



After long-term decline, are aspen recovering in northern Yellowstone?



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ABSTRACT

In northern Yellowstone National Park, quaking aspen (*Populus tremuloides*) stands were dying out in the late 20th century following decades of intensive browsing by Rocky Mountain elk (*Cervus elaphus*). In 1995–1996 gray wolves (*Canis lupus*) were reintroduced, joining bears (*Ursus* spp.) and cougars (*Puma concolor*) to complete the guild of large carnivores that prey on elk. This was followed by a marked decline in elk density and change in elk distribution during the years 1997–2012, due in part to increased predation. We hypothesized that these changes would result in less browsing and an increase in height of young aspen. In 2012, we sampled 87 randomly selected stands in northern Yellowstone, and compared our data to baseline measurements from 1997 and 1998. Browsing rates (the percentage of leaders browsed annually) in 1997–1998 were consistently high, averaging 88%, and only 1% of young aspen in sample plots were taller than 100 cm; none were taller than 200 cm. In 2012, browsing rates were much lower at 44%, and young aspen were taller on average with 34% >100 cm and 5% >200 cm. Most (62%) of the variation in height of young aspen in 2012 was explained by browsing intensity. Furthermore, in 2012, 25% of stands had at least five aspen saplings tall enough to escape elk browsing (≥ 200 cm spring height), a condition that has not occurred for decades and happened despite a recent drought. Sapling recruitment did not increase until browsing decreased, following substantial changes in elk density and distribution, and was not significantly related to stand productivity or climate fluctuations. These results suggest that large carnivore restoration, through effects on prey, may aid aspen recovery where aspen have been suppressed by elk.

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1. Introduction

In northern Yellowstone National Park (YNP), stands of quaking aspen (*Populus tremuloides*) declined during the 20th century as mature trees died but were not replaced by new trees (Romme et al., 1995). This lack of new aspen trees was primarily due to intensive herbivory by elk (*Cervus elaphus*) in winter, which suppressed the growth of young aspen (Kay, 2001; NRC, 2002; Barmore, 2003; Larsen and Ripple, 2003; Kauffman et al., 2010). The decline of aspen recruitment (i.e., growth of sprouts into saplings and trees) on the northern Yellowstone elk winter range (“northern range”) roughly coincided with the extirpation of wolves (*Canis lupus*). Some researchers (Ripple and Larsen, 2000; Ripple et al., 2001) hypothesized that the removal of these large predators contributed to aspen decline through a trophic cascade (Schmitz et al., 2000; Terborgh and Estes, 2010) when elk were released from predation pressure. Other factors that may have suppressed aspen recruitment in addition to herbivory included

suppression of fire, and a period of drought in the 1930s (Houston, 1982; Romme et al., 1995; YNP, 1997; Eisenberg et al., 2013).

Reintroduction of wolves to YNP in 1995–1996, and a concurrent increase in grizzly bears (*Ursus arctos*) (Schwartz et al., 2006; Barber-Meyer et al., 2008), provided an opportunity to observe the effects of large carnivore restoration on elk and possible effects on plants, with potential for increased survival and height of young aspen. After the return of wolves, Ripple and Beschta (2007, 2012b) found a decrease in browsing associated with “the first significant growth of young aspen in the northern range for over half a century,” and hypothesized that this was the result of a trophic cascade resulting from wolf reintroduction. Kauffman et al. (2010), using different methods, did not find evidence of reduced browsing or aspen recovery and concluded that no trophic cascade benefiting aspen had yet begun. These disparate findings and the ensuing debate demonstrated a need for further investigation of the extent and timing of a possible aspen recovery (Beschta and Ripple, 2013; Kauffman et al., 2013).

Trophic cascades in Canadian parks involving wolves, elk, and aspen have been attributed to a combination of low elk densities

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and predation-risk avoidance behavior (White et al., 1998, 2003; Hebblewhite et al., 2005; Beschta and Ripple, 2007; Hebblewhite and Smith, 2010). As in Yellowstone, bears (*Ursus* spp.) were present in these areas but it was wolves that were associated with lower elk densities and greater aspen recruitment. Evidence for trophic cascades involving wolves and cervids has also been found in the Great Lakes region (Callan et al., 2013) and in a national park in Poland (Kuijper et al., 2013).

Since the return of wolves to YNP, elk numbers have declined substantially on the northern range (White et al., 2012), so it may be reasonable to expect some response in plants browsed by elk. Conversely, relatively low elk numbers in the 1950s and 1960s did not result in new aspen recruitment (YNP, 1997; Barmore, 2003; Wagner, 2006), so aspen recovery with reduced elk numbers is not a foregone conclusion. If aspen recovery has now begun with similar elk numbers to those of 1950–1970, this would suggest a role for behavioral or trait-mediated responses to predation (Schmitz et al., 2004) in addition to simple reduction of elk numbers. Other factors besides predation also have affected elk population dynamics, including hunting outside the park, a severe winter in 1997, and perhaps a period of drought in the early 2000s. Some researchers have argued that these factors were more important than predation as causes of elk decline prior to 2006 (Vucetich et al., 2005; Eberhardt et al., 2007). However, winters after 1999 were mild, hunting was greatly reduced after 2005, and the drought ended by 2007, with little change in trends of declining elk density and shifting distribution (Hamlin and Cunningham, 2009; White et al., 2012; White and Garrott, 2013). In the same period of time, wolves became the primary cause of elk mortality in the northern Yellowstone herd (White and Garrott, 2005a; Hamlin et al., 2009; White et al., 2010), while bears became the leading cause of elk calf mortality (Barber-Meyer et al., 2008). Densities of these predators has been greatest in the park, while the winter elk hunt north of the park has been eliminated (White et al., 2012), allowing elk to reduce predation risk by wintering outside the park.

If aspen have begun to recover due to a reduction in elk herbivory, we would expect to find reduced rates of browsing associated with greater recruitment of tall aspen saplings above the browse level of elk, >200 cm in height (Kay, 1990; White et al., 1998). Reduced browsing intensity would also be likely to result in greater variation in the height of young aspen, due to differences in the amount of time since release from browsing or stand productivity affecting height after browsing is reduced. To test these hypotheses, we evaluated aspen stand conditions on the YNP northern range in the summer of 2012 and compared our results to similar data collected in 1997–1998, 14 years earlier (Larsen and Ripple, 2005), when wolves returned and the elk population began to decline. We used more extensive random sampling of aspen stands than in other recent studies of northern range aspen (Kauffman et al., 2010; Ripple and Beschta, 2012b) and sampled not only the population of young aspen within each stand, but also the tallest five as an indication of recent recruitment. We considered the possible effects of site productivity, climate, and annual snow accumulation on browsing intensity and aspen height, and analyzed the age distribution and recruitment history of trees in aspen stands.

2. Study area and background

2.1. Study area

Valleys of the upper Yellowstone River and its tributaries comprise YNP's northern range, the wintering grounds for elk, bison (*Bison bison*), deer (*Odocoileus* spp.), and small numbers of pronghorn (*Antilocapra americana*) and moose (*Alces alces*). In these

valleys, dry grasslands and sagebrush (*Artemisia* spp.) steppe are interspersed with groves of aspen. The upper slopes are forested with Douglas fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*) and Engelmann spruce (*Picea engelmannii*). Aspen and willow (*Salix* spp.) are often found along streams, and cottonwood trees (*Populus angustifolia* and *Populus trichocarpa*) along the larger rivers (Houston, 1982; NRC, 2002). The northern range extends outside of YNP north along the Yellowstone River basin (Lemke et al., 1998; White et al., 2012), but our sampling was limited to the portion within the park (Fig. 1).

2.2. Aspen and other woody browse plants

Quaking aspen stands greatly enhance wildlife habitat and species diversity, though they occupy only a small portion of the landscape in the northern Rocky Mountains (Romme et al., 1995; White et al., 1998; NRC, 2002). Fire can stimulate aspen reproduction and aid seedling establishment. In the absence of fire, sprouting from roots (suckering) accounts for most or all aspen reproduction, and trees in a stand generally share a single root system. Stands in the Yellowstone area are often small and widely separated in seeps or riparian areas, and may persist for centuries though individual trees typically survive less than 150 years. Coniferous trees may invade and replace aspen stands where conditions are suitable, unless fire resets succession. Aspen are highly palatable to elk, and intensive herbivory can eventually kill a stand if new root sprouts cannot survive to replace older trees (Romme et al., 1995; Kay and Wagner, 1996; Seager et al., 2013). This suppression by herbivory was the condition of most aspen stands on the Yellowstone northern range during most of the 20th century and young aspen were consistently very short, <50 cm (Kay, 1990; Renkin and Despain, 1996; NRC, 2002; Barmore, 2003; Larsen and Ripple, 2003). Thus, aspen stands in 2012 exhibited a gap in recruitment, as indicated by an overstory of mature trees and an understory of young aspen, but an absence of intermediate sizes and ages (Fig. 2). Similarly, willow, cottonwood, and other palatable browse species such as serviceberry (*Amelanchier alnifolia*) were suppressed by intensive herbivory (Kay, 1990; NRC, 2002; Singer et al., 2003; Beschta, 2005; Beyer et al., 2007; Wolf et al., 2007), but heights and canopy cover of these plants increased in portions of the northern range following wolf reintroduction (Smith and Tyers, 2008; Tercek et al., 2010; Baril et al., 2011; Ripple and Beschta, 2012b; Ripple et al., 2014). In some places willow heights are now influenced more by abiotic factors such as water and soil conditions than by browsing (Bilyeu et al., 2008; Tercek et al., 2010; Marshall et al., 2013), evidence of a significant reduction in herbivory (Singer et al., 2003; Hebblewhite and Smith, 2010).

2.3. Elk

Beginning in the 1930s, elk and bison herds in the park were culled to reduce numbers in an effort to reduce damage to vegetation on winter ranges (Houston, 1982; YNP, 1997; Wagner, 2006). After culling ended in 1969, annual counts of wintering elk on Yellowstone's northern range sharply increased (Fig. 3), from a low of about 3,200 in 1969 to 19,000 elk in the early 1990s. There were no counts in 1996 or 1997, but the winter of 1997 was unusually severe and many elk died from starvation or were killed by hunters when snow drove them out of the park (Garrott et al., 2003). In 1998 less than 12,000 elk were counted. By then, wolves were increasing on the northern range and elk numbers continued to decline, due to hunting outside the park (prior to 2006) and predation by wolves and bears (White and Garrott, 2005a, 2013; Eberhardt et al., 2007; Barber-Meyer et al., 2008). Drought prior to 2007 may also have affected elk recruitment (Vucetich et al.,

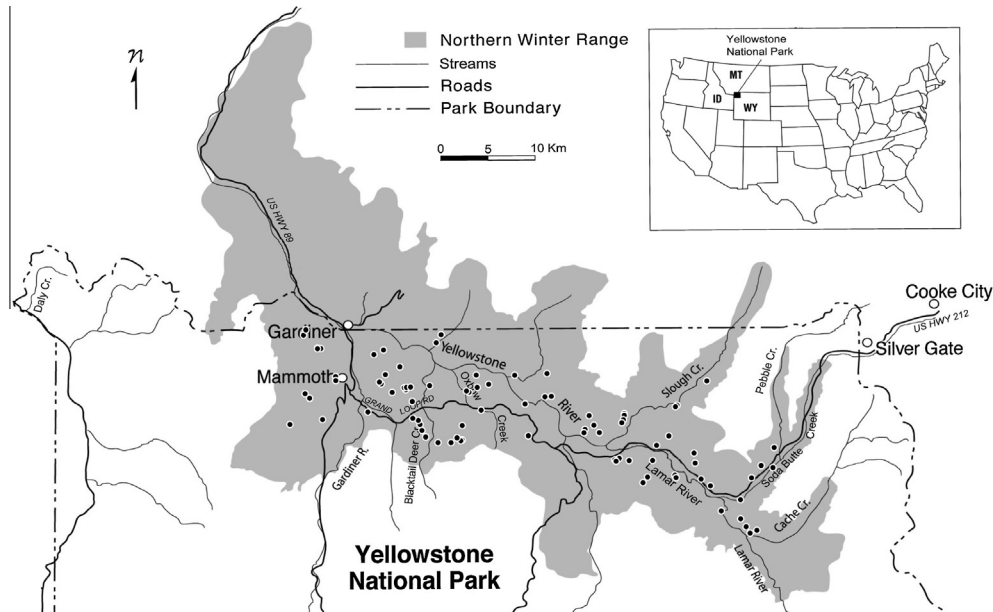


Fig. 1. The Yellowstone northern ungulate winter range (northern range); black dots mark locations of sampled aspen stands, all within the park boundary.

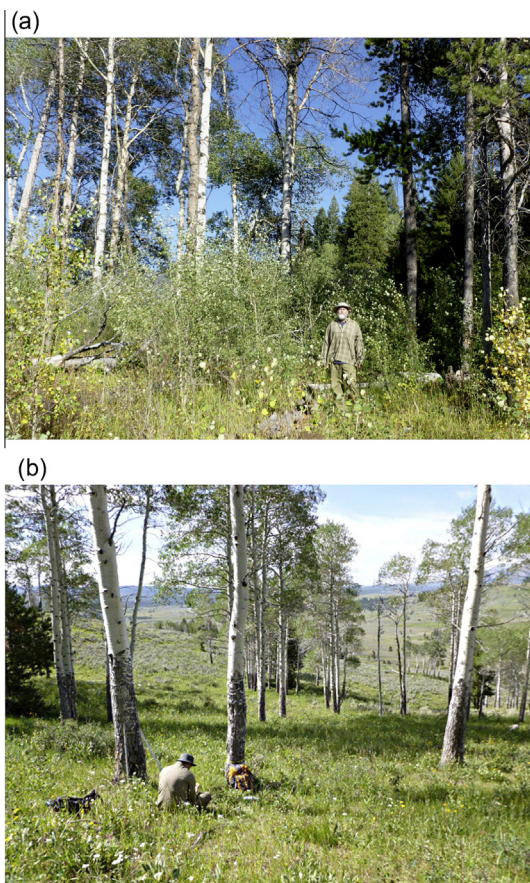


Fig. 2. Examples of aspen stand conditions in 2012 at two different study sites. (a) Stand with mature trees and young saplings but no intermediate size/age classes; tall saplings were about 3 m tall. (b) Suppressed stand with no saplings; sprouts were present but young aspen were repeatedly browsed and did not grow tall. Photos were taken in late summer 2012.

park has recently decreased to less than 50% (Wyman and Smith, 2012). Decreased hunting and increased predation have been associated with landscape-scale changes in the size and distribution of the northern Yellowstone elk herd (White and Garrott, 2005b, 2010; White et al., 2012; Painter, 2013).

2.4. Predators of elk

Wolves were extirpated from the Yellowstone area by the mid-1920s. After reintroduction in 1995–1996, wolf numbers in northern Yellowstone increased to 98 individuals in 2003 (Fig. 3), then declined to <40 in 2010–2012 (Smith et al., 2013). Disease, conflict between packs, and reduced elk numbers contributed to the decline in wolves. Nevertheless, throughout the study period 1997–2012 wolves were the most significant nonhuman predator of elk on the northern range (White and Garrott, 2005b, 2013; Eberhardt et al., 2007; White et al., 2010). Other predators included bears and cougars (*Puma concolor*), though the effect of cougars has been small due to low cougar densities (Barber-Meyer et al., 2008). Grizzly bear numbers increased in the 1990s and early 2000s (Schwartz et al., 2006; Barber-Meyer et al., 2008), and changes in the availability of other food sources may have contributed to an increase in bear predation on elk calves (Middleton et al., 2013). Bears take many elk calves in spring and could affect elk recruitment rates (Barber-Meyer et al., 2008; Hamlin et al., 2009), but wolves prey on young and adult elk throughout the year, and have the greatest potential to affect behavior of elk in fall and winter when most browsing of aspen occurs. The combination of wolves and bears has been found to limit cervid population densities in some other ecosystems (NRC, 1997; Kunkel and Pletscher, 1999; Ripple and Beschta, 2012a).

3. Methods

3.1. Climate data

Long-term climate data (for years 1895–2012) in the form of the Palmer Z Index were obtained for the Yellowstone Drainage Climate Division from two data sources, the National Climatic Data Center (NCDC, 2013) and the Western Regional Climate Center

2005). Recent elk counts have been the lowest since 1969 despite a large reduction in hunting after 2005 (White et al., 2012). Furthermore, the proportion of northern range elk wintering inside the

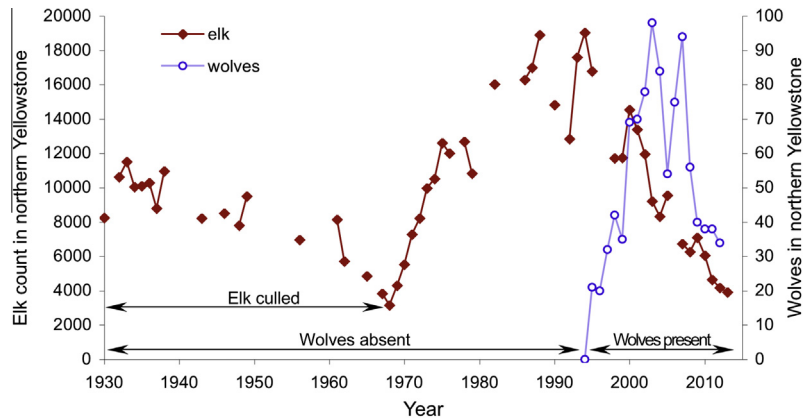


Fig. 3. Elk counts 1930–2013 (raw aerial count data; YNP, 1997; Wyman and Smith, 2012; Yellowstone Center for Resources, 2013) and wolf population estimates 1995–2012 (Smith et al., 2013) on the northern Yellowstone winter range. Line connects consecutive years, missing annual elk counts were not done or were considered inaccurate by park biologists due to weather and snow conditions. Elk counts included winter range north of the park, wolf estimates inside the park boundary only.

(WRCC, 2013). This Climate Division includes most of YNP (excluding the southwest portion). We averaged monthly values of the Palmer Z Index for each water year (October–September) to derive annual values, and compared results from the two models. The NCDC data have been widely used (Cook et al., 2004; McMenamin et al., 2008; Beschta and Ripple, 2009), but the WRCC model, based on the PRISM (Parameter-elevation Relationships on Independent Slopes Model) interpolation method (PRISM Climate Group, 2013), uses more monitoring stations and more physiographic variables and is likely to be more accurate than NCDC in mountainous areas (Daly et al., 2008; Abatzoglou, 2013). Palmer indices combine precipitation, temperature and estimated evapotranspiration into an index of soil moisture (Palmer, 1965; Heim, 2002), and are used as drought indicators. The Palmer Z or Moisture Anomaly Index is a measure of the departure of moisture conditions from monthly normals, and is the basis for other Palmer drought indices that include an additional cumulative effect of duration of a dry or wet period.

To assess relative winter severity, we used snow water equivalent (SWE) data from the Lupine Creek (10e01) snow course, in the west-central part of the northern range, combined with data from the Northeast Entrance (10d07s) SNOTEL station (NRCS, 2012) near the eastern edge of the range. Measurements of SWE for the first day of each month (January–May) were averaged for each year for the period of record 1967–2012, and yearly averages were used to calculate a long-term mean SWE.

3.2. Aspen data collection

Sampling methods were based on those used for baseline data collected in 1997–1998 (Larsen, 2001), but additional data were collected in 2012 for a more detailed analysis (Painter, 2013). Between July 24 and September 1, 2012 we sampled young aspen in 87 stands on the northern range within the park boundary (Fig. 1). These 87 stands were randomly selected in 1997–1998 and marked with GPS by Larsen (2001). Larsen collected data on young aspen in 76 of these stands in 1997–1998, plus an additional 3 stands that he did not mark with GPS, for a total of 79 stands with young aspen measurements in 1997–1998. A stand was defined as a group of aspen separated from other aspen by at least 30 m (Kay, 1990). Each stand was sampled with a single 2×30 m plot (belt transect), beginning at the nearest live tree on the perimeter of the stand closest to the GPS location (the “start tree”) and extending toward the centroid of the stand. If all trees were dead a standing dead tree was used. We defined an aspen “tree” as >5 cm dbh (diameter-at-breast-height); aspen <5 cm dbh were “young

aspen,” and “saplings” were young aspen >200 cm in height, tall enough to escape most browsing by elk (Kay, 1990).

Each 2×30 m sampling plot was classified as mesic or xeric, based on understory vegetation as an indication of soil moisture (see Larsen and Ripple, 2005). In each plot, we recorded the dbh of aspen trees (live or standing dead) and any other tree species >200 cm in height. For young aspen in the sampling plot, we recorded the height and browsing status (browsed or not) of each plant’s leader for late summer 2012 (fall height), spring 2012 and spring 2011, as indicated by bud scars and browsing scars (Ripple and Beschta, 2007). If a 2×30 m plot had <15 young aspen, the plot was extended in increments of 30 m^2 to reach a count of 15, or until the entire stand was censused. We also located the five tallest young aspen in each stand (within 60 m of the 2×30 m sampling plot) and used bud and browsing scars to measure height and browsing during previous years. For details of this plant architecture method see Ripple and Beschta (2007); we did not include aspen protected from browsing with no history of browsing (e.g., surrounded by jackstraw downfall). Conifer cover in aspen stands was classified as 0% cover, $<10\%$, 10–50%, or $>50\%$.

3.3. Aspen analysis

In 1997–1998, fall heights of young aspen were recorded in two height categories, ≥ 100 cm or ≥ 200 cm. We used these data to compare heights from 1997–1998 and 2012 as the mean percentage of young aspen ≥ 100 cm (including >200 cm), or ≥ 200 cm. We also compared the mean percentage of leaders browsed (browsing rate), not including saplings (≥ 200 cm in height) that are typically too tall to be browsed. Values were first calculated within a stand, and then averaged across stands. We used bootstrapping (function “boot.ci” in software R; R Development Core Team, 2008) to generate bias-corrected 95% confidence intervals (CI) (Efron and Tibshirani, 1993) to compare browsing and height between the two time periods. Bootstrapping was used because the 1997–1998 data were much more skewed than the 2012 data. To calculate the proportion of plots containing saplings, plot size was limited to 2×30 m even if the plot had been extended, to avoid biasing the comparison with 1997–1998.

In 1997–1998, new sprouts that had not been exposed to winter browsing were not distinguished from other young aspen, so the calculated browsing rate underestimated the actual annual rate. For further analysis of 2012 data we calculated an adjusted browsing rate for each stand that did not include new sprouts. The mean height increase of stems in 2012 (leader length) for each plot was used as an index to stand productivity, calculated as the difference

between spring height and fall height. Confidence intervals (95%) for mean browsing rate, height, and leader length in 2012 were calculated using t-statistics. Linear regression was used to test the significance of leader length and browsing rate as explanatory variables for the spring height of young aspen, using a log transformation of height to meet the assumption of constant variance. We also tested elk count and snow water equivalent (SWE, see climate Section 3.1) as explanatory variables for browsing rates of the five tallest young aspen over time. Regression coefficients were tested for significance using extra-sums-of-squares F-tests, and fit was assessed using the coefficient of determination (R^2). For aspen trees (>5 cm dbh) in the sampling plots, age was estimated from dbh using an equation derived from northern range aspen (Kay, 1990): $\text{Age} = 2.89 * \text{dbh}(\text{cm}) + 4.86$ ($R^2 = 0.84$, $n = 895$). Age estimates were grouped by decade to display the overall age structure.

4. Results

4.1. Climate

The two long-term climate data sources (NCDC and WRCC) gave somewhat different results (Fig. 4a and b), with only moderate correlation between the two datasets ($R^2 = 0.46$). Both datasets showed a recent drought, but data from NCDC, a widely used source (e.g., McMenamin et al., 2008), showed the drought as

extreme and unprecedented with a strong trend of increasing drought over the century. These indications may be misleading given the likelihood that WRCC data based on PRISM are more representative of actual conditions, and the WRCC data show the recent drought to be less severe than the drought of the 1930s with no long-term trend. The winter of 1997 had unusually high SWE (Fig. 5b), but average annual SWE for the period 2000–2012 was below the long-term average every year except 2011.

4.2. Aspen

Age structure of sampled trees ($n = 136$) is shown in Fig. 4c. The smallest overstory aspen tree (i.e., >5 cm dbh) in sample plots was 27 cm dbh (est. age ~83 years). The number of aspen trees within sampling plots (not counting the start tree) significantly decreased (t -test for unequal variances, $t_{102} = 8.6$, $p < 0.001$), from 2.8 trees/plot in 1997–1998 to 0.36 trees/plot in 2012. All stands we sampled contained at least one live aspen tree in 1997–1998, but 12% of stands in 2012 had no live overstory trees remaining.

Browsing rates of young aspen were generally lower and heights taller and more variable in 2012 compared to 1997–1998 (Fig. 5a). The percentage of leaders browsed (including new sprouts) was significantly lower in both 2011 and 2012, compared to 1997–1998 (95% CI, Fig. 5b), averaging 88% in 1997–1998 and 44% in 2012. There was no significant difference in browsing rate between 1997 and 1998, or between 2011 and 2012 (95% CI,

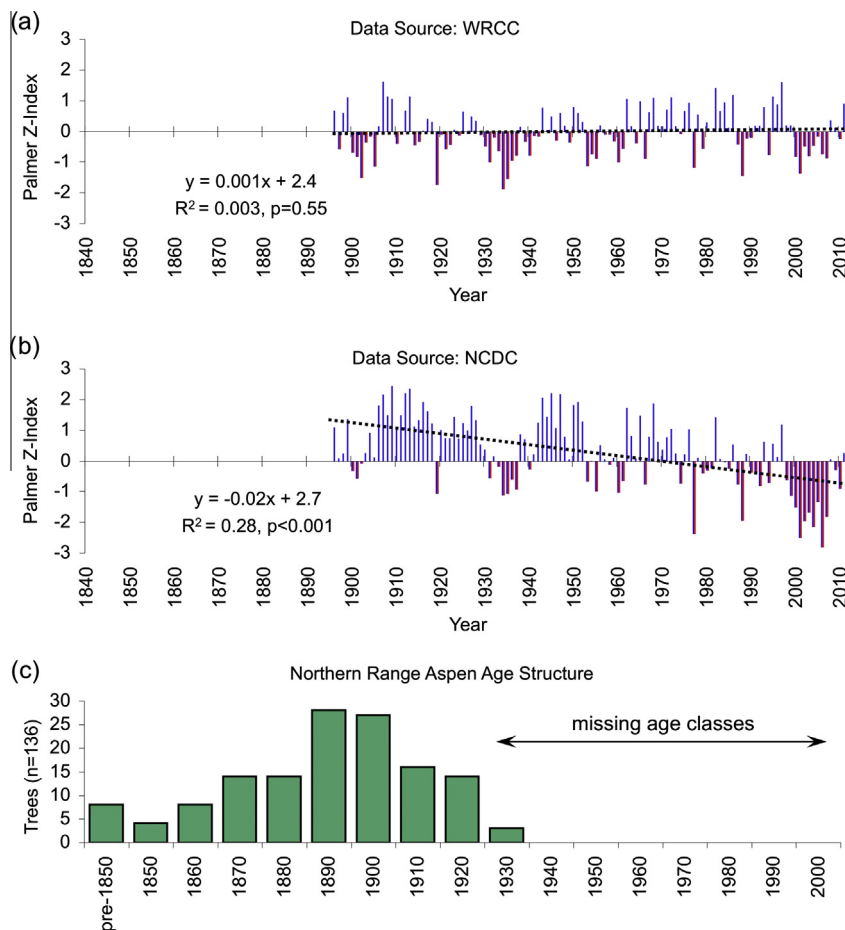


Fig. 4. Drought indicators and aspen recruitment. (a) and (b) Palmer Z Moisture Anomaly Index from two different data sources, averaged for each water year (October–September) 1896–2012 for the Yellowstone Drainage Climate Division; negative values indicate dry conditions. (a) Data from WRCC; drought in 1930s and 2000s is evident, but no overall trend; successive years have little correlation ($R^2 = 0.08$). (b) Data from NCDC, probably less accurate but commonly used, with a strong trend and greater correlation ($R^2 = 0.32$) between successive years. (c) Decade of origin of aspen trees (standing live or dead) sampled in 2012, showing continuous recruitment in the 1800s and early 1900s, but few trees recruited after the 1930s. Expected distribution would have more younger than older trees.

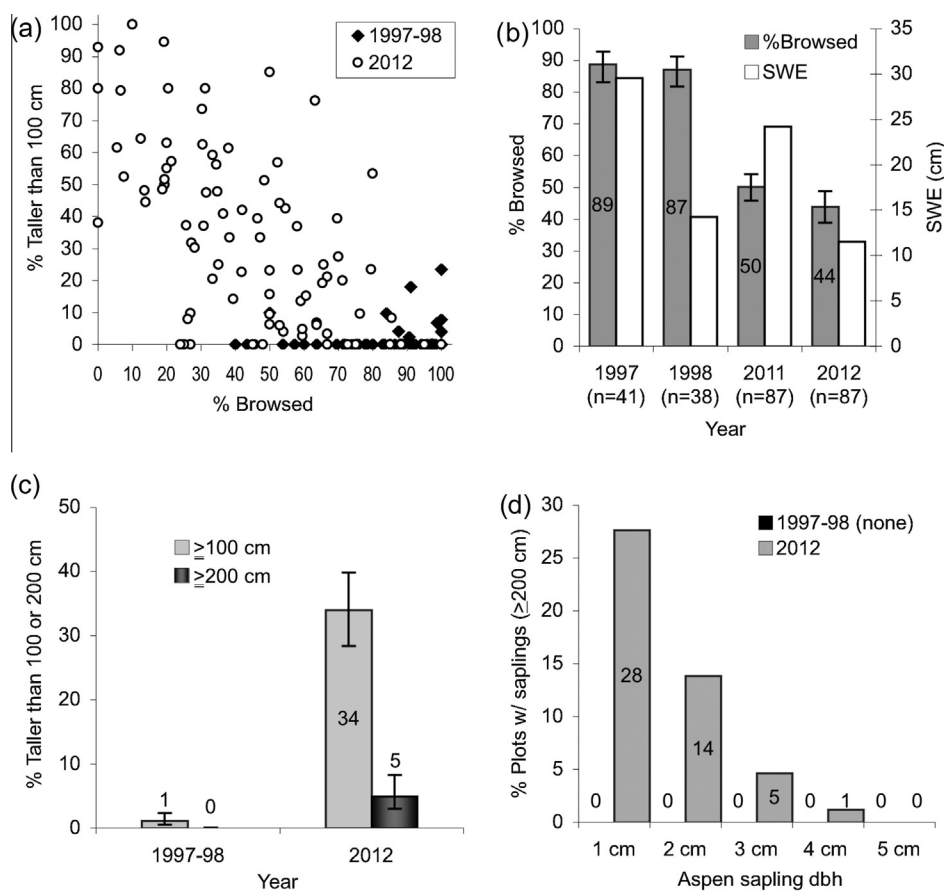


Fig. 5. Comparison of aspen height and browsing intensity in sampling plots. (a) Young aspen ≥ 100 cm (fall height) as a function of browsing rate in sampling plots in 87 aspen stands in 1997–1998 and 2012. Browsing rates included new aspen sprouts but did not include aspen >200 cm (see methods). (b) Mean browsing rate in plots (bars show 95% CI), with mean monthly snow water equivalent (SWE) for each sampling year; 41 stands were surveyed in 1997, an additional 38 in 1998; browsing for 2011 was assessed in 2012 using browse scars. (c) Mean percentage of young aspen ≥ 100 cm or ≥ 200 cm in sampling plots (95% CI). (d) Percentage of plots with at least one sapling (i.e., ≥ 200 cm) in five dbh classes; there were no saplings in 1998.

(Fig. 5b), despite large differences in annual SWE (Fig. 5b). Young aspen were significantly taller in 2012 than in 1997–1998, measured as the mean percentage ≥ 100 cm or ≥ 200 cm in sampling plots (95% CI, Fig. 5c), and variance among plots in the percentage ≥ 100 cm was 57 times greater in 2012 ($F_{81,86} = 0.02$, $p < 0.001$). Aspen plots in 1997–1998 had no saplings ≥ 200 cm (fall height), but 28% of plots in 2012 had at least one sapling ≥ 200 cm (Fig. 5d), most of small diameter. In 1997–1998, 6% of plots included conifers >200 cm tall, but in 2012 this had increased to 26% of plots. Coniferous trees were absent or had $<10\%$ cover in 54% of stands in 2012, with 18% of stands more than half-covered. Mesic or wet conditions were found in 80% of stands, xeric in 20%.

After removing from the analysis any aspen newly sprouted in 2012, browsing rates in sample plots averaged 67% (CI 62, 72) in 2011 and 52% (CI 46, 58) in 2012 for an average of 59% (CI 54, 65) for both years. Mean heights of young aspen in spring 2012 were strongly and inversely related to browsing rates (Fig. 6a, $p < 0.001$, $R^2 = 0.62$), but not to mean leader length (Fig. 6b, $p = 0.2$, $R^2 = 0.02$). Mean height (spring 2012) of young aspen in sampling plots, averaged first by plot then across plots, was 67.2 cm (CI 60, 74); fall height (2012) at the end of the growing season was 90.7 cm (CI 84, 98). Mean height (spring 2012) of the five tallest young aspen in each stand was 165.2 cm (CI 147, 183); fall height was 213.6 cm (CI 196, 231).

The five tallest young aspen in each stand increased in average height following a decrease in browsing after about 2005 (Fig. 7a), with a strong inverse relationship between browsing rate and

height in the years 2003–2012 ($R^2 = 0.93$, $p < 0.001$). The tallest young aspen sprouted in about 2003, but nearly half (47%) began after 2006. In spring of 2012, 46% of stands had at least one sapling >200 cm (Fig. 7b). Browsing rates for 2003–2012 were positively correlated with annual elk counts (Fig. 7c, $R^2 = 0.79$, $p < 0.001$), but there was no relationship between browsing rates and SWE (Fig. 7d, $R^2 = 0.03$, $p = 0.64$). Annual leader growth in 2012 averaged 48 cm (range 15, 113) for the five tallest young aspen in a stand versus 30 cm (range 8, 70) in sampling plots. Mean heights of young aspen (y) in sampling plots were significantly correlated with mean heights of the five tallest (x) in a stand ($R^2 = 0.59$, $y = 0.3x + 18$, $p < 0.001$).

5. Discussion

Almost all overstory aspen trees in our sampling plots were established before 1930 (Fig. 4c), consistent with previous research (Kay, 1990; Romme et al., 1995; Ripple and Larsen, 2000; Halofsky and Ripple, 2008; Beschta and Ripple, 2013; Kauffman, 2013). However, by 2012 the multi-decade hiatus in aspen recruitment appeared to be ending. In the last decade some saplings survived to grow above the reach of elk, in contrast with the absence of tall saplings in sampling plots in 1997–1998 (Fig. 5d). Browsing of young aspen was also much less than in 1997–1998 (Fig. 5), and in general young aspen were taller where browsing intensity was

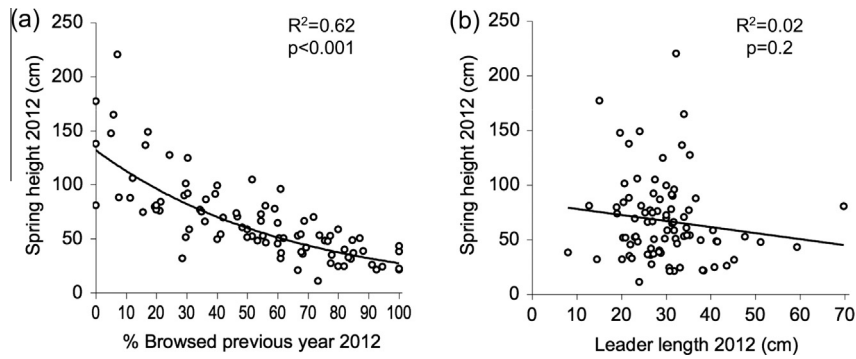


Fig. 6. Mean height as a function of browsing and leader length from sampling plots in 87 aspen stands. Regression lines were fitted to the log of height, for constant variance. (a) Browsing rates were calculated without new sprouts, and so were slightly higher than in Fig. 5. (b) Height as a function of leader length, an index for productivity.

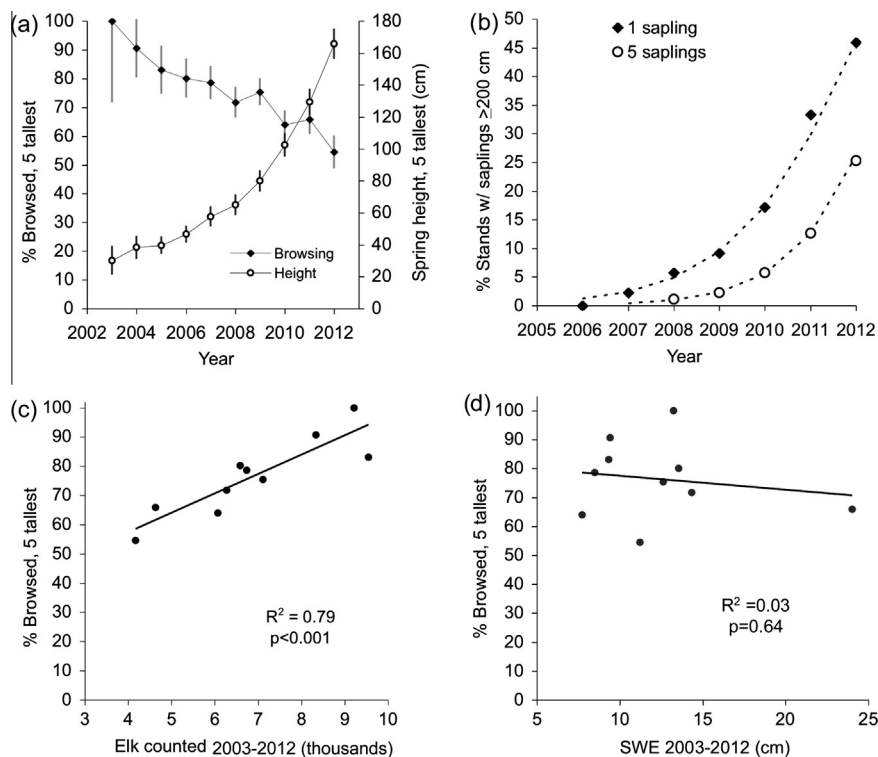


Fig. 7. Results for the five tallest young aspen in each stand based on plant architecture measurements in 2012. (a) Browsing rates and heights (95% CI) over time pooled from 87 stands. (b) Percentage of stands with one or five saplings ≥ 200 cm spring height. (c) Browsing rate as a function of annual winter elk count, 2003–2012. (d) Browsing rate as a function of average winter snow water equivalent, 2003–2012.

less (Fig. 6a). These changes occurred despite a recent drought (Fig. 4).

The presence of aspen saplings (i.e., >200 cm) in stands with reduced herbivory is evidence that the difference in browsing intensity in 2012 compared to 1998 represented a multi-year trend with a cumulative effect over time. The growth history of the five tallest saplings in each stand showed a steady decline in browsing rates after about 2003, followed by a height increase beginning about 2005 (Fig. 7a and b), similar to the findings of Ripple and Beschta (2012b) in the eastern portion of the northern range. The timing of the recent height increase of saplings was also consistent with the findings of Kauffman et al. (2010), who did not find tall saplings in 2004–2007 in a sampling of 16 stands. Our results indicate that aspen recovery in the northern range was just beginning at that time. Recent growth of saplings above the browse level of elk (Fig. 7b) was evidence of an important change that is likely to result in new trees. Similarly, in the portion of the range north of

the park boundary, Kimble et al. (2011) found in 2006 that most aspen stands were still suppressed by browsing from elk and cattle, but since that time aspen recruitment has increased in at least one area (Runyon et al., 2014).

5.1. Trophic cascade hypothesis

New sapling recruitment in northern Yellowstone is consistent with the hypothesis of a trophic cascade following large carnivore restoration. Release from browsing began after a substantial reduction in the northern Yellowstone elk herd, a reduction due at least in part to predation by wolves and bears, though hunting was also an important factor prior to 2007 and drought may have had some effect (Vucetich et al., 2005; White and Garrott, 2005a; Eberhardt et al., 2007; Barber-Meyer et al., 2008; Hamlin et al., 2009; White et al., 2010, 2012). Historically, hunting outside the park did not prevent increases in elk density inside the park, and the

number of elk killed by hunters was linked to winter severity forcing elk out of the park (Rush, 1932; Houston, 1982; White and Garrott, 2005a). A decline in elk numbers such as occurred in 1998–2012 did not happen in the past century without additional culling inside the park, regardless of the hunting (or climate) regime (Houston, 1982; Barmore, 2003). Thus the recent elk decline, which has been most pronounced inside the park (White et al., 2012; Painter, 2013), is evidence that predators may now be exerting some top-down control over elk numbers and distribution (Hamlin et al., 2009; White and Garrott, 2013).

5.2. Behavioral or trait-mediated effects of predation

Changes in the behavior or movements of elk, in combination with reduced elk density, may also have contributed to release of aspen from herbivory (White et al., 2003, 2009; Fortin et al., 2005; Hebblewhite et al., 2005; Mao et al., 2005; Gude et al., 2006; Muhly et al., 2010). Prior to wolf restoration, aspen seemed doomed to intensive browsing, and culling of elk before 1969 did not result in significant aspen recruitment despite more than two decades with relatively low elk numbers on the northern range (Fig. 3) (Barmore, 1967; Houston, 1982; YNP, 1997). In contrast, comparably low elk numbers since 2005 have been accompanied by new recruitment of aspen saplings (Figs. 5d and 7b). This difference suggests that something more than simple reduction of the elk population was necessary to reverse aspen decline. Possible sources of this difference include changes in elk foraging behavior or habitat use at large or small scales. The spatial distribution of northern range elk has shifted as the population has declined, so that a greater proportion of the herd now winters outside the park, and the density of elk inside YNP has been greatly reduced (White et al., 2012; Painter, 2013). In addition to direct effects of predation, this landscape-scale shift in elk distribution may be evidence of behavioral changes in response to higher densities of wolves and bears inside the park, as well as greater vulnerability to wolves in the east sector of the range where snow is typically deeper than in the west (White et al., 2010, 2012; White and Garrott, 2013). Other factors that could affect elk distribution include changes in hunting and land use outside the park (Haggerty and Travis, 2006; Proffitt et al., 2013; Wilmsers and Levi, 2013), and increased competition from bison in the park (Ripple et al., 2010; Painter and Ripple, 2012).

5.3. Alternative hypotheses: fire, climate, and growth rate

Suppression of fires and changes in climate have been proposed as possible explanations for the historical decline of aspen on the northern range (Houston, 1982; Romme et al., 1995; but see Halofsky and Ripple, 2008). Rapid growth and high densities of sprouts resulting from fire may have allowed aspen to escape elk browsing in the past. The fires of 1988 provided a test of the fire hypothesis since some burned stands had high densities of new sprouts; however, most of the new sprouts did not survive on the northern range, primarily due to herbivory by elk (Romme et al., 1995; Kay and Wagner, 1996; Renkin and Despain, 1996; YNP, 1997). There have been no other fires that could account for recent sapling recruitment.

Lack of successful aspen regeneration following the 1988 fires led park scientists to hypothesize that climate may have been unsuitable, and that “wetter winters with deeper snows, may contribute to a return to the circumstances that prevailed the last time that aspen escaped browsing and grew to tree height on the northern range” (YNP, 1997, p. 55). This climate hypothesis was suggested by the fact that the period of historical aspen recruitment in the late 19th and early 20th centuries was relatively moist, followed by drought in the 1930s; however, a moist period in the

1960s (Fig. 4) with low elk numbers (Fig. 3) did not result in significant recruitment of aspen trees. The Yellowstone region was again in drought from 2000 to 2007 (Fig. 4) (Wilmsers and Getz, 2005; McMenamin et al., 2008; Frank et al., 2013), and in northern YNP every winter from 2000 to 2010 had snow accumulations below average. Contrary to the climate hypothesis, the tallest young aspen in 2012 had increased rapidly in height after 2005 (Fig. 7), during the drought and despite the adverse climate trend (Hanna and Kulakowski, 2012). In 2012, 80% of stands had plant communities indicative of moist conditions, suggesting that moisture did not limit growth in most stands, though it may limit the area occupied by a stand.

This climate hypothesis is essentially about productivity, postulating that young aspen could escape from browsing if they grew faster, and that climate could make this difference by increasing growth rate with increased moisture. Another possibility is that slightly longer growing seasons due to warmer temperatures have resulted in greater annual growth (Despain, 2006; Hebblewhite and Smith, 2010). Regardless of the mechanism, if increased growth has resulted in some aspen escaping the reach of elk, where previously they were kept short, this would first be seen in stands with the highest rates of growth. The tallest young aspen (the leading edge of recovery) would be in stands with the fastest growth, and we would find a positive relationship between height and leader length. This relationship in 2012 was slightly negative and not statistically significant (Fig. 6b), so the productivity hypothesis was not supported. Changes in climate also cannot explain the relatively rapid switch from decades of young aspen height suppression to increasing sapling recruitment in the last decade. In contrast, browsing intensity was significantly and inversely related to height of young aspen (Fig. 6a).

In addition to affecting aspen productivity, climate could affect herbivory. Browsing could be reduced when elk leave the park in severe winters (White and Garrott, 2005a; White et al., 2012), and deep snows could make stands less accessible (Brodie et al., 2011). Very mild winters could leave other forage more accessible, perhaps reducing browsing (Hebblewhite and Smith, 2010). We found a strong relationship between browsing and the number of elk (Fig. 7c), but no evidence for a relationship between browsing and amount of snow (Fig. 7d). Snow was unusually deep in 1997, followed by below average SWE in 1998, yet browsing intensity was high in both years (Fig. 5b). In 2011 snow was deep, and in 2012 below average, yet browsing for both years was much lower compared with 1997–1998 regardless of snow. Most aspen browsing on the winter range occurs in fall and early winter when elk return to the range (Barmore, 1967, 2003), diminishing the potential for late winter severity to affect herbivory of aspen.

5.4. Persistence and regeneration of aspen stands

In many of the stands we sampled in 2012, browsing rates of young aspen remained relatively high (Fig. 2b). For example, about 40% of stands had browsing rates >60% (Fig. 6a) and young aspen in these stands were consistently short and hedged by browsing. Bison numbers have increased since the 1990s, and browsing by this large herbivore on cottonwood and willow, as well as aspen, may compensate in part for reduced elk herbivory in places used intensively by bison (White and Garrott, 2005b; Painter and Ripple, 2012; Painter, 2013). However, even with lower browsing intensity, some aspen stands may not recover if a trend toward warmer, drier conditions increases stress on stands in xeric habitats, and some stands may have already exhausted their ability to reproduce (Barmore, 1967; Kay and Wagner, 1996). The number of coniferous trees in aspen stands has been increasing, so forest succession may suppress some aspen stands in the absence of fire. Nevertheless, with recent new recruitment of saplings many aspen

stands are now more likely to persist on the northern range rather than dying out as was the previous trajectory, and reduced herbivory increases the potential for future fires to stimulate successful aspen regeneration (Seager et al., 2013). In 2011, we found a similar pattern of reduced browsing with increased height of young aspen in the Shoshone National Forest east of YNP (Painter, 2013), suggesting a wider pattern of beginning aspen recovery. Researchers in some other portions of the Yellowstone ecosystem have not found such changes (Kimble et al., 2011; Winnie, 2012), however, aspen recruitment increased after 2005 in the Eagle Creek area north of the park boundary following a decrease in browsing (Runyon et al., 2014), similar to what has happened inside the park.

6. Conclusions

Widespread but patchy recruitment of saplings above the browse height of elk demonstrates that an important shift in aspen dynamics has occurred on Yellowstone's northern range, a change that did not occur in the period 1930–1998, even when overall elk numbers were low in the 1950s and 1960s. Many aspen stands are in the early stages of recovery as indicated by decreased browsing and increased height of young aspen. It is unlikely that climate caused these recent changes, which happened despite a period of drought. The recent reduction in herbivory and associated increase in young aspen height are linked most plausibly to changes in elk density and distribution following the restoration of wolves, as wolf predation interacted with other factors affecting elk such as hunting by humans and predation by bears (White et al., 2012; White and Garrott, 2013). The northern Yellowstone example is consistent with previous research in Canada (White et al., 1998, 2003; Hebblewhite et al., 2005; Beschta and Ripple, 2007) suggesting that large carnivores may aid aspen conservation where aspen have been suppressed by elk.

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