

Restoration of the iconic Pando aspen clone: emerging evidence of recovery

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Abstract. Quaking aspen (*Populus tremuloides* Michx.) is being stressed across the America West from a variety of sources including drought, herbivory, fire suppression, development, and past management practices. Rich assemblages of plants and animals that utilize aspen forests, as well as economic values of tourism, grazing, hunting, and water conservation, make aspen ecosystems among the most valuable vegetation types in this region. The 43-ha Pando clone near Fish Lake, Utah, is an iconic example of an aspen community undergoing rapid decline due to overstory mortality and chronic recruitment failure. As part of a larger project to restore Pando, we fenced, treated, and monitored a portion of this famous grove with the intent of documenting regeneration responses and using such practices at larger scales. Twenty-seven randomly stratified monitoring plots were placed across this landscape in order to better understand herbivory and regeneration responses to distinct treatment categories: protected and unprotected, and passive (fenced only) and active (burning, shrub removal, selective overstory cutting) treatments. At each site, we measured basal area and mortality on mature trees, made counts of juvenile and intermediate suckers, documented browse levels and herbivore scat presence, and characterized environmental conditions in terms of aspen and common juniper cover, treatment type, elevation, slope, and aspect. Our results confirmed a positive regeneration response to browsing cessation after fencing, whereas non-fenced areas showed no improvement. Within the fence, there was a significantly better response of active treatment vs. passive and there was no significant difference between treatment types in terms of level of regeneration. Both active and passive management produced regeneration levels that were sufficient to replace dying canopy trees if managers continue to protect suckers until they exceed the reach of browsers. These results support a growing body of research suggesting managers need to invest in continuous protection from herbivory in stable aspen forests, as well as targeting additional post-treatment protection, to ensure adequate regeneration. We examine ramifications of these results for broader restoration purposes in the remainder of Pando, as well as other aspen communities regionally, with the ultimate goal of restoring ecological process toward greater ecosystem resilience.

Key words: cattle; herbivory; management; monitoring; mule deer; *Populus tremuloides*; recruitment; restoration; Utah.

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INTRODUCTION

As a highly adaptable species, quaking aspen (*Populus tremuloides* Michx.) thrives from the boreal forest to central Mexico and from the Atlantic

to Pacific coasts. While united under a single species moniker, aspen's broad range is facilitated by distinct functional types; though, land manager oversight of these key differences has commonly led to inappropriate forestry applications

(Rogers et al. 2014). Concurrently, multiple lines of inquiry are advancing rapidly in the study of quaking aspen ecology in North America (*Forest Ecology and Management*, Special Issue, Volume 299, 2013), which are leading us to reexamine precepts and adjust field practices. For example, researchers are only beginning to realize that the occurrence of aspen germinating from seeds is more common than once thought and that these discoveries are likely to have far-reaching implications for modern silviculture (Long and Mock 2012, Krasnow and Stephens 2015). Similarly, we now acknowledge that the role of fire in influencing aspen environments is more complex, with some forests being highly dependent, while others are marginally influenced by burning (Shinneman et al. 2013). The mixed effects of treatment, fire, climate, and seedling establishment have become fruitful ground for aspen research and application (Landhäusser et al. 2010, Krasnow and Stephens 2015, Yang et al. 2015). This resurgence in aspen science is in need of parallel field trials to test developing theory.

In the past decade, substantial energy has been focused in the arena of plant–animal relations, trophic cascades, and large ungulate herbivory due to widely documented impacts of both wild and domestic animals to aspen ecosystems (Rogers et al. 2010, Eisenberg et al. 2013, Seager et al. 2013). This effort is justified given widespread impacts to aspen systems from ungulates (Seager et al. 2013). In some regions, reintroduced predators appear to be mediating the level of hardwoods browsed by large ungulates (Beschta and Ripple 2009). While there is some dispute surrounding the idea of indirect effects of predators through “behaviorally mediated trophic cascades” (Kauffman et al. 2010, Painter et al. 2014), there is little argument that the direct effects of overabundant ungulate populations can have dramatic impacts on aspen regeneration, recruitment, and biodiversity of dependent species (Bailey et al. 2007, Durham and Marlow 2010, Martin and Maron 2012, Bork et al. 2013, Seager et al. 2013). Further, in the high-elevation relatively dry-system environment of the Colorado Plateau, a concerted effort has begun to examine interactive effects of wildfire size and intensity, regeneration response, and recruitment success in the face of domestic and wild ungulate pressure (Wan et al. 2014). While results are promising for aspen

rejuvenation where fire is a viable stimulant of vegetative reproduction (Wan et al. 2014), there is less understanding of recruitment and restoration strategies for non-fire-prone stable aspen (Shinneman et al. 2013) where excessive herbivory occurs (Yang et al. 2015).

The Pando aspen grove, located in central Utah, is a 43-ha genetically identical clone comprising an estimated 47,000 ramets (Barnes 1975, Mitton and Grant 1996, DeWoody et al. 2008). This clone has garnered international attention for its immense size and presumptive extreme age (Ally et al. 2008). The Pando clone is representative of the Colorado Plateau stable type described by Rogers et al. (2014) in which aspen trees do not compete with conifer species in a classic successional progression. Stable aspen are represented by structural stand complexity (height, size, condition) as opposed to tree species diversity. Aspen, as a single species, dominates stands for multiple generations through processes more akin to gap-phase dynamics and not stand replacement (Harniss and Harper 1982). Stable aspen forests are sustained by ongoing or episodic recruitment that contrasts with strong flushes of regeneration following catastrophic disturbance (Kurzel et al. 2007, Rogers et al. 2014). Sustained interruption of regular recruitment due to excessive, multi-year, browsing exposes stable aspen forests to significant risk of prolonged decline and potential stand failure (Weisberg and Coughenour 2003, Binkley 2008, Rogers and Mittanck 2014). Stand-replacing disturbance cannot be relied on to restore such communities (Rogers et al. 2014, Yang et al. 2015). Visual inspection of the Pando clone suggests it is on just such a trajectory today (Appendix S1): Where stems are unprotected by fencing, there is little regeneration or recruitment, often a single mature age-class, and a rapidly dying overstory comprised ramets from 110 to 120 yr of age (DeRose et al. 2015). While significant research has been devoted to Pando’s genetic properties (e.g., DeWoody et al. 2008, Mock et al. 2008), less focus has been placed on causes for its current condition, likely need for restoration, and methods for accomplishing a sustainable state in the face of chronic herbivory.

We undertook a study of forest conditions at the Pando clone to determine response to experimental fencing and active management (burning, shrub removal, tree cutting) as a precursor to developing a defensible restoration strategy. It is

visually evident that little recruitment has taken place at this site for years and perhaps even decades. Accordingly, both pre- and post-treatment monitoring relies heavily on documenting the status of young regeneration stems at Pando. If our actions result in higher levels of new aspen stems, this suggests not only that browsing is limiting regeneration, but that some forms of stand treatment may result in stronger regeneration responses than others. With this in mind, the current work has three prime objectives: (1) to determine whether fencing only is an effective strategy for restoration of the Pando clone; (2) to measure three active treatments—burning, shrub removal, and tree cutting—to assess which technique produces the strongest stem response; and (3) to examine the implications of this work in the context of stand- and regional-level aspen restoration where herbivory is an underlying threat to community resilience. Findings from this work will have ramifications at a variety of scales for aspen as a keystone component of western North American forests (Bartos and Campbell 1998), as well as among managers who are beginning to examine intercontinental links between *Populus* ecosystems (Myking et al. 2011, Boonstra et al. 2016), anticipated drought and warming (Worrall et al. 2013, Yang et al. 2015), and persistent herbivory (Seager et al. 2013).

METHODS

Study area

The Pando aspen clone is located in south-central Utah at the southwest edge of Fish Lake on the Fishlake National Forest (UTM 434701 E, 4264266 N). There is little variation in topography at the site, with the average elevation being 2707 m and the average slope 5–10%. Soils are mixed gravelly and cobbly in both loamy A-horizons and clayey B-horizons (Draft Survey, Fishlake National Forest, National Cooperative Soil Survey [UT651]) originating from tertiary volcanic materials—likely basalt, rhyolite, and latite welded tuff (M. Domeier, *personal communication*, NRCS Utah). Much of the forest floor is sparsely vegetated with exposed volcanic boulders and bare ground being common. However, dense patches of common juniper (*Juniperus communis* L.) and mountain big sagebrush (*Artemisia tridentata*, ssp. *vaseyana* Rydb.) are scattered throughout the site alongside

a wide range of montane grasses and forbs. The Pando clone is located in a relatively dry site (466 mm/yr precipitation, SNOTEL 1149, 6-year average), although winter snow accumulations make up the bulk of annual precipitation. Pando is bisected by a paved state highway accessing a popular resort area and bordered by a U.S. Forest Service campground, as well as summer vacation homes. Thus, human presence is relatively common. Currently, domestic cattle (*Bovis* spp.) are permitted to forage at Pando under a U.S. Forest Service grazing allotment for approximately 2 weeks annually during ingress and egress from higher-elevation pastures. Mule deer (*Odocoileus hemionus* Raf.) and North American elk (*Cervus elaphus* L.) access this area freely during the approximately 7-month snow-free season. (Though elk are clearly in the broader landscape, we have not seen them on site nor found scat in Pando surveys, whereas both siting and fecal evidence are common for deer.) Though human visitations in the surrounding area are high, most are unaware of the significance of this unique forest nor do they actually set foot within the clone itself. Our sampling took place each year prior to the onset of peak human use periods to avoid unwarranted attention to sample locations which may result in permanent marker removal or excessive vegetation damage.

Field methods

Our sampling design was intended to characterize forest conditions and experimental practices within a portion of the 43-ha Pando aspen clone. The focus of this study consists of a ~6-ha fenced enclosure erected in late 2013 in which experimental treatments were conducted in 2014 after initial sampling (Appendix S2). The experimental design used three treatment–control pairs within the fence consisting of at least two plots in each of those six polygons, plus an additional six plots located in the enclosure, but not within a specified treatment–control pair zone (Fig. 1). Individual plots in this study are the prime sample units: independent replicates within treatment designations. Specifically, though sometimes found in close proximity to each other, all plots are statistically independent due to (1) randomly selected locations within treatments; (2) significant within-treatment variability related to patchy vegetation cover, large rock outcrops, and uneven treatment

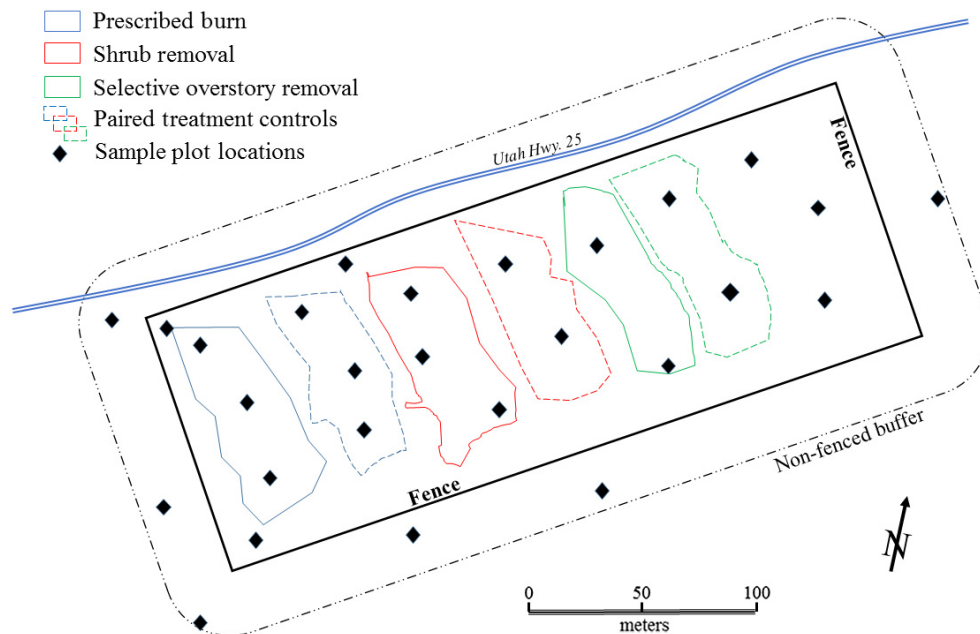


Fig. 1. Schematic of sampling design at Pando clone near Fish Lake, Sevier County, Utah (UTM 434701 E, 4264266 N). Twenty-seven plots (black diamonds) were sampled in various combinations of treatment types, controls, fenced, and non-fenced conditions.

application. The three treatments were prescribed burning, common juniper removal, and a 50% basal area-selective overstory removal. Due to spatial arrangement and varying flammability of understory plants and overstory trees, it was impossible to apply vegetative manipulations uniformly, though this does not discount the fact that treatment applications, overall, may show effects on dependent variables (e.g., aspen regeneration). Each experimental treatment (and paired control) was approximately 0.4 ha in size. Every attempt was made to locate an equal number of sample plots in each treatment polygon using random coordinate selection; however, in three instances, only two plots were located within treatment or control areas to avoid overlapping plot space (Fig. 1). Shrub removal and tree cutting were conducted by U.S. Forest Service work crews using hand tools and did not involve heavy equipment. Sample plots outside the fence were selected within a 60-m buffer to gain an understanding of background (unprotected) browse conditions. Thus, the total sample area covers ~16 ha (37%) of Pando, while the fenced portion within which manipulations occurred represents 14% of the aspen clone. In sum, there are 27 sample locations:

13 within-fence controls (including treatment pairings and at-large controls), three burned, three juniper removal, two selective overstory removal, and six outside the fence (Fig. 1).

In Year 1 (2014), we sampled all sites prior to treatment immediately following fencing; thus, measures in this first sample year represent pre-treatment conditions. All sample plots were re-measured in each of the following 2 yr. Stand characteristics not expected to significantly change over the life of this three-year study (e.g., mature tree diameters, live/dead trees, and environmental conditions) were measured in the first year. Variables measured were regeneration counts, growth, browse, and herbivore scat counts.

At each sample plot, we recorded data elements characterizing overall plot conditions and specific tree and browse characteristics. Environmental variables describing each sample location (plot) included geographic position (UTM), elevation, number of stand layers, stand condition, percent aspen cover (14 observation points averaged), treatment type, juniper cover (averaged two transect-based estimates), and a comments section for describing notable conditions not covered by other measures. Due to near-uniformly

poor values across the study area for the number of layers and stand condition (see Rogers and Mittanck 2014, Rogers et al. 2015), we did not conduct further analysis on these elements, though we still felt it important to document baseline conditions for future study. Tree- and browse-centered data elements were recorded within two 30×2 m transects arranged in a perpendicular fashion. For our purposes, the fixed area within transects is synonymous with the “plot” and is assumed to characterize conditions across that portion of the treatment area. This approach allowed us to easily expand values to a ha^{-1} basis for analysis. We began by photo documenting transects at each end facing toward the plot center, thus archiving a record of repeat photography in the four cardinal directions along measurement transects upon each visit. For all trees within transects ≥ 8 cm diameter at breast height (dbh), we recorded tree species, status (live/dead), and tree diameter class (≥ 8 –15, >15 –25, >25 cm). A count of aspen regeneration (i.e., stems ≤ 2 m height) was made within three height classes (0–0.5, >0.5 –1, and >1 –2 m). The lack of terminal buds due to browsing was recorded for each regenerating ramet. Live aspen recruitment (i.e., stems >2 m height, <8 cm dbh) was also tallied within sample transects. Stems were considered separate ramets if they forked from each other below the soil litter layer. Finally, we counted domestic and wildlife herbivore scat presence within sample transects (Rogers and Mittanck 2014). Domestic livestock feces was tallied per individual deposit. For wild ungulates, “piles” were considered separate if distinct groupings of pellets included at least three pellets (Bunnefeld et al. 2006). After counting, piles were removed from transects to ensure that re-measurements would only tally new scat. Scat presence on plots within the fence after the first year of baseline monitoring is indicative of some degree of unsuccessful enclosure.

Analytical methods

Our prime analytical objective was to determine significant differences in paired and group responses to treatments. In order to accomplish this, we first checked browse and scat count data to establish that herbivores were no longer entering the fenced area after Year 1 of the experiment. Once that statistical point was determined, we set

about testing for differences in the various combinations of fenced and unfenced, passive and active treatments within the fence, treatment–control pairs. Finally, response rates of the three active treatments were compared to each other. For all of these tests, our response variable was regeneration/ha, although we do make some qualitative comparisons between years and height classes on a stem count basis. Due to high variance and non-normal distribution in our dataset, we used only non-parametric statistics to determine results. Plots were randomly located and independent of each other. For the assessment of significant difference between dataset pairs (inside vs. outside fence and active vs. passive treatments inside fence), and as an equivalent to the parametric *t*-test, we used the two-sided Wilcoxon–Mann–Whitney *U* test. Output from this test is shown in Wilcoxon mean scores (*Z*-score). A *Z*-score beyond normal distribution (critical value) would confirm a significant difference between groups; level of significance is reported as a *P* value. The Kruskal–Wallis test, a non-parametric equivalent to analysis of variance, was the primary means of assessing statistical differences between treatment or year groups. Output from this test is also shown in terms of mean Wilcoxon scores. Results are considered significant where a Monte Carlo-simulated chi-square test (χ^2) using 10,000 runs produced an estimated *P* value of <0.05 . We used SAS software to conduct group tests and were guided by statistical groundings found in Zar (1999). Results for all analyses in this study were considered significant when $P \leq 0.05$.

RESULTS

Pre-treatment stand conditions

Overall, our beginning dataset (Year 1, pre-treatment) was highly variable, even within short distances and over environmental conditions estimated to be similar (e.g., treatment vs. control pairs), as evidenced by often high standard deviations of mean values (Table 1). We ran an initial test for differences in regeneration prior to treatments (Year 1) between all data pairings (fence–no fence, treatment–control pairs, and all treatment–control plots inside the fence) and found that only the inside–outside pairing was significantly different ($Z = -1.81$, $P = 0.03$; Table 1).

Table 1. Summary statistics for all locations prior to treatment (Year 1).

Treatment	Number of sample plots	Percent juniper cover	Percent aspen cover	Aspen regeneration/ha	Pre-treatment difference Z-score	Percent browse†	Live trees/ha	Basal area live trees m ² /ha	Dead basal area as % of live
Outside fence	6	7 (5)	23 (16)	83 (118)	-1.81 (0.03)	50 (50)	583 (623)	21.69 (19.69)	4.55 (6.78)
Inside fence					-1.81 (0.03)				
Prescribed burn control	3	40 (19)	17 (5)	861 (991)	-0.8729 (0.19)	1 (2)	305 (142)	11.55 (3.55)	68.37 (74.97)
Prescribed burn	3	38 (13)	21 (8)	639 (171)	-0.8729 (0.19)	23 (17)	333 (168)	19.12 (1.09)	1.49 (2.10)
Juniper removal-control	2	9 (6)	15 (5)	83 (83)	-1.4434 (0.07)	0 (0)	208 (42)	7.19 (0.43)	34.64 (38.64)
Juniper removal	3	20 (11)	22 (5)	278 (39)	-1.4434 (0.07)	0 (0)	361 (142)	7.40 (5.73)	73.77 (25.83)
Selective cut control	2	25 (20)	26 (8)	625 (125)	-0.3873 (0.35)	75 (25)	500 (250)	13.72 (1.07)	38.41 (15.01)
Selective cut	2	9 (1)	19 (1)	42 (42)	-0.3873 (0.35)	0 (0)	292 (125)	15.26 (2.41)	20.28 (20.28)
Random control	6	20 (12)	18 (4)	208 (208)	0.5118 (0.30)	14 (20)	305 (258)	6.56 (3.80)	24.95 (24.95)

Notes: All values represent group means (SD), except for number of plots. Pre-treatment difference refers to results of the Mann-Whitney *U* test for significant difference in regeneration per ha between groups in Year 1. Results are expressed in Z-scores (*P* value), and significant differences are shown in bold type. Outside and inside fences are compared, while all other groups are treatment-control pairs. The random control value is a comparison of all inside fence controls (including random control) and all treatments.

† Percent browse derived from live aspen stems <2 m height. Many locations, at Year 1, had few or even no stems (see aspen regeneration/ha), thus potentially yielding misleading values (e.g., low stem counts are likely due to past browsing levels).

Some additional basic study site patterns emerge in descriptive statistics. All treatment groups were similar, except where outside the fence juniper cover was lowest, and trees/ha and basal area were highest. Outside there was generally a much lower percent of dead basal area (although the prescribed burn plots had very low standing dead basal area). Standard deviations are too large to make clear sense of several initial measures (e.g., percent browse), mainly due to the low number of individuals sampled on many plots. A dominant trend for all plots was a low or very low number of regeneration/ha. For example, previous work suggests that 1200 stems/ha is a minimum standard for stand replacement (Mueggler 1989). Aspen recruitment, those trees >2 m and less than 8 cm dbh, totaled 11 individuals for the entire study area—a total insufficient to conduct meaningful analysis. Similarly, browse levels derived as a percent of regeneration tallied contribute limited information because totals were small and that itself may reflect high browse intensity, but are reported here as a documentation (albeit weak) of baseline conditions.

Percent browse numbers may be misleading due to very low counts in Year 1 and outside the fence every year; very low regeneration numbers

indicate that many young ramets were browsed to the ground level and not detectable. In Year 1, we counted a total of 103 suckers and 21% were browsed (12% inside, *N* = 97; 100% outside, *N* = 6); however, eight sample plots contained no live suckers (five plots inside and three plots outside). By Year 3, those numbers changed considerably: 440 total and 19% browsed (0.0% inside, *N* = 428; 100% outside, *N* = 12) and a single plot outside the fence contained no suckers (this plot contained the highest deer scat count, nine, of the entire study). We tallied only mule deer and cattle scat within our study plots. Mule deer scat proved very difficult to detect, perhaps because recently melted snow had matted vegetation making small pellets easy to overlook. Nonetheless, 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 enclosure. By Year 3, cattle deposits were 64 and deer scat was 14, all outside the enclosure.

Treatment effects

We used total regeneration/ha and stem count values in three height classes (0–0.5 m, >0.5–1 m, and >1–2 m) to assess effects of fencing over a

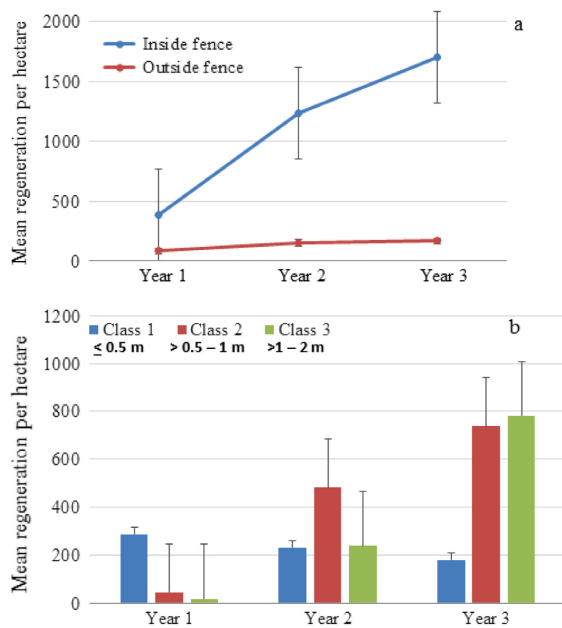


Fig. 2. Two views of aspen regeneration change over the three-year study period (Year 1 = pre-treatment): (a) mean regeneration/ha inside and outside the fenced enclosure. Mann–Whitney U tests for difference between groups showed a significantly more aspen inside the fence compared to outside in Year 1 ($Z = -1.81$, $P = 0.03$); however, those differences were much larger by Year 3 ($Z = -3.65$, $P = 0.0001$). Outside fence error bars: Year 1 = 135, Year 2 = 151, Year 3 = 111; and (b) mean regeneration/ha by year and height group for sample locations within the fenced area only depicting a progression of overall growth during the study period. Error bars describe 95% confidence interval for each data point.

three-year period. We measured significantly more regeneration inside the fence than outside at the end of this period ($Z = -3.65$, $P = 0.0001$). There was a >fourfold increase in the mean regeneration/ha as a result of fencing (Fig. 2a). Both overall height and total number of regeneration/ha increased within the enclosure as the study progressed. Within the fenced area, we documented an increasing mean regeneration/ha trend by height class with each additional year (Fig. 2b). The Kruskal–Wallis test yielded significant differences ($\chi^2 = 31.14$, $P < 0.0001$) between years of measurement in terms of regeneration for all sample locations within the fenced area regardless of treatment type (Fig. 3).

A closer examination of treatment types and active vs. passive treatments was conducted to understand the most effective practices. Results indicate that all sample sites benefited from herbivory protection (Fig. 2; Appendix S3). However, passive (fencing only) was significantly less effective than active (all treatments combined) in stimulating regeneration (Fig. 4, $Z = 1.74$, $P = 0.04$). Fencing without treatment resulted in a mean regeneration/ha 1359 ($N = 13$, $SD = 785$), a level thought to be sufficient for stand replacement (Mueggler 1989, Rogers and Mittanck 2014) and far beyond regeneration levels reported outside the fence that were also untreated (105, $SD = 43$; Fig. 2a). We compared treatment–control pairs and found no significant differences in regeneration production regardless of treatment type (Fig. 5), although the juniper removal–control pair yielded the most significant results ($Z = -1.44$, $P = 0.07$). The Kruskal–Wallis test for between-group differences in regeneration for active treatments also revealed non-significant results ($\chi^2 = 4.56$, $P < 0.10$); however, a general trend emerges of greatest-to-least ramet reproduction

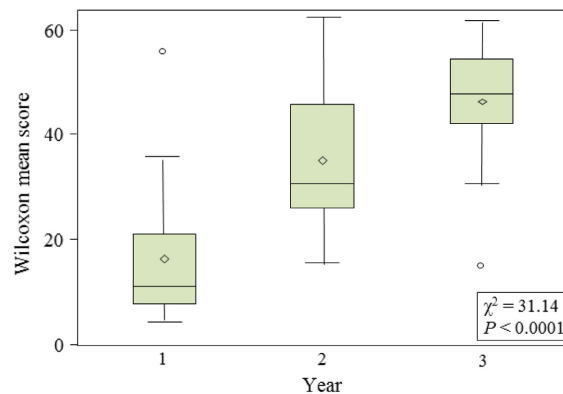


Fig. 3. Box plots depicting a significant difference ($\chi^2 = 31.14$, $P < 0.0001$) in terms of the Kruskal–Wallis test for differences between years (groups) of regeneration measurement (Year 1 = pre-treatment) for plots within the fenced enclosure. Output from Kruskal–Wallis test is shown in Wilcoxon mean scores on the y -axis (SAS). Whiskers show minimum and maximum values, boxes represent 25–75% data ranges, horizontal lines within boxes are medians, and diamond symbols are means. Results are considered significant where a Monte Carlo-simulated chi-square test using 10,000 runs produced an estimated P value of < 0.05 .

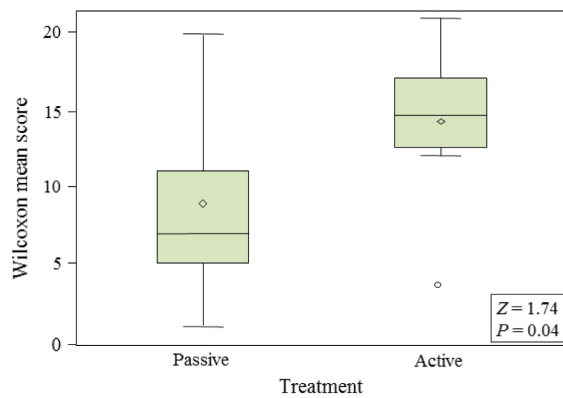


Fig. 4. Wilcoxon–Mann–Whitney U test results displayed in box plots showing significant differences ($Z = 1.74$, $P = 0.04$) in regeneration/ha between all treatment types (active) and all control plots (passive) within the fenced enclosure. Output from the test is shown in Wilcoxon mean scores on the y -axis (SAS). Whiskers show minimum and maximum values, boxes represent 25–75% data ranges, horizontal lines within boxes are medians, and diamond symbols are means.

from prescribed burning, to juniper removal, and finally selective cutting (Fig. 6). Although sample size is small, selective cutting ($N = 2$) produced fewer average regeneration/ha (1292, $SD = 458$) than non-treatment plots within the fence (1359).

DISCUSSION

Fencing as a management option

Our analysis of an experimental portion of the giant Pando aspen clone suggests that fencing to preclude ungulate herbivory has been successful. While this may appear to be an obvious conclusion, support of a likely outcome with empirical data establishes a basis for further examination of treatments within the fence. (Anecdotally, an adjacent enclosure at Pando has thus far not yielded visible regeneration after 2 yr; we assume deer are breaching the fence in some way there.) While there was an initial (Year 1; Table 1) difference showing statistically greater regeneration inside the fence vs. outside, we believe this may be attributed to the approximately nine-month gap between fence construction and baseline monitoring. Nonetheless, highly significant differences between regeneration at Year 3 confirm an overall trend that, even with an initial gap, is indisputable (Fig. 2). A fivefold increase in progressively taller

aspen suckers in our study area during this period resulted in marked improvements in vegetative regeneration within a 3-year period (Fig. 2b). At Year 3, we observed many stems inside the fence

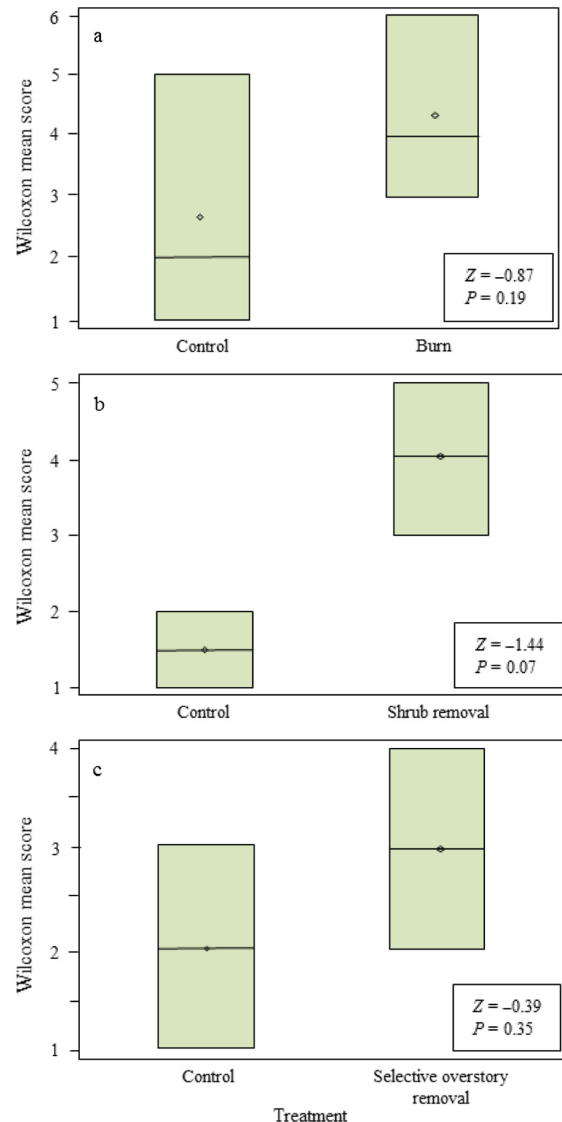


Fig. 5. Wilcoxon–Mann–Whitney U test results displayed in box plots showing insignificant differences in regeneration/ha between treatment pairs within the enclosure: prescribed burn ($Z = -0.87$, $P = 0.19$), shrub removal ($Z = -1.44$, $P = 0.07$), and selective overstory removal ($Z = -0.39$, $P = 0.35$). Output from the test is shown in Wilcoxon mean scores on the y -axis (SAS). Boxes represent 25–75% data ranges, horizontal lines within boxes are medians, and diamond symbols are means.

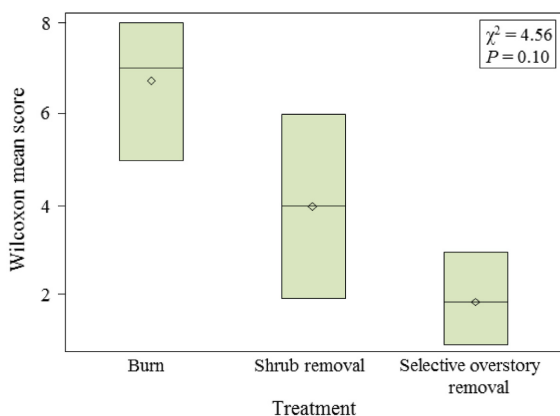


Fig. 6. Box plots depicting an insignificant difference ($\chi^2 = 4.56$, $P = 0.10$) in terms of regeneration/ha using the Kruskal–Wallis test for differences between all treatment types (groups). Output from Kruskal–Wallis test is shown in Wilcoxon mean scores on the y -axis (SAS). Boxes represent 25–75% data ranges, horizontal lines within boxes are medians, and diamond symbols are means. Results are considered significant where a Monte Carlo-simulated chi-square test using 10,000 runs produced an estimated P value of <0.05 .

growing near or just over the 2-m threshold where they may be considered beyond browse height (i.e., “recruitment”; Appendix S3). Outside the fenced study area, regeneration remained nearly unchanged during this time at levels far below those necessary for overstory replacement (Fig. 2a). Based on prior research, we conservatively target a ratio of at least 0.5 successful recruitment ramets for each live overstory stem (Rogers and Mittanck 2014). This guideline allows for moderate survival associated with an additional ramet flush that commonly follows stand disturbance. 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 has taken place at Pando.

Our expectations were exceeded by the level of regeneration resulting from fencing alone—so-called passive treatment—compared with active treatments (burning, shrub removal, and selective overstory cutting). Results indicate that all treatments combined produced significantly more suckers than fencing alone, although that outcome was marginally less than the 0.05 criteria used

here ($P = 0.04$, Fig. 4). In cases where sample plots fell near recently installed fence, it may be that tree cutting and soil compaction associated with the enclosure construction process stimulated a suckering response (Shepperd 1996). However, most control plots inside the fence were not located near enclosure edges, which suggests that active stimulation is not required to initiate replacement levels of recruitment. Particularly in stable aspen communities, stand-replacing disturbance is not thought to be the primary mechanism of renewal (Harniss and Harper 1982, Shepperd 1990, Kurzelt et al. 2007, Rogers et al. 2014). Instead, small gap openings and continuous regeneration and recruitment into the mid-story seem to form the basis of stable aspen functional ecology (Rogers et al. 2014, Nlungu-Kweta et al. 2016). Thus, if our approach to forest management is to use techniques that emulate natural disturbance processes, we may reasonably question the means of active treatment used here which go beyond individual tree and small gap openings. We may further reexamine the appropriateness of fire use in stable aspen forests that are not expected to burn under natural fire scenarios (Shinneman et al. 2013).

It is worthwhile to make a distinction between fencing to exclude herbivores for management purposes (i.e., allowing heavily browsed stands or landscapes to recover) vs. erecting small enclosures as demonstration or research test sites. Some would argue that use of fencing to reverse ill-effects of herbivory in aspen is only possible for relatively small-scale project areas (<5000 ha); fencing at landscape or larger scales presents formidable funding and maintenance challenges (Kota and Bartos 2010), as well as potentially limiting landscape connectivity.

A minimum size for active management to encourage aspen recruitment while overwhelming herbivore appetites has been difficult to establish and likely depends heavily on herbivore numbers, species, movement, and accessibility. Establishing such thresholds is a key research need for vegetation, range, and wildlife management. Given the prohibitive expense of managing aspen landscapes via large-scale fencing, it is difficult to demonstrate a cost to benefit advantage for most managers. Other than providing a visual demonstration of suckering potential, what can be derived from such efforts? Inside fences allow no browsing,

while outside fences permit complete browsing; neither scenario emulates ecological process, or a balanced herbivory prescription, to establish a sustainable pathway for aspen communities. At smaller scales such as the Pando clone, a riparian corridor, a campground, or small private parcels, temporary fencing may provide a reprieve while new ramets grow above the typical browsing heights of offending herbivores. A more difficult, but perhaps more ecologically sound, course is to address appropriate numbers and regular movement of large herbivores rather than relying exclusively on fenced exclosures. Certainly scale of restoration, but also coordinated animal–plant management, plays significant roles in planning sustainable aspen strategies.

Treatment efficacy at Pando Clone

Ecologists have a strong understanding of methods for stimulating regeneration in aspen forests under varying conditions (DeByle and Winokur 1985, Shepperd et al. 2006). In the present study, we examined passive vs. active treatments, as well as burning, shrub removal, and selective cutting within a large, genetically uniform, aspen grove. When each treatment was compared to an adjacent control area, we found no significant differences in regeneration response (Fig. 5), although the juniper removal treatment–control pairing yielded promising results (Fig. 5b). This result suggests that protection alone is sufficient to regenerate stable aspen communities. Most previous work of this nature has focused on seral aspen—systems known to regenerate vigorously following disturbance (Schier et al. 1985, Shepperd 1990). Seral and stable communities react differently to perturbations (Harniss and Harper 1982, Rogers et al. 2014), and this may partially explain the lack of more robust regeneration associated with the disturbances we tested here. Comparison between all three treatment types showed no significant advantage of one over the others (Fig. 6). Taken together, all forms of treatment, including fencing alone, strongly indicated positive regeneration trends over the three-year test period (Fig. 2), suggesting that the one common factor among all of them is protection from herbivory.

As mentioned earlier, the Pando clone falls within the definition of a stable aspen community and more precisely in the Colorado Plateau functional subtype described by Rogers et al. (2014).

The understory is dry and largely depauperate of vegetation, though there are ample patches of common juniper, grasses, and limited forbs scattered throughout the site. Understory growth is probably limited by herbivory, as well as large basalt boulders and outcrops. There is potential for the site to support more plants if moisture retention was increased by greater shading found in the complex vertical structure expected in stable aspen communities (Mueggler 1985). In terms of appropriate treatments emulating natural disturbance, this community is unlikely to experience wildfire due to the near-complete absence of successional conifers (Shinneman et al. 2013). Similarly, though common juniper may carry fire at a micro-topographic scale (as witnessed in our prescribed burn; Appendix S3: Fig. S3a), natural fire spread is unlikely given its patchy nature and short stature—characteristics known to limit crown-to-crown fuel continuity. Complete juniper removal, though apparently stimulating suckering, has little ecological precedent. Selective harvest, perhaps at a lower rate than our experimental 50% felling, most closely resembles sporadic die-off commonly experienced in stable aspen (Rogers et al. 2014). This method, however, produced fewer ramets than other treatments (Fig. 5) and resulted in the weakest significance (difference vs. adjacent control) compared to regeneration by fencing alone (Fig. 4c). It may be that additional time will reveal a more robust response in this disturbance type.

Evidence presented here provides a number of leads for advancing restoration of the Pando clone. First, we documented positive effects of short-term exclusion of herbivores via fencing. This implies that long-term herbivory patterns at Pando are the ultimate cause of the current decline in the clone's condition. Given the immense size and likely longevity of Pando, we can conservatively assume some pre-settlement balance between herbivory and growth which has more recently been disrupted. Second, ecologically appropriate management actions for Colorado Plateau stable aspen point more toward selective tree harvest or simply allowing current mortality levels alongside continuous regeneration (Rogers et al. 2014). This approach could be achieved via a passive only (fencing; Appendix S3: Fig. S3b) or modestly active strategy combining fencing and selective cutting, although our results did not

demonstrate a clear advantage to supplemental cutting at Pando. Third, though fencing at such an iconic location is not socially desirable, promotion of long-term ecological benefits through public education at the site may alleviate potential social conflicts over restoration actions. Fourth, while we have not undertaken a formal cost-benefit analysis here, we do acknowledge the expense of fencing even at this localized scale. However, similar expenses may be incurred using other treatments where poor results would be expected in the absence of fences. Finally, it is difficult to fully understand the historic changes that have led to the current predicament at Pando. While we know that mule deer are responsible for a portion of aspen sucker browsing, cattle reduction and enclosure 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. Likely there are combined effects of these two species and human actions have clearly influenced their fluctuating numbers over the past century. While elk browsing of aspen is a serious concern regionally (Seager et al. 2013), we did not see elk or record their scat at Pando. Reductions in numbers of wild or domestic ungulates, as mentioned earlier, will begin to address the base cause though it is politically unpopular. Most importantly, active treatment of the entire Pando clone without adequate temporary protection from herbivory would pose a more serious risk than inaction alone. Given previous documented cases in the area of significant aspen browsing and mortality on unfenced aspen treatments (Kay and Bartos 2000), it is highly likely that Pando could be significantly damaged or lost were active management to be followed by unfettered browsing.

Lessons for sustainable aspen in North America

Pando is an internationally known aspen clone that is currently at a critical juncture: Inaction by managers is likely to lead to total collapse or, at minimum, significant reduction in extent and viability. Experimental actions taken here have documented promising signs of recovery within a portion of the clone. Stable aspen communities, such as the Pando clone, are reliant on regular regeneration and recruitment. Further, as overstory trees continue to die, carbohydrate energy in root system reserves is diminished in proportion

to lessening total basal area (Frey et al. 2003). Herbivory of new recruits combined with overstory mortality increasingly enables a pattern where there is less capacity to produce suckers as basal area decreases. Deer and cattle are the prime large herbivores in this area. To our knowledge, deer populations are not abnormally high and cattle browsing has been reduced in the area over recent years. While it is clear that interruption of this recruitment pattern has occurred at some point, it remains unclear what changes in herbivory triggered were responsible for the deviation from sustainable aspen reproduction. A key message, then, is that while we cannot state unequivocally that there are “too many” herbivores at Pando, we do know that there too many for current conditions. Increasing drought and/or earlier spring snow melt may be abating recent curtailment of ramet recruitment, though evidence presented here suggests that herbivory alone provides ample explanation for this phenomenon.

In many respects, the Pando clone presents a unique location for examining stand-level aspen management. In regard to herbivory, it is rare that researchers can hold genetic variation constant in a field setting. Other researchers have shown that genetic make-up is closely linked to defense chemistry, leaf palatability, and ultimately susceptibility to mammalian herbivore browsing (Bailey et al. 2007, Wooley et al. 2008, Lindroth and St Clair 2013). Thus, we can assume in our study area minimal, if any, variation is sucker palatability. Based on visual evidence in the remainder of this clone, as well as tests of protected vs. unprotected regeneration (Fig. 2), it is clear that whatever suckers available to browsing are being consumed. Defense chemistry appears to be having no discernable effect as a browsing deterrent. On broader landscapes, with multiple aspen genotypes, we might expect to see wide variation in phenolic glycosides, for example, a defense chemical shown to reduce palatability when present in higher amounts (Smith et al. 2011, Holeski et al. 2016).

Regionally, implications from this work coincide with greater understanding of appropriate management based on ecological function at the community level (Rogers et al. 2014). It is important to note, for instance, that not all aspen types are governed by stand-replacing disturbance and

therefore should not be subjected to parallel management actions (Shinneman et al. 2013). Kurznel et al. (2007) documented a large proportion of stands that were “persistent” aspen, and of these, 70% were thought to be regenerating without stand-replacing events. Whether through episodic or continuous regeneration, we know that aspen stands may sustain themselves over long periods without loss of apical dominance (Schier et al. 1985, Crawford et al. 1998, Zier and Baker 2006, Kurznel et al. 2007) once thought to be an exclusive triggering mechanism for reproduction. The requirement of continuous or sporadic regeneration in the absence of disturbance makes stable aspen communities even more vulnerable to herbivory-caused collapse than seral communities (Rogers and Mittenack 2014). Conifer succession gradually increases the probability of mixed-severity fire and opportunity for more intense regeneration, which may overwhelm moderate herbivory. Such events are less probable in stable aspen, with limited stand-replacing events, which makes successful continuous recruitment even more critical. In relation to climate warming alongside herbivory, we should expect greater opportunity for increased wildfire in seral communities than in stable aspen (Yang et al. 2015). Drought and warming may increase the pace of mature tree die-off (Worrall et al. 2013), while continued herbivory will curtail chances of stand renewal. In such instances, if persistence of aspen cover is a management goal, managers will need to redouble efforts to address the root causes of herbivory-related aspen decline by directly focusing on ungulate populations and movements.

CONCLUSIONS

Recent efforts to preserve an ecologically functional Pando aspen clone in central Utah are showing early signs of success. Here, we have documented initial responses after 3 yr of fencing a portion of the clone and experimentally burning, removing shrubs, and selectively cutting subsets within this enclosure. Results indicate the most effective action was the fencing itself, though we acknowledge that treatments may prove more robust given additional time. Nonetheless, this protection allowed aspen suckers to progress toward recruitment that has been absent at Pando

for at least two decades. We must assume that ramets had been sprouting continuously, but that these stems were being browsed prior to fencing to the ground level, making them difficult to detect. Areas within the clone that are unprotected by fencing show no signs of recovery and will likely continue to decline. In stable aspen communities, such as the one studied here, long-term patterns of little or no successful recruitment will result in clonal decline as mature trees die. Without a concerted management effort (i.e., implementing lessons learned here), we should expect Pando to eventually experience system collapse and replacement by another more browse- and drought-tolerant vegetative type, such as montane sage meadow. Herbivory resulting from past livestock and wildlife management decisions is responsible for aspen decline on this local scale, as well as in many larger landscapes across the west. Not all aspen communities are affected in this way, so it is important to demonstrate through monitoring that excessive herbivory is an impediment to resilience before proceeding based on broad assumptions. Though we have demonstrated effective treatment for renewed regeneration by fencing a portion of Pando, more complicated solutions working across institutional and disciplinary lines will be required to address unsustainable browsing at landscape and regional scales.

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