What's Eating the Pando Clone?
Two Weeks of Cattle Grazing Decimates the Understory of Pando and Adjacent Aspen Groves

by Jonathan B. Ratner, Erik M. Molvar, Tristan K. Meek, and John G. Carter

Western Watersheds Project

What's Eating the Pando Clone?
Two Weeks of Cattle Grazing Decimates the Understory of Pando and Adjacent Aspen Groves

by Jonathan B. Ratner,[1] Erik M. Molvar,[1] Tristan K. Meek,[1] and John G. Carter[2]

EXECUTIVE SUMMARY

The Pando Clone is an aspen grove on the Fishlake National Forest in south-central Utah that was heralded in 1992 as the world's largest single living organism. Adult trees that are joined by a single rootstock and share identical chromosomes comprise the Pando Clone and, like many aspen groves across the West, it has suffered for a number of years from die-back and failure to regenerate new shoots to replace the aging adult trees for a number of years.

The U.S. Forest Service created fenced exclosures to protect a portion of the Pando Clone from herbivory (browsing - the consumption of woody growth - by mule deer and domestic cattle), and initiated some small-scale vegetation treatments. Aspen regeneration has responded inside the exclosures in both treated and untreated areas, while outside the exclosures, on public lands leased for livestock grazing, regeneration failure and die-backs continue to plague the Pando Clone as well as other aspen groves subjected to the same pattern of livestock and mule deer hebivory, and die-back continues.

Western Watersheds Project initiated a one-year monitoring project in order to quantify ungulate use in the area, using stationary motion-sensing cameras to quantify by species the use of the area and document levels of herbivory by both domestic cattle and mule deer over the 2018 growing season in the unfenced portions of the Pando Clone and in adjacent aspen groves. At our monitoring sites, we documented 4.5 times the amount of cattle use herbivory in two weeks than the mule deer use over six months. Forage utilization by mule deer prior to the onset of livestock grazing was unobservable, while forage utilization by livestock (plus mule deer) during the 2 weeks of cattle grazing consumed 70 to 90 percent of the understory vegetation's annual production.

Cattle have a greater propensity to consume aspen sprouts in autumn, when the nutritional quality of other understory vegetation declines, and the virtual elimination of understory vegetation by this high intensity livestock use may also cause mule deer to switch to aspen shoots, further amplifying the impacts. Our results show that the brief but intense cattle grazing appears to be a major contributor to the decline of the Pando Clone, as well as other aspen groves in the immediate vicinity, in addition to the much lighter continuous herbivory by mule deer. Based on comparisons of the exclosures with the area open to both livestock and mule deer that this high level of use in the unfenced areas effectively eliminates regeneration. A previous study (Rogers and McAvoy 2018) attributed the failure of the Pando Clone to regenerate solely to mule deer, but our results indicate that cattle are also having a major impact on understory vegetation. Our results suggest that livestock herbivory may be having a synergistic interaction with mule deer foraging to suppress aspen sprout growth, and that trampling of soils by livestock may also play a role in depressed aspen recruitment in unfenced portions of the Pando Clone and adjacent aspen stands.

Based on our results, we recommend removal of livestock from the Pando Clone area to protect this globally significant organism, and also recommend that livestock be removed from public land pastures elsewhere where aspen groves show signs of depressed regeneration.

[1] Western Watersheds Project, P.O. Box 1770, Hailey, ID 83333
[2] Keisha's Preserve, P.O. Box 363, Paris, ID 83261

Introduction

Aspen (*Populus tremuloides*) stands are found across the interior West from southern Arizona to the Canadian Rockies, and typically occur in montane or sage steppe environments, often in association with abundant soil moisture. Aspen groves range along a spectrum from fire-dependent transitional communities that regenerate through periodic fires to stable communities that do not require fire for persistence (Shinneman et al. 2013). Reproduction via seeds happens most commonly in conjunction with severe disturbance such as fire (Long and Mock 2012). More frequently, aspens reproduce by sending up new shoots, or "suckers," from the existing rootstock, and the resulting aspen grove may persist for thousands of years (Jones and DeByle 1985a).

Aspen groves are frequently clones, where a single root system sends up hundreds or even thousands of individual stems (Barnes 1975), with each "tree" being a genetically identical surface expression of one large organism connected through its common root network. Gardner (2013) found that areas with high clonal diversity in aspens occurred in areas with a more frequent fire history, while areas with low aspen clonal diversity, often larger clones, corresponded to areas with less frequent fires. Clones may be long-lived; Kay (2003) hypothesized that aspen clones in north-central Nevada have maintained their presence for thousands of years via vegetative regeneration. As aspen trees age (i.e., exceed 100 years of age), they generally produce relatively few suckers (O'Brien et al. 2010).

For the purpose of clarity, it is useful to define some terms that will be used throughout this report. Aspens growing from a common rootstock are called *ramets*, a term that encompasses fully-grown adult ramets ("trees") as well as immature, regenerating trees rising as *adventitious shoots* ("shoots" or "suckers" in this report). Both new shoots with terminal buds and branches that have lateral buds can be referred to as "stems." The term "seedling" is used in this report exclus-ively to refer to young aspens growing from a seed, and excludes young aspens growing from adventitious buds on an existing root-stock. Aspen reproduction can be sexual ("seeding") or asexual ("suckering") from buds on the root system. Aspen recruitment occurs when young plants grow above the upper browse level of large herbivores. Clusters of aspen are referred to as "groves." Where such clusters are comprised of genet-ically identical trees joined by a common root system they are called "clones" and represent a single organism with many adult trees, sometimes thousands. "Regeneration" occurs when the recruitment of aspen suckers replaces the die-off of adult trees.

Aspens commonly grow where soil moisture is relatively abundant. However, in forested areas, sites containing aspens may be wetter simply because they transpire less water into the atmosphere than do conifers (Jones and DeByle 1985b). Aspen groves often contribute more water to drainage systems than do coniferous trees because they transpire only during the part of the year when they have leaves (versus year-round transpiration for conifers) and collect more snow in the understory than do conifers (DeByle 1985c). Aspens also have chlorophyll in their stems, and can photosynthesize throughout winter when leaves are absent (Grant and Mitton 2010). Presumably, water loss is minimal during winter when leaves are absent.

Aspen groves are hotspots of biodiversity and a number of bird species appear to be dependent on aspen habitats. Aspen groves harbored the greatest number of native species (45) of any habitat type in Grand Staircase – Escalante National Monument (Bashkin et al. 2003). Red-naped sapsucker, black-capped chickadee, house wren, warbling vireo, and northern saw-whet owl are closely associated with aspen woodlands (Hejl et al.,1996). Loose and Anderson (1995) found that 30 of 33 woodpecker nests in their Sierra Madre study area were found in aspens, and among these, there was a significant pref-erence for large, old trees. According to Winternitz and Cahn (1983), 40% of species

that inhabit aspen are cavity nesters, with a significant preference for large trees over 100 years old and trees infected by heartrot fungus. Heartrot-infected aspens are easier for birds and mammals to hollow out to create cavity nests. Aspens also are of critical importance as a food source for beavers (Williges 1946).

Jones and DeByle (1985c) compiled a thorough analysis of the role of fire in aspen ecology. According to these biologists, almost all even-aged aspen stands in the western U.S. appear to be the result of severe fire, presumably in coniferous forests. In Yellowstone National Park, Romme and Knight (1982) found that fire suppression has led to denser coniferous forests, a decrease in aspen, and an increase in sagebrush in meadow areas. Forest fires can foster aspen regeneration because fallen timber provides refugia for aspen seedlings to escape browsing by ungulates (Ripple and Larsen, 2001).

Strong aspen regeneration typically occurs even after severe burns. An abundance of aspen woodlands in the coniferous forest zone often indicates the prevalence of past stand-replacement fires. But Fornwalt and Smith (2000) noted that old, multi-storied aspen stands can maintain their productivity over time and are in many cases self-perpetuating. Thus, previous assumptions that aspen stands require periodic disturbance to maintain themselves are not universally true, and some stands (particularly old, multi-story stands) perpetuate themselves in the absence of any management treatment.

Although aspen habitats are viewed as valuable grazing resources by the livestock industry, these areas are very sensitive to overgrazing. Meuggler (1985b) reported that heavy grazing by domestic sheep can turn the rich and diverse herbaceous understory that occurs in ungrazed stands into a depauperate understory of grasses. In aspen stands that are overgrazed, invading, unpalatable plants can form a stable grazing disclimax (an unnatural, disturbed plant association that can persist indefinitely), reducing the wildlife habitat value of the grove (Mueggler 1985a). In addition, in older stands, heavy livestock

grazing can prevent regeneration and speed the decline of the aspen stand itself (DeByle 1985a). Cole (1993) found that aspen-forb communities are highly susceptible to trampling damage even from human foot traffic. The physical trampling of nests and habitat degradation associated with livestock grazing can be detrimental to ground-nesting birds that prefer aspen habitats, such as the hermit thrush, junco, white-crowned and Lincoln's sparrows, veery, ovenbird, and nighthawk (DeByle 1985b). Because livestock grazing is currently permitted on more than 232 million acres of federal public land in the western United States (Beschta et al. 2013), the potential for ecological damage from livestock grazing is widespread.

The Pando Clone

The name "Pando" comes from the Latin "to spread." Kemperman and Barnes (1976) originally proposed the Pando Clone as a single living thing covering approximately 108 acres in area and made up of approximately 47,000 *ramets*, or stems. Grant et al. (1992) concluded that the Pando Clone represents the largest single organism in the world, with an areal extent of approximately 106 acres (43 ha) and an estimated weight of more than 6,600 tons (6 million kg). The Pando Clone was confirmed through genetic testing to be a single massive organism by DeWoody et al. (2008). Some of the trees in the Pando clone show triploid chromosome patterns (in effect, possessing a third set of chromosomes), and these individuals have a competitive advantage over diploid stems in terms of height and diameter growth (DeRose et al. 2015). This gives these stems an advantage in the 'self-thinning' stage of stand development, when only the most fit stems survive to attain tree form.

The age of the Pando Clone is a matter of substantial scientific debate. Kemperman and Barnes (1976) hypothesized that the Pando Clone was originally established more than 8,000 to 10,000 years before present. Aspen clones in this southern, unglaciated portion of the species' range, including Utah, can be unusually large and of much greater age
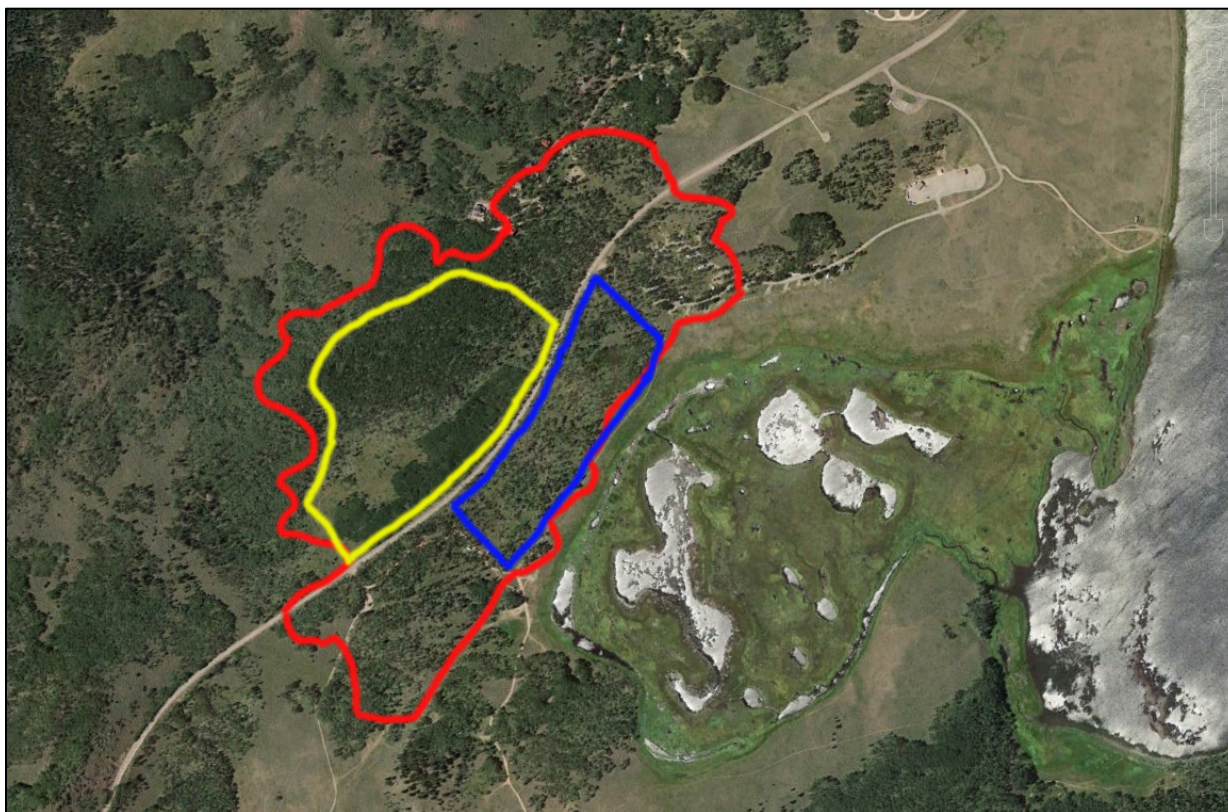
Figure 1. The boundary of the Pando Clone, in red (after Kemperman and Barnes 1976), showing the 2013 exclosure fence (in blue) which more successfully excludes mule deer, and the 2014 exclosure fence (in yellow) which has been less successful in excluding mule deer. State Highway 25 can be seen bisecting the Pando Clone, and Fish Lake appears at the right of the image. Image courtesy Google Earth.

(Barnes 1975). Mock et al. (2008) identified a number of other genetically distinct aspen clones along the fringes of Pando, and hypothesized that the relatively few mutational variants within the Pando Clone may indicate a much less ancient age for Pando. DeRose et al. (2015) hypothesized that the Pando Clone initially became established as recently as the 1880s. However, this conclusion is based on core sampling of existing trees; it is unlikely that the 108-acre root system of the Pando Clone arose spontaneously in a single year or two; indeed it is far likelier that the clone spread gradually over a long span of years. Thus, the definitive overall age of the Pando Clone remains undetermined at this time. Grant and Mitton (2010) estimated the age of the Pando Clone at 80,000 years.

On the Fishlake National Forest, where the Pando Clone grows, aspen cover has declined by 60% from historic levels (Wooley et al. 2008). Fragmentation of the Pando Clone stand itself is currently occurring, due to browsing by herbivores suppressing sapling recruitment, rural real estate development, and a fungal infection called sooty-bark canker (DeWoody et al. 2008). As a result, sapling recruitment in unfenced portions of the Pando Clone is failing to replace aging adult trees. According to Rogers and Gale (2017: 9), "Judging from the near-complete lack of recent recruitment (> 2 m height) and mid-story aspen throughout the study area, it has been many years, likely even decades, since this amount of stand renewal [0.5 ramets per overstory tree] has taken place at Pando." As overstory trees continue to die without replacement by sucker recruitment, the overall size of the Pando clone ultimately will shrink (*id.*). Mule deer and cattle affect the Pando Clone and its ability to regenerate through browsing adventitious suckers and trampling.

Elk do not appear to be affecting the Pando Clone. According to Rogers and Gale (2017: 11, internal citation omitted), "While elk browsing of aspen is a serious concern regionally, we did not see elk or record their scat at Pando." Rogers and McAvoy (2018) reported that "[e]lk sign is evident in the broader area" and used that as a basis for asserting that elk were presently accessing the Pando Clone, but documented no elk sightings and no elk scat during the course of their study.

In 2012, the Forest Service issued a decision to fence 67 acres (22 ha) of the Pando Clone's 108-acre (43-ha) extent (see Figure 1) to prevent herbivory from domestic and wild ungulates and authorized some small-scale, experimental cutting inside the exclosures to stimulate suckering (USFS 2012). The exclosures were built of 8-foot tall woven wire topped with a barbed-wire strand. One exclosure of 17 acres (7 ha) was constructed in 2013 to the east of State Highway 25, and it appears to mostly exclude both mule deer and livestock (Rogers and Gale 2017, Rogers and McAvoy 2018), although Coles-Ritchie documented deer sign and evidence of browsing inside this exclosure. Aspen recruitment is progressing well inside the Pando Clone ungulate exclosure, even though the presence of mule deer has been documented inside the exclosure (Coles-Ritchie 2018). A second exclosure of 37 acres (15 ha) was constructed in 2014 to the west of the highway, incorporating a 22-year-old section of fence, and mule deer appear to be able to enter this fenced exclosure (Rogers and McAvoy 2018). Rogers and Gale (2017) found that the portions of the Pando Clone that had been fenced to exclude large herbivores showed a positive response in terms of regeneration (irrespective of cutting treatments), while the remaining 52 acres (21 ha) of the Pando Clone outside the exclosure showed no improvement. Rogers and Gale (2017) found that fencing alone resulted in an average of 550 regenerating suckers per acre inside the 2013 exclosure, a level sufficient for stand replacement according to earlier scientific findings (Mueggler 1989).

Aspen Declines

The regeneration problems experienced by the Pando clone mirror widespread declines in aspen regeneration, both on the Fishlake National Forest and throughout the West. In addition to the gradual replacement of aspen woodlands through the invasion of conifers in certain areas, aspen die-offs also occur in the absence of conifer encroachment. These die-offs can eliminate adult stems within a period of two years, and are often accompanied by an absence of sapling recruitment (Bartos 2008). On Cedar Mountain in south-central Utah, aspen stands showed depressed sucker recruitment and almost one-fifth showed crown dieback greater than 20% (Rogers et al. 2010). Evans (2010) found that drought weakened aspen on Cedar Mountain, Utah, making them more susceptible to a long-term decline that reduced the area of aspen woodland by 24% over a 23-year span. Many aspen stands in northern Nevada are in poor condition and have not regenerated in more than 100 years, due primarily to heavy livestock browsing (Kay 2003). Brown (1995) attributed the decline of aspen in eastern Oregon and Washington to intensive grazing and fire exclusion. Fairweather et al. (2007) documented a sudden decline of aspens on the Coconino National Forest in Arizona following a severe frost event, followed by a severe drought and an outbreak of tent caterpillars. Smooth brome, an invasive perennial grass, may affect aspen suckering (O'Brien et al. 2010). Overall, multiple factors can contribute to the decline of adult aspens, but reproduction through suckering typically occurs unless it is suppressed be herbivory by non-native livestock or by native herbivores such as deer and elk.

While the gradual decline of aspen groves over time may be widespread, aspen die-offs also occur that eliminate adult stems within a period of two years, with an absence of sapling recruitment (Bartos 2008). Sudden Aspen Death syndrome is associated with aspens at high altitude under water stress (Worrall et al. 2010). The decline of the Pando Clone appears to be of the more gradual

variety, rather than Sudden Aspen Death syndrome.

Aspens most commonly reproduce adult stems via suckering from the rootstock; its seeds, while abundant, are short-lived and have demanding germination requirements (Schier 1981, Kay 2003, Long and Mock 2012). As a result, seedling establishment typically occurs only during extremely wet summers (Jones and DeByle 1985b).

Schier (1975) described the dynamics of sucker production as governed by apical dominance, a phenomenon whereby hormones from the terminal buds of aboveground stems (auxins) inhibit hormones in the root system that stimulate sucker growth (cytokinins). When disturbance of the stems reduces the flow of auxins, the cytokinins can initiate the regenerative process. However, when aboveground stems weaken and die, the root system dies back due to a lack of photosynthate being furnished to the roots. Schier (1976) suggested that sucker regeneration is proportional to above-ground disturbance, citing examples from clearcut logging studies where the number of suckers generated is proportional to the number of stems removed by logging. Where suckering is suppressed by ungulate browsing, the die-off of adult aspens can result in areal reductions in aspen habitats across the landscape.

Shepperd (2001) proposed hormonal stimulation, a proper growth environment, and sapling protection as the three elements of an aspen regeneration triangle. Natural disturbances such as fire can stimulate suckering and regenerate aspen stands, but if livestock are not excluded from the aspen grove for several years following fire, their browsing can severely suppress sucker growth (Kay 2003).

The Role of Herbivory in Aspen Declines

Heavy ungulate browsing over extended time periods can cause regeneration failure over spans of many decades, resulting in an even-aged grove of older trees that is less resilient to drought and other stressors (Lindroth and St. Clair 2013). In the Book Cliffs of northeastern Utah, Rogers and Mittanck (2014) found that only three of 77 aspen stands (less than 4%) contained adequate levels of recruitment to perpetuate the stand, due substantially to browsing by wild and domestic herbivores. Herbivory by both domestic livestock (sheep and cattle) and wild ungulates (deer and elk) can suppress aspen shoot recruitment, and thus impair regeneration.

In some circumstances, large herbivore grazing and/or browsing in aspen stands may not put significant pressure on aspen reproduction. For example, Beck and Peek (2005) found only a 3% dietary overlap between spring and summer mule deer and cattle diets in aspen stands, with deer preferring browse and cattle preferring grasses and forbs, and also found that elk and cattle did not have significantly different diets. However, this study found that all of the herbivores studied had a 0% dietary consumption of aspen, with the exception of spring diets in one of three years, which showed <1% aspen contribution to the elk diet. Mower and Smith (1989) found that elk and mule deer diets in northern Utah were quite similar, and although shrubs made up a significant component of both, aspens were not noted as a significant component of the diet. Notwithstanding the preference of native and domestic ungulates for other forage plants, overbrowsing of aspen shoots to the point of regeneration failure is widespread.

Aspens have defensive compounds – phenolic glycosides and tannins – that provide adequate defense against insects and mammalian herbivores when browsing is light, but which is an inadequate defense under heavy browsing, which results in high levels of damage to the trees (Lindroth and St. Clair 2013). Elk may respond negatively to increasing phenolic glycoside content (Wooley et al. 2008). However, the scientific consensus is that while the tannins and phenolic glycosides present in aspens evolved as a defense against herbivory, they are insufficient to prevent browsing by either domestic or wild ungulates.

Deer and Elk Browsing

Aspen communities often are an important source of protein for mule deer in summer, whereas Utah serviceberry and big sagebrush communities may only provide maintenance amounts of protein (Austin and Urness 1985). This dietary advantage of aspen communities may contribute to mule deer preference for them. Severe browsing by elk and deer virtually eliminated sapling recruitment during an aspen die-off in northern Arizona (Fairweather et al. 2007). Additionally, population irruptions of mule deer on the Kaibab Plateau of northern Arizona in the 1920s had, between 1953 and 1962, completely suppressed aspen recruitment on the Kaibab Plateau of northern Arizona (Binkley et al. 2006). In Michigan, Randall and Walters (2011) found that increasing densities of white-tailed deer in aspen stands suppressed suckering and reduced forb density and species richness.

Livestock grazing in aspen groves may come at a cost for resident mule deer. Loft et al. (1991) suggested that as a result of livestock grazing, displacement of mule deer from these habitats and expansion of deer home ranges resulted in a lowering of inclusive fitness for mule deer. According to Loft et al. (1991: 22, internal citation omitted), "Once aspen stands had been occupied by cattle for a few weeks, there was little forage or hiding cover available, and deer essentially quit using the habitat." These studies indicate the likelihood that forage removal by cattle or domestic sheep can alter mule deer habitat selection and/or diet choices.

The likelihood of suppressed aspen regeneration from concentrated elk browsing appears to be greater than for mule deer. Compton (1974) found that elk in the Sierra Madre Range in Wyoming concentrated their summer use in subalpine parks, and found heavy autumn use in aspen cover types. Beck et al. (1997) reported that aspen made up 10% of elk summer diet, versus 3% of domestic sheep summer diet, in north-central Utah. Elk foraging on winter ranges has been shown to depress growth and prevent reproduction of aspen in Rocky Mountain National Park (Baker et al. 1997, Suzuki et al. 1999, Binkley

2008). Aspen are likely to be suppressed where elk density exceeds four elk per square kilometer (Painter et al. 2018). Elk also damage aspens by browsing new shoots, rubbing flexible saplings with their antlers, and by gnawing tree bark to get at the phloem underneath (Fairweather et al. 2007).

In the absence of large native predators, elk can suppress aspen sapling recruitment (Binkley 2008, Beschta and Ripple 2009). Ripple and Larsen (2000) found that due to heavy browsing by elk, following removal of wolves, only 5% of the current overstory aspen in the Northern Range of Yellowstone National Park originated after 1921. Painter et al. (2018) found that the percentage of aspen suckers browsed annually in Yellowstone National Park was 80-100% in 1997-98, decreasing to 30-60% in 2011-15 after the re-establishment of a wolf population. Elk shifted their habitat use and herbivory intensity away from Yellowstone National Park and toward the lower Madison River Valley in response to increasing wolf populations in the Park (Painter et al. 2018). However, in some localities within Yellowstone National Park, elk densities have remained high enough to continue to suppress aspen suckering (*id.*). White et al. (1998) found that elk browsing suppressed aspen recruitment in Canadian Rockies national parks, except under conditions when elk densities were reduced by wolves. There is now a broad scientific consensus that the absence of large native predators can result in depressed recruitment of aspen and other woody species (Beschta and Ripple 2009, Painter et al. 2018).

Browsing Pressure from Domestic Livestock

Livestock often concentrate their grazing activity in aspen groves due to the availability of shade and preferred understory forage species. In the Sierra Nevada mountains, cattle utilized meadow riparian and aspen habitats most strongly, selecting them over other habitats (Loft et al. 1991). According to Kay (2003: 41), "Even on allotments where livestock use has been controlled, aspen stands near water may still be in poor ecological condition because cattle tend to

concentrate in those areas." Bailey et al. (1990: 213) found that cattle impacts on aspen are so severe that livestock can be used as a means to suppress aspen reproduction, stating "Overgrazing is generally considered to be detrimental to range stability and productivity over the longer term, but short duration heavy grazing may have a place in forage establishment and control of woody species." These researchers (*id.*: 214) recommended, "Clearly, for immediate control of aspen suckers, top removal or defoliation must be timed similarly to the late grazing treatment in this study. However, aspen suckers are suitable forage for cattle provided they are maintained within reach."

Beschta et al. (2014) found that aspen recruitment rates plummeted in the late 1800s with the onset of cattle grazing on the lands that would become Hart Mountain National Wildlife Refuge in southern Oregon, and increased by an order of magnitude after livestock were removed in 1990. These researchers attributed the decline of aspen groves on Hart Mountain to top-down forcing by cattle browsing, which suppressed aspen sapling recruitment, rather than climate changes. On Monroe Mountain in south-central Utah, Bartos and Campbell (1998a) provided photographic documentation of the effects of livestock preventing aspen regeneration using fenceline contrasts of a previously burned and logged area which remained barren in the presence of livestock and failed to regenerate. Across the fence, on habitats accessible to native herbivores but where livestock were excluded, dense regeneration was evident. Alexander (1995) documented that trampling by livestock broke 40% of aspen samples under both moderate and heavy grazing in his Alberta study; trampling caused damage in the form of basal scars that were present on 25% of surviving aspen saplings. By the second spring of cattle grazing, aspen sapling mortality in this study was 25%, 70%, and 89% for the ungrazed, moderately grazed, and heavily grazed sites, respectively.

Cattle selection for aspen shoots differs by season. According to Kay (2003: 32), "Year-

long or season-long grazing is particularly detrimental to aspen, while early-season or dormant-season use may allow aspen to successfully regenerate." According to Jones et al. (2011: 629), "Aspen suckers received no early-growing season use by cattle but received the heaviest late-growing season use of all three vegetation types. Utilization was the same for all vegetation types at mid-growing season. Mean late-growing season use of aspen suckers was greater than 60%, and some stands received 100% use." Jones et al. (2011: 630) observed, "By mid-growing season, the quality of meadow and aspen understory vegetation approached minimum nutritional levels required for cattle." Alexander (1995) found that aspen suckers that have not yet begun to lignify, or become woody (i.e., one-year-old suckers), are a palatable forage for cattle, while two-year-old suckers were "not readily used" by cattle.

Even moderate levels of livestock grazing can suppress aspen regeneration. Alexander (1995) found that moderate and heavy grazing by cattle were equally effective at preventing aspen regeneration, with both moderate and heavy grazing both had a significant negative effect on understory biomass production in aspen stands.

Methods

We quantified ungulate use of the Pando Clone area with two motion-triggered cameras (Cameras 2 and 3) that were placed in portions of the Pando Clone outside the fenced exclosures, and two cameras that were placed in neighboring aspen groves (Cameras 1 and 4) subjected to the same pattern of livestock and mule deer herbivory. The cameras were sited in areas open to grazing and browsing by both domestic livestock and wild ungulates. The cameras were set to take photographs of all motion-triggered events separated by at least 1 minute. Cameras were installed on May 11th, 2018 and retrieved on November 22nd, 2018 to record herbivore activity throughout the growing season. The cameras were more sensitive to motion than

expected. As a result, two of the cameras (Cameras 1 and 4, the cameras sited in neighboring aspen groves) ran out of battery power well before the end of the monitoring period, and therefore failed to record photographs during the livestock grazing period. These cameras, when remaining operational throughout the summer and into the fall, provide useful comparisons of forage utilization during cattle-free and cattle grazing periods, but could not be used to compare animal unit equivalents between deer and cattle due to the absence of livestock records.

After retrieval, the photographs were individually examined and the counts of ungulates were tallied for each camera. In order to more accurately compare total use by ungulate species, use was calculated based on body size/forage consumption by the Animal Units Equivalents (AUEs). A literature search found a range of estimates for mule deer, ranging from 0.2 (Pratt and Rasmussen 2001, NRCS 2003) to 0.17 (Ogle and Brazee 2009). For our calculations, we used 6 deer per 1 cattle animal unit (AU) (0.167), which is conservative being based on a 1,000-pound cow with calf. Cattle weights have increased significantly over the last 40 years with current average slaughter weight is presently 1,382 pounds (628 Kg) as of December 2017, (NASS 2018). We graphed the AUE data by week to display use over the monitoring period. It should be noted that the ratio of six deer per cow greatly underestimates the difference. A 1,382-pound (628 kg) cow consumes 3% of its body weight per day, or 41.6 lbs (18.9 Kg) (Ogle and Brazee, 2009). A 150-pound (68 kg) mule deer consumes 1.5 kg/day (UWSP 2019). This

current information indicates a mature cow consumes 12.6 times the forage demand of a mule deer. However, we used the lower value to provide a conservative comparison.

We created time lapse videos of the photographs from each camera to help visualize conditions and herbivore use throughout the growing season.

The Interagency Landscape Appearance Method

This method's descriptions classify forage utilization into the following Herbaceous Utilization classes (USFS 1993; *see also* BLM 1996):

1. No Use (0-5%). The rangeland shows no evidence of grazing use; or the rangeland has the appearance of negligible grazing.

2. Slight (6-20%) The rangeland has the appearance of very light grazing. The key herbaceous forage plants may be topped or slightly used. Current seedstalks and young plants of key herbaceous species are little disturbed.

3. Light (21-40%) The rangeland may be topped, skimmed, or grazed in patches. The low-value herbaceous plants are ungrazed and 60 to 80 percent of the number of current seedstalks of key herbaceous species remain intact. Most young plants are undamaged.

4. Moderate (41-60%) The rangeland appears entirely covered as uniformly as natural features and facilities will allow. Fifteen to 25 percent of the number of current seedstalks of forage plants are utilized. (Moderate use does not imply proper use.)

5. Heavy (61-80%) The rangeland has the appearance of complete search. Key herbaceous species are almost completely utilized with less than 10 percent of the current seedstalks remaining. Shoots of rhizomatous grasses are missing. More than 10 percent of the number of low-value herbaceous forage plants have been utilized.

6. Severe (81-100%) The rangeland has a mown appearance and there are indications of repeated coverage. There is no evidence of reproduction or current seedstalks for key herbaceous species. Key herbaceous forage species are completely utilized. The remaining stubble of preferred grasses is grazed to the soil surface.

These videos can be accessed at https://www.westernwatersheds.org/pando-clone-time-lapse/. We also took photographs along the 2013 exclosure fence to document the contrasting rates of regeneration within and outside the exclosure.

Utilization of vegetation by herbivores was estimated using the interagency Landscape Appearance Method descriptions, an estimation procedure used on the Fishlake National Forest (USDI Technical Reference 1734.3), see accompanying box. Utilization was estimated at the photo location on the day prior to livestock entry, 7 days after livestock entry (half of the livestock use period) and again after livestock removal.

Results

The exclosures constructed by the Forest Service in 2013 and 2014 within portions of the Pando Clone provide a clear contrast between natural recovery rates inside the exclosures with the effects of this heavy to severe level of utilization outside the exclosures. The exclosures were built of 8-foot tall woven wire topped with a barbed-wire strand. Figures 2 and 3 are taken from the same location, with one looking into the interior of the 2013 exclosure and the other looking into the grazed allotment, and area used by both deer and cattle.

From the ongoing aspen recovery that has occurred since the exclosures were constructed in 2013 and 2014, and the complete lack of any recruitment of aspen sprouts occurring outside the exclosures, it is clear that current management outside the exclosures prevents the regeneration of the Pando Clone in areas open to livestock grazing. Inside the 2013 exclosure fence, we found successful aspen recruitment is occurring irrespective of any mule deer that may have found a way to enter the exclosure area.

Camera 1 recorded from May 11th, 2018 through August 13th, 2018, prior to the onset

Figure 2. A view inside the 2013 exclosure. Note abundant regeneration 8-12 feet tall after 5 years of exclusion. June 10th, 2019.

Figure 3 (above). Looking into an unfenced portion of the Pando Clone from the same location with no regeneration. June 10th, 2019.

Figure 4 (below). - Fenceline contrast with abundant regeneration inside the 2013 exclosure (left) and no regeneration occurring outside (right). June 10th, 2019.
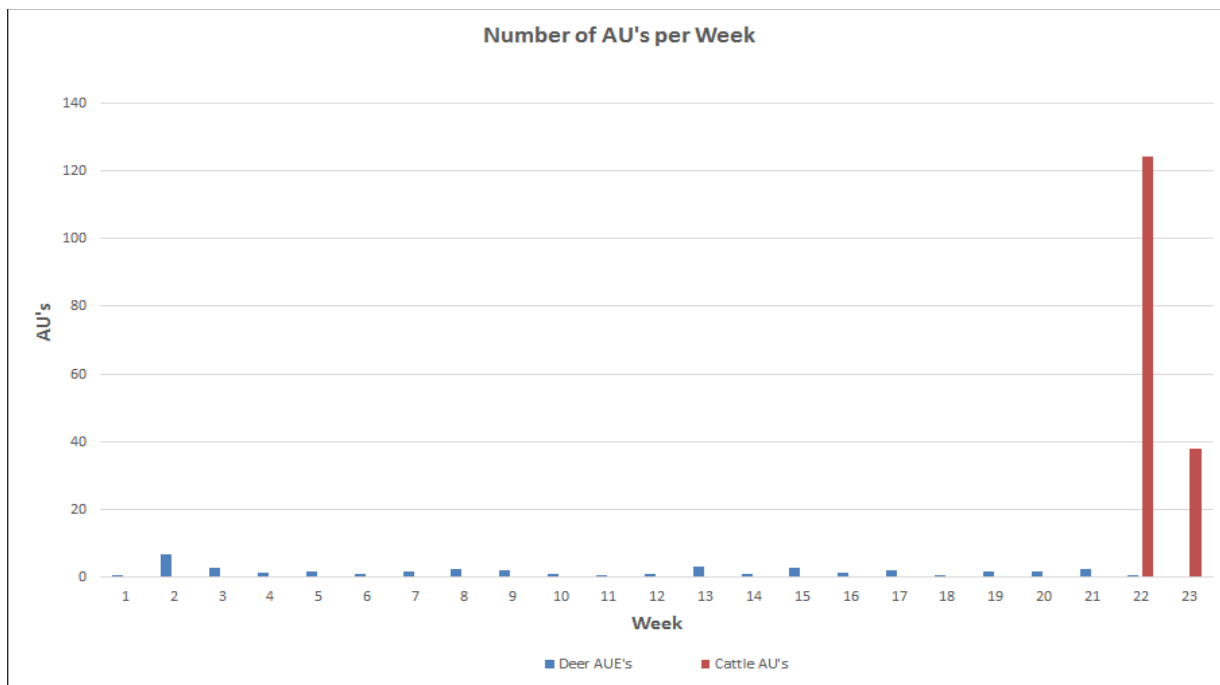
Figure 5. Camera 2, within an unfenced portion of the Pando Clone, deer versus cattle Animal Units by week.

of livestock grazing. Camera 2 recorded from May 11th, 2018 through October 9th, 2018.

Camera 3 recorded from May 11th, 2018 through November 22nd, 2018. Camera 4 recorded from May 11th, 2018 through September 22nd, 2018, prior to the onset of livestock grazing. The livestock use period

began on October 4th and ended October 16th for a total of 13 days, during which domestic cattle were the type of livestock present in the project area. The area under study received use by mule deer (*Odocoileus hemonius*) throughout the monitoring period.
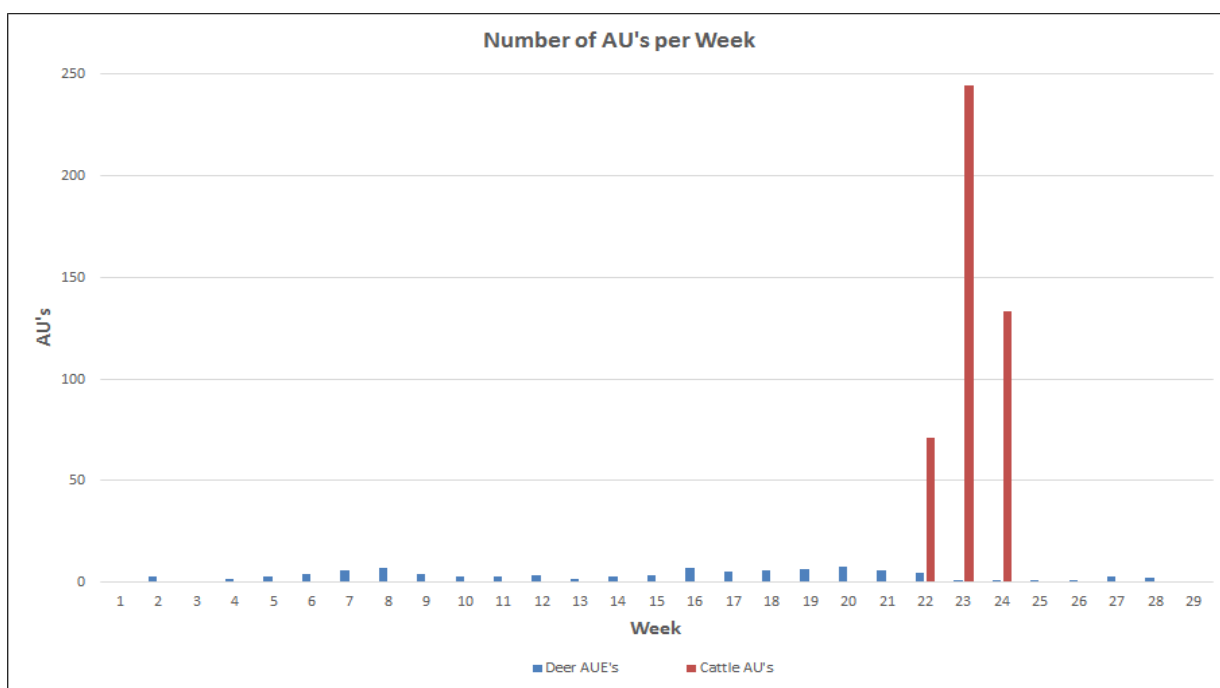

Figure 6. Camera 3, within an unfenced portion of the Pando Clone deer versus cattle Animal Units by week.

Rogers and McAvoy (2018) reported that "[e]lk sign is evident in the broader area" and used this as a basis for asserting that elk might presently be accessing the area. We documented no elk sightings in the Pando Clone, but Camera 1 recorded four elk in one instance in an adjacent aspen grove.

For Camera 1, motion from grass moving in the wind depleted the power supply by August 13th, 2018, so only forage utilization observations could be made. For Camera 2, deer use during the 6-month period totaled 42 AUE's, while cattle use during the 6 days (slightly less than 50% of the cattle use period) totaled 162 AU's. For Camera 3, deer use during the 6-month period totaled 101 AUE's, while cattle use during the 13 days totaled 448 AU's. For Camera 4, motion from grass moving in the wind depleted the power supply by September 27th, 2018, so only utilization observations could be made. On average, the index for animal use documented for cameras that lasted into the livestock grazing season was found to be four times higher for cattle during the 13 days of livestock grazing than for mule deer over the course of the entire growing season. Camera

4, on the eastern shore of Fish Lake, documented a similar result.

During the months prior to the arrival of livestock all cameras documented no observable utilization of the vegetation, whereas within 7 days after the arrival of livestock utilization was in the "heavy" category (61-80% utilization) for Cameras 2 and 3, inside the Pando Clone. After livestock removal, use was in the upper "heavy" to mid "severe" (81-100%) categories at all four sites (see Figures 10, 16, 22, 27, 28, and 29).

Figure 10 shows conditions following livestock removal for Camera 1, in an aspen grove adjacent to Pando. Based on the descriptions in the Landscape Appearance Method this would fit in the upper end of the "heavy" (61-80%) category. Within the Pando Clone, patterns of herbivory by mule deer and livestock were essentially identical to Pando's genetically distinct neighboring groves. For Camera 2, livestock use was near the upper end of the "heavy" category by day 7, with significant utilization on rabbitbrush (*Chrysothamnus* sp.), which has low palatability (see Figure 15). By the time livestock were removed, forage utilization levels, based on

Figure 7. Camera 1 (in an aspen grove immediately adjacent to the southeast corner of the Pando Clone) at deployment. Note mountain lion.

Figure 8 (above). Camera 1, mid-June.

Figure 9 (below). Camera 1, mid-summer.

Figure 10 (above). Camera 1 location on November 22nd, 2018, after livestock removal. Forage utilization shown here is in the upper end of the "heavy" (61-80%) category.

Figure 11 (below). Camera 2, within the Pando Clone, at deployment.

Figure 12 (above). Camera 2, inside the Pando Clone, in mid-June.

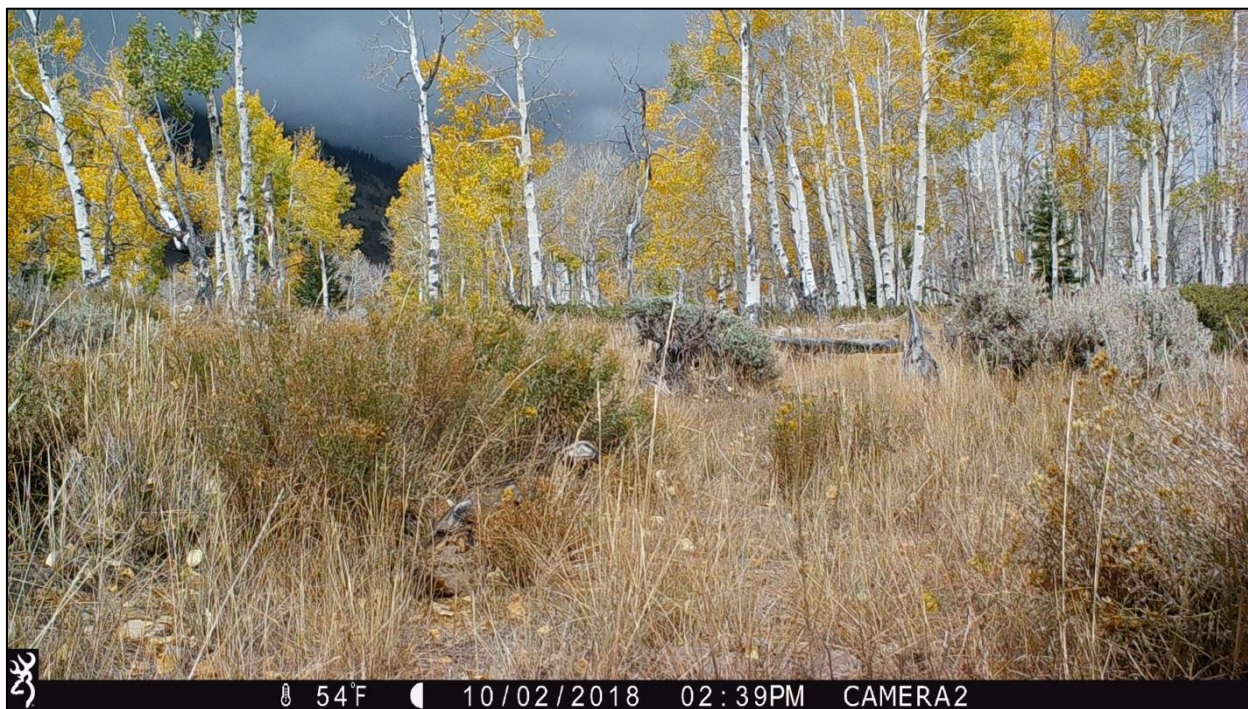**Figure 13 (below).** Camera 2 in late summer.

Figure 14 (above). Camera 2 just prior to livestock entry.

Figure 15 (below). Camera 2 after 7 days of livestock use.

Figure 16 (above). Camera 2 location on November 22nd, 2018, taken in the general direction the remote camera had been pointed, after livestock removal. Forage utilization shown here is in the mid to upper end of the "severe" (81-100%) category.

Figure 17 (below). Camera 3 (within the southeastern edge of the Pando Clone) at deployment.

Figure 18 (above). Camera 3 in mid-June.

Figure 19 (below). Camera 3, mid-summer.

Figure 20 (above). Camera 3 just before livestock entry. Note for reference the two large bunchgrasses on the left and the scattered fallen limbs on the ground.

Figure 21 (below). Camera 3 after 7 days of livestock use.

Figure 22 (above). Camera 3 after livestock removal. Forage utilization shown here fits in the upper end of the "heavy" (61-80%) category.

Figure 23 (below). Camera 4, above the eastern shore of Fish Lake, at deployment.

Figure 24 (above). Camera 4 in mid-June.

Figure 25 (below). Camera 4, mid-summer.

Figure 26 (above). Camera 4 just before livestock entry.

Figure 27 (below). Camera 4 location, taken in the general direction of the remote camera, on November 22nd, 2018 after livestock removal. Based on the descriptions in the Landscape Appearance Method this level of herbivory fits in the upper end of the "heavy" (61-80%) category.
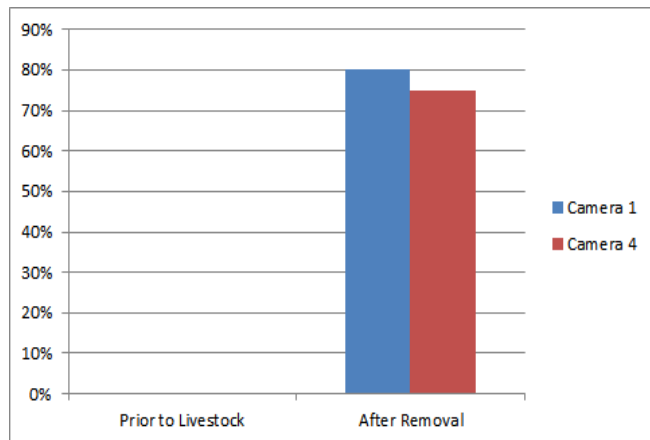
Figure 28. Forage utilization levels before livestock entry and after removal for Cameras 1 and 4, in aspen groves adjacent to the Pando Clone.

the descriptions in the Landscape Appearance Method grazing levels shown by Camera 2 this would fit in the mid to upper end of the "severe" (81-100%) category. By day 7 of livestock use documented by Camera 3 (see Figure 21), the large bunchgrasses had been completely grazed and only a small fraction of the seedheads remained. Note the difference in visibility of the fallen branches at ground level between Figures 20 and 21. Figure 22 shows conditions for Camera 3 following livestock removal. Based on the descriptions in the Landscape Appearance Method this would fit in the upper end of the "heavy" (61-80%) category. By the time livestock were removed, forage utilization levels shown by Camera 2 (see Figure 16) would fit in the mid to upper end of the "severe" (81-100%)
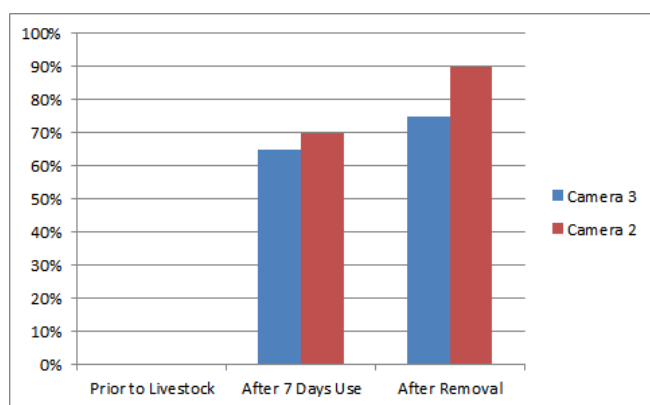

Figure 29. Forage utilization levels before livestock entry and after removal for Cameras 2 and 3, sited within the Pando Clone.

down to the same level as the rest of the forage base.

While we hoped to document direct herbivory by deer and/or cattle on aspen sprouts with the remote cameras, in fact we were unable to document any aspen sprouts at all during the growing season period over which our cameras were deployed. This is consistent with the findings of Rogers and Gale (2017), who also reported essentially no aspen sprouts outside the exclosure fence. Thus, like Rogers and McAvoy (2018), we are unable to measure direct herbivory of aspen by either mule deer or cattle, and are left with making inferences from indirect measures (in the case of this monitoring report, overall forage consumption and animal use). The level of trampling by cattle appears to be heavy in all locations we monitored.

Our findings support the conclusions of Loft et al. (1991), that the presence of livestock results in habitat abandonment by deer. Deer use dropped to nearly zero after the arrival of livestock and only returned after livestock removal and then at much lower levels than prior to livestock entry.

Discussion

We documented levels of herbivory by mule deer that were too light to quantify throughout the summer, measured by the Landscape Appearance Method used by the Forest Service to estimate forage utilization. This was followed by heavy to severe understory utilization by cattle that virtually eliminated understory vegetation during the 14-day period in October when cattle were turned out both in unfenced portions of the Pando Clone, and in neighboring aspen groves subjected to the same pattern of livestock grazing. The level of livestock forage utilization we documented (70 to 90%) was consistent with heavy grazing as defined by Alexander (1995), who classified 73% forage utilization by cattle as "heavy" and found this level – entailing the browsing of 95% of aspen saplings – to be sufficient to suppress aspen regeneration (see Figures 28 and 29). This is

supported by scientific observations at Pando itself. Rogers and Gale (2017: 11) concluded, "A key message, then, is that while we cannot state unequivocally that there are 'too many' herbivores at Pando, we do know that there are too many for current conditions."

These heavy to extreme levels of forage utilization exceed the Forest Service allowable utilization level of 50% (USDA 2018). In addition, these levels are much greater than the 25% level supported by leading range scientists (Galt et al 2000).

By quantifying the ungulate use of the Pando area and tracking utilization over the study period, our data and analysis demonstrates, based on Animal Unit Equivalents, that more than 4 times the animal use occurs in the unfenced portion of the Pando Clone and in neighboring aspen groves from livestock than for mule deer. Nearly all of the observable forage utilization in the understories of aspen groves in this area during the monitoring period was the result of livestock. According to Rogers and Gale (2017: 6),

> we counted only one mule deer scat pile, but 219 cattle deposits in Year 1. In Year 2, we counted no scat piles of any species within the fence, but 72 cattle and five deer piles outside the exclosure. By Year 3, cattle deposits were 64 and deer scat was 14, all outside the exclosure.

Our results are consistent with these findings.

Our findings contrast with Rogers and McAvoy 2018, which concluded that mule deer are the primary factor in regeneration failure in the Pando Clone. The Rogers and McAvoy study used "browse level, and feces counts as a surrogate for ungulate presence." Its analysis identified deer presence (indexed by density of pellet groups) as the key factor relating to failure of aspen sprouts to recruit. Cattle presence as indexed by feces was negatively related to both recruitment and aspen density but was not identified as a major factor by this exploratory analysis. It is troubling that while pellet groups were

negatively related to aspen regeneration in the Rogers and McAvoy study, browse level was not a significant factor. Browsing of aspen saplings would presumably be the direct means by which either mule deer or cattle would directly affect sapling survival and recruitment.

In addition, Rogers and McAvoy's identification of cattle concentration as an unimportant factor in aspen recovery runs contrary to earlier findings that aspen recruitment is lowest in portions of the Pando Clone accessible to livestock, and higher in fenced areas, whether these are accessible to mule deer or not (Rogers and Gale 2017, Coles-Ritchie et al. 2018). Rogers and McAvoy (2018) concluded that deer were the cause of regeneration failure. But in their analysis of regeneration, the 2014 exclosure was accessible to deer but not cattle, and had a browse level of 24%, while in the unfenced area, where both deer and cattle were present, the browse level was 55%. Furthermore, aspen recruitment was highest in the 2014 exclosure (1,204 stems/ha) in the presence of deer and lowest in the 2013 exclosure from which both deer and livestock were absent, further muddying this conclusion.

The season of livestock grazing can also have a major impact on regeneration. Livestock show greater preference for browsing aspen shoots in autumn than in spring (Fitzgerald et al. 1986). Aspen suckers have higher nutritional quality than other forage types throughout the year, but cattle focus their foraging on meadow and understory vegetation in early and late summer, increasing utilization of aspen suckers only late in the growing season when other forage types were of low nutritional quality and depleted by grazing (Jones et al. 2011). However, experimentally browsed aspens showed greater growth when browsed in the autumn than when browsed in early or late summer (Jones et al. 2009). Balancing aspen's greater resilience to livestock grazing in fall with the far greater tendency of cattle to select aspen browse at this same time of year thus becomes critical.

Late-season grazing by cattle (just before leaf drop) is the most effective season for cattle grazing to suppress aspen regeneration, and livestock grazing during this time of year can eliminate aspen seedling recovery after six consecutive seasons of grazing post-fire (Bailey et al. 1990). Jones et al. (2011) recommended avoiding late-season grazing by cattle in aspen stands to minimize browsing on aspens, and recommended that mid- and late-season grazing by cattle not occur in consecutive years. Jones et al. (2011) recommended avoiding late-season grazing by cattle in aspen stands to minimize browsing on aspens, and recommended that mid- and late-season grazing by cattle not occur in consecutive years. In the case of the Pando Clone, livestock use this pasture in the fall every year, at the very time of year when the greatest selection by cattle for aspen shoots occurs. In this case, cattle were turned out in the Pando Clone in early autumn, precisely the season when the tendency of cattle to browse on aspen saplings would be expected to be greatest based on the science.

In our monitoring, we found livestock use in the "heavy" to "severe" categories that would result in complete use on any aspen suckers that had emerged. Our cameras were unable to detect aspen sprouts – or either mule deer or cattle herbivory on them – but the end result was that aspen sprouts were virtually completely suppressed outside the exclosure fences, based on the absence of any aspen sprouts visible in our photographs. This finding is consistent with other reports documenting little or no aspen recruitment outside exclosure fences that prevent grazing by livestock (but do not always prevent access by mule deer).

Cattle grazing in parts of the Pando Clone outside the exclosure, and in neighboring unfenced aspen groves, may also have a synergistic effect with the herbivory by native mule deer, resulting in impacts to aspen recruitment that may be greater than simply adding the two types of impact together. Wild herbivores may be drawn to ungrazed areas where livestock have been excluded (O'Brien et al. 2010). Aspen habitats are preferred by mule deer when cattle are absent, but preference declines under moderate to heavy grazing to the point where deer use aspen habitats roughly in proportion to their availability (Loft et al. 1991). Mueggler and Bartos (1977) studied an exclosure accessible to deer but not livestock in which production of forbs, or broad-leaf understory herbs, occurred inside the exclosure. This abundance of forage likely concentrated deer foraging activity inside the exclosure, to the detriment of aspen suckers, which failed to survive to reach tree status between 1905 and 1934, based on subsequent tree-ring analysis.

Austin and Urness (1985) reported that aspen proportion in mule deer summer diets ranged from 0.2 – 3%, but increased to 9% in September. The heavy level of understory utilization by cattle in the unfenced parts of the Pando Clone and in nearby aspen stands (70-90% as found in our study) during a time of year when deer intrinsically increased their herbivory on aspen saplings may, through competition, further increase mule deer browsing on aspen shoots by leaving behind few alternative sources of forage.

Kay and Bartos (2000) studied exclosures on the Dixie and Fishlake National Forests that excluded deer and livestock both, or livestock only. Complete failure of new regeneration occurred in the presence of both livestock and deer herbivory outside the exclosures at 4 of the 5 sites where portions of the exclosures prevented access by both deer and livestock, and at 3 of the 8 sites having livestock-only exclosures new regeneration failed in areas where the livestock were excluded. Kay and Bartos found that excluding livestock and/or native herbivores increased recruitment of aspen saplings in the 2-meter to 5-centimeter diameter-at-breast-height range, with an average of 4,474 surviving aspen ramets under livestock and cervid exclusion, 2,498 ramets surviving by excluding livestock only, and an average of 1,012 surviving ramets outside the exclosures, where aspens were subject to herbivory by cattle, sheep, deer, and/or elk. Rogers and Gale (2017) documented a more than fourfold increase in aspen regeneration

inside the Pando Clone's fenced exclosure compared with outside.

In this monitoring project, we found little visual evidence of aspen recruitment outside the exclosure fences, indicating either that aspen sprouts were browsed away prior to the onset of the growing season for grasses, or that deer and/or livestock herbivory was eliminating them prior to the point at which they would become visible to the camera. Given the extreme level of understory herbivory by cattle during the 13-day grazing period that we recorded in 2018, it is entirely possible that mule deer returning to the Pando Clone following cattle grazing would have found little understory forage, increasing the likelihood of 100% utilization of aspen sprouts that emerged prior to the onset of the following season. In this way, the overgrazing by cattle that we recorded within unfenced portions of the Pando Clone may be interacting with herbivory by mule deer to eliminate aspen recruitment outside the ungulate exclosures.

Bailey et al. (1990: 214) found fall cattle grazing to be an effective tool for eliminating aspen regeneration:

> Suckers defoliated by grazing in August, late in the growing season, were nearly eliminated after only 1 defoliation (FitzGerald and Bailey 1984) whereas suckers defoliated earlier in the season continued to regenerate and took 7 years to decline to 7% of original stem densities…. Schier (1976) indicated that repeated removal of tops and consequent initiation and growth of new suckers leads to a gradual depletion of nonstructural carbohydrates in the roots. Exhaustion of carbohydrates by annually repeated destruction of growing points appears to take from 6 to 8 years…. Clearly, for immediate control of aspen suckers, top removal or defoliation must be timed similarly to the late grazing treatment in this study.

These authors conclude by stating, "If the first priority is to nearly eradicate regenerating aspen suckers, then late season, short duration heavy grazing should be applied." Unfortunately, this is exactly what is happening within the unfenced Pando Clone and surrounding aspen groves.

Trampling damage by ungulates has often been implicated as a potentially significant cause of aspen regeneration failure (Schier 1981, DeByle 1990, Brown 1995). With regard to cattle, Weatherill et al. (1969: 5) concluded that "[c]onsumption reduces photosynthesis, trampling may break stems and leaves, while soil compaction can injure root systems and decrease soil aeration and water holding capacity." While Dockrill et al. (2004: 261) found that damage from cattle due to direct browsing and trampling damage killed individual aspen sprouts, these researchers concluded that "[h]igh mortality among stems without observed injuries might have been indirectly associated with cattle damage resulting from soil compaction, reduced root oxygen and subsurface severing of lateral roots." Because adventitious buds forming on lateral roots are the genesis of aspen sprouts, and because the level of trampling by cattle appears to be substantial based on our monitoring, more detailed study of the effect of trampling by livestock on the roots, adventitious buds, and initiation of suckering in the Pando Clone is necessary prior to concluding that herbivory by deer or livestock (or some synergistic combination of the two) is primarily responsible for the failure of sprout recruitment outside fenced exclosures.

Livestock appear to have the heavier impact than mule deer on aspen regeneration, based on exclosure studies that differentially exclude cattle and wild cervids. Based on a study of 30 grazing exclosures in aspen habitats in Nevada, Kay (2003: vi) stated,

> The [declining] status and trend of aspen communities in north-central Nevada, however, is not related to climatic variation, fire suppression, or browsing by mule deer. Instead, the condition of individual aspen communities is related to past and present levels of livestock grazing. That

is, aspen is declining throughout most of north-central Nevada due to repeated browsing of aspen suckers by cattle and/or domestic sheep – repeated browsing eliminates sucker height growth, which prevents their maturation into aspen saplings and trees. Without stem replacement, aspen clones are consigned to extinction.

Livestock in mountain ranges of central Nevada contributed to poor aspen clone condition, and grazing by sheep and cattle accounted for 99.5% of the grazing pressure based on feces counts (Kay 2001).

While mule deer have been implicated as the cause of regeneration failure in the Pando Clone (Rogers and McAvoy 2018), the bulk of science thus far published (reviewed herein) does not necessarily support this conclusion, and our own monitoring photos show quite clearly that cattle, rather than mule deer, are having the heaviest impact on understory vegetation in the Pando Clone and on the understories of neighboring aspen groves.

Recommendations

We recommend eliminating livestock grazing during all seasons for the entire Pando Clone, and for aspen habitats generally, livestock should be removed if aspens are experiencing regeneration failure. This should be done until aspen regeneration is above browse height, and will require periodic repetition to prevent future aspen sprout suppression. Kay (2003) recommended fencing critical aspen stands or restricting livestock to only early-season grazing. According to Beschta et al. (2014: 36, internal citations omitted), "Our results indicate that for areas grazed by livestock and where aspen recruitment is either absent or occurring at low levels, implementing strategies that eliminate or minimize the effects of livestock herbivory may be needed. Given the vast amount of public land annually utilized by domestic ungulates and the large losses in aspen those lands have experienced to date,

reducing livestock grazing effects within and across ecoregions may be required for attaining ecological restoration of herbivore-altered plant communities." According to Alexander (1995: 120), "even though aspen sucker density was still high after two years [cattle] grazing, it was the author's opinion that if the grazing treatments were continued, the prognosis for successful aspen forest regeneration would be poor."

Mechanical treatments such as coppice logging do not appear to be warranted in the Pando Clone based on the science. Aspen stands can reach high densities without stagnating because they are self-thinning (DeByle 1984). Thus, the thinning or logging of aspen stands is unwarranted from a silvicultural perspective. Bird species richness increases with aspen patch size (Johns 1993), suggesting that fragmenting aspen stands into progressively smaller patches through clearcutting may lead to a loss of bird diversity. In the Pando Clone, coppice logging of aspens might also inadvertently cause a loss of genetic diversity by completing the dominance of triploid aspens (DeRose et al. 2015). The successful regeneration of aspen saplings inside the Pando Clone's exclosure fence in the absence of mechanical treatments is proof positive that mechanical interventions are unnecessary.

The idea of eliminating grazers from aspen stands struggling to reproduce is not a new concept. Mueggler (1989) recommended protecting aspen groves with exclosures where the stand is heavily grazed or browsed. According to Shepperd (2001: 363), "Fencing is the only guaranteed means of directly protecting sprouts from browsing animals." O'Brien et al. (2010: 28) recommended, "In situations where the relative impact of domestic livestock versus wildlife has not been determined, a livestock exclusion fence alone (followed with monitoring) may be a reasonable first choice."

The significant role of cattle grazing in the Pando Clone has been acknowledged by scientific researchers. According to Rogers and Gale (2017: 11), "While we know that mule deer are responsible for a portion of

aspen sucker browsing, cattle reduction and exclosure seem to also play an important role as evidenced by the combination of scat counts, browse levels, and overall regeneration response inside and outside our study area."

At a minimum, the existing exclosures should be expanded to encompass the entire perimeter of the Pando Clone, plus a quarter-mile buffer to allow for expansion, and livestock grazing should cease in this area. A better solution would be to permanently close the Dry Ponds pasture and any other pasture that encompasses the Pando Clone, to livestock grazing. Further research is needed to determine thresholds at which mule deer and/or cattle density reduce aspen recruitment below self-sustaining levels, and the degree to which soil trampling by livestock contributes to sprout suppression and root damage in aspen clones.

Aspens and mule deer have been evolving together for thousands of years. In light of our findings that heavy cattle utilization of aspen understories in the unfenced portions of the Pando Clone and in neighboring aspen stands, and the likelihood that this heavy level of grazing could work synergistically with mule deer browsing to suppress aspen regeneration, previous hypotheses that mule deer browsing alone is responsible for the decline of Pando Clone sucker establishment appear highly unlikely. Taken together, the evidence brought forward thus far suggests that livestock grazing and/or trampling may be the critical factor(s) tipping browsing pressure over the threshold at which aspen regeneration begins to fail. Removing livestock grazing from the pastures south of Fish Lake and measuring suckering and recruitment for a period of 5 years would be a logical method to determine whether the primary driver of the failure to recruit is deer or livestock.

Literature Cited

Alexander, M.J. 1995. The response of mature decadent and healthy sapling aspen forest communities to prescribed burning and controlled livestock grazing. M.S. Thesis, U. of Alberta, 164 pp.

Austin, D.D., and P.J. Urness. 1985. Values of four communities for mule deer on ranges with limited summer habitat. J. Range Manage. 38: 167-171.

Bailey, A.W., B.D. Irving, and R.D. Fitzgerald. 1990. Regeneration of woody species following burning and grazing in aspen parkland. J. Range Manage. 43: 212-215.

Baker, W.L., J.A. Munroe, and A.E. Hessl. 1997. The effects of elk on aspen in the winter range in Rocky Mountain National Park. Ecography 20(2):155-165.

Barnes, B.V. 1975. Phenotypic variation of trembling aspen in western North America. Forest Sci. 21: 319-328.

Bartos, D.L., 2008. Great Basin Aspen Ecosystems. Pp. 57-60 *in* Collaborative Management and Research in the Great Basin – Examining the Issues and Developing a Framework for Action, Chambers, J.C., Devoe, N., Evenden, A., (Editors). USDA Forest Service Gen. Tech. Rep. RMRS-GTR-204.

Bartos, D. L., J. K. Brown and G. D. Booth. 1994. Twelve Years Biomass Response in Aspen Communities Following Fire. Journal of Range Management 47:79-83.

Bartos, D.L., and R.B. Campbell, Jr. 1998a. Decline of quaking aspen in the Interior West: Examples from Utah. Rangelands 20: 17-24.

Bartos, Dale L. and Robert B. Campbell, Jr. 1998b. Water Depletion and Other Ecosystem Values Forfeited When Conifer Forests Displace Aspen Communities. Proceedings of American Water Resources Association Specialty Conference, Rangeland Management and Water Resources. American Water Resources Association, Herndon, Virginia TPS-98-1. 474 p.

Bartos, Dale L. and Walter F. Mueggler. 1979. Influence of Fire on Vegetation Production in the Aspen Ecosystem in Western Wyoming. North American Elk Ecology, Behavior and Management. Mark S. Boyce and Larry D. Hayden-Wing, eds. University of Wyoming, Laramie, Wyo.

Bashkin, M., T.J. Stohlgren, Y. Otsuki, M. Lee, P. Evangelista, and J. Belnap. 2003. Soil characteristics and plant exotic species invasions in the Grand Staircase—Escalante National Monument, Utah, USA. Appl. Soil Ecol. 22: 67-77.

Beck, J.L., and J.M. Peek. 2005. Diet composition, forage selection, and potential for forage competition among elk, deer, and livestock on aspen-sagebrush summer range. Rangeland. Ecol. Manage. 58: 135-147.

Beck, J.L., J.T. Flinders, D.R. Nelson, C.L. Clyde, H.D. Smith, and P.J. Hardin. 1997. Diet selection and importance of management indicator species to elk and domestic sheep in a north-central Utah aspen ecosystem. Pp. 131-137 *in* Proc.1997 Deer/Elk Workshop, Rio Rico, AZ. Arizona Game and Fish Department, Phoenix.

Beschta, R.L., and W.L. Ripple. 2009. Large predators and trophic cascades in terrestrial ecosystems of the western United States. Biol. Conserv. 142: 2401-2414.

Beschta, R.L., D.L. Donahue, D.A. DellaSala, J.J. Rhodes, J.R. Karr, M.H. O'Brien, T.L. Fleischner, and C.D. Williams. 2013. Adapting to climate change on western public lands: Addressing the ecological effects of domestic, wild, and feral ungulates. Environ. Manage. 51: 474-491.

Beschta, R.L., J.B. Kauffman, D.S. Dobkin, and L.M. Ellsworth. 2014. Long-term livestock grazing alters aspen age structure in the northwestern Great Basin. Forest Ecol. Manage. 329: 30-36.

Binkley, D. 2008. Age distribution of aspen in Rocky Mountain National Park, USA. Forest Ecol. Manage. 255: 797-802.

Binkley, D., M.M. Moore, W.H. Romme, and P.M. Brown. 2006. Was Aldo Leopold right about the Kaibab deer herd? Ecosystems 9: 227-241.

(BLM) U.S.D.I. Bureau of Land Management. 1996. Utilization Studies and Residual Measurements: Interagency technical reference. Technical Reference 1734-3. Denver, CO: BLM, 174 pp.

Brown, M. 1995. Aspen decline in the inland Northwest: A review of some relevant literature. USDA Forest Service Pacific Northwest Research Station, 28 pp.

Cole, D.N. 1993. Trampling effects on mountain vegetation in Washington, Colorado, New Hampshire, and North Carolina. USDA Forest Service Research Paper INT-464, 57 pp.

Coles-Ritchie, M. 2018. Removal of invasive plants from Pando exclosure 2018. Aspen Bibliography, Paper 7771. Online at https://digitalcommons.usu.edu/aspen_bib/7771.

Compton, T.L. 1974. Some interspecific relationships among deer, elk, domestic livestock and man on the western Sierra Madre of southcentral Wyoming. PhD Thesis, Univ. of Wyoming, 247 pp.

DeByle, N.V. 1984. Managing wildlife habitat with fire in the aspen ecosystem. Pp. 73-82 *in* Fire's effects on wildlife habitat--Symposium proceedings. USDA Forest Service Gen. Tech. Rept. INT-186, 97 pp.

DeByle, N.V. 1985a. Animal impacts. Pp. 115-123 *in* Aspen: Ecology and management in the western United States, N.V. DeByle, and R.P. Winokur, eds. USDA Forest Service Gen. Tech. Rept. RM-119, 283 pp.

DeByle, N.V. 1985b. Wildlife. Pp. 135-152 *in* Aspen: Ecology and management in the western United States, N.V. DeByle, and R.P. Winokur, eds. USDA Forest Service Gen. Tech. Rept. RM-119, 283 pp.

DeByle, N.V. 1985c. Water and watershed. Pp.153-160 *in* Aspen: Ecology and management in the western United States, N.V. DeByle, and R.P. Winokur, eds. USDA Forest Service Gen. Tech. Rept. RM-119, 283 pp.

DeRose, R.J., K.E. Mock, and J.N. Long. 2015. Cytotype differences in radial increment provide novel insight into aspen reproductive ecology and stand dynamics. Can. J. For. Res. 45: 1-8.

DeWoody, J., C.A. Rowe, V.D. Hipkins, and K.E. Mock. 2008. "Pando" lives: Molecular genetic evidence of a giant aspen clone in central Utah. W. N. Am. Nat. 68: 493-497.

Dockrill, C.W.M., P.V. Blenis, A.W. Bailey, and J.R. King. 2004. Effect of summer grazing on aspen stem injury, mortality and growth. Forestry Chron. 80: 257-261.

Evans, D.M. 2010. A spatiotemporal analysis of aspen decline in southern Utah's Cedar Mountain, using remote sensing and Geographic Information Systems. M.S. Thesis, Utah State Univ., 185 pp.

Fairweather, M.L., B.W. Geils, and M. Manthei. 2007. Aspen decline on the Coconino National Forest. Pp. 53-62 in Proc. 55th West. Int. Forest Disease Work Conf., October 15-19 2007, Sedona, AZ, McWilliams, M.G. (comp.). Salem, OR: Oregon Department of Forestry.

Fitzgerald, R.D., R.J. Hudson, and A.W. Bailey. 1986. Grazing preferences of cattle in regenerating aspen forest. J. Range Manage. 39: 13-18.

Fornwalt, P.J., and S. Smith. 2000. Production and total root carbon allocation for single-storied and multi-storied aspen stands in southern Wyoming. P. 449 *in* Sustaining aspen in western landscapes: Symposium proceedings. USDA Forest Service Proceedings RMRS-P-18.

Galt, D., F. Molinar, J. Navarro, J. Joseph, and J. Holechek. 2000. Grazing capacity and stocking rate. Rangelands 22(6):7-11.

Gardner, R.S. 2013. Clonal diversity of quaking aspen (*Populus tremuloides*): How multiple clones may add to the resilience and persistence of this forest type. M.S. Thesis, Utah State Univ., 77 pp.

Grant, M.C., J.B. Mitton, and Y.B. Linhart. 1992. Even larger organisms. Nature 350: 216.

Grant, M.C., and J.B. Mitton. 2010. Case study: The glorious, golden, and gigantic quaking aspen. Nature Educat. Knowledge 3(10): 40.

Hejl, S.J., R.L. Hutto, C.R. Preston, and D.M. Finch. 1995. Effects of silvicultural treatments in the Rocky Mountains. Pp. 220-244 *in* Ecology and management of neotropical migratory birds, T.E. Martin and D.M. Finch, eds. New York: Oxford University Press.

Johns, B.W. 1993. The influence of grove size on bird species richness in aspen parklands. Wilson Bull. 105:256-264.

Jones, J.R., and N.V. DeByle. 1985a. Morphology. Pp. 11-18 *in* Aspen: Ecology and management in the western United States, N.V. DeByle, and R.P. Winokur, eds. USDA Forest Service Gen. Tech. Rept. RM-119, 283 pp.

Jones, J.R., and N.V. DeByle. 1985b. Soils. Pp. 65-76 *in* Aspen: Ecology and management in the western United States, N.V. DeByle, and R.P. Winokur, eds. USDA Forest Service Gen. Tech. Rept. RM-119, 283 pp.

Jones, J.R., and N.V. DeByle. 1985c. Fire. Pp. 77-81 *in* Aspen: Ecology and management in the western United States, N.V. DeByle, and R.P. Winokur, eds. USDA Forest Service Gen. Tech. Rept. RM-119, 283 pp.

Jones, B.E., D.F. Lile, and K.W. Tate. 2009. Effect of simulated browsing on aspen regeneration: Implications for restoration. Rangeland Ecol. Manage. 62: 557-563.

Jones, B.E., D.F. Lile, and K.W. Tate. 2011. Cattle selection for aspen and meadow vegetation: Implications for restoration. Rangeland Ecol. Manage. 64: 625-632.

Kay, C.E. 2001. The condition and trend of aspen communities on BLM administered lands in central Nevada, with recommendations for management. Final Report to the Battle Mountain Field Office, BLM, 155 pp.

Kay, C.E. 2003. Aspen management guidelines for BLM lands in north-central Nevada. Final Report to the Battle Mountain Field Office, BLM, 62 pp.

Kay, Charles E. and Dale L. Bartos. 2000. Ungulate Herbivory on Utah Aspen; Assessment of Long-term Exclosures. Journal of Range Management 53:145-153.

Kemperman, J.A., and B.V. Barnes. 1976. Clone size in American aspens. Can. J. Bot. 54: 2603-2607.

Krebill, R.G. 1972. Mortality of Aspen on the Gros Ventre Elk Winter Range. USDA Forest Service Research Paper INT-129. Intermountain Forest and Range Experiment Station, Ogden, Utah.

Lindroth, R.L., and S.B. St. Clair. 2013. Adaptations of quaking aspen (*Populus tremuloides*) for defense against herbivores. Forest Ecol. Manage. 299: 14-21.

Loft, E.R., J.W. Menke, and J.G. Kie. 1991. Habitat shifts by mule deer: The influence of cattle grazing. J. Wildl. Manage. 55: 16-26.

Long, J.N., and K. Mock. 2012. Changing perspectives on regeneration ecology and genetic diversity in western quaking aspen: Implications for silviculture. Can. J. For. Res. 42: 2011-2021.

Loose, S.S., and S.H. Anderson, 1995. Woodpecker habitat use in the forests of southeast Wyoming. J. Field Ornith. 66(4):503-514.

Mock, K.E., C.A. Rowe, M.B. Hooten, J. DeWoody, and V.D. Hipkins. 2008. Clonal dynamics in western North American aspen (*Populus tremuloides*). Molecular Ecol. 17: 4827-4844.

Mower, K.J., and H. D. Smith. 1989. Siet similarity between elk and deer in Utah. Great Basin Nat. 49: 552-555.

Mueggler, W.F. 1985a. Vegetation associations. Pp. 45-55 *in* Aspen: Ecology and management in the western United States, N.V. DeByle, and R.P. Winokur, eds. USDA Forest Service Gen. Tech. Rept. RM-119, 283 pp.

Mueggler, W.F. 1985b. Forage. Pp. 129-134 *in* Aspen: Ecology and management in the western United States, N.V. DeByle, and R.P. Winokur, eds. USDA Forest Service Gen. Tech. Rept. RM-119, 283 pp.

Mueggler, W. F. 1989. Age Distribution and Reproduction of Intermountain Aspen Stands. West. J. . Appl. For. 4(2):41-45.

Mueggler, W.F. and D.L. Bartos. 1977. Grindstone Flat and Big Flat exclosures: A 41-year record of changes in clearcut aspen communities. USDA Forest Service Research Paper INT-195. Intermountain Forest and Range Experiment Station, Ogden, UT.

(NASS) National Agricultural Statistical Service. 2018. Livestock slaughter. USDA, 18 pp.

(NRCS) Natural Resources Conservation Service. 2003. National Range and Pasture Handbook. Washington, DC: U.S. Dept. of Agriculture, 214 pp.

O'Brien, M., P. Rogers, K. Mueller, R. MacWhorter, A. Rowley, B.Hopkin, B. Christensen, and P. Dremann. 2010. Guidelines for aspen restoration on the national forests in Utah. Western Aspen Alliance, Utah Forest Restoration Working Group. Logan, UT: Utah State Univ., 48 pp.

Ogle, D., and B. Brazee. 2009. Estimating initial stocking rates. Boise, ID: USDA Natural Resources Conservation Service Tech. Note, 39 pp.

Painter, L.E., R.L. Beschta, E.J. Larsen, and W.J. Ripple. 2018. Aspen recruitment in the Yellowstone region linked to reduced herbivory after large carnivore restoration. Ecosphere 9(8):e02376. 10.1002/ecs2.2376.

Pratt, M., and G.A. Rasmussen. 2001. Determining your stocking rate. Utah State Univ. Coop. Range Ext. Fact Sheet NR/RM/04, 7 pp.

Randall, J.A., and M.B. Walters. 2011. Deer density effects on vegetation in aspen forest understories over site productivity and stand age gradients. Forest Ecol. Manage. 261: 408-415.

Ripple, W.J., and E.J. Larsen. 2000. Historic aspen recruitment, elk, and wolves in northern Yellowstone National Park, USA. Biol. Conserv. 95: 361-370.

Ripple, W.J., and E.J. Larsen. 2001. The role of postfire coarse woody debris in aspen regeneration. West. J. Appl. For. 2: 61-64.

Rogers, P. C., and J. A. Gale. 2017. Restoration of the iconic Pando aspen clone: emerging evidence of recovery. Ecosphere 8(1): e01661.10.1002/ecs2.1661.

Rogers, P.C., and D.J. McAvoy. 2018. Mule deer impede Pando's recovery: Implications for aspen resilience from a single-genotype forest. PLoS ONE 13(10): e0203619.

Rogers, P.C., and C.M. Mittanck. 2014. Herbivory strains resilience in drought-prone aspen landscapes of the western United States. J. Veg. Sci. 25: 457-469.

Rogers, P.C., J. Leffler, and R.J. Ryel. 2010. Landscape assessment of a stable aspen community in southern Utah, USA. Forest Ecol. Manage. 259: 487-495.

Romme, W.H., and D.H. Knight, 1982. Landscape diversity: The concept applied to Yellowstone National Park. BioScience 32(8):664-670.

Schier, G.A. 1975. Deterioration of aspen clones in the middle Rocky Mountains. USDA Forest Service Research Paper INT-170, 14 pp.

Schier, G.A. 1981. Physiological research on adventitious shoot development in aspen roots. USDA Forest Service Gen. Tech. Rep. INT-GTR-107. Ogden, UT: Intermountain Forest and Range Experiment Station, 12 pp.

Shepperd, W.D. 2001. Manipulations to regenerate aspen ecosystems. Pp. 355-365 *in* Sustaining Aspen in Western Landscapes: Symposium Proceedings, W.D. Shepperd et al (compilers). USDA Forest Service Proceedings RMRS-P-18. Fort Collins, CO: Rocky Mountain Research Station.

Shinneman, D.J., W.L. Baker, P.C. Rogers, and D. Kulakowski. 2013. Fire regimes of quaking aspen in the Mountain West. Forest Ecol. Manage. 299: 22-34.

Suzuki, K., H. Suzuki, D. Binkley, and T.J. Stohlgren. 1999. Aspen regeneration in the Colorado Front Range: Differences at local and landscape scales. Landscape Ecol. 14(3): 231-237.

(USFS) U.S.D.A. Forest Service. 1993. Utilization Study Data: Key forage plant method. Form R4-2200-47 (1/93).

(USFS) U.S.D.A. Forest Service. 2012. Decision Memo: Pando Clone Restoration Project. Richfield, UT: Fishlake National Forest, 7 pp.

(USFS) U.S.D.A. Forest Service. 2018. Annual Operating Instructions 2018 Seven Mile Allotment. Fremont Ranger District, Fishlake National Forest. Available online at https://www.fs.usda.gov/Internet/FSE_DOCUMENTS/stelprdb5157689.pdf.

(UWSP) University of Wisconsin Stevens Point. 2019. Mule Deer Feeding Habits. University of Wisconsin Stevens Point Wildlife Ecology College of Natural Resources. Available online at https://www.uwsp.edu/wildlife/Ungulates/Pages/Mule%20Deer/Mule-Deer-Diet.aspx. Site last visited 06/21/2019.

White, C.A., C.E. Olmstead, and C.E. Kay. 1998. Aspen, elk, and fire in Rocky Mountain national parks of North America. Wildl. Soc. Bull. 26: 449-462.

Williges, W.A. 1946. A beaver survey on the Pole Mountain division of the Medicine Bow National Forest. M.S. Thesis, Univ. of Wyoming, 106 pp.

Winternitz, B.L., and H. Cahn. 1983. Nestholes in live and dead aspen. Pp. 102-106 *in* Snag habitat management: Proceedings of the symposium, USDA Forest Service Gen. Tech. Rept. RM-99, 226 pp.

Wooley, S.C., S. Walker, J. Vernon, and R.L. Lindroth. 2008. Aspen decline, aspen chemistry, and elk herbivory: Are they linked? Rangelands 30: 17-21.

Worrall, J.J., S.B. Marchetti, L. Egeland, R.A. Mask, T. Eager, and B. Howell. Effects and etiology of sudden aspen decline in southwestern Colorado, USA. Forest Ecol. Manage. 260: 6380648.