Wolves, elk, and aspen in the winter range of Jasper National Park, Canada

R.L. Beschta and W.J. Ripple

Abstract: We undertook a retrospective study of aspen age structure in the winter range of Jasper National Park to assess potential trophic cascades in wolf–elk–aspen systems. We compiled historical wolf (*Canis lupus* Linnaeus, 1758) and elk (*Cervus elaphus* Linnaeus, 1758) population data and, in 2005, sampled 42 trembling aspen (*Populus tremuloides* Michx.) stands within the Palisades site along the Athabasca Valley near Jasper townsite and another 30 stands within the Willow Creek site in a relatively remote portion of the park. Results indicated that aspen recruitment (suckers or seedlings growing into tall saplings and trees) occurred at both sites in the early 1900s but decreased in the 1940s as elk numbers were reaching a maximum. Wolves were largely eliminated from the park in the mid-1900s, and aspen recruitment during that time ceased at both sites, apparently because of heavy browsing by elk. With recovery of wolf populations in the late 1960s and increasing predation risk, elk use of the Willow Creek site declined, and aspen recruitment resumed. However, at the Palisades site, an area of relatively low predation risk due to human use and developments, renewed aspen recruitment has not occurred. Results indicate that historical wolf or ungulate control programs and human developments influenced trophic cascades involving wolves, elk, and aspen in these winter ranges.

Résumé : Nous avons entrepris une étude rétrospective des structures d'âge du peuplier faux-tremble dans les quartiers d'hiver du Parc national de Jasper pour évaluer les chaînes trophiques dans les systèmes loup-wapiti-peuplier. Nous avons compilé les données historiques de populations de loup et de wapiti et, en 2005, nous avons échantillonné 42 peuplements de peuplier dans le secteur des Palissades, le long de la vallée de l'Athabasca, près de l'agglomération de Jasper et 30 autres peuplements dans le secteur de Willow Creek, un secteur peu accessible du parc. Nos résultats indiquent que la régénération de peuplier (gourmands/semis poussant au travers des grandes gaules et des arbres) était bonne au début des années 1900 dans les deux secteurs, mais qu'elle a décliné dans les années 1940 lorsque le nombre de wapitis culminait. Le loup a été pratiquement éliminé du parc vers les années 1950 et la régénération du peuplier a alors cessé, apparemment à cause du broutement intense du wapiti. Avec le regain des populations de loup à la fin des années 1960 et l'accroissement du risque de prédation, le wapiti a de moins en moins utilisé le secteur de Willow Creek et la régénération du peuplier a repris. Toutefois, la régénération n'a pas repris dans le secteur des Palissades, un secteur où le risque de prédation est faible à cause de la présence humaine et du développement. Ces résultats indiquent que les programmes historiques de contrôle du loup et des ongulés, combinés à l'activité humaine, ont influencé les chaînes trophiques impliquant le loup, le wapiti et le peuplier faux-tremble dans ces quartiers d'hivernage.

[Traduit par la Rédaction]

Introduction

Nearly a half-century ago, ecologists Hairston et al. (1960) proposed a model for trophic interactions often referred to as the "green world hypothesis." Implicit in this concept is the idea that plant communities evolved in predator-regulated ecosystems in contrast to a bottom-up model of ecosystem structure where, for example, plants utilize a vast array of chemical compounds and other mechanisms to reduce or prevent herbivory (Fraenkel 1959; Murdoch 1966). Ongoing discussions on terrestrial food webs continue to question the relative strength of top-down forcing versus bottom-up controls (Polis et al. 2000; Schmitz et al. 2000; Terborgh 2005). Recently, Bowyer et al. (2005) concluded that existing models of predator–prey dynamics are not well suited for understanding top-down and bottom-up regulation of ungulates. In a review of trophic cascade studies, Borer et al. (2005) found few examples illustrating the effects of large mammalian carnivores in structuring plant communities. Thus, uncertainty continues to persist regarding the relative role of top-down and bottom-up mechanisms upon ecosystem structure and function.

Long-term, landscape-scale studies of trophic cascades involving an apex predator (wolves, *Canis lupus* Linnaeus, 1758), consumers (ungulates such as elk, *Cervus elaphus* Linnaeus, 1758), and producers (woody browse species such as trembling aspen, *Populus tremuloides* Michx.) have seldom been designed and implemented. The scarcity of such research is likely attributable to the difficulty of undertaking assessments at relatively large spatial and temporal scales, a need for significant long-term funding, and the difficulty of experimentally manipulating populations of large carnivores. However, wolves experienced large population fluctuations across substantial areas of Alberta during the

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20th century. Thus, a retrospective study of aspen age structure could provide important insights regarding any top-down progression of lethal (predation) and nonlethal (predation risk) effects across successively lower trophic levels in areas where wolves, a highly interacting predator (Soulé et al. 2005), were removed and subsequently recolonized.

Quaking aspen is not only the most widespread deciduous tree species in western North America but is relatively unusual in reproducing primarily by suckering (root sprouts) from the parent root system of a clone. Such clones have been able to perpetuate themselves for thousands of years (Kay 1997*a*). Suckers in open-grown clones normally form a dense thicket along the clone periphery, whereas the entire clone may sprout prolifically following fire or overstory removal (DeByle and Winokur 1985). Aspen trees are long lived (~100–130 years) relative to understory shrubs, grasses, and forbs and, thus, can provide important insights as to the long-term status of these other plants. Furthermore, aspen plant communities are utilized by a numerous species of wildlife, including ungulates, to help satisfy habitat needs.

In Alberta's Jasper National Park (NP), early research by Cowan[2] and a later study by Dekker (1985) found ungulate herbivory a major concern regarding aspen recruitment. In both Jasper and Banff NPs, Lulman (1976) identified a lack of aspen regeneration even though conifer invasion was not a significant occurrence. Across much of North America, aspen stands have experienced significant decline during the last century (Kay 1997*a*, Bartos 2001). Once lost from a landscape, aspen is unlikely to return through normal seeding processes (Bartos and Campbell 1998). Long-term herbivory from either wild or domestic ungulates, altered fire regimes, and conifer encroachment have been long identified as important factors related to aspen stand dynamics. Although the role of top carnivores has been of concern since at least the 1930s (Leopold 1943), the potential consequences of removing apex carnivores such as wolves has received relatively little critical research until recently (Ripple and Larsen 2000; White 2001; Binkley et al. 2005; Beschta and Ripple 2006).

Because wolves in Jasper NP had been functionally extirpated twice in the 20th century followed by periods of recovery, we undertook this study to evaluate lower trophic-level responses over time. Specific objectives included (*i*) to evaluate the potential effects of wolf presence–absence (via trophic cascades) upon the age structure of winter-range aspen communities in Jasper NP and (*ii*) to determine whether alternative factors such as climate fluctuations, conifer invasion, and fire may have also influenced aspen age structure.

We postulated that 20th century management of wolf populations has been a pivotal factor affecting trophic cascades involving wolves–elk–aspen and has significantly altered the recruitment of winter-range aspen stands in Jasper NP. Although aspen is typically characterized as a "fire species" (regenerates prolifically following fire), we also hypothesized that herbivory by elk may limit the capability of fire to improve aspen recruitment.

Study area

Jasper NP, consisting of 10 900 km^2 along the eastern side of the Canadian Rockies in western Alberta, is one of the largest national parks in North America. Carved by glaciers that receded from valley bottoms <10 000 years ago, the park occupies a series of roughly parallel mountain ranges trending southeast–northwest. Originally established as a forest park in 1907, it officially became a national park in 1930. Adjoining Jasper NP to the south is Banff NP, to the north Willmore Wilderness Park, and across the Continental Divide to the west, Mount Robson Provincial Park in British Columbia.

Three ecological zones are found in the park: (*i*) montane, (*ii*) subalpine, and (*iii*) alpine tundra; both the montane and subalpine zones contain significant areas of nonforest vegetation. The montane zone comprises <10% of the park and occupies the lowest elevations (1000–1350 m) along the Athabasca River and its major tributaries (Rhemtulla et al. 2002). Tree species common to the montane zone include lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*), white spruce (*Picea glauca* (Moench) Voss), and aspen. The mixed forest and grassy areas of the montane zone provide important winter habitat for ungulates such as elk, caribou (*Rangifer tarandus* (Linnaeus, 1758)), moose (*Alces alces* (Linnaeus, 1758)), mule deer (*Odocoileus hemionus* Rafinesque, 1817), white-tailed deer (*Odocoileus virginianus* (Zimmerman. 1780)), as well as travel corridors for ungulates and large carnivores. Also found in the park are bighorn sheep (*Ovis canadensis* Shaw, 1804) and mountain goats (*Oreamnos americanus* (de Blainville, 1816)). Large carnivores in Jasper NP include black bears (*Ursus americanus* Pallas, 1780), grizzly bears (*Ursus arctos* Linnaeus, 1758), cougars (*Puma concolor* (Linnaeus, 1771)), and wolves.

History of wolves and elk in Jasper National Park

Regardless of any influence First Nations may have had on wolf–ungulate populations, wolves were apparently abundant in prairie and foothill areas utilized by bison when European explorers entered present-day Alberta (Gunson 1995), but were infrequently encountered in the mountains, possibly because of low prey densities (Kay et al. 2000). By the late 1800s, large numbers of wolves in Alberta had been killed or poisoned, and market hunting of ungulates further reduced prey populations. A wolf bounty was implemented in 1899, and by the early 1900s, wolves in the southern part of the province had been largely extirpated (Gunson 1984).[3] However, control efforts in the early 1900s failed to prevent a slow population increase in Jasper NP, eventually attaining 40–60 wolves by the 1940s (Cowan 1947; Soper 1970 Carbyn 1974; Fig. 1*a*).[4]

From 1943 to 1954, 72 wolves in Jasper NP were reported killed with snares, cyanide guns, and rifles (Carbyn 1974) decreasing the population to very low levels by the mid-1950s. In the early 1950s, thousands of wolves were killed

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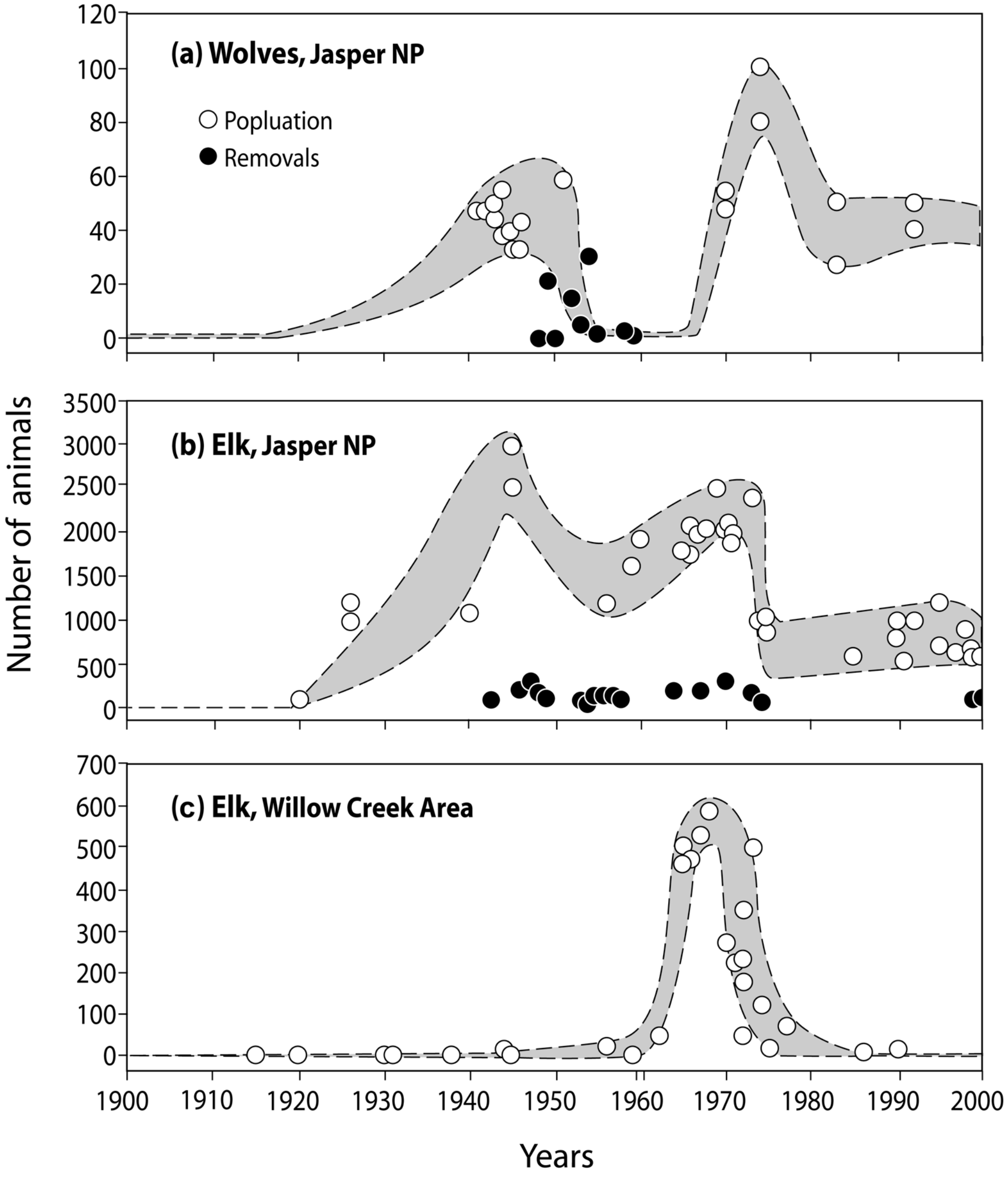
[2] I.M. Cowan. 1946. General report upon wildlife studies in the Rocky Mountain Parks, 1946. Unpublished report. Parks Canada, Ottawa, Ont.

[3] W. Bradford. 1995. A history of elk in Jasper National Park with a reflection on the wolf history, the history of elk in the Willow Creek area, and the history of elk/human interactions. Unpublished report. Jasper National Park, Jasper, Alta.

[4] R.G. Kaye and J.M. Roulet. 1980. The distribution and status of wolves. Unpublished report. Parks Canada, Ottawa, Ont.

Fig. 1. Population estimates (○) and removals (●) of (*a*) wolves and (*b*) elk in Jasper National Park and (*c*) elk in the Willow Creek winter range of northeastern Jasper National Park. The shaded area represents general population trends over time as well as an indication of uncertainty in population estimates at any point in time. Data sources: (*a*) Cowan (1947), 1943 (Report on game conditions in Banff, Jasper and Kootenay National Parks, 1943. Unpublished report. Parks Canada, Ottawa, Ont., and 1946 (General report upon wildlife studies in the Rocky Mountain Parks, 1946. Unpublished report. Parks Canada, Ottawa, Ont.)), Carbyn (1974), R.G. Kaye and J.M. Roulet (1980, The distribution and status of wolves. Unpublished report. Parks Canada, Ottawa, Ont.), Dekker (1985), Dekker et al. (1995), and W. Bradford. 1986. A discussion on elk (*Cervis canadensis*), moose (*Alces alces*), sheep (*Ovis canadensis*), and wolf (*Canis lupus*) population trends in Jasper National Park. Unpublished report. Jasper National Park, Jasper, Alta.; and W. Bradford. 1995. A history of elk in Jasper National Park with a reflection on the wolf history, the history of elk in the Willow Creek area, and the history of elk/human interactions. Unpublished report. Jasper National Park, Jasper, Alta. (*b*) D.R. Flook. 1955. An appraisal of the elk situation in the Athabasca Valley of Jasper Park. Unpublished report. Canadian Wildlife Service, Edmonton, Alta.; Jasper National Park (warden wildlife census 1965–1970), Bradford (1995) unpublished report (see section *a*), Dekker et al. (1995), R. Ralf. 2001. Aerial elk census 2001, Athabasca and Miette Valley, Jasper National Park. Unpublished report. Jasper National Park, Jasper, Alta.; and R. Ralf. 2004. Jasper National Park, Roadside elk surveys 2004. Unpublished report. Jasper National Park, Jasper, Alta., and M. Bradley (Jasper NP, personal communication, 2005); (*c*) Stelfox and Service (1974) and Bradford (1986, 1995) unpublished reports (see section *a*).



across Alberta, mostly by poisoning (Gunson 1995). Although predator control programs were abandoned in Jasper NP in 1959,[4] reduced levels of control continued outside the park until 1966 (Gunson 1991). Wolves increased inside the park in the late 1960s and attained a population of 80–100 animals by the mid-1970s.[3] Infrequent estimates of wolf numbers since then indicate a smaller wolf population, perhaps in response to lower elk numbers. Highway and railroad mortality from 1980 to 1990 indicates a mean loss of two wolves per year (Jasper NP, Warden Service files).

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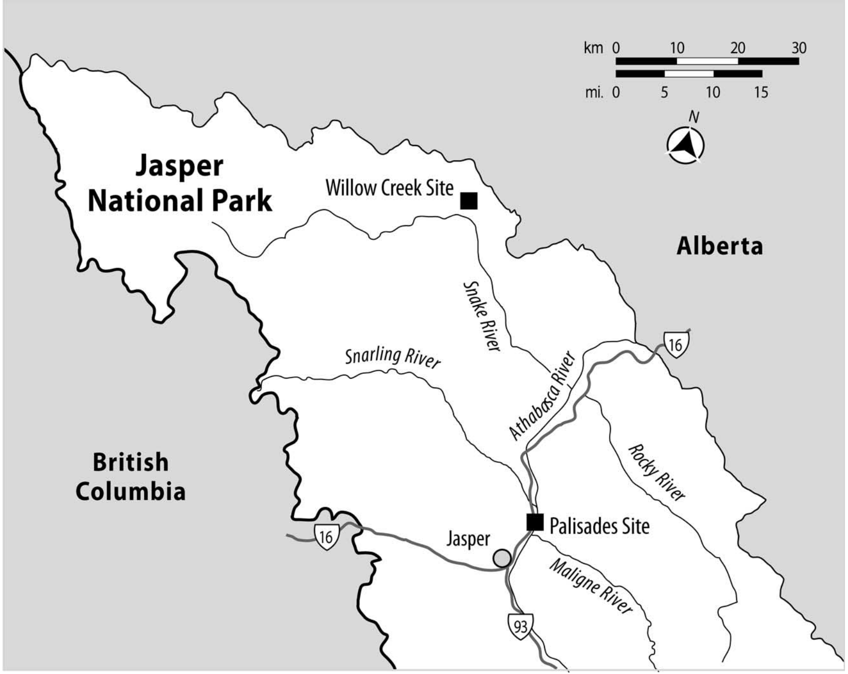
Fig. 2. Location of study sites in Jasper National Park, Alberta.



Widespread hunting in the late 1800s reduced ungulate numbers across southern Alberta, with local extirpations of some species. By the early 1900s, elk were entirely absent from the area that was later to become Jasper NP (Dekker et al. 1995). Wild ungulates in Alberta became increasingly protected in the early 1900s and ~90 elk from Yellowstone NP were released into the park in 1920. Elk numbers rapidly increased (Fig. 1*b*) as they dispersed and filled "new ranges" during the 1920s and 1930s (Flook 1964). Within a few years after the 1920 release, elk became habituated to people and an increasing annoyance at Jasper townsite.[3] Because of their impacts on winter range and periodic nuisance at Jasper townsite, more than 2200 elk were slaughtered or culled between 1942 and 1970. Decreased elk numbers from the early 1940s through the late 1950s were mainly due to park service culling, severe winters in combination with a deteriorated winter range, and predation by wolves.

With wolves heavily controlled in the 1950s, elk numbers again began to increase (Fig. 1*b*). Elk also began to utilize winter-range habitat in the Willow Creek area of the park (Fig. 1*c*), where horses were wintered in the late 1960s and early 1970s. Here, elk often "followed horses around and fed in areas horses had pawed [through the snow] and exposed forage".[3] Decreased numbers of elk in the Willow Creek area after the early 1970s was thought to be a result of "overhunting" (elk from this herd were heavily hunted along the park boundary in the adjacent Rock Creek area), severe winters in the early 1970s, high wolf numbers, reduced forage due to previous use by large numbers of elk and horses (Dekker 1985),[3] and perhaps a loss of forage accessibility in deep snow after the overwintering of horses was curtailed (W. Bradford, Jasper NP, personal communication, 2005).

A depleted winter range, cold weather, and exceptionally deep snowpack resulted in a major die-off of Jasper NP's elk during the winter of 1973–1974, with wolf populations helping to maintain lower elk numbers in subsequent years.[3] Since the mid-1970s, estimates indicate ≤1000 elk reside within the park, representing a winter-range density of <1 elk/km^2. Highway and railroad mortality from 1980 to 2004 averaged 51 elk/year (Jasper NP, Warden Service files).

Methods

We utilized two study sites within Jasper NP for evaluating aspen stands. The Palisades site (~2 km^2) is located 9 km north of Jasper townsite along Highway 16, where aspen occur on post-Pleistocene glaciofluvial terraces (former floodplains) of the Athabasca River (Fig. 2). The Willow Creek site (~3 km^2) is located in the northeastern part of the park and includes aspen stands in portions of the Willow Creek and Rock Creek drainages. Aspen stands here occurred primarily along the edges of meadows and adjacent toeslopes. The Willow Creek site is relatively remote from humans, although it experiences seasonal use by hikers and groups on horseback.

During August 2005, we measured aspen tree diameters within 42 stands at the Palisades site and 30 stands at the Willow Creek site. A "stand" was defined as a group of aspen trees separated from any adjacent group by approximately 30 m or more. A 4 m wide belt transect, starting at the edge of the stand and passing through the stand's centroid to the opposing edge, was used for sampling aspen at the Palisades site. Transects ranged from 20 to 70 m in length. Along each transect, we measured the diameter at breast height (DBH, cm) and status (i.e., alive or dead) of any aspen stem ≥1 cm in diameter. At the Palisades site, aspen stands occurred on both sides of Highway 16. Some of the stands to the east of the highway (between the highway and the Athabasca River) had experienced prescribed fire in recent years; all stands to the west of the highway had not. Along approximately 4 km of highway, we sampled all as-

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pen stands along the east (burned and unburned) and west (unburned) sides of the highway.

At the Willow Creek site, individual aspen stands typically had their longitudinal axis paralleling the edge of a meadow or forested toeslope. Because these stands contained a relatively large number of small-diameter aspen, we used a 2 m wide belt transect through each stand, with transects ranging from 15 to 40 m in length. Each transect was oriented perpendicular to the stand's longitudinal axis. For stands ≤100 m in length, the belt transect was established midway along this axis. Occasionally, we encountered a stand >100 m in length, in which case we divided the longitudinal dimension of the stand into thirds and established a separate belt transect between each of these divisions.

At both study sites, we sampled only stands dominated by aspen, thus excluding a few stands where conifers represented a major component of the overstory. Measured DBHs were summarized in frequency histograms to illustrate general patterns of stand structure for each site.

Across each study site, we obtained increment cores at breast height (1.4 m) from aspen trees representing a range of diameters. The cores were sealed in plastic straws for transport to a laboratory where they were dried and sanded. Tree rings were counted using a binocular microscope and regression analysis was used to develop relationships between the number of growth rings (i.e., tree age at breast height) and tree DBH. From these relationships and assuming that, on average, 5 years were required for an aspen stem to attain breast height (Peterson and Peterson 1995), the calculated total age was subtracted from 2005 to estimate each tree's date of establishment. Frequency histograms of establishment dates, by decade, were compiled to identify temporal patterns of aspen recruitment at each site.

Available long-term databases associated with climate and fire were obtained to help assess their potential influence on elk populations and (or) aspen recruitment. To characterize general climatic conditions during winter months as well as identify years of abundant snowfall, we tabulated annual snowfall amounts (cm) over the months of November through March between 1917 and 2000 for the Jasper weather station (elevation ~1060 m). Because temporal patterns of fire occurrence provide an important context regarding general forest conditions (e.g., aspen recruitment, forage availability, and conifer crown closure), we summarized the proportion of the park that had burned, by 50 year periods from 1700 to 1900 and 20 year periods after 1900, from a fire-history map of Jasper NP (Jasper NP, Warden Service, undated). The map included fires of natural, anthropogenic, and unknown causes.

In 1998, Jasper NP established two 10 m × 10 m ungulate exclosures within aspen stands at the southern end of the Palisades site. One of these "Palisades" exclosures experienced a moderate-intensity burn in 1999, whereas the other remained unburned. At the northern portion of this site (~4 km further north along Highway 16), two additional ungulate exclosures (each 15 m × 40 m) had been established in 1998 near the airport (Amiro et al. 2004). Although the "airport" exclosures were established primarily to evaluate the effects of controlled burning on stands of lodgepole pine, aspen were present inside and outside each exclosure. In 2001, one of the airport exclosures experienced a low-intensity burn, and the other, a high-intensity burn. At the Willow Creek site, a 10 m × 10 m ungulate exclosure located ~0.5 km west of the Willow Creek Warden Cabin had been established in 1998 within an unburned aspen stand.

One or more large aspen were present at each of the ungulate exclosures and, thus, provided a viable root system from which suckers could develop; suckers were present inside and outside all exclosures. Because the exclosures had been constructed within the last 7 years, we were primarily interested in evaluating any aspen that had regenerated since their installation. A 10 m × 10 m sampling plot was established inside and outside each exclosure. For a plot on the inside, we measured the height and current annual growth of all young aspen stems. For a plot outside, we also measured the height of all young aspen stems and, using plant architecture techniques (Keigley and Frisina 1998), determined the percentage of stems that had been browsed the previous winter. For comparative purposes, we considered $p \leq 0.05$ from any statistical analysis to represent a "significant" difference.

Results

Aspen

At the Palisades site, we measured 420 live aspen ≥1 cm DBH within belt transects through 30 unburned aspen stands. For 12 stands that had experienced prescribed burning, we measured 108 live aspen. DBHs were 19.5 ± 5.2 cm (mean ± SD) and 19.6 ± 5.3 cm for the unburned and burned stands, respectively. A paired *t* test (two-tailed, equal variances) indicated mean diameters for the two groups of stands were not significantly different (p = 0.88). Thus, DBH data were combined for developing a frequency distribution of diameters (i.e., stand structure) at the Palisades site (Fig. 3*a*). An additional 142 and 36 dead aspen ≥1 cm DBH were measured within the unburned and burned stands, respectively, at this site. The mean DBH of these dead trees was 14.0 cm, indicating that contemporary mortality is largely occurring within smaller diameter classes.

We measured 657 live aspen, all ≥1 cm DBH, within belt transects through 26 stands in the Willow Creek drainage and 68 live aspen from four stands in the Rock Creek drainage. DBHs were 5.0 cm ± 5.6 cm for trees in the Willow Creek drainage compared with 6.5 ± 7.4 cm for trees in the Rock Creek drainage. A paired *t* test (two-tailed, unequal variances) indicated the mean diameters of these two groups of stands were not significantly different (p = 0.10), and their diameter measurements were combined to illustrate stand structure for the Willow Creek site (Fig. 3*b*). An additional 277 dead aspen with a mean DBH of 2.2 cm were measured at the Willow Creek site.

Stand structure provides a convenient means of summarizing major variations in aspen recruitment, and it is apparent from the histograms in Fig. 3 that the size-class distributions for aspen at the two study sites are considerably different. Although trees <9 cm DBH are entirely absent at the Palisades site, the Willow Creek site has relatively large numbers of trees in these smaller size classes but, instead, is missing trees 11–15 cm DBH.

We obtained a total of 71 increment cores from aspen

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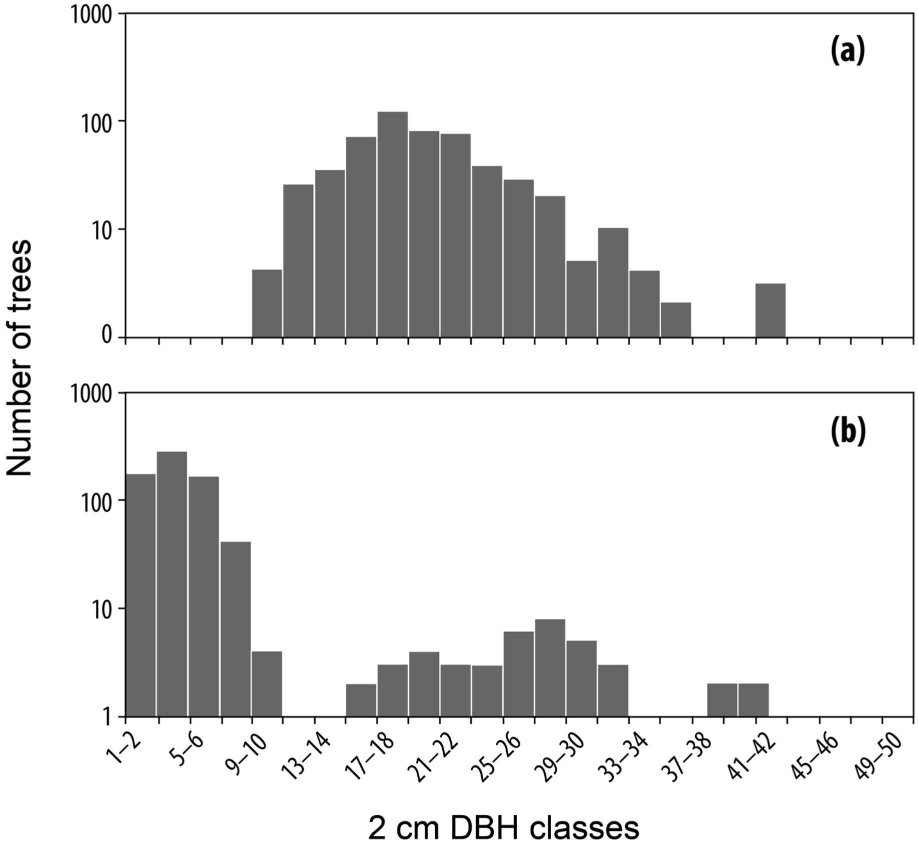
Fig. 3. Histograms of aspen frequency by 2 cm DBH (diameter at breast height) classes at the (*a*) Palisades site and (*b*) the Willow Creek site.



trees ranging from 6.6 to 49.7 cm DBH, of which 25 were from the Palisades site and 46 from the Willow Creek site. After inspection of the dried and sanded cores, eight of them were unreadable. The remaining cores included 14 from unburned stands and 7 from burned stands at the Palisades site, 23 from stands in the Willow Creek drainage, and 19 from stands in the Rock Creek drainage. Based on regression analysis of tree rings and DBH for each site, an establishment date for each measured aspen was calculated using the relationships in Fig. 4.

Our age data for the Palisades (Fig. 5*a*) and Willow Creek (Fig. 5*b*) sites indicate aspen recruitment was ongoing in the early decades of the 20th century when both wolves and elk were absent. However, recruitment of aspen at the Palisades site decreased in the 1930s and 1940s and then ceased entirely from the 1950s to the present (i.e., "missing age-classes" in Fig. 5*a*). Aspen recruitment at the Willow Creek site also shows a downward trend in the 1930s and 1940s, followed by cessation of recruitment during the 1950s and 1960s (Fig. 5*b*). At Willow Creek, Dekker (1985) noted that "suckering shoots [of aspen] began to grow in abundance" during the late 1970s. Our age structure data similarly indicate a recovery of aspen recruitment beginning in the 1970s, which continued into the 1980s and 1990s.

Climate

Snowfall records over the period 1917–2000 for the Athabasca Valley indicate a mean November–March snowfall of 110 cm with snowfall of ≥185 cm occurring, on average, approximately once every 10 years. The early 1970s represent a period of relatively large snowfall amounts. For example, over 200 cm of November–March snowfall were recorded during the 1970–1971 and 1971–1972 winters followed by a record 243 cm in 1973–1974. A 10 year moving average of November–March snowfall amounts generally indicates that they were below average from the 1920s through the 1940s, above average from the 1950s through the 1970s, and then near average for the 1980s and 1990s (Fig. 6).

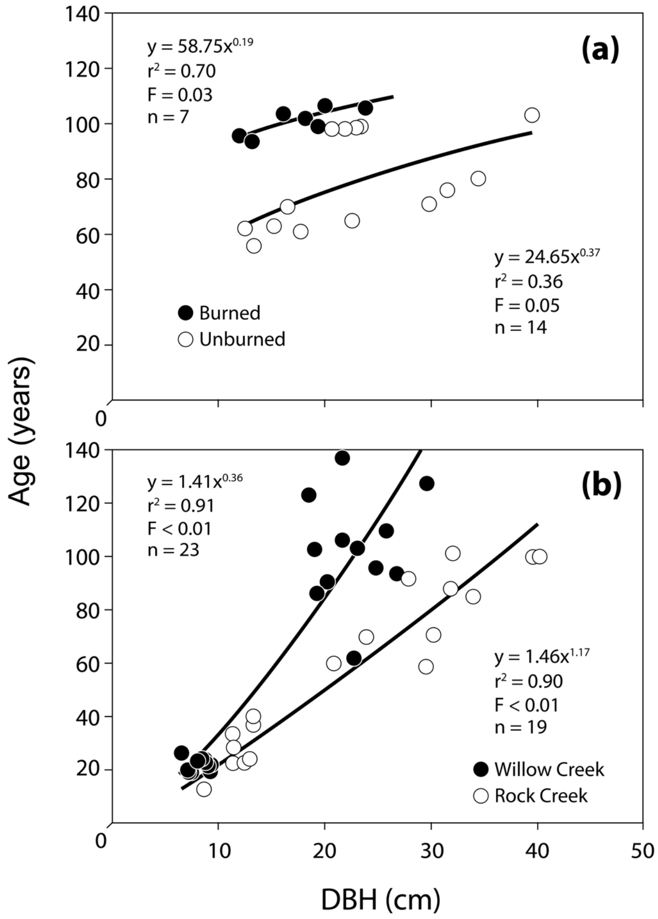
Fire history

Analysis of the fire history map indicated that 14% of the park's area last experienced burning during the 1700s. Another 19% of the park was last burned during the 1800s, with nearly three-fourths of this occurring in the latter half of that century. Many of the lodgepole pine forests along the Athabasca Valley originated during the major fires of 1889 (Tande 1979; Fig. 7). Only 5% of the park's area experienced fire in the 1900s, and of this, three-fourths occurred prior to 1920. Thus, when elk were introduced into the park in 1920, significant portions of summer and winter range had experienced fire in the three previous decades. After 1920, burned areas in Jasper NP became uncommon, thus allowing conifers to reoccupy former sites.

Exclosures

For the Palisades and airport exclosures, mean heights of young aspen inside the exclosures ranged from 94 to 173 cm and were significantly greater (p = 0.03, two-tailed paired t test, unequal variances) than mean heights outside the enclosures, which ranged from 25 to 69 cm (Fig. 8). Outside

Fig. 4. Tree age at breast height versus diameter at breast height (DBH) for aspen at the (*a*) Palisades site and (*b*) the Willow Creek site.



these exclosures, mean browsing ranged from 67% to 100% of the stems during the winter of 2004–2005. At the Willow Creek exclosure, the mean height of 91 cm for young aspen inside the exclosure was not significantly different ($p = 0.99$, two-tailed paired t test, unequal variances) from the mean height of 90 cm measured outside the exclosure, where 33% of the stems had been browsed during the winter of 2004–2005.

The current annual growth of aspen growing inside the Palisades and airport exclosures averaged 29 cm/year (range 16–45 cm/year) for 2005, indicating ~4.8 years were required for young aspen to attain breast height. A current annual growth of only 6 cm/year was measured at the Willow Creek exclosure and may reflect the effects of disease that was observed (e.g., chlorotic leaves, sparse canopies, blackened bark, and a high proportion of dead stems) for aspen inside and outside the exclosure.

Discussion

Wolves–elk–aspen

Although aspen is a relatively long-lived deciduous species, our age structure data were insufficient for assessing potential effects of First Nations or Europeans upon wolf–elk–aspen relationships prior to the early 1900s. However, the age structure of aspen (Fig. 5) confirm ongoing recruitment when wolves and elk within Jasper NP were absent in the early 1900s (Figs. 1*a* and 1*b*). As elk and wolf numbers increased through the 1930s and 1940s, these data hint at the beginning of a downturn in aspen recruitment during the 1930s (Fig. 5), a downturn that was well underway during the 1940s when Cowan (1947)[2,5] documented deteriorating range conditions from high levels of elk herbivory along the Athabasca Valley. Such browsing reduced reproduction of palatable woody species such as aspen, willow (*Salix* spp.), russet buffalo-berry (*Shepherdia canadensis* (L.) Nutt.), and wolf-willow (*Elaeagnus commutata* Bernh.) and allowed low-palatability herbaceous species to increase in dominance. Even mature shrubs were either dying from heavy browsing or had lost vitality to a point where fruiting was greatly curtailed or absent. A more recent study (Kay 1990), approximately 1000 km to the south in the northern elk winter range of Yellowstone NP, similarly found that heavy browsing by elk was capable of suppressing nearly all berry production of saskatoon (*Amelanchier alnifolia* (Nutt.) Nutt.), buffalo-berry, and choke cherry (*Prunus virginiana* L.).

In the early 1930s, the Athabasca Valley was "superlative beaver range" and maintained a large population of beaver (*Castor canadensis* Kuhl, 1820; Cowan 1947). However, by the 1940s, the removal of large stems of aspen and willows by beaver, while ungulates were eliminating regeneration of these plants, rendered large areas of the valley unsuitable for beaver. Thus, from the early 1930s through the mid-1940s, there was a marked decrease in beaver populations inside Jasper NP because of depleted food supplies (Cowan 1947).[5] Studies in other mountain ecosystems have similarly found heavy browsing of willows in elk winter range represents an important mechanism underlying a decline of beaver habitat and populations (Smith et al. 2004; Baker et al. 2005).

During severe winters or other periods of the 1940s when food was in short supply, elk in Jasper NP also utilized the bark of aspen trees for nutritional value. Thus, throughout much of the park's winter range, Scharff (1972) found bark along the base of mature aspen trees blackened (scarred) up to a height of ~2 m as a result of elk "barking" during previous decades.

Because of deteriorated ungulate winter range, Jasper NP began to reduce elk numbers in the early 1940s, while, ironically, control efforts were underway that nearly eliminated wolves from the park and across much of Alberta. Even though ~80 elk/year were slaughtered in Jasper NP over a period of 28 years, aspen recruitment during Jasper NP's second functional extirpation of wolves in the 1950s and 1960s was essentially nonexistent at both the Palisades and Willow Creek sites (Fig. 5).

It was not until the 1960s that elk began to heavily utilize the relatively remote area of winter range at the Willow Creek site, yet our age structure data (Fig. 5*b*) indicate a total lack of recruitment in the 1950s. We hypothesize that as-

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[5] I.M. Cowan. 1943. Report on game conditions in Banff, Jasper, and Kootenay National Parks, 1943. Unpublished report. Parks Canada, Ottawa, Ont.

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Fig. 5. Histograms of aspen frequency by decade of establishment at the (*a*) Palisades site and (*b*) the Willow Creek site. Exponential functions (broken lines) were fit through decades with frequent establishment to highlight periods with missing age-classes.

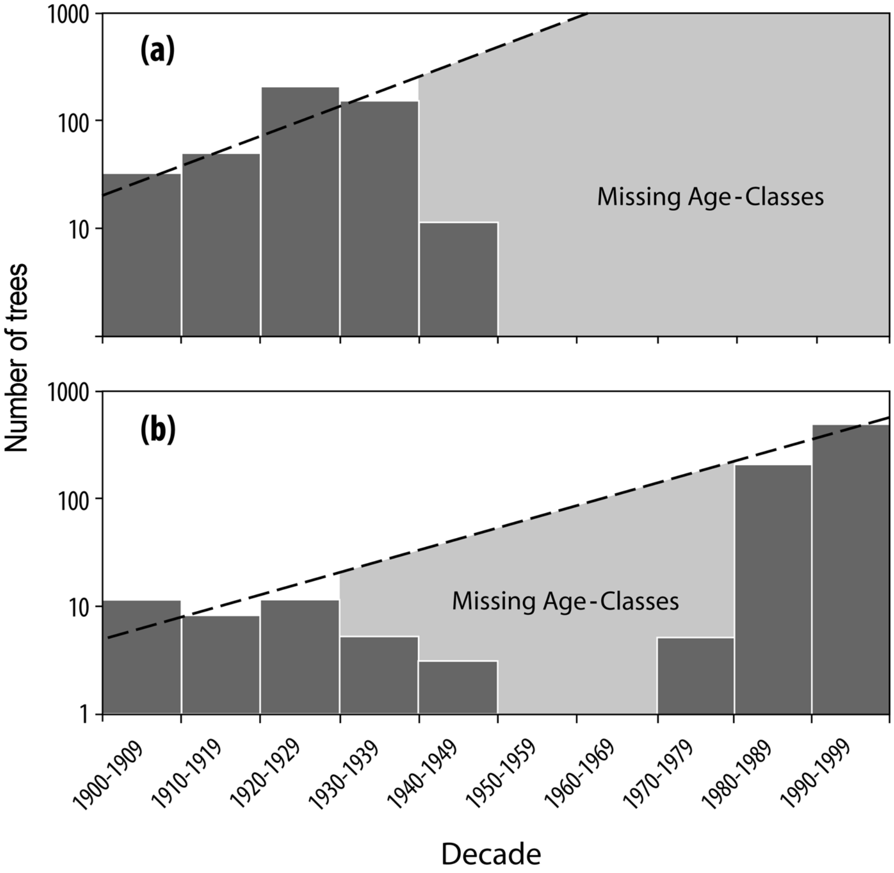


Fig. 6. November through March snowfall totals by year at the Jasper townsite from 1917 to 2000.

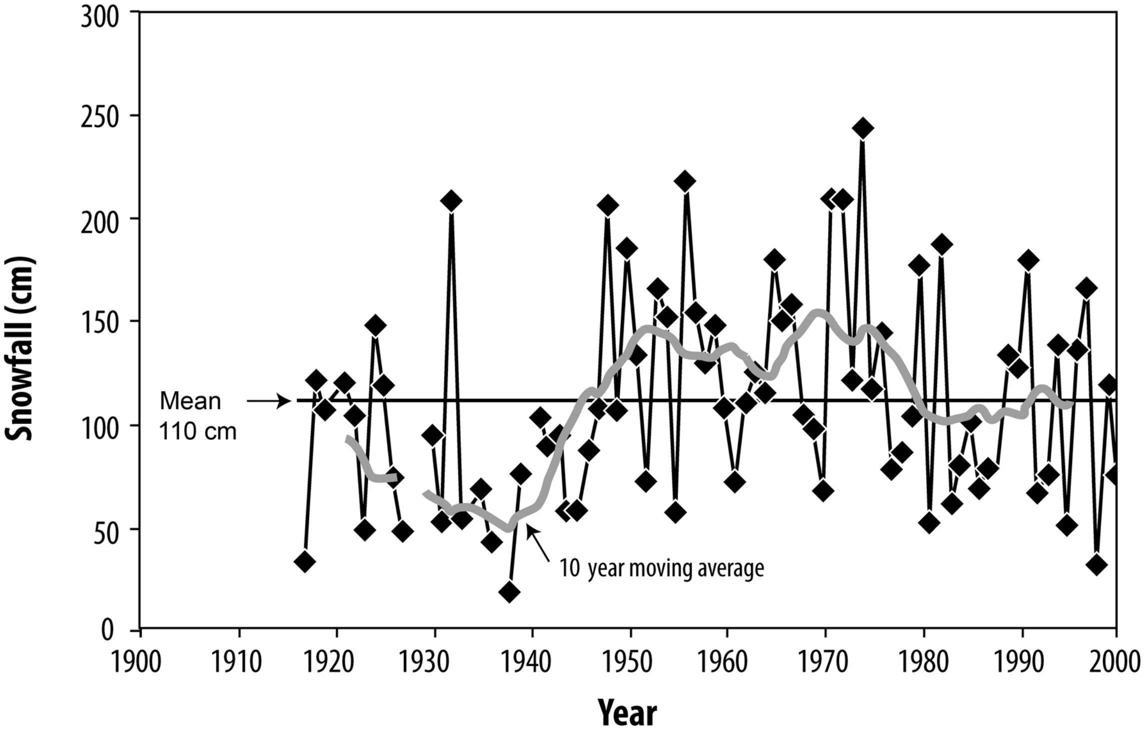
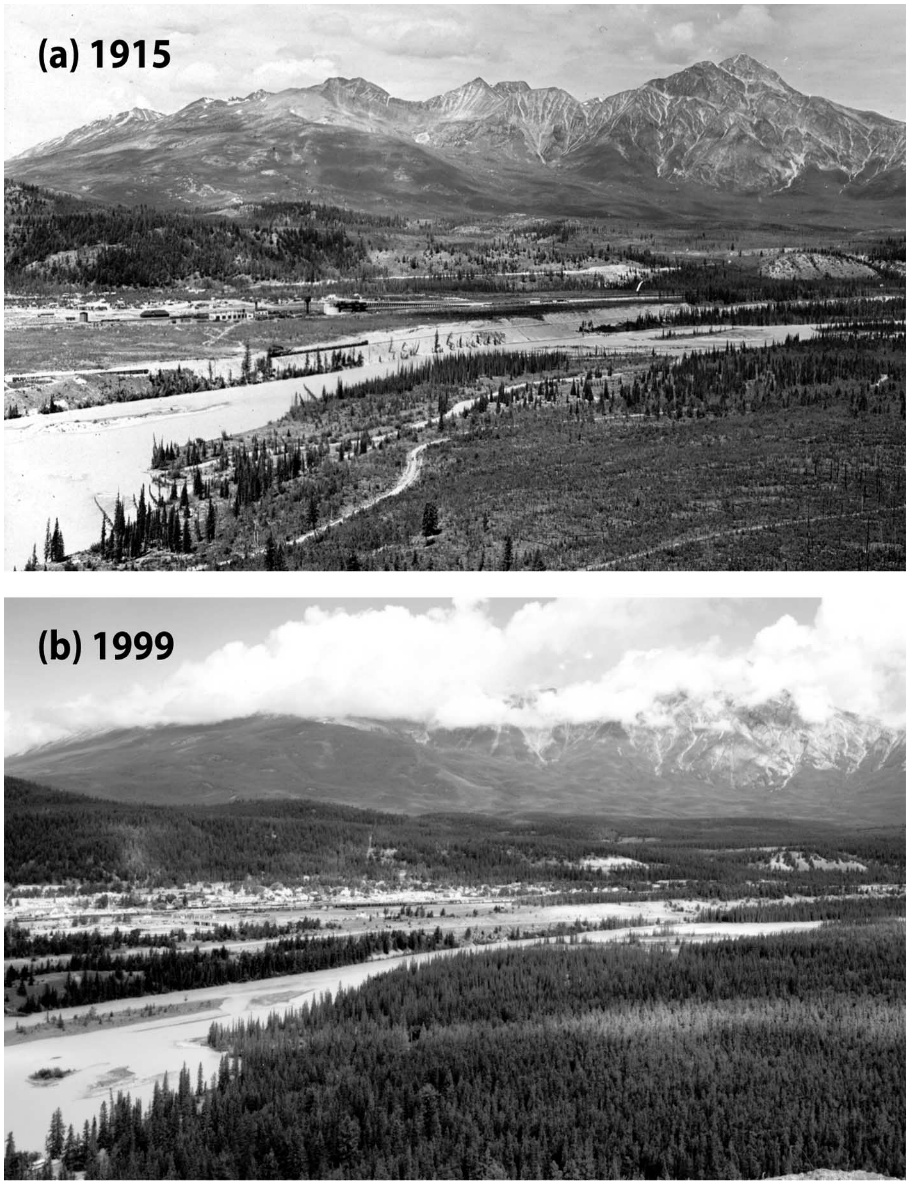


Fig. 7. Chronosequence of photographs in (*a*) 1915 and (*b*) 1999 from Old Fort Point looking northwest across the Athabasca River towards the Jasper townsite; note the loss of ungulate winter range in the foreground following conifer reestablishment following fires in the late1800s – early 1900s. Photo credits: (*a*) M.P. Bridgland, Jasper Yellowhead Museum and Archives (84.21.5 volume 3A, station 26 and (*b*) Copyright J. Rhemtulla and E. Higgs (photo 216, station 26).

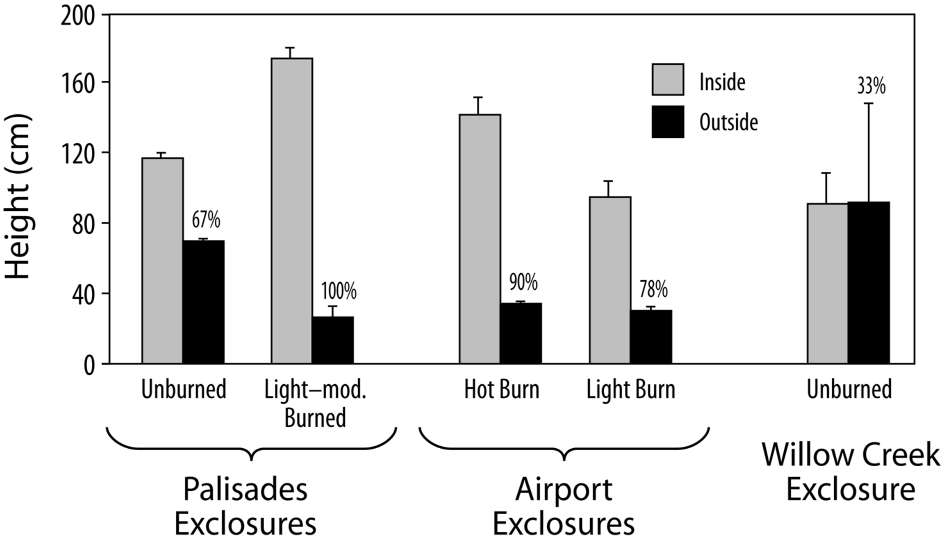


pen utilization by 500–600 elk and the wintering of up to 200 horses by the park service in the late 1960s[3] was sufficient to damage and eventually kill any aspen that might have become established in the 1950s.

The reduction in habitat use by elk in the Willow Creek area after the mid-1970s (Fig. 1*c*) and subsequent recovery of aspen recruitment measured at the Willow Creek site is in direct contrast to the continued lack of aspen recruitment at the Palisades site in the Athabasca Valley. Since Dekker (1985) found that wolves denned in the Willow Creek area from the mid-1960s into the early 1980s, this would suggest increased predation risk may have contributed to the reduced habitat use by elk in this area that began in the 1970s and continued through the 1990s. Long-term observations in Jasper NP led Dekker and Bradford (2001) to indicate that "the catalyst that drives elk movements appears to be wolf predation." After the 1970s, elk generally avoided using winter range in the Willow Creek area even though widespread recruitment of aspen and the growth of willows in recent decades provided abundant browse. Initial recruitment of willow, cottonwood (*Populus* spp.), and aspen (at least locally) has also been observed following the 1995–1996 reintroduction of wolves into Yellowstone NP (Ripple and Beschta 2004, 2007; Beyer 2006).

At the Palisades site, the cessation of aspen recruitment that began in the 1950s and which has continued to the present appears to confirm the effect of long-term foraging or browsing by elk in areas close to human developments and activities (e.g., highways, campgrounds, and the townsite). In recent decades, this situation may also reflect an at-

Fig. 8. August 2005 mean heights of young aspen inside and outside of ungulate exclosures (constructed in 1998). Errors bars are SEs. Values above the bars show the percentage of plants outside the exclosures that were browsed during the 2004–2005 winter.



tempt by elk to reduce predation risk (from wolves). Similarly, with the occurrence of recolonizing wolves in Banff NP, elk have increasingly utilized habitats close to and within areas of human development (White and Feller 2001; Hebblewhite et al. 2002).

In western Alberta, White (2001) evaluated age structure of aspen stands in nine sample areas distributed along nearly 300 km of the eastern Rocky Mountains. In the vicinity of our Willow Creek site, sampled aspen stands showed a bimodal age structure, much like that presented in Fig. 5*b*, whereas all remaining sites illustrated a decrease in aspen recruitment during the last 50 years. The “state and transition model” of White et al. (2003) indicates that high elk densities reduce aspen recruitment and eventually put at risk the maintenance of a viable root system and survival of a stand (clone). Kay (1997*b*) also found decreased aspen recruitment at Kootenay and Yoho NPs from about the mid-1930s and attributed it to several factors including the elimination of aboriginal burning, fire suppression, and intense ungulate browsing. Only where ungulate browsing remained low were aspen able to successfully regenerate. At least in Kootenay NP, the 1930s and 1940s also represent a time when wolves were absent and elk numbers increased (Park service files).

Aspen forests are the most species-rich forests in Jasper NP, containing >100 species of vascular plants (Lulman 1976; Achuff and Corns 1982). Commonly occurring shrubs include prickly rose (*Rosa acicularis* Lindl.), buffalo-berry, common snowberry (*Symphoricarpos albus* (L.) Blake), honeysuckle (*Lonicera* spp.), and common juniper (*Juniperus communis* L.). Other berry-producing plants, such as saskatoon, redosier dogwood (*Cornus sericea* L.), wolf-willow, currants (*Ribes* spp.), grayleaf red raspberry (*Rubus idaeus* L. ssp. *strigosus* (Michx.) Focke), and low-bush cranberry (*Viburnum edule* (Michx.) Raf.) also provide an important contribution to the biodiversity of these plant communities. Earlier, Moss (1932) similarly documented more than 100 vascular plant species comprising aspen communities in the parklands and boreal forests of Alberta. Because heavy ungulate browsing of these deciduous species can reduce food for berry- and seed-eating birds and small mammals, the major reductions or cessation of aspen recruitment found in this study, White et al. (2003) in western Alberta, and Kay (1997*b*) in Kootenay and Yoho NPs of British Columbia, likely indexes significant impacts to a variety of plant and faunal species.

Climate

Variations in weather patterns may directly or indirectly influence the temporal patterns of vegetation establishment, growth, and mortality. Additionally, winter snowfall amounts can influence the amount and spatial distribution of herbivory within plant communities that comprise a winter range. In other instances, winters of exceptionally high snowfall may cause major die-offs of elk and other ungulates, thus reducing herbivory pressure in subsequent years. In this study, the distinctly different patterns of age structure for the Palisades and Willow Creek sites (Fig. 5), which experienced essentially the same climatic regimes, preclude climate as an important control of aspen recruitment in the winter range of Jasper NP. Others (Baker et al. 1997; Hessl and Graumlich 2002) have similarly concluded that climate fluctuations are not a major factor affecting aspen community dynamics.

Fire regimes

Throughout forest and rangelands of the Rocky Mountains in Canada and the United States, fires represent an important disturbance regime. Fires that occurred in Jasper NP during the late 1800s and early 1900s, involving ∼18% of the park’s area, created and maintained open areas of herbs and shrubs, rejuvenated suckering in aspen stands, and reset plant succession where forests had burned. However, as conifers reoccupy burned-over sites or invade open areas, their crowns eventually limit the availability of light needed to sustain understory herb–shrub species (Lieffers and Stadt 1994). Thus, by the 1940s, when the effects of large ungulate foraging or browsing was being identified as a major

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concern in Jasper NP, increasing tree densities and canopy closure of conifers was well underway or may have already occurred in many of the areas that had burned during previous decades.[2]

Historically, the periodic occurrence of fires in southwestern Alberta maintained areas of open habitats interspersed with aspen stands (White et al. 2003). Predation-sensitive elk, held at low densities by humans and carnivores, foraged in these open habitats but tended to infrequently utilize aspen thickets. However, with predator control efforts, reduced human hunting, and the habituation of elk to humans during the 20th century, elk densities increased, while a reduced occurrence of fire (and subsequent regrowth of conifers) decreased the overall forage base available to ungulates. Thus, the ensuing high levels of herbivory resulted in few aspen stems surviving beyond the sapling age-class.

Exclosures

Young aspen inside the Palisades and airport exclosures were consistently taller than those on the outside where browsing pressure was relatively high. Long-term exclosure studies in the winter range of Yellowstone NP have similarly shown that aspen suckers and other woody browse species can quickly establish and grow inside exclosures, once browsing pressure from elk is curtailed (Kay 1990, 2001). Heavy annual browsing by elk outside the Yellowstone exclosures, when wolves were absent from the park, resulted in aspen sucker heights of only 31 ± 10 cm for over half a century (1935–1989); willows, cottonwoods, and other deciduous woody species were similarly suppressed by browsing during this period (Kay 1990; Singer 1996; Barmore 2003; Beschta 2005). At the Willow Creek exclosure in Jasper NP where browsing pressure was relatively low, heights of young willow inside and outside the exclosure were essentially the same.

Fire, normally considered an important disturbance mechanism for initiating increased aspen sucker production, was insufficient for ensuring successful recruitment of aspen into tall saplings outside of the Palisades and airport exclosures because of ungulate herbivory. White et al. (1998, 2003) earlier concluded that fire in areas of high elk density will likely “accelerate the demise of aspen,” because it may remove overstory trees with no assurance of successful recruitment by postfire suckering. Similarly, Hessl and Graumlich (2002) determined that heavy browsing effectively “decouples” the normally expected increase in aspen recruitment following fire. Conversely, Kay (1997*b*) found that, where ungulate browsing pressure was low, aspen stands in Kootenay and Yoho NPs were multiaged, because they continued to regenerate without fire disturbance. Our age structure data for the Willow Creek site (Fig. 5*b*) similarly show that, once elk herbivory decreased in the 1970s, aspen recruitment readily occurred in the absence of fire.

Conclusions

Across western North America, aspen stands have successfully sustained themselves for thousands of years during which fires (natural and human-caused), ungulate browsing, and hunting of predators and ungulates by First Nations were part of their natural history. However, results herein and in conjunction with other studies indicate that fire occurrences in areas where herbivory pressure from elk is high are unlikely to improve aspen recruitment or the maintenance of palatable shrub–herb species.

From a trophic cascades perspective, direct and indirect human interventions during the 20th century appear to have had a major role in affecting aspen age structure and the biodiversity of winter-range plant communities in Jasper NP. Direct interventions include the periodic extirpation and recovery of wolves as well as the extirpation and reintroduction of elk. Indirect interventions include those associated with human developments and activities that tend to displace wolves, thereby locally reducing predation risk experienced by elk. In conjunction with a broader literature regarding predators, prey, and plants, it appears that the removal of wolves was a predisposing factor contributing to high levels of ungulate herbivory and a cessation in aspen recruitment at the Palisades and Willow Creek sites.

The current diversity and spatial distribution of plant species in heavily browsed aspen forests of Jasper NP, and in other areas of North America similarly experiencing high levels of herbivory from wild or domestic ungulates, likely has been appreciably altered from what was originally present prior to European contact. Thus, protecting and maintaining functionally intact plant communities susceptible to herbivory and restoring those that have been impacted represent a major challenge to ecologists and society. In Jasper NP, long-term ecosystem states (elk and wolf populations and aspen stand structure) and processes (predation, herbivory, fire, and aspen recruitment) were significantly altered over much of the 20th century. Over time, it will be important to evaluate whether reestablished predator–prey interactions and future fire regimes within the park will be able to sustain recruitment of woody browse species at landscape scales as well as promote recovery of other plant species that historically comprised aspen communities and the faunal species that depended upon them for habitat needs. Perhaps the largest unknown is how humans will continue to influence these interactions.

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