



Berry-producing shrub characteristics following wolf reintroduction in Yellowstone National Park

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ABSTRACT

Gray wolves (*Canis lupus*) were reintroduced into Yellowstone National Park in 1995–96, thus completing the park's large predator guild. In the fall of 2010, approximately 15 years after wolf reintroduction, we sampled ten genera/species of berry-producing shrubs within 97 aspen (*Populus tremuloides*) stands in the park's northern ungulate winter range. Regression analysis indicated shrub heights for five of the ten genera/species were positively correlated with height of understory aspen; greater shrub richness was found in aspen stands with the tallest understory aspen. In addition, the proportion of shrubs with berries was positively correlated with shrub height for six of the ten genera/species. Results were consistent with the re-establishment of a tri-trophic cascade involving wolves, elk (*Cervus elaphus*), and palatable woody plants in northern Yellowstone. After multiple decades of browsing suppression by elk, it appears that aspen and at least some genera/species of berry-producing shrubs are in the early stages of recovery. If shrub recovery continues, improved food-web and habitat support could benefit a wide range of terrestrial wildlife species in northern Yellowstone.

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1. Introduction

In tri-trophic systems, carnivores provide top-down forcing that can mediate the behavior and density of herbivores (consumers), thus allowing plant communities (producers) to maintain high levels of abundance, biomass, and productivity (Pace et al., 1999; Ripple and Beschta, 2012a). However, in the late 1800s–early 1900s, an increasing Euro-American presence in the western United States (US) resulted in widespread extirpation of gray wolves (*Canis lupus*) and grizzly bears (*Ursus arctos*), as well as reduced numbers of ungulates (Laliberte and Ripple, 2004). Although ungulate populations across much of this region were recovering by the mid-1900s, incomplete large predator guilds have remained.

Even national parks in the western US were not immune to the loss or displacement of large mammalian carnivores (e.g., Cahalane, 1941; Leopold et al., 1963). Thus, increased herbivory by elk (*Cervus elaphus*) and/or deer (*Odocoileus* spp.) began to alter the structure and dynamics of plant communities as well as other ecosystem processes (Hess, 1993; White et al., 1998; Prichard, 1999; Beschta and Ripple, 2009). In the eastern US, intensive herbivory on young deciduous woody plants from an increased population of white-tailed deer (*Odocoileus virginianus*), in the absence of gray

wolves and cougars (*Puma concolor*), similarly initiated major shifts in plant diversity and patterns of succession across many of the region's deciduous forests (Rooney et al., 2004).

Following the extirpation of wolves and grizzly bears in the American West, many aspen (*Populus tremuloides*) communities experienced long-term decline during the latter half of the 20th century due, in part, to high levels of herbivory from native and domestic ungulates (Kay, 1997; Bartos, 2001). The status and dynamics of these communities are of particular importance to the biodiversity and resilience of terrestrial ecosystems because numerous species of vascular plants may occur in the understories, including multiple genera of shrubs (e.g., *Rosa*, *Symphoricarpos*, *Amelanchier*, *Prunus*, *Berberis*). These understory plants are key sources of food and physical habitat for an extensive array of wild-life species (DeByle and Winokur, 1985).

Gray wolves, initially extirpated from Yellowstone National Park in the early 1900s, were reintroduced in 1995–96, again completing the park's native predator guild (Smith et al., 2003). Consistent with the re-establishment of a tri-trophic cascade involving wolves-elk-plants, improved recruitment (i.e., growth of seedlings/sprouts above the browse level elk) of young aspen, cottonwood (*Populus* spp.), and willow (*Salix* spp.) have been documented in portions of the park's northern ungulate winter range (Beyer et al., 2007; Ripple and Beschta, 2012b; Baril, 2009; Beschta and Ripple, 2010). However, the status of shrub communities in aspen stands has not been previously reported. We hypothesized that the increased heights of young aspen (ramets) in recent years

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may similarly be reflected in shrub community dynamics. Thus, the objective of this study, some 15 years after wolf reintroduction, was to assess the heights, diversity, and presence/absence of fruit on berry-producing shrubs within recovering aspen stands in northern Yellowstone.

2. Study area

Yellowstone's northern ungulate winter range contains a mix of grassland and forest vegetation distributed across the more than 1500 km² of mountainous terrain (NRC, 2002; Barmore, 2003), two-thirds of which lies within the park's boundaries. Steppe and shrub-steppe plant communities are often dominated by big sagebrush (*Artemisia tridentata*) and, with increasing elevation, grade into coniferous forests comprised principally of lodgepole pine (*Pinus contorta*) and Douglas-fir (*Pseudotsuga menziesii*). Aspen stands occur in riparian and upland settings and occupy 2.4% of the northern range (Savage, 2005), with cottonwood and willow communities predominantly found along stream courses and adjacent floodplains.

When ungulates in Yellowstone National Park were being protected during the early 1900s and wolves systematically removed, Smith et al. (1915) observed that willows and various shrubs such as "mountain maple, service berry, wild rose, snow-berry, fly honey suckle" were showing evidence of considerable winter browsing. Some four decades later, the park's elk management plan indicated the severity of effects this large herbivore was having on northern range ecosystems (YNP, 1958; pp. 1–2):

"The cumulative effects of grazing and trampling by excessive numbers of elk for many decades are obvious today. Meadows once covered by lush thickets of willows now have a grass-type aspect; likewise former groves of aspen now have only a few trees which cannot be replaced while elk consume reproduction. Sagebrush has disappeared from ridges and other places where snow lies shallow, and even bunchgrass, which comprises the bulk of the elk's diet, is in poor condition on that range where grazing animals must feed later in the winter."

"Damaging effects of this abuse are manifold. Animals, whether they be the elk or bighorn which graze, the beaver which feeds on aspen and willow, small songbirds which demand food and protection from vegetation, ducks which suffer from fluctuating water levels, or fish which find a shortened food supply as silt fills stream beds, all suffer from this damaging chain reaction started by the elk."

Based on long-term age structure data for aspen (Romme et al., 1995; Ripple and Larsen, 2000), cottonwood (Beschta, 2005), and willow (Wolf et al., 2007), the extent to which intensive browsing by elk impaired Yellowstone's northern range deciduous plant communities during the last half of the 20th century was unprecedented. Trophic downgrading and impacts to channels following the loss of wolves similarly occurred in the upper Gallatin elk winter range along the park's northwest corner (Ripple and Beschta, 2004; Beschta and Ripple, 2006; Halofsky and Ripple, 2008).

After wolves were reintroduced into Yellowstone during the mid-1990s, their numbers in the northern range increased annually, attaining a population of nearly 100 wolves in 2003. Since then, the northern range population has fluctuated between 40 and 95 wolves (Smith et al., 2011). Following the return of this apex predator, various changes in elk behavior were observed (Laundré et al., 2010) and their population declined from >15,000 elk in the 1990s to ~5,000 elk by 2010. Furthermore, annual population surveys (White et al., 2012) indicate that relatively few elk have been wintering in the eastern portion of the northern range in recent years.

3. Methods

In September of 2010, we revisited 98 aspen stands in the eastern portion of Yellowstone's northern range that had been previously sampled in August of 2006 (see Ripple and Beschta, 2007). They included 44 riparian and 54 upland stands distributed along Crystal Creek, Rose Creek, Slough Creek, and the Lamar River. One of the original riparian stands along Rose Creek had experienced conifer blowdown and human disturbance during removal of the downed conifers; it was thus excluded from remeasurement. In 2006 we had selected the five tallest understory aspen (i.e., of those that became established since the reintroduction of wolves) within each stand and determined temporal patterns of leader heights and browsing levels from plant architecture (e.g., Keigley et al., 2003). In 2010 we again selected the five tallest understory aspen and determined leader heights as of the spring of 2010 as well as whether each leader had been browsed during the winter of 2009–10. From the 2006 and 2010 data sets, we summarized annual browsing intensity of aspen leaders (% browsed) by three height classes (i.e., 1–100, 101–200, and 201–800 cm). We were unable to consistently distinguish annual patterns of browsing and height growth for berry-producing shrubs from plant architecture measurements, thus we utilized browsing measurements of young aspen as an index of herbivory within each stand. The forage value of as least some of the shrubs we sampled (e.g., serviceberry and chokecherry) was similar to that of aspen (Nelson and Leege, 1982).

For each measured understory aspen, a 10-m radius plot was delineated around its base for sampling shrubs. Within the collective area of these 10-m radius plots in each stand, we measured the height (cm) of the five tallest berry-producing shrubs for each of ten genera/species as well as whether fruit were present/absent on an inventoried plant. The following genera/species were encountered (listed in frequency of occurrence from the most frequent to the least frequent): (1) rose (*Rosa woodsii* and *R. acicularis*); (2) snowberry (*Symphoricarpos albus* and *S. oreophilus*); (3) gooseberry (*Ribes lacustre* and *R. oxycanthoides*); (4) serviceberry (*Amelanchier alnifolia*); (5) buffaloberry (*Shepherdia canadensis*); (6) chokecherry (*Prunus virginiana*); (7) twinberry (*Lonicera involucrata*); (8) thimbleberry (*Rubus parviflorus*); (9) currant (*Ribes cereum*); (10) raspberry (*Rubus idaeus*). Except perhaps for snowberry, currant, and raspberry, most of these species are capable of attaining heights of 200 cm; serviceberry and chokecherry can attain heights considerably greater than 200 cm (Hitchcock and Cronquist, 1973; Cronquist et al., 1997).

We use the terminology "berry-producing shrubs" herein to collectively represent a diverse group of deciduous woody plants that produce a prominent fruit. While most of the shrubs evaluated in this study generate a fruit that meets the strict definition of a "berry" – a fleshy fruit developed from a single pistil (Derig and Fuller, 2001) – some do not. For example, rose produces a rose hip, serviceberry a pome, and chokecherry a drupe. Nevertheless, we included them in our study since they have a fleshy fruit that is generally "berry-like". Some of the shrubs we encountered in the field may hybridize (e.g., *Rosa* spp.), thus precluding easy confirmation of species.

We used linear regression of shrub height (*y*) and aspen height (*x*) for each genera/species category to assess whether the heights of berry-producing shrubs were associated with the increased heights of young aspen that had been occurring in recent years. We also calculated shrub richness (the average number of genera/species categories, ±95% CL) by height class of aspen leaders to identify possible relationships in shrub richness relative to the height of recovering understory aspen. Kay (1995) had earlier found that taller plants produced more fruit, thus we used logistic

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