

Historic aspen recruitment, elk, and wolves in northern Yellowstone National Park, USA

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Abstract

We conducted an analysis of aspen (*Populus tremuloides*) overstory recruitment on the northern range of Yellowstone National Park (YNP) using information provided in a monograph published by Warren (Warren, E.R., 1926. A study of beaver in the Yaney region of Yellowstone National Park, Roosevelt-Wildl. Ann. 1, 1–191), increment cores collected from riparian aspen stands in 1998, and an extensive random sample of aspen increment cores collected over YNP's entire northern range in 1997 and 1998. We summarized aspen size classes reported by Warren and estimated overstory origination dates of the stands he described using a linear regression based on our riparian aspen diameter/age relationship. Applying our regression results to Warren's diameter measurements, we predicted that the stands measured by Warren contained aspen that originated between approximately 1751 and 1920. The random set of aspen increment cores were used to analyze the age distribution of the current aspen overstory on YNP's northern range. These increment core data showed that approximately 10% of the current overstory aspen originated before 1871, 85% between 1871 and 1920, and 5% after 1921. Based upon our analysis of the Warren data and our aspen increment cores, we conclude that successful aspen overstory recruitment occurred on the northern range of YNP from the middle to late 1700's until the 1920's, after which it essentially ceased. Rocky Mountain Elk (*Cervus elaphus*) browsing has been identified as significantly impacting aspen overstory recruitment on YNP's northern range. We hypothesized why elk browsing has a different influence on aspen now than it did historically. We discussed several potential social and ecological factors and hypothesize that a main factor is YNP's loss of significant predator/prey relationships in the early 1900's, especially the influence of gray wolves (*Canis lupus*). We found that aspen overstory recruitment ceased during the same years that wolves, a significant source of elk predation, were removed from YNP. Wolves may positively influence aspen overstory recruitment through a trophic cascades effect by reducing elk populations, modifying elk movement, and changing elk browsing patterns on aspen. © 2000 Elsevier Science Ltd. All rights reserved.

1. Introduction

Yellowstone National Park's (YNP) northern ungulate winter range has seen a steady decline of overstory aspen in this century (Houston, 1982; Despain, 1990; Kay, 1990; Meagher and Houston, 1998). Aspen in YNP reproduces principally by vegetative means, producing suckers from existing clones (Kay, 1993). During winter, elk browse the leaders off the aspen suckers and thereby prevent their escapement to tree height, a

process that has been documented in YNP and elsewhere in the northern Rocky Mountains (Bartos and Mueggler, 1981; Kay, 1993; Romme et al., 1995). Kay (1990) and Wagner et al. (1995) stated that the decline of overstory aspen is due primarily to overbrowsing caused by an overabundance of elk. Singer et al. (1998) suggested that aspen decline might be related to the increase in the aridity of the 20th century climate, leading to suboptimal conditions for aspen overstory recruitment. This warming and drying climatic trend has been hypothesized as possibly influencing aspen's production of certain chemical compounds that discourage grazing of suckers by herbivores (Despain 1990, YNP 1997). Some researchers have hypothesized that

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changes in northern range vegetation, including aspen, may be related to a reduction in the occurrence of natural fires (Houston, 1973; Singer et al., 1998). Conversely, Baker et al. (1997) failed to find any relationship between aspen recruitment and climatic fluctuations or fire suppression in Colorado's Rocky Mountain National Park. Romme et al. (1995) suggested that an interaction of several variables including fire suppression, climatic variation, elk abundance and a lack of mammalian predators may account for the failure of aspen to reach tree height in this century. Kay (1994, 1998) suggested that elk were much rarer in the YNP area during pre-European times, principally due to heavy predation by native Americans.

Romme et al. (1995) conducted a limited age structure analysis of aspen on the northern range. They found that most of the current northern range aspen overstory originated during the 1870's and 1880's and concluded that this was the only major period of recruitment of overstory aspen trees in YNP since about 1800. Warren (1926) collected increment cores from 31 aspen in a restricted geographic area near Camp Roosevelt in 1921, with the majority of these trees also originating during the 1870's and 1880's. Several authors have suggested that this period (1871–1890) may have provided unusually favorable conditions for the development of aspen, including frequent fires, favorable climatic conditions, and low levels of herbivory due to ungulate reductions from market hunting (Romme et al., 1995; YNP, 1997; Meagher and Houston, 1998).

The years 1872–1886 were a unique period in the history of YNP, being the “market hunting” era when all large wild animal populations in the park were being decimated (Schullery and Whittlesley 1992). Bison (*Bison bison*), elk, and other large animals were shot for their hides and the carcasses were baited with poison to eliminate the coyote (*Canis latrans*) and the wolf (Schullery and Whittlesley, 1992). Hunting was prohibited in the park in 1883 but enforcement was ineffective until the US Army assumed park administration in 1886 (Weaver, 1978). The coming of the Army helped curtail large-scale poaching and allowed YNP animal populations to begin rebuilding from their low levels.

By the turn of the century a protectionist attitude was developing toward native ungulate populations and by 1912 wolf populations were also increasing (Weaver, 1978; Houston, 1982). Concerns regarding the effects of a large predator base on the ungulate herds led to the effective removal of the wolf from YNP in the period of 1914–1926 (Weaver, 1978). According to park records, at least 136 wolves were killed in YNP during this period. The last occupied den found in YNP was destroyed near Tower Fall in 1923 and only unverified sightings of large wolf-like canids appear in park records after 1927 (prior to wolf reintroduction in 1995). Since the 1920's the elk population has been limited principally by park

service removals (until 1968), regulated hunting adjacent to YNP, and natural regulatory factors.

Previous YNP studies have qualitatively compared aspen abundance and age structure in historic photographs to conditions on the same sites in recent times (Houston, 1982; Kay, 1990; Meagher and Houston, 1998). Warren (1926) published the first quantitative study of aspen in Yellowstone. The aim of his investigation was to make accurate descriptions, maps, and photographic records of beaver, their works, and the character of riparian vegetation, especially aspen, which was their primary food source. Warren photographed, measured, and described the character and diameter sizes of YNP riparian aspen stands existing in 1921 and 1922.

Park officials have stated, “there remains no question that ungulate browsing is the immediate cause of the decline of aspen on the northern range, but there is considerable uncertainty over why that browsing has a different influence now than it has had historically” (YNP, 1997, p. 56). This raises the question of whether the growth of aspen was suppressed before or after the 1920's, when Warren did his fieldwork.

The objectives of our study were to investigate the following questions:

1. Are previous studies correct in asserting that the period between 1870 and 1890 was the only major episode of aspen tree recruitment on YNP's northern range during the last 200 years?
2. Did the elimination of historic YNP predator/prey relationships and the absence of wolves give ungulate browsing patterns a different influence on aspen now than they had historically?

In the second objective, it was not our goal to analyze all the numerous competing hypotheses regarding aspen decline on YNP's northern range. Our aim was to investigate if the absence of wolves was potentially an important factor in the decline of aspen, through an incomplete trophic structure involving wolves, elk and aspen (Mills et al., 1993; Estes, 1996).

1.1. Study area

This study was conducted on YNP's northern range; the 100,000-hectare (ha) wintering ground for YNP's largest elk herd (Fig. 1). Northern range vegetation consists of sagebrush steppe (primarily Big Sagebrush, *Artemisia tridentata*) and grassland interspersed with small stands of conifer (primarily Douglas Fir, *Pseudotsuga menziesii*) and aspen (Houston, 1982). More continuous conifer forests occur on north facing slopes and above 2000 m in elevation. Aspen occupy approximately 2–3% of the northern range landscape, occurring mostly in small stands on wet midslope

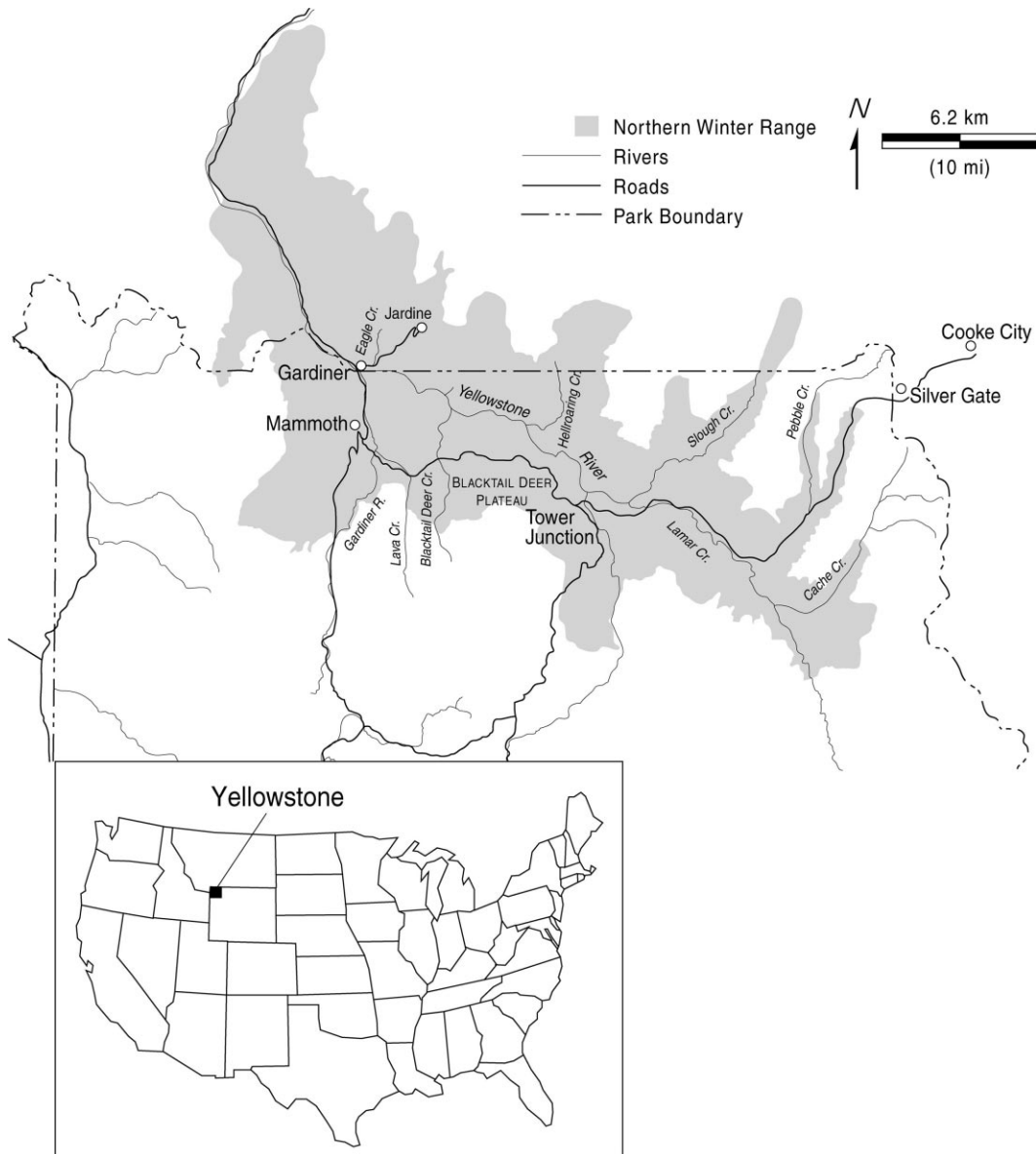


Fig. 1. Study area map of YNP's northern range (Source: YNP, 1997).

benches and along the conifer/steppe ecotone (Despain, 1990).

2. Methods

We searched Warren's (1926) text for quantitative information on as many different YNP northern range aspen stands as possible. We located references to 20 different stands where Warren (1926) gave measurements of aspen trees. From each of these 20 references we selected the largest diameter tree Warren (1926) reported as representing a stand dominant tree and indicative of that stand's overstory origination date (Mueggler, 1989).

To estimate growth rates of the likely trees encountered by Warren, we collected a set of increment cores from riparian aspen on the northern range in 1998 ($n = 30$). Cores were obtained from aspen trees at Geode Creek ($n = 15$), Lost Creek ($n = 2$), Slough Creek ($n = 2$), near Yellowstone Bridge ($n = 1$), and adjacent to a pond near Tower Fall ($n = 10$). Since riparian aspen are uncommon in the Park, we collected additional increment cores from the riparian areas of Eagle Creek ($n = 19$), just north of the YNP boundary in the Gallatin National Forest. The aspen trees we cored ranged from 5 to 48 cm diameter at breast height (DBH). Aspen were cored at a height of 1.0 m and we did not add an estimate of age at the coring height. All of the riparian aspen we cored ($n = 49$) were less than 46 m in horizontal distance

from the surface water of the streams or the pond, with a mean distance of 15 m to water. The increment cores were mounted, sanded, and the growth rings were counted using a dissecting microscope. Simple linear regression was used to predict the age of the aspen based on its DBH. The 49 cores used to develop the regression model were not used in any of the other analysis described in this paper.

Warren's (1926) report also contained numerous photographs of aspen stands being utilized by beaver. We analyzed these photographs for further evidence of the 1921 status of aspen overstory regeneration.

A second set of increment cores was collected to obtain a comprehensive age structure of overstory aspen on YNP's northern range. The purpose of collecting this sample was to determine whether the period of 1871–1890 was the only significant period of overstory recruitment for existing northern range aspen. Using a 1988 1:24,000 set of color infrared aerial photographs, we inventoried existing (post-1988 fires) aspen stands on YNP's northern range. We then randomly selected and visited 92 aspen stands during 1997–1998. From this sample we obtained 98 readable aspen cores from 57 different stands. The cores were obtained from a variety of site conditions and included a gradient of moisture conditions. To sample the range of aspen ages present, we attempted to obtain two cores from each of three different size classes (5–9, 10–19, and >20 cm DBH) in each stand. However, we observed that aspen <20 cm DBH were exceedingly rare on the northern range and we were able to collect only seven cores between 10 and 19 cm DBH and no cores from trees less than 10 cm DBH. A maximum of nine cores were drilled in each stand, with trunk rots being the reason cores could not be obtained from many stands. The trees were cored at a height of 1 m and were mounted, sanded and aged using the same procedures as the riparian set discussed above. We did not add an estimate of age at coring height and some stems may be older than our estimates due to missing rings or because browsing pressure kept them in shrub form for an unknown length of time. Ring widths were measured and skeleton plots were developed but cross-dating was not successful due to the complacency of the rings (Stokes and Smiley, 1968).

3. Results

Our linear regression of riparian aspen ages with DBH (cm) resulted in the simple linear equation of $\text{AGE}(\text{years}) = -6.8624 + (3.12587 * \text{DBH})$ with an $R^2 = 0.75$ (Fig. 2). The analysis of Warren (1926) showed that he encountered a wide variety of aspen size classes in the stands measured. Based on our regression model and using the largest diameter aspen in each stand, the

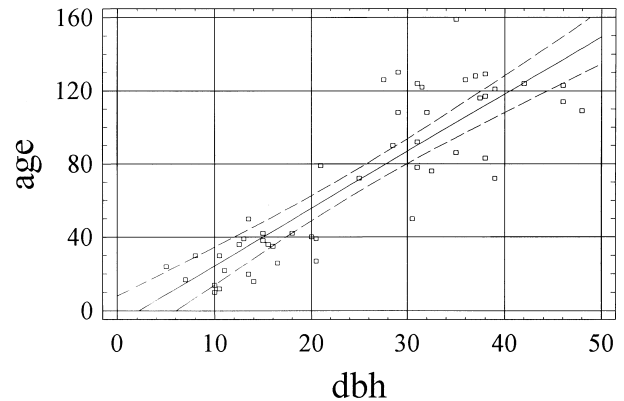


Fig. 2. Simple linear regression of aspen ages with diameter at breast height (DBH) in cm for riparian aspen cores collected on YNP's northern range and on Eagle Creek (Gallatin National Forest). The regression equation was $\text{AGE}(\text{years}) = -6.8624 + (3.12587 * \text{DBH})$. ($R^2 = 0.75$, $n = 49$). The dashed lines represent the 95% confidence interval.

stands measured by Warren (1926) contained aspen that originated from approximately 1751–1920 (Fig. 3).

In our analysis of the photographs taken by Warren, we found 23 different images with tall aspen saplings (approximately >2 m tall and less than 5 cm DBH), indicative of recent recruitment success into the aspen overstory. Fig. 4 is an example of this aspen recruitment as photographed by Warren in the early 1920's.

The current age distribution derived from the increment cores taken from the randomly selected aspen stands indicates that 10% of the sample originated before 1871, 85% between 1871 and 1920, and 5% from 1921 to 1998 (Fig. 5).

4. Discussion

To examine aspen overstory regeneration on the northern range we considered three different historical periods. These included the years prior to 1871, 1871–1920, and 1921–1998. The period prior to 1871 represents the era preceding park establishment, 1871–1920 represents the period of park creation, increasing Euro-american influence, and the origination of much of the current aspen overstory and 1921–1998 represents the current era of essentially no overstory recruitment.

Warren (1926) provides evidence that northern range aspen successfully recruited overstory stems in the period of 1751–1870. Our analysis of Warren (1926) considered every instance of size diameter he reported, not just the results from the 31 increment cores collected from a restricted geographic area near Camp Roosevelt cited in the YNP (1997) report. The 31 increment cores were collected by Warren (1926) to measure diameter growth rates, not to present an age structure analysis of YNP aspen in 1921–1922. Of the 20 aspen stands that Warren (1926) supplied diameter or circumference data

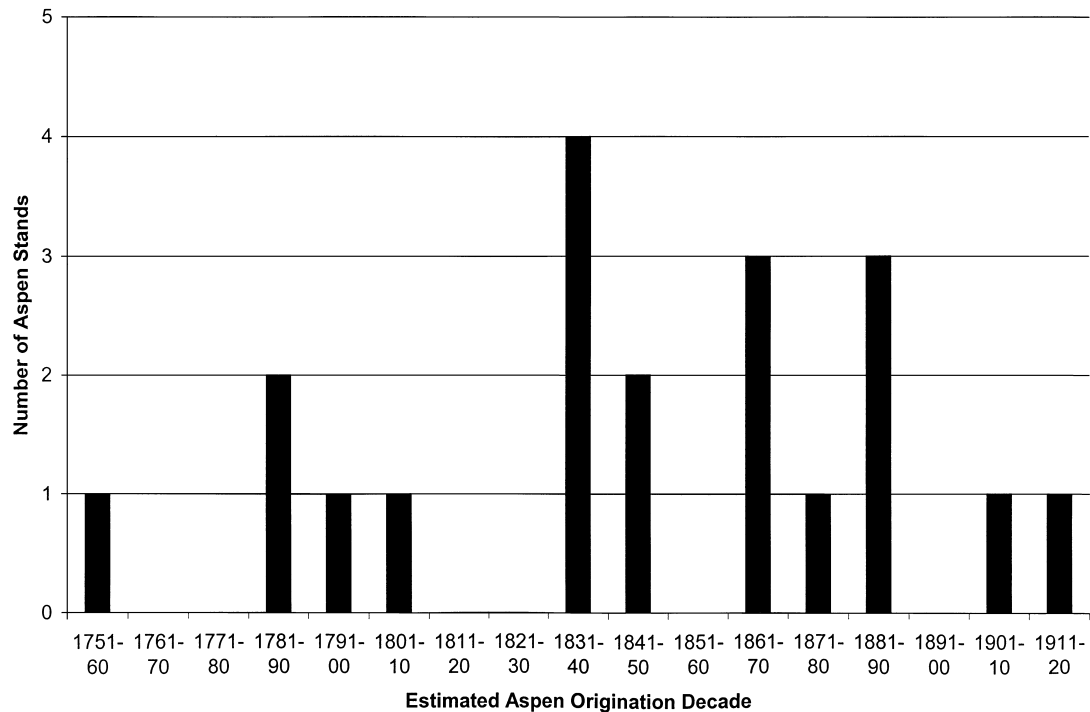


Fig. 3. Estimated aspen origination decades based on the largest diameter trees in 20 northern YNP aspen stands described by Warren (1926) in 1921. Predicted aspen origination dates were based on the aspen diameter/age regression shown in Fig. 2. The original maximum aspen diameters in the 20 stands included the following sizes in cm (inches): 1.65 (0.65), 7.62 (3), 12.70 (5), 12.70 (5), 12.70 (5), 15.24 (6), 19.91 (7.84), 20.32 (8), 20.32 (8), 25.40 (10), 25.40 (10), 30.48 (12), 30.48 (12), 30.48 (12), 30.48 (12), 38.10 (15), 43.18 (17), 44.70 (17.6), 45.72 (18), 55.88 (22).



Fig. 4. Multiple sized aspen stand near Elk Creek in Yellowstone National Park (Source: Warren, 1926, Fig. 120). The photo was taken on August 10, 1921.

for, our regression equation predicted that the overstory of 14 (70%) originated before 1871 (Fig. 3).

We found 10% of our 1998 random set of aspen cores originated prior to 1871 (aspen > 127 years old, Fig. 5). Romme et al. (1995) also reported 10% of their sampled northern range aspen originated prior to 1871. Kay (1997) found 10% of aspen stands he sampled belonged to stems greater than 120 years old in Yoho and Kootenay

Parks in the Rocky Mountains of British Columbia, Canada. In Wyoming's Gros Ventre valley, Krebill (1972) reported 8% of the sampled aspen stems to be older than 120 years. Mueggler (1989) reported 11% of his cores to be older than 129 years in a study of more than 1500 aspen cores collected in 9 National Forests in Utah, southeastern Idaho, and western Wyoming. All of the age structure studies listed indicate that aspen is a tree species with a relatively short life span and show that YNP's percentage of aspen > 120 years is consistent with other Rocky Mountain areas.

There is ample evidence of successful aspen overstory regeneration in the period of 1871–1920. We dated 85% of our aspen cores to the 1871–1920 period while Romme et al. (1995) dated 86% of their cores to this period (Fig. 5). There are significant differences in the two data sets however, for the periods of 1871–1890 and 1891–1920. We found a much lower percentage of aspen trees originating between 1871 and 1890 (21% versus 52%) than did Romme et al. (1995). Conversely, we found a significantly higher proportion of aspen originating during the 1891–1920 period (46% versus 10%) than Romme et al. (1995). Differences between the two data sets can at least partially be explained by differences in methodology and research objectives. We cored three different DBH classes (5–10 cm, 10–20 cm, and > 20 cm) to attempt to capture the range of ages in the aspen overstory while Romme et al. (1995) sampled

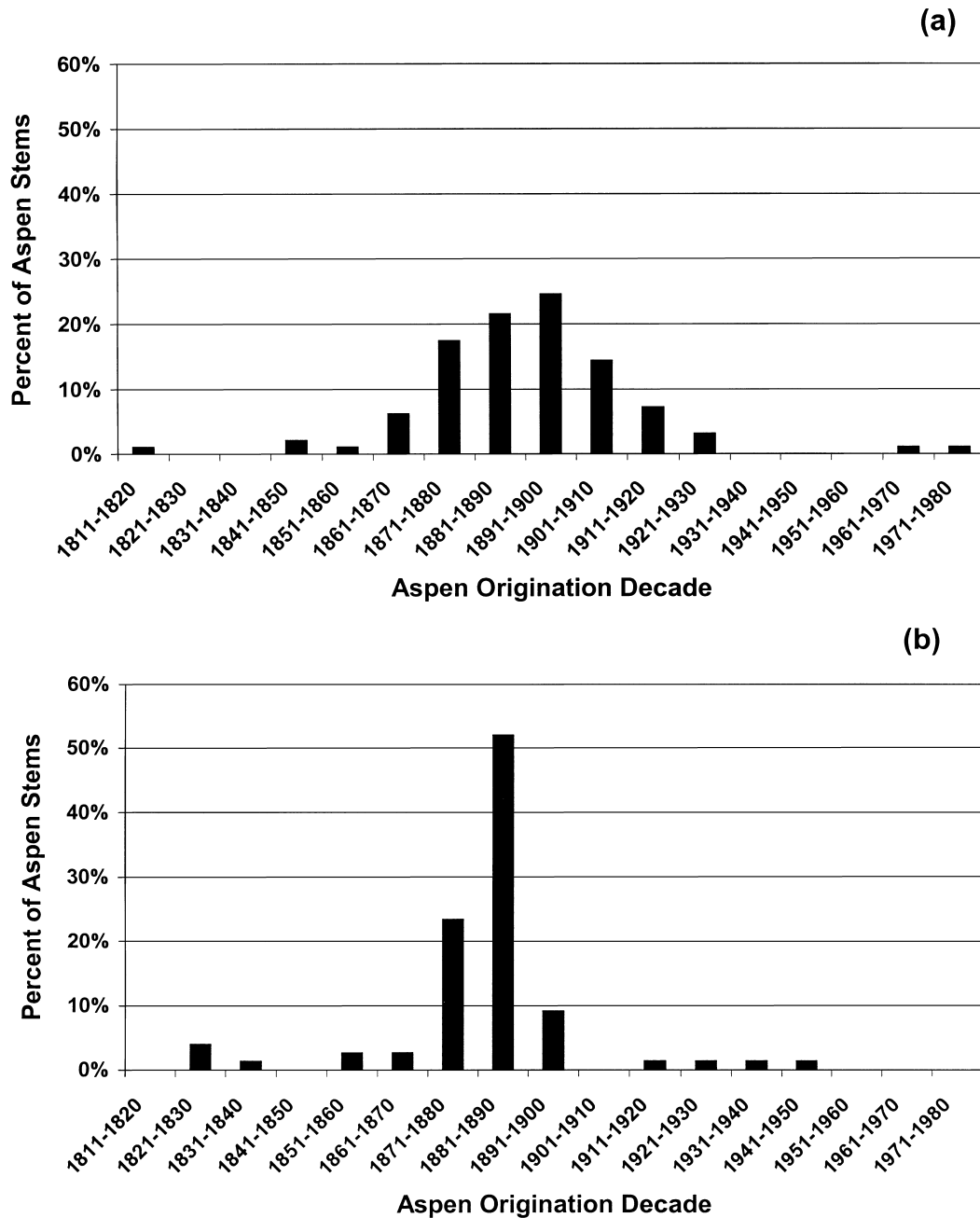


Fig. 5. The percentage of current overstory aspen stems established by decade on YNP's northern range. The source for the top histogram (a) is from the current study (98 cores), while the data for the bottom histogram (b) was adapted from Romme et al. (1995, 77 cores).

only canopy dominant trees. We also obtained cores from a much greater number of aspen stands (57 versus 15). The Romme et al. (1995) increment core sample was the only YNP aspen age study we have found in published literature. However, its non-random and clustered nature may make it statistically inappropriate to infer the aspen age structure over the entire northern range.

Warren (1926) also provides strong corroborating quantitative and photographic evidence of aspen overstory regeneration between both 1871–1890 and 1891–

1920 (Figs. 3 and 4). His photographs as well as other research involving historic photographs support the conclusion that aspen overstory recruitment was occurring during the 1871–1920 period (Warren, 1926; Houston, 1982; Kay, 1990; Meagher and Houston, 1998).

The period of 1921–1999 was characterized by no significant recruitment of new stems into the aspen overstory. We found 5% and Romme et al. (1995) reported 3% of sampled aspen trees originating since 1921. The two aspen cores we collected with origination

dates after 1929 (1962 and 1974) were both on sites protected from elk browsing. One of the aspen was protected by scree and the other by down woody debris (jackstrawed conifers).

These findings bring us back to a consideration of why northern range aspen overstory recruitment has essentially ceased since the 1920's, when there is evidence of success from approximately 1751 to the 1920's. Based on dendroclimatic indices since the 1920's, climatic conditions affecting tree growth varied from the poor growing conditions in the 1930's to above average conditions from 1945 to 1954 and 1965 to 1969 (Stockton, 1973; Romme et al., 1995). Yet these favorable climatic periods failed to produce any evidence of successful aspen overstory recruitment either in our core sample or previous research (Jonas, 1955; Barmore, 1965; Kay, 1990). More importantly, from 1871 to 1920 our core data (Fig. 5) show aspen overstory recruitment both during periods of favorable climatic conditions and also during the unfavorable climatic period of 1901–1905 (Stockton, 1973). Therefore, at least since the 1870's, dendroclimatic evidence linking YNP aspen overstory recruitment success with periods of favorable climatic conditions is lacking.

We agree with Baker et al. (1996) that fluctuations in beaver populations cannot explain the aspen decline process, since nearly all beaver occupancy is found in and adjacent to streams and their range does not extend to YNP's common upland aspen stands. In addition, processes related to fire suppression or conifer invasion do not appear to be significant factors in YNP aspen decline, since aspen recruitment has been documented in YNP exclosures and on the elk winter range just north of the YNP boundary (Kay, 1990). Further evidence was provided by the 1988 YNP fires, which stimulated aspen sucker production and led to significant seedling establishment, yet failed to produce a new cohort of aspen overstory stems in YNP (Kay, 1993; Romme et al., 1995; Romme et al., 1997).

Euroamerican influences may have played multiple roles in YNP aspen decline. YNP was established as the world's first National Park in 1872, but hunting remained legal until 1883 and poaching continued even after that date (Haines, 1977). Park visitation steadily increased and a major transportation route crossing the northern range developed, with possible effects on elk abundance and browsing patterns. North of the YNP boundary, human settlement, livestock, fences, and regulated hunting may also have reduced elk migration onto the lower elevation winter range north of the park (Wagner et al., 1995). Euroamericans also disrupted existing predator/prey relationships. The market hunting era (1872–1886) reduced populations of both predator and prey species, thereby potentially reducing browsing pressure on aspen. A major change occurred in the early 1900's, when policies to eradicate predators

and protect prey species (elk and bison) were introduced (Weaver, 1978). Skinner (1926) reviewed YNP administrative records and reported that between 1904 and 1925, 121 mountain lions (*Puma concolor*), 2805 coyotes and 132 wolves were killed in YNP. Skinner (1926) also stated that he believed that more predators were killed than official records indicated. A major ecological difference between the two eradication events is that in the first (1872–1886), both predator species and elk were reduced, while during the second (1914–1926), only predators were eradicated. This difference may have been an important factor in explaining why aspen overstory recruitment occurred during and after the market hunting era (potentially low elk browsing levels) and became almost nonexistent after the second predator eradication campaign (potentially high elk browsing levels). Within the boundaries of YNP, elk herd reduction programs continued (until 1968) but these programs were of a fundamentally different nature than historic predator/prey relationships. Rather than the constant threat provided by wolf presence, the periodic elk herd reductions were a management tool carried out as quickly and efficiently as possible to minimize disruptions to park visitation (Wright, 1998).

We hypothesize that predator eradication and the subsequent loss of historic predator/prey relationships may be an important factor in the decline of northern range aspen. References to aspen decline began to be noted in the literature beginning in the 1920's and 1930's, concomitant with the final phase of YNP wolf eradication (Warren, 1926; Rush, 1932; Grimm, 1939). Our analysis of the Warren data and our random set of increment cores both show successful aspen recruitment during the 1800's and early 1900's, a period when predator/prey relationships had not yet been so fundamentally altered. After 1900, human predation on elk was brought under increasing control in YNP and wolves were essentially eliminated between 1914 and 1926, with northern range aspen overstory recruitment ceasing at the same time.

The 1995 re-establishment of wolves on YNP's northern range may be of long-term benefit to aspen. Given YNP's policy of natural regulation, wolves may help re-establish an ecologically significant and historically important predator/prey relationship in the park. In addition to reducing elk populations, potential keystone predators such as wolves may also affect aspen overstory recruitment by influencing ungulate movement and browsing patterns. Our hypothesis on modifying elk behavior is based on predation risk effects theory. We agree with Schmitz et al. (1997) who state that the risk introduced by the mere presence of a predator could have widespread effects by causing many prey individuals to alter their foraging behavior.

Singer (1991) suggested that some changes in habitat use by ungulates in response to wolves might have gone

undetected in YNP's past. When wolves were present, elk may have used antipredator strategies and avoided areas frequented by wolves. Studies have shown that wolves can affect the spatial organization and hence browsing patterns of ungulates. During a period of a declining numbers, white-tailed deer (*Odocoileus virginianus*) in Minnesota were observed to be more numerous in wolf-pack buffer zones, as wolves avoid these areas to minimize the chances of fatal encounters between packs (Mech, 1977). In Canada's Jasper National Park, Dekker (1985) and Dekker et al. (1996) noted increased aspen overstory recruitment in areas frequented by wolves. Recent work by White et al. (1998) supported Dekker's conclusions and suggested that aspen may be regenerating in areas avoided by elk following a predator avoidance strategy. Since wolves recolonized the Canadian parks in the 1970's, researchers have found higher elk densities in low wolf predation areas (White et al., 1998). Dekker et al. (1996) found elk cow:calf ratios were 100:18–19 near wolf denning sites and cow:calf ratios were 100:48 along roadways and near areas inhabited by humans. Based on tree ring data, White et al. (1998) reported that a new cohort of aspen suckers has regenerated into trees 3–5 m tall since wolves were reintroduced into Jasper National Park, with particularly robust overstory recruitment near high-use wolf trails.

McLaren and Peterson (1994) investigated food chain relationships between wolves, moose and balsam fir (*Abies balsamea*) on Michigan's Isle Royale. According to tree ring data, the balsam fir on Isle Royale showed depressed growth rates when wolves were rare and moose densities were high, due to moose herbivory suppressing foliar biomass and annual wood accrual on the firs (McLaren and Peterson, 1994). They concluded that the Isle Royale food chain appeared to be dominated by top-down control where predation determined herbivore density and hence plant growth rates. McLaren and Peterson (1994) emphasized that the unprecedented low wolf populations of recent times (1988–1991) had led to very high levels for the moose population and strong suppression of balsam fir growth. Angelstam (pers. comm., 1998) also noted an inverse relationship between wolf abundance and aspen recruitment in Sweden, Finland, and northern Russia.

Historic photographs provide evidence of aspen and willow thickets occurring on the northern range in the early years of this century (Houston, 1982; Kay, 1990; Meagher and Houston, 1998). Aspen thickets in the uplands of the northern range may have been more common in the 1800's due to a higher fire frequency (Houston, 1973). Elk may have used antipredation strategies to avoid wolves around the patches of aspen thickets on the open uplands of the northern range. Houston (1982, p. 314) commented on the visible effects of ungulate browsing along the edge of an aspen thicket

in a photograph taken on the northern range in 1900. We hypothesize that elk may typically have browsed only on the edge of the upland aspen thickets to avoid predation by wolves. This type of antipredator behavior has been observed for Caribou (*Rangifer caribou*) in skirting willow (*salix* spp.) thickets to avoid predation by wolves in Alaska (Roby, 1978).

Wolves have been shown to frequent riparian areas (Peterson, 1977). In Minnesota, Mech (1970) stated that frozen riverbeds, streams, and beaver ponds were used by wolves for travel. Allen (1979) reported that wolves on Isle Royale prospected the beaver ponds and lake-edge lodges for beaver sign during the thaws of February and March. Paquet (1993) provided evidence of wolf activity in beaver occupied riparian areas of Banff National Park, Canada. We hypothesize that elk may have avoided riparian aspen stands that were located in wolf travel corridors. This type of antipredation behavior may have increased aspen recruitment in some riparian zones in northern YNP.

As a potential keystone species, wolves may increase aspen recruitment indirectly through poorly understood trophic structure interactions. For example, wolf-killed elk carcasses may benefit the grizzly bear (*Ursus arctos horribilis*) population and possibly help it expand. This could increase grizzly predation on elk, thus possibly changing or further reducing elk herbivory effects. Grizzly bears have been found to be significant predators of neonatal elk in YNP (Singer et al., 1997). Orians et al. (1997) reviewed previous studies and found that the coexistence of wolves and bears usually drives prey to lower population densities.

We noted a potential wolf influence on elk behavior and aspen sucker heights in a pilot study during the 1998 field season. Therefore, in cooperation with YNP biologists, in 1999 we initiated a long-term study of aspen, elk, and wolves using 115 permanent plots on YNP's northern range. Our objectives are to obtain data on elk use and aspen regeneration at random locations within and outside of three core wolf pack territories on the northern range.

We have provided strong evidence of long term aspen overstory recruitment in YNP up until the 1920's. We hypothesize that disturbance to predator/prey relationships, especially between wolves and elk, has been a major factor in YNP aspen decline. Other human influences, as discussed above, may have also played a role in YNP aspen decline. In addition to direct predation on elk, we suggest that cascading trophic interactions involving predator presence and movement may have had spatially specific effects on elk behavior and herbivory. Our hypothesis is based on theory involving trophic cascades as well as empirical evidence from both the literature and our data. Further research involving the potential influence of wolves on ecosystem processes will greatly enhance our knowledge of how

these keystone predators potentially regulate terrestrial systems.

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