices and annual precipitation cannot explain the pattern of aspen overstory recruitment in the winter ranges we studied.

Houston (1973) estimated a historic fire interval of 20–25 years on the northern range, an interval that has been altered by fire-suppression efforts begun by European–Americans in the late 1800s. Fire can stimulate high levels of ramet production in aspen clones for 1–3 years afterward, with mean densities of 38,000 ramets/ha recorded on the northern range after the 1988 fires (Romme et al., 1995). However, the 1988 fires have not led to a cohort of aspen reaching tree size on the Yellowstone National Park portion of the

northern range (Romme et al., 1995). On the Gallatin's portion of the northern range, the best 20th-century periods of aspen overstory recruitment (1920–1929, 1930–1939, 1970–1979, Fig. 2b) were not associated with major fires (Houston, 1973, 1982).

In the Sunlight/Crandall area, there were at least two major fires in the 20th century: the 1935 Crandall/ Closed Creek fire and the 1988 Willow Mist fire (Dawson, personal communication, 2001). In the Crandall Basin, 28% (11 of 39 cores) of the sampled aspen originated between 1935 and 1939, and this cohort of aspen may be the result of the 1935 Crandall fire. However, there are very little data available on elk populations in the Sunlight/Crandall area in the 1930s, and browsing levels during this period are unknown. The Wyoming Game and Fish Department estimates that the Clarks Fork elk herd grew from approximately 1800 elk in 1949 to a mean of 5000 for the 1985–1995 period, so the elk population in the Sunlight/Crandall area is likely to have increased since the 1930s (Emmerich, unpublished data, 2000). The Willow Mist fire of 1988 burned large areas in the Sunlight Basin, but did not burn extensively in areas occupied by aspen, and our data do not show a large cohort of aspen developing from this fire. Fire also would appear to be unrelated to the large cohort of aspen we dated to the 1970–1979 period, since no large fires occurred in the Sunlight/Crandall basins during that decade (Dawson, personal communication, 2001). Our data were substantially in agreement with other studies that have concluded that aspen can recruit new overstory stems in the absence of wildfire (Kay, 1990; Baker et al., 1997; Suzuki et al., 1998; Hessl, 2000).

The pattern of successful recruitment of new overstory aspen stems in Yellowstone National Park changed during the 1920s (Fig. 2a and d). Prior to 1920, aspen overstory recruitment occurred in all habitat types (Table 2) and Warren (1926) documented a multi-aged aspen overstory along several riparian corridors on the northern range of Yellowstone National Park. Using increment cores and the aspen diameters supplied by Warren (1926), Ripple and Larsen (2000) developed a regression equation predicting that the 1920s-era aspen overstory consisted of trees originating from the mid-to-late 1700s to the 1920s. In addition to the Warren photographs (1926), other compilations of historic photographs also show evidence of several size classes of aspen evident on the

northern range in the late 1800s to early 1900s (Houston, 1982; Kay, 1990; Meagher and Houston, 1998).

Between 1920 and 1998, the aspen stands on the park's northern range that were most successful in recruiting new overstory stems were located in scree habitat types, fenced exclosures, and jackstraw piles (Kay, 1990; Ripple and Larsen, 2001). All of these areas are at least partially protected from browsing; hence, this pattern of aspen overstory recruitment is consistent with the suggestion that ungulate browsing is the major factor limiting aspen growth in Yellowstone National Park. In contrast, our aspen increment cores from the Gallatin and the Sunlight/Crandall elk winter ranges document continuous aspen overstory recruitment in all habitat types between 1920 and 1998, which brings us to a consideration of why aspen outside the park has been more successful at recruiting overstory stems than has aspen within the park boundaries.

Historically, both humans and other mammalian predators pursued elk throughout the area, and there has long been debate over possible changes in elk migration and behavior due to anthropogenic changes on the northern range. Elk have been shown to change their migration patterns and behavior in the presence of predation (Boyce, 1989). Changes to the northern range outside of Yellowstone National Park included European–American settlement, unrestricted grazing of livestock (until 1926), and the establishment of the "firing line" just north of the park border, where hunters would gather and shoot elk immediately after they crossed the boundary (Rush, 1932; Murie, 1947; Haines, 1977). Within the park, 1895–1930 was the era of complete protection of elk, when wolves were eliminated as a source of predation (by 1926), humans were no longer allowed to hunt, and elk populations rose (Houston, 1982; Singer and Mack, 1999). The lack of forage outside Yellowstone National Park due to overgrazing by cattle, coupled with the "firing line" style of hunting, encouraged elk to stay within Yellowstone Park boundaries all winter. We hypothesize that the observed differences in the aspen age structures inside and outside the park have been principally due to predation risk effects affecting the movement, behavior, and browsing patterns of elk. Predation risk effects describe a trade-off in foraging strategy, where elk may avoid certain areas to reduce their chances of being killed by human or animal predators (Lima and

Dill, 1990; Schmitz et al., 1997). Historically, predators may have affected elk behavior and movement sufficiently to allow for regeneration of aspen overstories at sites with high levels of predation risk. Outside the park, lower elk densities along with foraging strategies influenced by the risk of predation may have led to different browsing patterns, resulting in increased aspen overstory recruitment in the Gallatin and Sunlight/Crandall elk winter ranges.

After 1930, the ''direct reduction'' (killing and live-trapping) program of elk management began in Yellowstone National Park (Singer and Mack, 1999). The failure of aspen to recruit overstory stems within the park during this period (1930–1968) has long puzzled scientists. Craighead et al. (1972) and Houston (1982) studied the effects of direct reduction on elk distributions and both concluded that this program had disproportionately reduced the migratory segment of the herd. This may help explain why the direct reduction program had little or no effect on aspen overstory recruitment within the park, and may have actually assisted aspen recruitment outside park boundaries by reducing browsing pressure. In the Gallatin National Forest, St. John (1995) concluded that aspen stands <500 m from roads were less impacted by ungulates than were those farther away, suggesting that elk adjusted their foraging behavior to avoid human contact and possible predation. Suzuki et al. (1998) suggested that management strategies to disperse elk might help alleviate local aspen declines in the Rocky Mountain National Park area.

On elk winter ranges in the northern greater Yellowstone ecosystem, aspen have more successfully recruited overstory stems in national forest areas than within the park. However, recent ecological changes may again alter the behavior and browsing patterns of ungulates on the northern and Sunlight/Crandall elk winter ranges. Wolves were reintroduced into Yellowstone National Park in 1995 and may be affecting the differential risk of predation and elk browsing patterns inside and outside park borders (Larsen and Ripple, 2001; Ripple et al., 2001). Cooperative efforts to purchase additional elk winter range north of Yellowstone National Park and within the Gallatin National Forest matrix have also been undertaken in recent years. Between 1976 and 1998, greater numbers of elk have migrated out of the park during the winter months and have more than doubled the area they occupy in the Gallatin National Forest during the winter (Lemke et al., 1998). This increase in the density of elk and the area they occupy on the Gallatin's portion of the northern range may also affect future spatial patterns of browsing and aspen overstory recruitment. Additional research into elk behavioral and browsing patterns in the presence of predators and aspen reproduction at the landscape or ecosystem scale is needed, and is especially urgent in the national forest areas surrounding Yellowstone National Park.

Acknowledgements

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