The effects of elk on aspen in the winter range in Rocky Mountain National Park

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Baker, W. L., Munroe, J. A. and Hessel, A. E. 1997. The effects of elk on aspen in the winter range in Rocky Mountain National Park – *Ecography* 20: 155–165.

National parks face problems in managing wild ungulates and their forage resources, including small park sizes and incomplete protection of winter ranges, absence of major predators, and influences from exterior management activities. Our study focuses on the effects of elk *Cervus elaphus* browsing on aspen *Populus tremuloides* in the elk winter range of Rocky Mountain National Park. Elk can prevent successful regeneration of aspen by suckers, and increase the mortality of established trees. Here we quantify the effect of elk on aspen in the elk winter range of the park, particularly since the adoption of a policy of “natural regulation” in 1968. We collected a stratified-random sample of aspen cohorts in the elk winter range, and also inside two long-term exclosures. In each cohort we tallied live and dead trees by diameter, recorded the height and percentage of stem surface covered by bark-stripping, and estimated the date of regeneration of the cohort using increment cores. We also tallied live and dead aspen suckers (young trees <2.5 m tall) by height and the number of live and dead branches on each sucker. Aspen outside the exclosures are declining as evidenced by 1) high mortality among established trees, including entire stands that are dead, 2) low density of live suckers, insufficient to regenerate the stand, 3) suckers that are excessively branched and seldom surviving to reach tree height, and 4) almost no cohort regeneration since adoption of natural regulation. Exclosures and early photos of the elk winter range suggest these are anomalous conditions. Over the last century, aspen cohorts regenerated only when there were fewer than ca 600 elk on the park's elk winter range, far fewer than the present estimated 1600 head. Fire suppression, natural succession, fluctuations in beaver populations, climatic fluctuations, and other factors are of no or lesser importance than elk in the regeneration and survival of aspen cohorts on the elk winter range. The decline of aspen is a concern when management is focused on the ecosystem scale rather than simply the scale of wildlife and their primary forage resources.

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National parks face several difficulties in managing wild ungulate populations, their forage resources (Houston 1971), and the ecosystems in which they occur. First, parks often do not include sufficient land area or necessary resources, such as winter ranges. Second, many parks, such as those in the western United States, lack predators that formerly played a role in limiting ungulates. Third, management outside parks may influence the parks. In Rocky Mountain

National Park in Colorado, for example, the montane zone winter range for herds of elk *Cervus elaphus* is only partly contained within the park border. Major predators, such as gray wolf *Canis lupus* and grizzly bear *Ursus arctos*, were extirpated before park establishment. Outside the park there is much private and National Forest land on which elk can be hunted.

Our focus is on the repercussions of these problems for populations of quaking aspen *Populus tremuloides*,

Accepted 31 July 1996

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ISSN 0906-7590

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the primary deciduous tree in the park and a significant component of the park's biodiversity. Aspen provides important habitat for birds and other animals (DeByle 1985a, Turchi et al 1995), as well as attracting tourists in the fall, which adds to the economic prosperity of the surrounding communities. However, aspen is also a forage resource for elk in their winter range in the park. It has been suggested that aspen populations in the park may be declining because of over-browsing by elk, fire suppression, and other factors (Hess 1993). There has been similar concern about elk-related declines in high-elevation willows and white-tailed ptarmigan dependent upon these willows (Braun et al 1991).

Elk strip the bark and browse the twigs of aspen primarily in winter when understory forage is minimal or covered by snow (Olmsted 1979). Bark-stripping contributes to an increase in disease, such as fungal infections, in the larger trees (Hinds 1985). Excessive browsing during the sapling stage reduces their chances for survival (DeByle and Winokur 1985), and can also significantly reduce or eliminate new root sprouts or suckers, the primary mode of aspen regeneration. However, there are no quantitative data on present effects of browsing on aspen or the extent of successful aspen regeneration in the park's elk winter range.

In Yellowstone National Park there is similar concern about whether a decline in aspen and willows since the middle 1800's is due to over-browsing by elk or to other factors, such as climatic fluctuations and fire suppression (Kay 1990, Boyce 1991, Coughenour and Singer 1991, Singer et al 1994, Romme et al 1995). Climatic events, such as drought or late spring or summer frosts, can decrease growth and prevent suckers from regenerating (DeByle and Winokur 1985). Moist weather may favor aspen regeneration (Romme et al 1995). Aspen is confined to mesic sites (>41 cm annual precipitation) at lower elevations (DeByle 1981), reinforcing the importance of moisture to aspen regeneration. However, some researchers believe that fire suppression may be more important than elk browsing in the decline of aspen (Houston 1982). Beavers, who fell aspen near streams and wetlands, might also contribute to aspen fluctuations. A decline in beavers might lower water tables, as their ponds decay and drain, which increases moisture stress for nearby aspen in the riparian zone (Singer et al 1994).

To assess the quantitative effects of elk browsing, climatic fluctuations, and other factors on aspen in the elk winter range of Rocky Mountain National Park, we tested the null hypotheses (H_1) that aspen stands have sufficient suckers, though elk-induced mortality is high in some areas, to remain stable on the elk winter range, and (H_2) in spite of elk browsing, aspen cohorts are regenerating at a rate sufficient to balance cohort losses. We also compared the present age distribution of aspen cohorts on the elk winter range with recent

climatic records to assess the role of climatic fluctuations in aspen regeneration. We argue that fire suppression and beavers have not caused the failure of aspen regeneration on the elk winter range.

Study area

The study area is the part of the elk winter range within the boundaries of Rocky Mountain National Park in north-central Colorado (Fig. 1). The elk winter range was determined based on migration observations (Bear 1989) and maps in park files. The study area includes the open meadows of Horseshoe Park, Beaver Meadows, and Moraine Park, bounded by ridges and moraines, such as Bierstadt Moraine and Lateral Moraine (Fig. 1). The elevation of the park varies from 2378 to 4337 m, but the elk winter range occurs <2800 m. The elk winter range contains small areas of montane grassland interspersed with forest dominated by *Pinus ponderosa* and *Pseudotsuga menziesii*, as well as scattered aspen stands (Peet 1981).

Elk populations within the park have been managed in several ways (Hess 1993). Elk were hunted to near extirpation in the area of the park by AD 1900 as they were in other parts of Colorado (Swift 1945). In 1913, 49 elk were transplanted into the park area, and the herd was considered successfully established at 30 head by 1915 (Gysel 1959 says 50 head in 1915), the year the park was established (Hess 1993). The population increased rapidly, and was causing damage to the elk winter range by the 1930's (Packard 1942, 1947). Bark stripping was first reported in 1931 (Hess 1993). By the late 1930's Packard (1942, p. 480) reported that, in Beaver Meadows "every aspen in this meadow is heavily scarred as high as the elk can reach, and no branches survive below that height. There is almost no reproduction. The trees bordering the meadow are dead or dying by the hundreds. . . . It is almost certain that in comparatively few years all of these aspen will have died." In 1942, following a peak in the population at ca. 1200 head, elk were shot by park personnel, with 1045 elk removed between 1944 and 1953 (Gysel 1959). Elk numbers approximately stabilized at an average of 587 elk until 1967 (Hess 1993). Elk shooting ceased in 1962 (Olmsted 1979), but trapping and relocation continued through 1967 (Hess 1993).

In 1968, a new "natural regulation" management policy was implemented. The policy of natural regulation developed largely in Yellowstone National Park with a changing perception that predation is unimportant compared to density-dependent competition for food, space, and mates combined with weather events (e.g. extreme winters), in regulating ungulate populations (Cole 1971). This natural regulation policy has been reviewed and criticized by Chase (1986) and Kay

Fig 1 The study area and the elk winter range in Rocky Mountain National Park

(1990) Rocky Mountain National Park's version of natural regulation actually included increased hunting of elk outside the park's boundaries as a means to control populations inside the park. Hunting outside the park may have slowed the increase in elk inside the park since adoption of natural regulation. During the 1980's an average of 355 elk was harvested per year

adjacent to the park (Spowart pers comm). This amounts to ca 12% of the winter range herd, as the total herd on the elk winter range is now ca 3000 head, with an average of ca 60% of these (1800 head) on the park's part of the elk winter range over the last 5 yr (Johnson pers comm.) However, 200 of these are using alpine ranges

Methods

We identified potential aspen stands to be sampled using 1:40 000 scale color infrared aerial photographs taken in 1990. We ground-truthed each potential stand identified on the aerial photos, and mapped all stands containing more than ca. 10 contiguous live or dead trees on 1:24 000 scale U.S. Geological Survey topographic maps. Seventy-two stands suitable for sampling were mapped in the elk winter range. We then divided the elevational range (2400–2800 m) of the 72 stands into 4 strata, each 100 m wide, and allocated the sampling effort among the strata based on the percentage of stands in each stratum. The actual stand to be sampled within each stratum was chosen randomly. Aspen were also sampled in two long-term exclosures, erected in the 1960's, in Beaver Meadows and in two stands adjacent to these exclosures.

Aspen stands we sampled often contain a single predominant size class or distinct patches of different size classes that are spatially segregated. Patches of abundant suckers, for example, tend to be found around the margins or in the gaps of an overstory of large trees or in distinct patches adjacent to these trees. This mosaic pattern of size classes has been observed in other species of *Populus* (Baker 1988), where it has been shown to represent distinct episodes of regeneration. We will call the patches in this mosaic "cohorts." Whether these cohorts represent separate clones is not important for our study. Aspen stands in this area are typically even-aged, but can be uneven-aged where the overstory canopy has broken up allowing regeneration (Betters and Woods 1981). The clonal habit and even-aged structure suggest that trees might age and senesce in synchrony (Mueller-Dombois 1986), so there is a logical basis for our cohort-based sampling.

Within each stand we sampled each cohort separately using a 10 × 10 m plot, or multiple 10 × 10 m plots when the density of trees was low. A "tree" is a stem > 2.5 m tall, taller than that of the highest reach of elk browse we observed. We tallied the number of standing dead and live trees in 2 cm size classes based on diameter at breast height (dbh). Suckers, defined as stems < 2.5 m tall, were tallied in 25 cm height classes. The number of dead and live branches on each sucker was counted, excluding the current year's growth, since most browse by elk on current growth will not occur until the following winter. We used a Biltmore stick to estimate the dbh of fallen, dead trees. To determine whether or not successional replacement of aspen by conifers is occurring, we tallied conifers in each plot by height (if < 2.5 m) or dbh (if > 2.5 m).

To determine the approximate date of regeneration of a cohort, we extracted an increment core from the largest 5–10 trees at 25–50 cm above the base. We determined the difference between the age at the base and at 50 cm above the base for 15 saplings from 3

cohorts in 3 locations in the elk winter range, the mean difference was 2.87 yr with a standard deviation of 1.73 and a range of 1–7 yr. The date of regeneration of the cohort is assumed to be the date of origin of the oldest of the 5–10 trees. Tree rings were counted in the laboratory after moistening each core for better ring visibility. The rings are generally complacent, and cross-dating was not attempted. Uncorrected estimated regeneration dates are plotted by year on the graphs along with a 5-yr running mean that is a representation of the dating precision. We compared these dates versus elevation, topographic position (valley bottom, hillside, and ridge or high hillside), and by watershed (Fall River, Big Thompson, and Glacier Creek).

Several sources were used for climate data and estimates of elk abundance. We used U.S. Weather Bureau records of mean annual temperature and total annual precipitation for Fort Collins, CO, ca. 50 km northeast of the elk winter range, which has the nearest, reliable long-term weather records. Weather records from Estes Park have inconsistencies, due to movement of the station, that make them unreliable for long-term analyses (Doesken pers. comm.). April snow depth is from a station ca. 15 km south of the elk winter range. Annual total runoff (streamflow) is from the gauging station for St. Vrain Creek at Lyons, CO, which includes part of our study area in its drainage area. We used several elk population estimates (Packard 1947, Stevens 1980, Hess 1993), including records in Rocky Mountain National Park files. We searched the park's historical collection for photographs showing the condition of aspen on the elk winter range prior to park establishment.

Results

Aspen stands inside and outside the exclosures are very different in present levels of mortality and in age, reflecting the absence of elk browsing inside the exclosures since their establishment (Fig. 2). Data from inside the two exclosures were pooled, as were data from outside the exclosures, for the following comparisons. The ratio of live to dead trees is twice as high inside the exclosures (3.25:1) as outside (1.47:1) (Fig. 2b). Most of the mortality inside the exclosures is in the smallest size-classes of trees (Fig. 2a), probably reflecting a self-thinning process, while the mortality outside is more evenly distributed across the size-classes, indicating high rates of mortality even among established trees (Fig. 2b). The largest trees (> 20 cm dbh), however, do not appear to be dying at as high a rate as the smaller trees (Fig. 2b). Two of the 23 cohorts sampled outside the exclosures consist entirely of standing dead and downed trees and no live trees. Similar cohorts composed entirely of dead trees were observed in other parts of the elk winter range. The dead trees

Fig 2 Mean size class distribution of live and dead aspen inside and outside exclosures in the elk winter range

contain typical heights (1.75–2.25 m) and levels of elk browse markings on the stems (usually 60–90% of the stem surface below 2.25 m). The number of dead trees in a cohort is not correlated with either mean browse height or the percentage of stem surface that is browsed. Inside the exclosures, the larger trees are 30–36 yr old, reflecting regeneration following establishment of the exclosures, but there are also many smaller trees inside the exclosures (Fig 2), suggesting continuing regeneration. Outside the exclosures, cohorts regenerated at several times, but no cohorts regenerated near the exclosures after the increase of elk following the onset of natural regulation in 1968.

The density and morphology of suckers also differ inside and outside the exclosures. There is a much higher density of live suckers inside (mean = 2450 ha⁻¹) than outside (mean = 473 ha⁻¹, range = 0–1200 ha⁻¹) the exclosures, and a lower density of dead suckers inside (mean = 150 ha⁻¹) than outside (mean = 450 ha⁻¹) the exclosures. The corresponding mean ratio of live to dead suckers is ca 16:1 inside the exclosures and 1:1 outside the exclosures. The mean ratio of live to dead branches is much higher on the suckers inside the

exclosures (3.24:1) (also Fig 3a) than outside the exclosures (0.12:1) (also Fig 3b). The number of branches per sucker is lower inside the exclosures (8.73 per sucker) than outside the exclosures (14.69 per sucker), because of increased bud sprouting following loss of buds to browsing by elk. Many suckers inside the exclosures survive to reach the height above which elk browsing is most intense (<2.5 m) (Fig 3a), while very few suckers outside the exclosures reach this height (Fig 3b). Similarly, the number of suckers that have survived to sapling or small tree size (e.g. <6 cm dbh) is very low outside the exclosures (Fig 2b).

Climatic and hydrologic fluctuations correspond only weakly, if at all, with the approximate pattern of regeneration of cohorts (moving average in Figs 4a–d). Aspen regenerated during cooler periods prior to 1930, as well as during warmer periods in the 1930's and since 1960 (Fig 4a). Aspen cohorts regenerated during periods with lower than average total annual precipitation, such as the 1930's, as well as during periods with above average total annual precipitation, such as between 1910–1925 (Fig 4b). More direct measures of available moisture, such as snow depth and streamflow are simi-

larly equivocal Aspen cohorts, for example, regenerated during periods with above average April snowdepth, such as between 1945–1955, and during periods of fluctuating snowdepth, as between 1956–1966, but failed to regenerate during above average snowdepth periods in the late 1930's to early 1940's (Fig 4c) Similarly, aspen cohorts regenerated during periods with high annual runoff, low annual runoff, or average annual runoff (Fig 4d)

Fluctuations in elk numbers correspond more closely with the time of regeneration of cohorts (Fig 4e) Until the late 1930's, when elk numbers on the elk winter range reached above ca 750–1000, cohorts regenerated every few years on the elk winter range Then, during the 1940's, when elk numbers remained very high, there was a hiatus in aspen regeneration Intentional herd reductions did not consistently decrease elk numbers

until ca 1950 At this point, aspen cohort regeneration began again (Fig 4e) and continued through the 1960's while elk control continued When the elk populations began to increase again in ca 1970, two years after the natural regulation policy was adopted, aspen cohort regeneration essentially ceased (Fig 4e), with the exception of one cohort, regenerated in 1978, located on a steep slope west of Hallowell Park away from the middle of the elk winter range Other spatial trends in regeneration dates are not evident, there is considerable scatter in these dates within watersheds and within the three topographic positions

The sampled cohorts contain few conifers, suggesting that succession to conifers is generally not occurring in aspen stands on the elk winter range Thirteen of 23 cohorts sampled outside the exclosures lacked conifers, and in the other ten cohorts there were 22 conifer seedlings, 6 conifer saplings, and 22 coniferous trees Of these 50 conifers, 23 were found in a single stand

Mature aspen and suckers were present on the elk winter range at the time of EuroAmerican settlement, before elk were extirpated from the area of the park Several photographs in the historical collection at Rocky Mountain National Park, taken between 1900–1914, show mature aspen, an example of these photos includes Fig 5 taken on a trail along Fall River in 1905 These photos and others in the park collection show mature aspen 30 cm or more in diameter were present on the elk winter range in 1900–1914 Based on our dating of aspen trees in the elk winter range ($n = 114$), these trees would have been 70 or more years old in 1900–1914 These trees regenerated well before EuroAmerican settlers began extirpating elk from the area There also are smaller aspen, including suckers, visible in some of the photos Moreover, aspen trunks visible in these early photographs lack evidence of bark stripping, and suckers do not appear browsed Since evidence of bark-stripping persists for many decades (Olmsted 1979), it is unlikely that bark-stripping was common in the park's elk winter range in the decades prior to EuroAmerican settlement

Discussion

Sucker branching and sucker mortality, tree mortality, and cohort origin and death are the primary indicators of the health of the aspen population on the elk winter range While bark-stripping during the 1920's and 1930's is still evident on surviving trees (Olmsted 1979), there is no relationship in our sample between the amount or height of bark stripping and the number of dead trees in a cohort This is probably because bark stripping is commonly high throughout the elk winter range, and may precede tree death by decades Our results suggest that monitoring is needed at the level of

Fig 3 Mean density of aspen branches inside exclosures and outside exclosures in the elk winter range

Fig 4 Correlation of aspen cohort origin dates with environmental conditions and elk abundance. The estimated date of origin of each cohort is shown as a bar. Horizontal dashed lines represented means for the period of record. The curved lines beneath the bars represent the 5-yr moving average of the number of cohort origins. Environmental and elk data include (a) mean annual temperature at Fort Collins, (b) total annual precipitation at Fort Collins, (c) April snowdepth at the Wild Basin site, (d) total annual runoff for St Vrain Creek at Lyons for the water year (October of previous year to September of current year), (e) Elk population estimates by Stevens (1980) (summer and winter range), Hess (1993), and Johnson (pers comm) (park's part of the winter range).

the sucker and its morphology (Fig 3), the tree (Fig 2), and the cohort (Fig 4). Intentionally-placed exclosures provide supplementary evidence, but are not randomly located, and represent complete absence of elk browsing, a condition that may never have existed on the elk winter range. Random sampling of the browse-susceptible aspen population throughout the elk winter range is needed on an ongoing basis, supplemented by studies of aspen where elk are at lower densities, but still present.

Overall, our sample indicates that the aspen population in the elk winter range is declining, except in the exclosures where elk browsing has been eliminated. The indicators of decline are excessive levels of mortality in suckers (Fig 3b) and established aspen trees (Fig 2b), absence of successful regeneration of cohorts since 1978 (Fig 4e), and evidence that few of the suckers now alive will grow into trees (Figs 2b and 3b). The number of live suckers outside the exclosures (mean = 473 ha⁻¹, range = 0–1200 ha⁻¹) is well below the number (2500 ha⁻¹) estimated to be needed for successful stand regeneration in mature aspen stands (Mueggler 1989), whereas the density of suckers inside the exclosures (2450 ha⁻¹) is adequate. The excessive branching of suckers outside the exclosures (Fig 3b) suggests that

elk are causing apical suppression, which prevents these suckers from ascending to tree height (Olmsted 1979) to replace dying overstory trees. Even in cohorts with moderate live sucker densities (1200 ha⁻¹) these suckers are not surviving to reach tree height. We thus reject the null hypothesis (H₁) that the aspen stands on the elk winter range (outside the exclosures) are producing sufficient suckers to maintain the population.

There is a strong relationship between the number of elk and episodes of aspen cohort regeneration on the elk winter range (Fig 4e). Over the last 60–70 yr when elk abundance on the elk winter range rose above ca 600–750 head, aspen ceased regenerating new cohorts on the elk winter range. Elk abundance on their winter range rose above this level in ca 1970 following the adoption of the natural regulation policy, and since 1980 an average of ca 1600 elk have been on the part of the elk winter range that is the subject of this study. Since 1970 (ca 25 yr) only one aspen cohort regenerated in our sample of the elk winter range (in a marginal area away from the center of the range). During the 1950's and early 1960's, when elk were intentionally maintained at or below 600–750 head, six cohorts regenerated (ca 9 per 25 yr). Two of 23 cohorts we sampled are entirely dead and many others have high levels of mortality (Fig 2b). Aspen on the elk winter range does not appear to constitute a stable shifting mosaic of regenerating and dying cohorts, as all the cohorts we sampled lack sufficient suckers to replace dying overstory trees and new cohorts have not appeared. Our data suggest that aspen cohort loss exceeds aspen cohort regeneration since the onset of natural regulation. We reject H₂, and conclude that aspen are declining at the cohort level.

Earlier studies in Rocky Mountain National Park noted the consistent relationship between declining aspen viability (high mortality and lack of successful sucker regeneration) and increasing elk abundance over the last 60–70 yr (Olmsted 1979). Bark-stripping was noticed by 1931 on the elk winter range (Gysel 1959, Hess 1993) when elk numbers were ca 200–300 (Stevens 1980), but excessive aspen stem mortality was not mentioned at that time (Ratcliff 1941). Private lands were purchased in 1932 to expand the elk winter range. However, the increase in elk numbers must have offset this winter range expansion, or mortality from bark-stripping in the 1920's and 1930's had a delayed effect, because by ca 1940 Packard (1942) noted heavy aspen mortality along the stream in Beaver Meadows. After elk reductions between 1944 and 1953, Gysel (1959) noted (but did not quantify) dead and dying aspen, but did find (1959 p 699) that "in some areas where there is little browsing, these root suckers are numerous in the vicinity of both live and dead trees, enough to perpetuate the stands." The elk winter range was expanded again in 1962 by purchase of private land (Hess 1993), but this did not alleviate elk impacts on

Fig 5 Aspen along "a trail near Fall River" in 1905, taken by an unknown photographer (Photo courtesy of Rocky Mountain National Park). Note that more than one size class of aspen is present.

aspen. By the late 1970's following cessation of elk population control within the park in 1968, Olmsted (1979 p 91) reported that "only two of the thirteen clones examined within the study area retained volumes of seasonal twig growth sufficiently large to suggest that the clones can persist." Of these two, one clone was in an enclosure and in the other clone Olmsted reported (1979 p 91) that "sprouts are not developing into mature trees." He predicted (p 96) "the probable disappearance of most of the stands in the near future." Park reports on the condition of aspen on the elk winter range echoed this prediction through the 1980's (Hess 1993), and present levels of mortality support this prediction (Fig 2b).

On other elk winter ranges in the Rocky Mountains, elk browsing is similarly affecting aspen viability (Krebill 1972, Schier 1975, Kay 1990, Kay and Wagner 1994). In Yellowstone National Park, heavy utilization of aspen by ungulates suppresses vertical growth and lowers the probability of successful regeneration and perpetuation of the aspen population (Kay 1990, 1993, Kay and Wagner 1994, Romme et al 1995). Kay reported a 95% loss of aspen aerial extent since 1872. Areas in which excessive elk browsing is occurring also have a high mortality of overstory trees (Krebill 1972, Schier 1975).

Beavers may also play a role in aspen regeneration, although their effects are likely to be minor. Beavers cut aspen, then feed on the bark and small branches, and also use the stems in their dams (DeByle 1985b). Beavers were undoubtedly adversely affected during the early trapping period before 1840 (Wishart 1979), but their populations had generally recovered in the Front Range by ca 1910 (Yeager and Hill 1954), near the time of the early photographs we found showing aspen was common on the elk winter range. Beavers have declined on the elk winter range since elk increased in the 1930's (Hess 1993). Any effect of beavers and their decline in our study area is concentrated in the vicinity of wetlands and streams (Packard 1942). Early photographs show healthy aspen stands were present near streams and wetlands, as well as away from these areas. Most aspen stands in our sample are far from areas populated by beavers, but still have high levels of mortality.

Fire suppression has also been offered as an explanation of aspen decline. Fire may stimulate aspen seedling production (Kay 1993, Romme et al 1995) and sucker regeneration (Schier and Campbell 1978, Jones and DeByle 1985, Bartos et al 1991). Houston (1982) believed that periodic hot fires were necessary for aspen maintenance, and that the decline in aspen in Yellowstone National Park was mostly due to fire suppression. Hess (1993) argued that (p 60) "fire suppression in Rocky Mountain National Park is completing what elk began – the destruction of plant community and landscape diversity – and it is doing so on a much grander

scale than congregations of elk on the park's winter range." Hess directed these statements at the entire distribution of aspen in the park, rather than just the elk winter range.

Fire suppression cannot explain the decline in aspen on the elk winter range in the park for three reasons. First, there is no relationship between fluctuations in aspen regeneration and the history of fire suppression. There was a decrease in aspen regeneration in the late 1930's and early 1940's on the elk winter range (Fig 4e). Fire suppression has been practiced in the park since the 1920's, and continued beyond the 1940's to the present, so fire suppression cannot explain a decrease in aspen regeneration during this particular period. Also, there was successful aspen regeneration during the 1950's and 1960's despite ongoing fire suppression (Fig 4e). Second, fire clearly is not necessary for aspen regeneration on the elk winter range. In both Yellowstone National Park (Kay 1990) and our study area, aspen regenerated well in enclosures where there were no fires. Aspen also regenerated well during the 1950's and 1960's when fires were being suppressed. Third, even though more aspen suckers might be produced following a fire, virtually all of these suckers would fail to reach tree height at the present time due to elk browsing (Bartos et al (1991) and Kay (1990, 1993) similarly found that elk severely reduced post-fire seedling and sucker densities in Wyoming. Kay (1990) found that aspen did regenerate when elk populations declined in Eagle Creek near Yellowstone National Park in spite of ongoing fire suppression, as is the case in our study area. Fire suppression bears no relationship with the marked fluctuation in aspen regeneration we identified on the elk winter range (Fig 4e). Fire might temporarily stimulate sucker regeneration, but would not likely change the low probability that suckers will reach tree size.

There is also no evidence in our study area that aspen decline is simply normal succession from aspen to conifers. Hess (1993 p 61) linked this idea with the need for fire in aspen regeneration: "aspen in Rocky Mountain National Park is primarily a successional species, dependent on fire for its renewal, maintenance, and perpetuation." In Yellowstone National Park, repeat photography shows that most aspen stands present in the late 1800's have been invaded by conifers (Kay 1990), suggesting that the decline in aspen in that area is simply normal succession (Kay argues against this idea). Parker and Parker (1983) suggested that aspen persistence requires light surface fires, as more severe crown fires favor lodgepole pine *Pinus contorta*, and this species and other conifers tend to outcompete and overtop aspen. However, our sample of the elk winter range suggests there are few or no conifers present in most aspen stands on the elk winter range, and fire is unnecessary to maintain aspen dominance.

Our results suggest that aspen regeneration in the park is not clearly dependent upon favorable climatic

episodes Romme et al (1995) argued that most aspen in the northern part of Yellowstone National Park regenerated in the 1870's and 1880's during a moist climatic episode, but not successfully in that area since then. However, Kay (1990) found that aspen regenerated during the late 1960's and early 1970's in the Eagle Creek area just north of Romme et al's study area when elk browsing was reduced. In our study area aspen cohorts regenerated periodically over the last century, except during times of high elk abundance (Fig 4e). Rare, moist episodes do not appear to be important for aspen regeneration in Rocky Mountain National Park's elk winter range.

Our results and arguments together suggest that excessive elk browsing, rather than fire suppression, beavers, or climatic fluctuations, is significantly limiting aspen regeneration and survival in the park's elk winter range since the onset of natural regulation, but this was not the case prior to EuroAmerican settlement. Photographic evidence (e.g. Fig 5) suggests that in the decades prior to the influence of EuroAmerican settlers aspen were common on the elk winter range and did not show evidence of bark-stripping or sucker browsing by elk. Kay (1990) and Kay and Wagner (1994) similarly found that photos from ca 1870–1900 of aspen on the northern range in Yellowstone National Park show no evidence of bark-stripping or sucker browsing. Kay (1994) argued that there were few elk wintering on the northern range prior to EuroAmerican settlement, in part because Native American hunters kept elk populations at a low level. There is only anecdotal information about elk abundance in our study area prior to EuroAmerican settlement (Swift 1945), but the lack of elk browsing in early photographs suggests elk were less abundant on their winter range in the decades prior to EuroAmerican settlement than they are today.

If competition for food, space, and mates combined with adverse climate, rather than predation, are supposed to regulate elk densities, as the natural regulation model suggests (Cole 1971), then this regulation has been insufficient, for over 25 yr, to lower the elk population to a level that allows aspen regeneration. Ungulate populations may fluctuate in density, and regeneration of forage species may be heightened during ungulate population crashes (DeByle 1979), but there has not been a crash of sufficient magnitude during these 25 yr, in spite of severe winters and ample climatic fluctuation (Fig 4). If an elk population crash does not occur until after forage species have been depleted, then it could be argued that the theory of natural regulation is invalidated (Kay 1990). However, Boyce (1991) believes that elk should be expected to have major effects on vegetation, and if there are impacts such as we have documented, then this is insufficient to invalidate natural regulation. It also could be argued that since aspen is not the primary forage species expected to limit elk on the elk winter

range, it is a poor indicator of the success or failure of natural regulation (Romme pers. comm.). Our perspective is that if a significant component of the ecosystem, whether or not it is a primary forage species, is depleted relative to its pre-EuroAmerican abundance, then this is a strong indication that natural regulation is not an effective ecosystem management strategy, regardless of its value in managing the wildlife/forage part of the ecosystem.

This distinction between managing just the wildlife/forage system as opposed to the broader ecosystem is also reflected in the question of carrying capacity. Park staff in the 1940's suggested carrying capacity was ca 400 elk, but other estimates suggested perhaps 600 head (Hess 1993). However, Hobbs et al (1982) estimated the carrying capacity as between 991 ± 102 to 1674 ± 270 head over a two-year period, based on an analysis of energy and nutrient requirements of elk. However, these estimates consider only elk survival. Moreover, it can be argued that carrying capacity is dynamic, since elk clearly are influencing the future ability of their winter range to provide forage. DeByle (1979) argued that a more holistic interpretation of carrying capacity should include the sustainability of the other components of the ecosystem. In the context of our focused study of aspen, a significant part of the ecosystem, this species is unlikely to regenerate cohorts on the elk winter range and maintain existing cohorts unless elk are reduced to the level of the 1950's (average of ca 600 head). Other wildlife species, such as willow ptarmigan, also appear to be being adversely affected by high elk numbers (Braun et al 1991). The simple balance or imbalance between wild ungulates and their primary forage resources is an insufficient indicator for managing integrity or health on the ecosystem scale.

Acknowledgments – We appreciate the assistance of Richard Bachand, Therese Johnson, Frank Brown, and Richard Naumann. Comments by Dan Binkley, Mark Boyce, Therese Johnson, Karl Hess, Charles Kay, Charles Olmsted, John Pastor, William Romme, Francis Singer, and Thomas Stohlgren greatly improved an earlier version of this paper. This study was supported by a McNair Scholar award to J. A. Munroe, and by the National Park Service, Global Change Program, under Cooperative Agreement No. CA 1268-1-9009.

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