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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.

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.,