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Review

Riparian vegetation recovery in Yellowstone: The first two decades after wolf reintroduction

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ABSTRACT

During the seven decades of gray wolf (*Canis lupus*) absence in Yellowstone National Park intensive browsing by Rocky Mountain elk (*Cervus elaphus*) suppressed the growth of young deciduous woody plants within the park's northern ungulate winter range. Since wolf reintroduction, 24 assessments of deciduous woody plants in riparian areas have been published, including eleven on willow (*Salix* spp.), six on aspen (*Populus tremuloides*), five on cottonwood (*Populus angustifolia* and *Populus trichocarpa*), and one each on berry-producing shrubs and thinleaf alder (*Alnus incana* spp. *tenuifolia*). All but two of these studies found increases in plant height, stem diameter, stem establishment, canopy cover, or recruitment. More than half of the studies measured ungulate browsing and, in all instances, increased growth/cover of woody plants over time occurred concurrently with a decrease in browsing. Almost half of the studies also compared observed plant community changes to climatic/hydrologic variables but the results of these analyses were often inconsistent. Although the long-term warming and drying trends underway in northern Yellowstone appear unlikely to have contributed to the occurrence of improved riparian plant communities during the last two decades, these vegetation changes were consistent with reestablishment of a tri-trophic cascade involving an intact large predator guild, elk, and woody plant species. This early stage of vegetation recovery in northern Yellowstone, although not occurring everywhere, represents a major departure from the wide-spread suppression of woody plants by elk browsing that occurred in the decades when wolves were absent.

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1. Introduction

Riparian areas, occurring transitionally between terrestrial and aquatic ecosystems, characteristically have strong biophysical gradients (National Research Council, 2002b). The resulting diversity in structure, composition, and function of native plant communities occupying these gradients provide food-web support and habitat structure for numerous faunal species and are of fundamental importance to the inherent resilience of these systems (Tabacchi et al., 1998; Kauffman et al., 2001; Naiman et al., 2005). Vegetation diversity is also crucial for helping to stabilize alluvial streambanks, maintain channel morphology, shade

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streams, protect water quality, and provide allochthonous inputs, all of which contribute to productive and sustainable aquatic ecosystems (National Research Council, 2002b; Bennett and Simon, 2004).

After seven decades of absence, gray wolves (*Canis lupus*) were reintroduced into Yellowstone National Park in 1995–1996, again completing the park's large predator guild (Smith et al., 2003). Following reintroduction of this apex predator, young deciduous woody plants that had been suppressed by ungulate browsing in previous decades began to increase in height and recover in some riparian areas (Fig. 1). Two major hypotheses often have been presented to explain the changes in vegetation that are currently underway. One hypothesis indicates that the re-establishment of a trophic cascade following the return of wolves has decreased ungulate herbivory on palatable woody plants (e.g., Fortin et al., 2005; Beyer et al., 2007) thereby allowing height increases that, at least in some areas, have again begun to exceed the upper browse level (~200 cm) of Rocky Mountain elk (*Cervus elaphus*). Such a top-down cascade requires that reintroduced wolves, in conjunction with other large predators, mediate the behavior (e.g., foraging habits, spatial use of habitat) and/or density of elk. Alternatively, bottom-up forces (e.g., climatic trends and fluctuations, hydrologic disturbances, site productivity) could represent major factors initiating and subsequently influencing any recovery of riparian plant communities (e.g., Tercek et al., 2010; Marshall et al., 2014).

To help understand the relative importance these contrasting influences (i.e., top-down vs. bottom-up) might have on plant community dynamics, we undertook a synthesis of published studies that have evaluated changes to riparian vegetation in northern Yellowstone during the two decades following wolf reintroduction. We summarized the extent to which plant community dynamics have changed since 1995–1996 and the relative importance of top-down (herbivory) versus bottom-up influences (climate, hydrology) in affecting these dynamics.

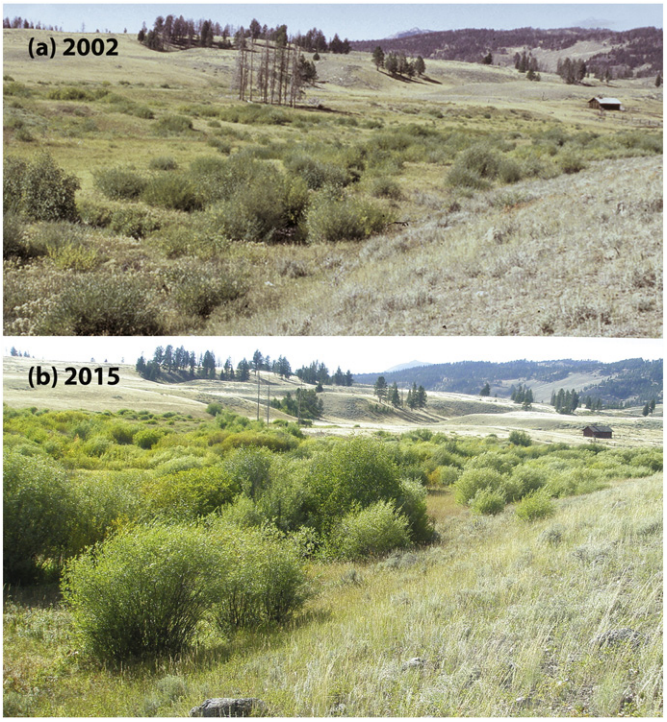

Fig. 1. Chronosequence of photos along the west fork of Blacktail Deer Creek in Yellowstone's northern range: (a) in 2002 young willows were beginning to increase in height after decades of suppression by intensive elk browsing; (b) in 2012 willow heights and cover have continued to increase and many plants now exceed 200 cm in height. Beaver have been active along the west fork of Blacktail Deer Creek in recent years and in late summer of 2015 eight beaver dams, averaging 51 cm in height (range = 20 to 100 cm), were present. Photo credits: (a) W.J. Ripple, 8/27/2002 and (b) R.L. Beschta, 8/31/2015.

Our synthesis focused on studies of deciduous woody species because they are (1) important to the biodiversity and functioning of riparian and aquatic systems (National Research Council, 2002b), (2) long-lived, and (3) generally resilient to disturbance (Kauffman et al., 1997). Furthermore, most of them had been height-suppressed by ungulate browsing during the decades when wolves were absent (Kay, 1990; Barmore, 2003).

2. Yellowstone National Park prior to wolf reintroduction

Although Native Americans resided within the area that was to eventually become Yellowstone National Park, aboriginal hunting, gathering, and burning came to an end when Indians were removed following the park's establishment in 1872 (Nabokov and Loendorf, 2004). Early park administrators attempted to protect ungulates from market hunters whereas wolves, bears (*Ursus* spp.), cougar (*Puma concolor*), and coyotes (*Canis latrans*) were persecuted. Even after the National Park Service assumed management responsibility in 1918, predators continued to be hunted, trapped, and poisoned (Schullery and Whittlesey, 1992; Wagner, 2006). Wolves were extirpated from the park by the mid-1920s, thus removing any effect this apex predator may have had on ungulate prey in the 1500 km^2 northern ungulate winter range, or "northern range", of which approximately two-thirds lies within the park. Additional information regarding northern range terrain, plant communities, wildlife, and management history can be found in Houston (1982); Schullery and Whittlesey (1992), and Yellowstone National Park (1997), but see also Chase (1986); Chadde and Kay (1991); National Research Council (2002a); Barmore (2003), and Wagner (2006).

Deciduous woody species commonly found within northern range riparian areas include willow (*Salix* spp.), thinleaf alder (*Alnus incana* spp. *tenuifolia*), and various species of berry-producing shrubs. Cottonwood (*Populus angustifolia* and *Populus trichocarpa*) typically occurs along major valley bottoms and aspen (*Populus tremuloides*) is often present along tributary streams as well as on moist-sites scattered across the northern range's shrub-steppe terrain (Despain, 1990).

Perhaps the first recorded observations of increased levels of elk browsing in northern Yellowstone were those of Smith et al. (1915). By the 1930s, ungulate herbivory of northern range vegetation had become of sufficient concern that park administrators initiated a program of ungulate culling (Grimm, 1939), reducing the elk population to <5000 animals by the mid-1960s. Culling of elk in the park was terminated after 1968 (Allin, 2000) and their population rapidly increased, approaching nearly 20,000 by the late 1980s. Between 1935 and 1989, studies of young willow, aspen, and other woody species consistently found these plants generally unable to grow above a height of 100 cm due to intensive elk browsing (Kay, 1990; Chadde and Kay, 1991; Singer, 1996; National Research Council, 2002a; Barmore, 2003). Relatively recent studies of cottonwood and aspen age structure (i.e., frequency of plants by date of establishment) in the northern range have confirmed a major decline in their recruitment (i.e., growth above the upper browse level of elk) between the early 1900s and the 1990s (Fig. 2). By 1990, the difference between observed and expected stem frequencies represented an estimated 51% and 89% decline in total number of cottonwood and aspen, respectively (Fig. 2). Results from Wolf et al. (2007) similarly indicate a 91% decline in willows. In other areas of the western North America, high levels of ungulate herbivory following the displacement or extirpation of large predators profoundly reduced the recruitment of woody species over time (e.g., Hess, 1993, White et al., 1998; Ripple and Beschta, 2004b; Beschta and Ripple, 2009). Additionally, Bork et al. (2013) found that summer browsing by various large herbivores, including bison, elk, and cattle (*Bos taurus*), could significantly increase mortality of aspen saplings in the northern Great Plains.

As a consequence of long-term and intensive ungulate herbivory in the northern range during the decades of wolf absence, depleted