

The Condition and Trend of Aspen, *Populus tremuloides*, in Kootenay and Yoho National Parks: Implications for Ecological Integrity

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Aspen (*Populus tremuloides*) communities were measured in and near Yoho and Kootenay National Parks to determine condition and trend. Most aspen stands were heavily invaded by conifers as they had not burned in 60 years or more due to modern fire suppression and the elimination of aboriginal burning. Aspen is also declining due to repeated ungulate browsing, primarily by Elk (*Cervus elaphus*). Even where disturbed by logging and burning outside the parks, many aspen stands failed to produce new stems greater than 2 m tall because all the suckers were repeatedly browsed. Only where ungulate numbers were low was aspen able to successfully regenerate. Aspen, though, is not "seral," as that term is commonly used because the species seldom grows from seed due to its demanding seed bed requirements. This, coupled with high biodiversity, makes aspen an excellent indicator of ecological integrity as mandated by Parks Canada statute.

Key Words: Aspen, *Populus tremuloides*, Kootenay National Park, Yoho National Park, ecological integrity, Elk, *Cervus elaphus*.

Aspen (*Populus tremuloides*) is an excellent indicator of ecological integrity because the species seldom grows from seed due to its demanding seed bed requirements (Perala 1990). In fact, there are no known instances of aspen clones having established from seed anywhere in the southern Canadian Rockies or in the Intermountain Western U.S. during the period of recorded history (Kay 1993). It is thought that environmental conditions have not been conducive to seedling growth and clonal establishment since shortly after the glaciers retreated 10 000 or more years ago (McDonough 1979, 1985; Perala 1990; Jelinski and Cheliak 1992; Mitton and Grant 1996). This means that the aspen clones found throughout the southern Canadian Rockies today have likely maintained their presence on those sites for thousands of years via vegetative regeneration. Thus, aspen may be among the oldest living organisms on Earth (Mitton and Grant 1996). In fact, Peterson et al. (1995:14-17) classified aspen as old-growth ancient forest.

Aspen seedlings are more common in the northern Canadian Rockies (Peterson and Peterson 1992, 1995) and there may be "windows of opportunity" that allow seedling establishment at infrequent, 200 to 400 year or longer, intervals (Jelinski and Cheliak 1992: 728), but successful sexual reproduction of aspen is still exceedingly rare (Mitton and Grant 1996). Aspen trees invariably occur as clones in which all the individual trees (ramets) are genetically identical, having grown from a common root sys-

tem by vegetative shoots (Shepperd and Smith 1993). If aspen clones are lost due to forest succession or other factors, there are no known means of reestablishment (Kay et al. 1994). As a relatively short-lived tree (< 150 years), long-lived aspen clones are often dependent on periodic disturbance such as fire to stimulate vegetative regeneration via root suckering, and to reduce conifer competition (Bartos and Mueggler 1979, 1981; Bartos et al. 1991, 1994; Shepperd 1993; Shepperd and Smith 1993). In the absence of fire or other disturbance, most aspen clones in the southern Canadian Rockies will eventually be replaced by more shade-tolerant species. Thus, the condition and trend of aspen provides information not only on an area's fire history, but also addresses the question of whether past fire suppression practices have had a significant impact on park resources (Walker and Irons 1993). While 70 or more years of active fire suppression may not have had a detectable effect on coniferous species (Masters 1990), fire exclusion may have had a greater impact on aspen communities (DeByle et al. 1987; Bunnell 1995).

In addition, aspen provides highly palatable forage for Elk (*Cervus elaphus*) and other ungulates in the Canadian Rockies (Nelson and Leege 1982; Poll et al. 1984; Timmermann 1991). Aspen is, however, sensitive to repeated browsing. High-density Elk populations commonly strip bark from mature aspen and severely browse aspen suckers, thus preventing stand regeneration which may eventually lead to the

*See Documents Cited section following Acknowledgments.

loss of aspen clones (Krebill 1972; Olmsted 1977, 1979; Weinstein 1979; DeByle 1985; Kay 1990; Shepperd and Fairweather 1994). Unlike herbaceous plants, the long-term grazing and fire histories of aspen communities can also be judged from historical and repeat photographs (Kay and Wagner 1994).

Moreover, aspen communities support an array of other species and may have the highest biodiversity of any forest type in the Canadian Rockies (DeByle and Winokur 1985; Peterson and Peterson 1992, 1995*; Stelfox 1995). Bird communities, for instance, vary with the size, age, and location of aspen clones, as well as with grazing intensity and history (Young 1973, 1977; Flack 1976; Winternitz 1980; Daily et al. 1993; Johns 1993; Westworth and Telfer 1993; Pojar 1995; Stelfox 1995). If aspen is lost, many birds and small mammals will decline; some precipitously (Ehrlich and Daily 1993).

In Yoho National Park (established 1886) and Kootenay (established 1920), aspen is common on lower-elevation montane slopes with southerly or westerly aspects (Kuchar 1978*; Achuff et al. 1984) — areas that are also rated as prime winter habitat for Elk and other ungulates (Poll et al. 1984; Van Egmond 1990). To the east in Banff National Park, high ungulate populations are believed to be having a negative effect on that park's aspen communities (Cowan 1944*, 1947, 1950; Flook 1964, 1970; Kay and White 1995). In U.S. national parks, such as Yellowstone and Rocky Mountain, Elk have had a major impact on aspen, often eliminating the species from many areas (Olmstead 1977, 1979; Kay 1985, 1990; Hess 1993; Kay and Wagner 1996). Aspen, however, has not previously been studied in Kootenay or Yoho. Moreover, none of the montane areas in either park have burned in more than 60 years due to active fire suppression programs (Kay and White 1995), which raises the prospect that Yoho and Kootenay's aspen communities may be declining due to advancing forest succession. To address these and other questions, I measured and surveyed aspen in and near Kootenay and Yoho National Parks.

Methods

I conducted a systematic survey of aspen communities in Kootenay and Yoho National Parks during September 1994 and September 1995. Both parks are situated immediately west of the continental divide in British Columbia between 50° 30' – 51° 40' N and 116° 10' – 117° 15' W. Due to both park's thick coniferous forests, steep terrain, and limited budget it was not possible to undertake a random survey of aspen stands. Instead, sampling was confined to established trails, old fire-roads, and along park highways. Each trail or road was first driven or walked and all aspen stands plotted on 1:50 000 topographic maps. Then a representative number of stands was selected for detailed measurement.

At each aspen community that was sampled during this study, a 2 x 30 m belt transect was placed perpendicular to the slope in the stand's center. To facilitate data recording, I subdivided each 30 m transect into 3 m segments and then recorded the number of live aspen stems by size classes within each 3 m segment. The following size classes were used: (1) stems less than 2 m tall, (2) stems greater than 2 m tall but less than 5 cm diameter at breast height (DBH), (3) stems between 6 and 10 cm DBH, (4) stems between 11 and 20 cm DBH, and (5) stems greater than 21 cm DBH. Ages of aspen within each size class were determined by counting annual rings. The ages of large aspen were obtained with the aid of an increment bore while smaller stems were cross-sectioned, usually those less than 5 cm DBH. Stems less than 2 m tall were not aged.

Within each stand, the following information was also recorded: (1) elevation as determined from topographic maps; (2) Universal Transverse Mercator (UTM) grid coordinates, again estimated from topographic maps; (3) aspect; (4) estimated slope in percent; (5) estimated stand size in meters; (6) bark damage — percent of stems that exhibited old black-scar, ungulate bark damage and the percent of stems with new or recent bark damage — wounds that had not yet healed over with black-colored bark, usually less than two years old (Krebill 1972); (7) an estimate of the mean percent of each stem that had been damaged by ungulate bark stripping; (8) if the stand had newly regenerated stems greater than 2 m tall but less than 5 cm DBH, an estimate of the percent that showed evidence of ungulate highlining — where the ungulates browse off all the lower branches as high as the animals can reach, usually 2 m; and (9) the percent of stems less than 2 m tall that exhibited ungulate browsing.

Items 6 to 9 provided an estimation of past ungulate use. Only Elk or Moose (*Alces alces*) strip-off and eat the bark of aspen, and bark damage usually occurs during winter when other foods are in short supply (Krebill 1972). Neither Mule (*Odocoileus hemionus*) nor White-tailed deer (*O. virginianus*) strip aspen bark, but both species of deer, as well as Elk and Moose browse aspen. Since at least 1940, however, Elk have dominated the ungulate communities in Kootenay and Yoho, especially during winter (Poll et al. 1984; Van Egmond 1990). In areas with high Elk populations, bark stripping can be so severe that the lower 2 m of aspen trunks are black instead of their normal white coloration (Kay 1990; Kay and Wagner 1994).

In addition, at each stand the number and species of conifers was recorded on the 2 x 30 m belt transect that was used to count aspen stems. Conifers were recorded by the same five size classes that were used for aspen. Total percent conifer canopy cover in each stand was also estimated according to guidelines

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community that was sampled during a 2 x 30 m belt transect was placed in the stand's center. To begin, I subdivided each 30 m transect into 10 segments and then recorded the stems by size classes within each segment. The following size classes were used: (1) stems less than 2 m tall, (2) stems greater than 2 m tall and less than 5 cm diameter at breast height, (3) stems between 6 and 10 cm DBH, (4) stems between 11 and 20 cm DBH, and (5) stems greater than 20 cm DBH. Ages of aspen within each stand were obtained by counting annual rings. Percentages of stems were obtained with the aid of a diameter tape. The smaller stems were cross-sectioned to determine diameter less than 5 cm DBH. Stems were then aged.

The following information was obtained as determined from a 2 x 30 m belt transect: (1) Universal Transverse Mercator coordinates, again estimated to the nearest meter; (2) estimated stand size in meters; (3) percent of stems that exhibited bark damage and the percent of stems with black-colored bark; (4) percent of each stem that had bark stripping; (5) if the stem was greater than 2 m tall, an estimate of the percent of ungulate highlining — the removal of all the lower branches — and the reach, usually 2 m; and (6) percent of stems greater than 2 m tall that exhib-

ed signs of past ungulate damage (e.g., stem strip-off by *Alces alces*) and bark damage usually associated with ungulate browsing. Other foods are in short supply in the area, including Mule Deer (*Odocoileus columbianus*) and deer (*O. virginianus*). The species of deer, as well as the percent of stems with bark stripping, were recorded. Since at least 1940, the impact of the ungulate community, especially during winter (Brunt 1990). In areas where bark stripping can be so severe, aspen trunks are black and the bark is missing (Kay 1990;

the number and species of stems. Conifers were recorded in each segment. Percent canopy cover in each segment was recorded according to guidelines

established by Mueggler (1988). Finally, understory species canopy cover was estimated for each stand but those data are not reported here (see Kay 1996*).

This was part of a larger project to assess long-term ecosystem states and processes in the southern Canadian Rockies (Kay et al. 1994; Kay and White 1995), but here I only report the results of my aspen research in and around Yoho and Kootenay. Aspen outside Yoho and Kootenay was included because other studies have found a marked inside-outside park difference in aspen community dynamics due to differences in ungulate use. Inside Yellowstone National Park, for instance, the area occupied by aspen has declined approximately 95% since park establishment in 1872 and even burned aspen stands have failed to successfully regenerate due to repeated ungulate browsing (Romme et al. 1995; Kay and Wagner 1996). Outside that park, however, where hunting limits Elk numbers, aspen stands have successfully regenerated without fire or other disturbance and display characteristics of climax communities (Kay 1985, 1990). The same is true in Colorado's Rocky Mountain National Park (Hess 1993). By measuring aspen stands in the same drainage with similar histories of disturbance, but with different histories of ungulate use, it is possible to determine if climatic change, fire suppression, or grazing is primarily responsible for any observed differences in community structure (Kay 1990). Kuchar (1978*), Achuff et al. (1984), Poll et al. (1984), Van Egmond (1990), and Tymstra (1991) provided information on vegetation, wildlife, and climatic conditions in Kootenay and Yoho.

Results

A total of 269 aspen stands were measured in or near Kootenay (n = 168) and Yoho (n = 101) National Parks. Most aspen stands were heavily invaded by conifers, primarily White Spruce (*Picea glauca*), Lodgepole Pine (*Pinus contorta*), or Douglas Fir (*Pseudotsuga menziesii*); mean conifer canopy cover = 38% (SEM = 2.6%). Ungulates have also had a significant impact on these aspen communities. Only where ungulate use was low had aspen stands been able to successfully regenerate — defined as producing new stems more than 2 m tall. In Kootenay National Park, aspen successfully regenerated in the Columbia Valley where there are few Elk, but not in the Kootenay Valley where most of the park's Elk winter. While in Yoho National Park, except for a handful of stands, no aspen communities successfully regenerated.

Even clear-cut stands were not able to successfully regenerate in the Cross River drainage south of Kootenay National Park. Although logging and associated soil disturbance increased sucker densities 60 fold (mean = 291 stems/ha unlogged vs. 17 337 stems/ha logged), aspen height growth was limited

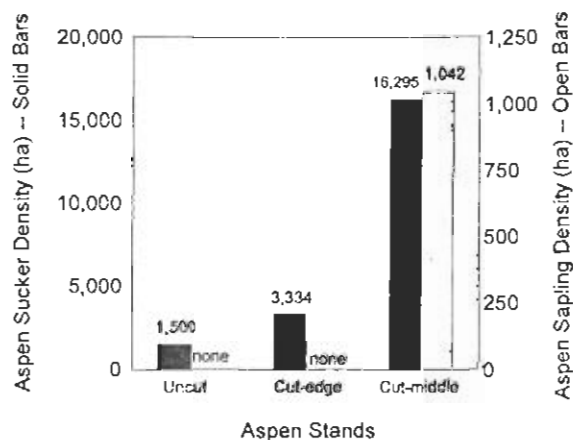


FIGURE 1. The impact of cutting and ungulate browsing on aspen regeneration west of Yoho National Park. Uncut stands had low sucker densities and no successful aspen regeneration. Fourteen years after they were treated, aspen stands within the edge of the cut-block had slightly elevated sucker densities but successful aspen regeneration was absent. In the center of the cut-block, however, where ungulate browsing was less (Brunt 1990: 88), aspen sucker densities were significantly higher and some stems had recently grown beyond the reach of ungulates. Aspen suckers = the number of aspen stems less than 2 m tall. Aspen saplings = the number of aspen stems more than 2 m tall but less than 5 cm DBH.

by ungulate browsing. A few stems, though, escaped browsing, and in only eight years, those plants attained 3 to 4 m in height, which suggests that both the site and the climate can support excellent aspen growth (Bartos et al. 1994). Similarly, in Yoho's Kicking Horse Valley, cutting and burning failed to regenerate aspen.

West of Yoho's Kicking Horse entrance, the British Columbia government cut and burned two large areas to increase forage for wintering ungulates, primarily Elk. The cut-blocks are on steep south-facing slopes above the Trans-Canada Highway. Prior to treatment, both areas were predominately aspen with low to moderate conifer invasion, primarily Douglas Fir. The trees were felled and then burned in place. That is to say, the areas were not technically logged, as none of the trunks were removed and no roads were built. Thus, unlike logging areas, there is no vehicle access to these cut-blocks. In addition, an approximately 100 m strip of vegetation was left along the highway so that the cut-blocks are not visible from the pavement. This prevents hunters shooting into the cut-blocks from the road.

At one cut-block, I measured four uncut aspen stands, four felled aspen stands at the edge of the cut-block, and four felled aspen stands in the center of the cut-block. Uncut aspen stands had low sucker

densities and had not successfully regenerated. While 14 years after they were treated, aspen within the edge of the cut-block had slightly elevated sucker densities, successful regeneration was absent because ungulate browsing prevented any of those stems from growing more than 1 m tall. In the center of the cut-block, however, where browsing was less intense, aspen sucker densities were significantly higher and some stems had recently grown beyond the reach of ungulates (Figure 1).

Elk use the edges of cut-blocks more frequently than they do the centers because the animals are reluctant to venture far from cover where they can be shot (Lyon 1979; Edge and Marcum 1985; Edge et al. 1985; Brunt 1990: 88; Lyon et al. 1985). Although sportsmen cannot drive into these cut-blocks, the areas are still hunted because they are so close to Trans-Canada Highway. Although there are no data on aspen sucker densities immediately following treatment, it is likely that the low sucker densities now seen around the inside edge of these cut-blocks are also a result of ungulate browsing (Kay 1990; Bartos et al. 1994; Shepperd and Fairweather 1994).

Only in areas where ungulate numbers were low did logged aspen stands successfully regenerate. For instance, clear-cut logging and broadcast burning on British Columbia crown lands north of Kootenay Park stimulated aspen regeneration. Mean ($n = 18$) stem densities 15 to 25 years after logging were: (1) < 2 m tall = 3288/ha; (2) > 2 m tall but less than 5 cm DBH = 6131/ha; (3) 6–10 cm DBH = 2593/ha; (4) 11–20 cm DBH = 269/ha, and (5) > 21 cm DBH = 0. The same was true along the Ice River south of Yoho Park. Mean ($n = 8$) stem densities 12 to 14 years after logging were: (1) < 2 m = 4313/ha (2) 2 m $<<$ 5 cm DBH = 6647/ha; and (3) 6–10 cm DBH = 832/ha. Many of the regenerated stems had reached heights of more than 6 m and showed little evidence of ungulate bark damage (mean proportion of individual aspen trunks scarred = 2%) or browsing (mean percent aspen suckers browsed = 9%).

There was also a correlation between ungulate use and aspen regeneration in undisturbed stands. Where ungulate use was high, no stands were able to successfully produce new stems greater than 2 m tall, but where ungulate use was low, as measured by the mean percent aspen suckers browsed and the mean percent aspen bark damage, collectively termed the ungulate use index, aspen stands successfully regenerated without disturbance. A linear regression of the ungulate use index and aspen sapling density produced a correlation coefficient of $r^2 = 0.96$, which suggests a strong negative relationship between ungulate use and aspen regeneration (Figure 2). Even stands with high rates of conifer invasion were able to regenerate successfully if ungulate use was low.

Aspen on Mount Wardle displayed a similar regeneration pattern. Mount Wardle is located north-

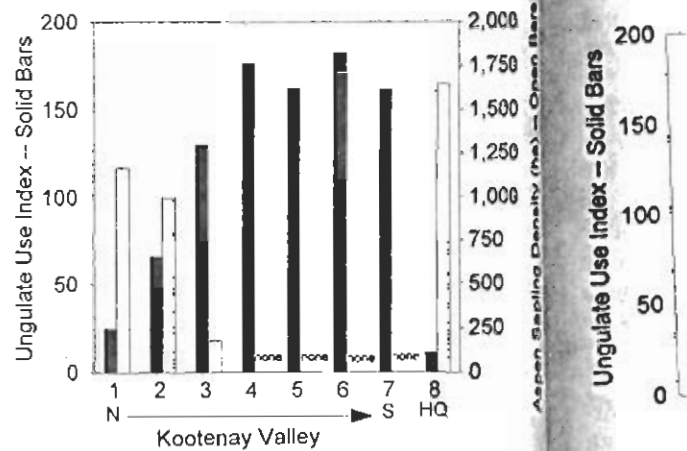


FIGURE 2. The relationship between ungulate use and aspen regeneration in Kootenay National Park. The ungulate use index (solid bars) is a combination of the mean percent aspen suckers browsed plus the mean percent aspen bark damage and is plotted with the density (ha) of aspen stems greater than 2 m tall but less than 5 cm DBH. Areas 1-7 are all in the Kootenay Valley from north to south, with one north of the park and seven south of the park while HQ is the area around park headquarters in the Columbia Valley. Where Elk use was low, undisturbed aspen stands had successfully regenerated at more than 1000 stems/ha but as ungulate use increased, stem density declined. At ungulate use levels above 140, stands failed to produce new stems greater than 2 m tall. Linear regression = Aspen Sapling Density (ha) = -9.36 (Ungulate Use Index) + 1567.73; $r^2 = 0.96$; $p < .01$. (1) Unlogged area north of the park including aspen stands KNP-131 to 133, 139, 146, 147, 153, and 156 to 158; (2) west Kootenay fire-road north — KNP-60 to 66; (3) west Kootenay fire-road south — KNP-86 to 99; (4) Highway 93 — KNP-80 to 86 and 100-102; (5) east Kootenay fire-road — KNP-27 to 42; (6) Cross River eastside fire-road — KNP-11 to 18; (7) south of park — KNP-7 to 10 and 51 to 54; and (HQ) park headquarters — KNP-43 to 50.

east of Kootenay Crossing in Kootenay National Park and its steep south-facing slopes support populations of Elk and Mountain Goats (*Oreamnos americanus*) during winter (Poll et al. 1984). Six aspen stands were measured on Mount Wardle beginning near the bottom and progressing upslope. Ungulate browsing decreased with elevation while aspen regeneration showed the opposite trend (Figure 3). Lower-elevation aspen stands had no regeneration greater than 2 m tall while upper-elevation stands had successfully regenerated without disturbance and were multi-aged. Elk use the lower slopes more intensely than they do the steeper, rockier, upslope areas. Mountain Goats neither strip the bark from aspen nor do they apparently find it very palatable. The oldest aspen in these stands were only $60 \pm$ years

FIGURE 3.

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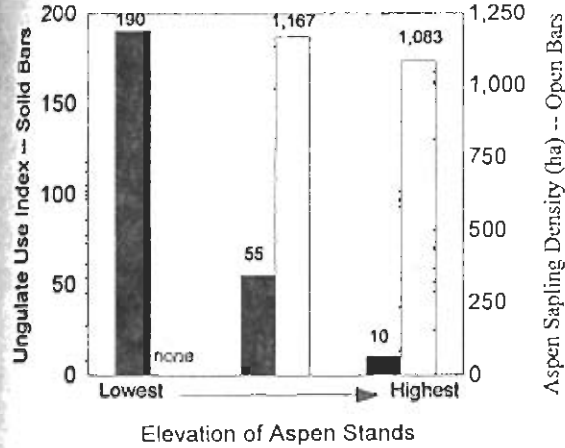
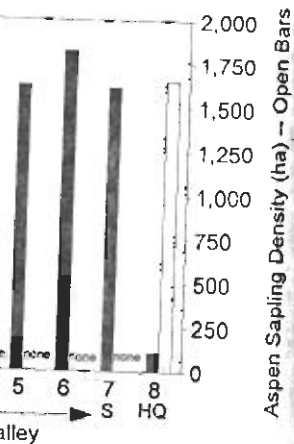


FIGURE 3. The relationship between ungulate use and aspen regeneration on Mount Wardle in Kootenay National Park. The ungulate use index (solid bars) is a combination of the mean percent aspen suckers browsed plus the mean percent aspen bark damage and is plotted with the density (ha) of aspen stems greater than 2 m tall but less than 5 cm DBH. Areas 1-7 are all in the north to south, with one area seven south of the park while area 8 and park headquarters in the south where Elk use was low, undisturbed and successfully regenerated at 1,400 stems/ha but as ungulate use declined. At ungulate use index 10 stems failed to produced new stems greater than 2 m tall. Linear regression — Aspen Sapling Density (ha) = -6.62 (Ungulate Use Index) + 1312.96; $r^2 = 0.91$; $p < .01$.

between ungulate use and aspen regeneration on Mount Wardle in Kootenay National Park. The ungulate use index (solid bars) is a combination of the mean percent aspen suckers browsed plus the mean percent aspen bark damage and is plotted with the density (ha) of aspen stems greater than 2 m tall but less than 5 cm DBH. Areas 1-7 are all in the north to south, with one area seven south of the park while area 8 and park headquarters in the south where Elk use was low, undisturbed and successfully regenerated at 1,400 stems/ha but as ungulate use declined. At ungulate use index 10 stems failed to produced new stems greater than 2 m tall. Linear regression — Aspen Sapling Density (ha) = -6.62 (Ungulate Use Index) + 1312.96; $r^2 = 0.96$; $p < .01$. (1) Unlogged aspen stands KNP-47, 153, and 156 to 158; (2) north — KNP-60 to 66; (3) south — KNP-86 to 99; (4) east — KNP-100 to 102; (5) west — KNP-27 to 42; (6) Cross — KNP-11 to 18; (7) south — KNP-50 and 51 to 54; and (HQ) KNP-43 to 50.

of age, but similarly aged trees were taller at the lower elevations. Thus, conditions are more conducive to aspen growth at lower elevations, but regeneration was better on the harsher sites. This suggests that climatic conditions are less important than ungulate browsing in determining whether or not stands can successfully regenerate.

Aspen in Kootenay and Yoho were difficult to age because many, and especially the older, stems had some type of heart rot or other disease (Peterson and Peterson 1992, 1995). This may be a natural phenomenon or it may be due to the high incidence of ungulate bark damage that has occurred in the parks (Hinds 1985). Cores without at least some heart rot were rarely encountered during this study. Many cores could not be read at all while in others, with only small bands of decayed wood, it was possible to establish approximate ages. That is to say, if there were x number of annual rings per cm before a short section of diseased core, I assumed that a cm of diseased core contained x number of growth rings. While this technique is not precise, it is the best that could be done under the circumstances. This was mainly a problem with the larger aspen as the smaller stems were usually not diseased. Thus, the younger stems were more accurately aged than the older aspen.

Because aspen "has a pronounced ability to express dominance, and overstocking to stagnation

of growth is extremely rare" (Perala 1990: 562), other studies have found a positive correlation of increasing age with increased stem DBH (Alder 1970:15-17; Masslich et al. 1988: 258; Kay 1990: 63). So it is not surprising that a linear regression of age in year and DBH in cms for all unlogged stands measured in Kootenay produced a significant positive correlation — age in years = 2.24 (DBH in cm) + 13.16; $r^2 = 0.69$; $n = 632$; $p < 0.01$. Thus for Kootenay in general, the smaller the aspen stems, the younger their age. Logged aspen stands north of the park were not included in this calculation because they had nearly double the DBH growth rate of unlogged stands which would have skewed the analysis. Instead, that regression was calculated separately — age in years = 1.45 (DBH in cm) + 6.22; $r^2 = 0.82$; $n = 147$; $p < 0.01$.

A linear regression of age in years and DBH in cms for all unlogged stands measured in Yoho also yielded a significant positive correlation — age in years = 2.24 (DBH in cm) + 29.54; $r^2 = 0.64$; $n = 121$; $p < 0.01$. This was similar to that obtained in Kootenay except the y-intercept was greater. This probably reflects the larger number of smaller-sized stems that were available for aging in Kootenay. In Yoho, only a few stands had successfully regenerated, while in Kootenay there were more sites that had successfully regenerated.

The aspen stand-age distribution for Kootenay and Yoho National Parks, or more correctly the age of

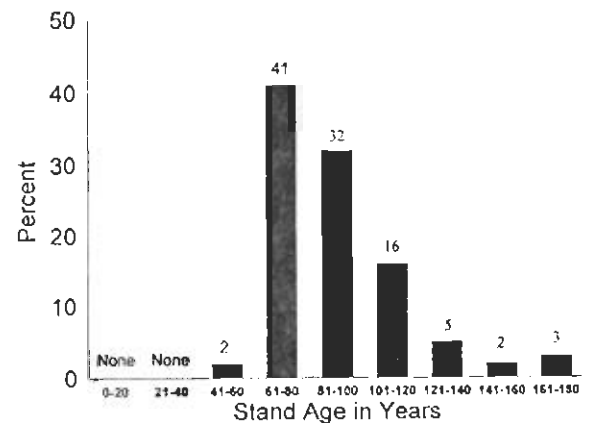


FIGURE 4. Age classes of aspen stands in Kootenay and Yoho National Parks. Fire suppression and ungulate browsing have had a dramatic impact on Kootenay and Yoho's aspen communities. There have been virtually no stand replacing fires during the last 60 years while before then aspen stands were frequently regenerated by fire when Elk populations were low. There are few stands with trees older than 150 years because that is near the maximum longevity of individual aspen stems and because historically fire-return intervals were very short; i.e., by chance alone, old age trees are uncommon in areas burned by frequent fires (Johnson et al. 1995; Lesica 1996).

in Kootenay National Park support populations of mountain goats (*Oreamnos americanus*; Peterson et al. 1984). Six aspen stands on Mount Wardle beginning to regenerate upslope. Ungulate use declined with elevation while aspen regeneration followed a opposite trend (Figure 3). Unlogged aspen stands had no regeneration on upper-elevation stands without disturbance and on the lower slopes more aspen regenerated deeper, rockier, upslope aspen regenerated over strip the bark from the stems. We find it very palatable. The aspen stands were only 60± years

the oldest aspen trees in the stands, indicates that aspen commonly regenerated ca. 1816 to 1935 (Figure 4). This probably reflects a history of frequent stand replacing fires (Van Wagner 1978) and low ungulate populations. During the last 60 years, however, few aspen stands have regenerated.

Discussion

Aspen is declining in Yoho and Kootenay National Parks due to advancing forest succession, an absence of fire, and high ungulate population densities. Aspen, however, is not "seral," as that term is commonly used. It is often claimed that aspen "is an early successional tree species [which] ... often occupies recently disturbed sites" (Campbell et al. 1994). This, though, is not true because aspen does not grow from seed either in the southern Canadian Rockies or the western United States (Mitton and Grant 1996). That is to say, if a coniferous forest is burned, aspen will not establish from seed. The only way aspen will "appear" after a burn is if it is already there; i.e. the clones are already established. By eliminating conifers and at the same time stimulating aspen growth, aspen does become more visible after fire, but only when the species is already present. So aspen is not really "seral," instead the presence of aspen indicates a long history of disturbance, primarily frequent fires.

Moreover, previous fire-history studies (Masters 1990; Tymstra 1991) underestimated the importance of fire in maintaining aspen. For aspen, it makes a difference if clones are burned once every 60 years or once every couple of hundred years. As fire-return intervals lengthen, aspen is eliminated (Shepperd and Smith 1993: 167). Noble and Slatyer (1980: 16) found that a 20 to 130 year fire frequency was necessary to maintain aspen in western Montana forests. The fire-return intervals in the southern Canadian Rockies are now longer than that necessary to maintain aspen (Kay et al. 1994).

Since Kootenay National Park was established, for instance, the fire-return interval for the Kootenay Valley increased from 92 to 165 years (Masters 1990). As few aspen trees live more than 100 to 150 years, the near doubling of the fire-return interval has probably contributed to the declining trend of aspen in Kootenay National Park. Moreover, Masters (1990) noted that the fire cycle for the entire park between 1928 and 1988 was in excess of 2700 years, while between 1788 and 1928 it was but 130 years, and between 1508 and 1778 it was only 60 years — this is a 45-fold decrease in the area burned since early historical times. The same is true in Yoho where fire-return intervals are now beyond their range of historical variability, especially in montane areas where most of that park's aspen is found (Tymstra 1991). This lengthening of the fire cycle is due to modern fire suppression and the elimination

of native burning, not climatic factors (Kay et al. 1994; Kay and White 1995; Wierzchowski 1995; Rogeau 1996).

Aspen in Kootenay and Yoho is also declining due to repeated ungulate browsing, primarily by Elk. Where ungulate populations are low, aspen has regenerated without disturbance and stands are multi-aged. At most locations, though, Elk and other ungulates browse all the aspen suckers and prevent height growth. Furthermore, forest succession with large numbers of Elk is different from succession with only a few Elk. It is clear that many "seral" aspen stands in southern Canadian Rockies can produce new stems greater than 2 m tall without disturbance if ungulate browsing is low. Thus, even "seral" aspen can maintain its presence on a site while it "waits" for the next fire to remove the encroaching conifers. So by limiting aspen regeneration, Elk in Kootenay and Yoho have not only contributed to that species' decline, but repeated browsing may also have eliminated some clones that could not "wait" for the next fire. In Yellowstone, repeated ungulate browsing has eliminated approximately one-third of the aspen clones present at park establishment (Kay and Wagner 1996).

Although logging outside Yoho and Kootenay National Parks stimulated aspen sucker production, browsing still prevented aspen height growth and successful regeneration, except where ungulate populations were low. This suggests that even if fire had been allowed to play its historical role for the last 60 years, aspen may still have declined. The very persistence of aspen in the southern Canadian Rockies over the millennia, indicates that ungulate usage, and especially Elk browsing, was not as intense in the past as it is now; i.e., the ecology of aspen suggests that Elk and other ungulate numbers were probably much lower in pre-Columbian times than they are at present — a conclusion supported by historical wildlife observations and archaeologically recovered faunal remains (Kay and White 1995).

Under current conditions, aspen's position in the ecosystem will continue to diminish from historical levels, and species that depend on aspen will also decline. If present trends continue, Kootenay and Yoho will lose the aspen communities that they once contained. The decline of aspen is not unique to the southern Canadian Rockies, but is also occurring throughout the western United States (Cartwright and Burns 1994). As discussed elsewhere, I believe that this decline has a common cause, namely the elimination of aboriginal land management practices; i.e., prior to European influence aboriginal burning stimulated aspen regeneration and native hunting in combination with carnivore predation kept ungulate populations low (Kay 1994, 1995; Kay and White 1995).

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and Yoho is also declining due to browsing, primarily by Elk. Browsing is low, aspen has disturbance and stands are young, though, Elk and other ungulates, aspen suckers and prevent forest succession with different from succession. It is clear that many "seral" stands in the Canadian Rockies can probably regenerate 2 m tall without disturbance. Thus, even in the presence of a site-specific fire to remove the site, aspen regeneration in Yoho have not only declined, but repeated browsing has eliminated some clones that could regenerate. In Yellowstone, repeated fires have eliminated approximately 50% of aspen present at park establishment (1996).

Yoho and Kootenay aspen sucker production, aspen height growth and density are low, except where ungulate browsing suggests that even if ungulate browsing is still its historical role for aspen, it has declined. The decline in the southern Canadian Rockies indicates that ungulate browsing was not as low; i.e., the ecology of aspen and other ungulate numbers in pre-Columbian times. A conclusion supported by radiocarbon dates and archaeological remains (Kay and White

1994). Aspen's position in the landscape diminish from historical times. The decline in aspen will also continue, Kootenay and Yoho communities that they once were. Aspen is not unique to the region but is also occurring in the United States (Cartwright 1994). Elsewhere, I believe the primary cause, namely the overmanagement practices that influence aboriginal land use and native ungulate predation (Kay 1994, 1995; Kay

Ecological Integrity

According to legislative directives, Canada is to manage her national parks "so as to leave them unimpaired for... future generations [and]... ecological integrity... of natural resources shall be [given] first priority...." (Woodley 1993). If we measure present ecological integrity by the state of the ecosystem that existed before European arrival, as others have proposed (Kay 1991a, 1991b; Woodley and Theberge 1992; Woodley 1993; Woodley et al. 1993; Wagner et al. 1995), then much of the southern Canadian Rockies today lack ecological integrity, especially if the condition and trend of aspen is used as an indicator of long-term ecosystem states and processes. Moreover, as coniferous forests replace aspen and grasslands, wildlife habitat is lost (Van Egmond 1990); i.e., fire suppression and a history of high ungulate populations work in concert to severely reduce ungulate carrying capacity in the future (Kay and White 1995).

Throughout North America, most national parks, wilderness areas, and nature reserves are managed to represent the conditions that existed in pre-Columbian times; i.e., so-called natural or pristine conditions. But what is natural? If Native Americans repeatedly fired the vegetation and in combination with other predators limited ungulate numbers, which, in turn, determined the structure of entire plant and animal communities, that is a completely different situation than letting nature take its course today (Wagner and Kay 1993; Kay 1995; Wagner et al. 1995). Moreover, Canada, like many countries, has chosen to use her national parks as baseline reference areas from which to judge the health of other, more developed ecosystems (Woodley et al. 1993). But again, what is natural? If ecological conditions in Canada's national parks are changing due to reduced predation on ungulates and lack of aboriginal burning, as the ecology of aspen and other data suggest, then are those parks the proper standard with which to measure ecosystem health and ecological integrity in other areas?

It must be remembered, though, that doing nothing, so called "natural regulation" or "hands-off" management, is really a value judgment and a decision that has wide-ranging consequences (Wagner et al. 1995). In Kootenay and Yoho, for instance, following the status quo means, among other things, that (1) Elk will continue to dominate the ungulate community, (2) aspen will continue to decrease and may eventually be eliminated, and (3) biodiversity will continue to decline as aspen communities are lost. In Banff National Park, the Minister of Canadian Heritage mandated Bow Valley Study recently recommended that Parks Canada implement an aggressive prescribed fire program and that steps should be taken to reduce the park's Elk herd so that aspen and other vegetation types can be maintained

at levels approaching their historical abundance (Bernard et al. 1995*; Page et al. 1996a, 1996b). I would suggest that Kootenay and Yoho National Parks implement similar active management programs if those park's biological diversity and ecological integrity are to be maintained.

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Cover: Typical aspen, *Populus tremuloides*, stand in Yoho National Park, British Columbia, showing extensive damage to bark by Elk, *Cervus elaphus*, no regeneration, and White Spruce, *Picea glauca*, invasion. Photo courtesy of Charles E. Kay. See article on the condition and trend of aspen in Kootenay and Yoho National Parks; implications for ecological integrity, pages 607-616.



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