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The Plight of Aspen: Emerging as a Beneficiary of Wolf Restoration on Yellowstone’s Northern Range

John Klaptosky

Quaking aspen (Populus tremuloides Michx.) is the most widely distributed tree in North America and is native to Yellowstone National Park’s (YNP) northern range, a 250,000 acre area including the valleys of Yellowstone, Lamar, and Gardner rivers. Aspen make up a small component of vegetation on Yellowstone’s landscape, and most stands on the northern range are less than five acres in size. However, aspen remain a persistent species because of its root-suckering ability, allowing aspen stands to proliferate as successive generations of shoots arise from a continually expanding root system. As a result of this characteristic, aspen usually occur in clones of genetically-identical individuals (Barnes 1966). Aspen seedling establishment is not common because of short-lived seed viability and demanding seedbed requirements. Major disturbance events, such as the 1988 Yellowstone fires, may play an important role in the preparation for aspen seedling establishment. Following the 1988 fires, there was widespread germination of aspen seedlings in burned areas (Kay 1993, Romme et al. 1997); however, most of those seedlings have since been browsed by ungulates (Romme et al. 2005, Forester et al. 2007), yet some have persisted in scattered high-elevation sites (Hansen et al. 2016). Although pure, self-sustaining stands exist, aspen is generally regarded as a species that requires major disturbance, such as fire or clearcutting, to reduce competition from other tree species and to stimulate growth of aspen suckers (Bartos and Mueggler 1979, Mueggler 1989).

Schier (1975) reported when major disturbances such as fire are excluded from the environment, aspen may be replaced by conifers, provided there is a seed source nearby. Many aspen stands in Yellowstone coexist along the edges of conifer forests or as a component of mixed conifer environment. Schier (1975) also stated aspen established on drier sites often revert to shrub-steppe community types, and heavy browsing by elk (Cervus elaphus) can hasten this transition. Additionally, as a result of multiple years of browsing, aspen develop a shrub-like form, which can be seen extensively on Yellowstone’s northern range (figure 1). Aspen in

Figure 1. The sprouting of new shoots each year, coupled with the continual hedging by elk, give aspen their shrub-like appearance.
this shrub-like form are a common appearance in aspen stands throughout the northern range, demonstrating aspen’s resiliency to persist on the landscape in spite of heavy browsing.

Warren (1926) provided one of the earliest data sets regarding aspen of Yellowstone in his classic study of beaver and aspen. Warren reported that aspen and beaver were abundant along most streams in the Tower Falls area. In the 1950s, reexamination of the status of beaver in the Tower Falls area (Jonas 1955) revealed no sign of beaver, where an estimated 200 had lived in the early 1920s. Aspen along streams and ponds had all but disappeared. It appears beavers eliminated the older aspen trees and elk browsed the young clone trees (Barmore 1967). It is during the same time period when Warren was conducting his study that park records reported on the extirpation of wolves (Canus lupus) from Yellowstone. Throughout the 20th century, other researchers on the northern range documented the failure of existing clones to regenerate replacement of overstory stems (Rush 1932, Grimm 1939, Kay 1990, Romme et al. 1995, Larsen and Ripple 2003). It is estimated aspen historically covered 4-6% of the northern range (Houston 1982) but have declined to cover 1-2% of the landscape (Renkin and Despain 1996).

The decline of aspen is of concern because it is a unique and important species in the park. Aspen is one of the few upland deciduous tree species present in the ecosystem, and is noted for very high rates of net primary productivity (Hansen et al. 2000). Aspen forests are important for biodiversity; they support a greater variety of plant associations than the typical conifer forests of the area, as well as increase bird species richness and total abundance (Turchi et al. 1995, Dieni and Anderson 1997, Hollenbeck and Ripple 2008).

The character of aspen stands has also changed from variable age classes to a recent state of mature, declining stands of older stems (Meagher and Houston 1998). According to Mueggler (1989), western aspen matures between 60 and 80 years, deteriorates rapidly after about 120 years, and in rare cases reaches ages over 200 years. According to age sampling done between 2003 and 2005, where 30 samples were randomly collected across the northern range and aged, the existing aspen overstory in the park established sometime between 1864 and 1919, with an average tree age of 119 years (YNP, unpublished data). This establishment period is consistent with other age structure analyses done on northern range aspen (Warren 1926, Romme et al. 1995, Larsen and Ripple 2003).

Aging aspen stands on the northern range are rapidly declining. As a result of stand deterioration, the reduction in crown area facilitates aspen suckering because apical dominance is weakened, and more solar radiation reaches and warms the surface floor (Schier 1975). In aspen, auxin (a plant hormone that causes elongation of cells in shoots) produced in undisturbed growing stems/trees is translocated downward into roots where it inhibits sucker formation, a phenomenon known as apical dominance (Farmer 1962, Eliasson 1971a,b, Schier 1973, Steneker 1974). Interference with or disturbance of the auxin supply (such as fire disturbance or mechanical damage like stem browsing) changes the hormonal balance in the roots, which enables growth promoters (such as cytokinins) to initiate the regenerative process. During aspen regeneration, variation in stand development may be affected by clones with inherently poor suckering capacity (Schier 1975), clonal genetic differences in susceptibility to pathogens (Mielke 1957, Wall 1971, Copony and Barnes 1974), as well as a host of insects.

NPS PHOTO - N. HERBERT
Wolves and Aspen

After almost 70 years of absence, wolves were reintroduced into Yellowstone in 1995. By the end of 1998, 112 wolves formed 11 packs in the Greater Yellowstone Ecosystem (GYE; Smith et al. 1999). Four packs established themselves on the northern range. In 1999, 113 permanent plots were established in aspen stands (defined as a group of aspen trees within 30 meters of one of its cohorts) across the northern range to assess the role of reintroduced wolves on elk use and aspen response (Ripple and Larsen 2000; figure 2). An inventory of YNP northern range aspen stands was created from a set of 1,240,000 color infrared aerial photographs taken in October 1998, at the conclusion of the fire season. A scanning stereoscope was used to identify grid cells containing large-stem aspen. A comprehensive list of cells containing aspen was compiled from the photographs to produce the inventory. Beginning with a live mature aspen tree running into the stand towards the centroid of the clone, a 1 x 20 meter transect was established. A metal tag was attached to the aspen start tree, and the transect was marked with nine-inch spikes for reference. From 1999-2013 (with the exception of year 2000), there has been an effort to visit and collect data for all 113 aspen sites annually near the end of the growing season in August/September. For 10 of those years, between 106 and 113 sites were visited. For the other four years, 60-90 sites were visited. Collected data included aspen stem height, current annual growth of the leader stem (the tallest stem when in shrub form), evidence of browsing from the prior year, and a count of new suckers.

Wolves’ primary prey species is elk. According to the Northern Yellowstone Cooperative winter elk count data, there has been a reduction of elk from 19,000 in 1993-1994 (the last census data prior to wolf reintroduction) to 5,000 in 2015-2016 (YNP, unpublished data, see page 8). As the number of elk has declined on the northern range, there has been a significant reduction of elk use in the number of browsed aspen stems (YNP, unpublished data; figure 3). It also appears the physiological response of apical dominance is beginning to express itself in aspen, as evident by the production of fewer suckers and increased stem height (figure 4). Given the decline in elk, the influence of apical dominance, and the significant average increase in stem height, the
early stages of stem elongation should be evident on the northern range landscape. Comparing the average stem heights for sites from 1999 (the first year aspen plots were read) to 2012 it appears aspen stand recovery is beginning to take place on the northern range (figure 5).

Are Aspen Benefitting from Wolves?

Together with other factors that influence the number of elk such as predation from bears, cougars, and hunting, aspen appears to be benefitting from the reintroduction of wolves. Barring any unforeseen circumstances, these large predators are here to stay in Yellowstone; and their continued presence on the northern range should help maintain the elk herds at lower densities, providing a long-term benefit to aspen, unlike the decades that followed the discontinuation of culling activities and the ensuing increase of elk on the landscape. Since the successful restoration of wolves along with other large predators in Yellowstone, the gradual decline in elk has significantly reduced browsing pressure, allowing for apical dominance to increasingly express itself in aspen. This physiological process is translating into the emergence of widespread aspen stand recovery, in spite of continued levels of browsing across the northern range. In light of this recent development, it is premature to say aspen have recovered or will return to anything like historic levels both in range and size. Many existing stands of mature aspen trees on the northern range established and flourished at the tail-end of the Little Ice Age, a period where conditions were predominantly wetter and cooler. These environmental conditions do not exist on the northern range today, so aspen is expected to behave and adapt differently. Recent data are highly encouraging and suggest a positive trend forward for aspen. How this plays out on the future landscape remains to be seen.

Literature Cited


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**John Klaptosky** acquired a master's degree in Sustainable Systems from the University of Slippery Rock, Slippery Rock, PA. He began his career with Yellowstone National Park in 2003, and has since served as a biological science technician in the vegetation department at the Yellowstone Center for Resources. John began his work with aspen in 2003, as the lead field technician for a research project involving the history of aspen browsing on Yellowstone’s northern range.