

Article

Regeneration and Herbivory Across Multiple Forest Types Within a Megafire Burn Scar

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Abstract

Human activities are increasing the occurrence of megafires that alter ecological dynamics in forest ecosystems. The objective of this study was to understand the impacts of a 610 km² megafire on patterns of tree regeneration and herbivory across three forest types (aspen/fir, oak/maple, and pinyon/juniper). Seventeen transect pairs in adjacent burned/unburned forest stands (6 aspen/fir, 5 oak/maple, and 6 pinyon/juniper) were measured. Sapling density, meristem removal, and height were measured across the transect network over a three-year period from 2019 to 2021. Tree species able to resprout from surviving roots (oak and aspen) generally responded positively to fire while species that typically regenerate by seeding showed little post-fire regeneration. Browse pressure was concentrated on deciduous tree species and was greater in burned areas but the effect diminished over the three-year study period. Meristem removal by herbivores was below the critical threshold, resulting in vertical growth over time. Our results indicate that forest regeneration within the megafire scar was generally positive and experienced sustainable levels of ungulate browsing that were likely to result in forest recruitment success.

Keywords: wildfire; novel fire regime; disturbance; sapling; forest recruitment; ungulate browse



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1. Introduction

The size, frequency, severity, and timing of wildfires are changing due to human activity, resulting in novel fire regimes that affect forest regeneration and ecosystem stability [1–3]. Megafires are becoming more common and are classified by being large (greater than 40,000 hectares) and having a uniquely large ecological and societal impact [4,5]. Megafire probability varies by season and increases during warmer and drier periods, which are increasing due to climate change [3,6]. Extreme drought brought on by climate change is making large, high-severity fires more frequent [6]. A comprehensive analysis of large fires conducted by Westerling et al. [7] found regional temperature to explain 66% of annual variation in fire frequency, with fires burning more often in warmer than cooler years. Early spring snowmelt due to warming temperatures also increases wild-fire activity [8], and because snowpack melts earlier in burned areas [9], fires are creating a self-perpetuating cycle. Fire suppression in forests increases fuel loads which increases wildfire extent and severity [10]. Megafires create burn mosaics across the landscape, which alters vegetation structure, productivity, and successional pathways in forest ecosystems

that likely have strong habitat feedbacks on the wildlife communities [11–13]. However, more studies are needed to understand the effects of megafires on forest ecosystems and its implications for wildlife behavior.

Because of their large size, megafires are increasingly burning across ecotonal boundaries and multiple plant community types leading to shifts in ecological processes that operate at landscape scales. Species are differentially adapted to unique habitats across landscapes, so larger and more severe fires will have different effects on plant species depending on their life history strategies [14,15]. Plant species that have co-evolved with fire have developed root and stem suckering, which is common in aspen, oak, and maple species [16–18]. In contrast, regeneration by seed common in gymnosperms including fir, pinyon pine, and juniper may have more variable regeneration responses in post-fire environments [19]. Furthermore, large fires can lengthen ecosystem recovery by increasing the dispersal distances of propagules [20–22]. Sparks et al. [23] found that forests with fire-adapted species have the lowest reduction in net primary production in the short term. Megafires can elicit even longer recovery timetables when they burn multiple forest types, especially when the forests are not fire resilient. The ecological effect of megafires that cross multiple forest types on forest regeneration is not well understood.

Changing fire regimes create a range of conditions that influence both forest regeneration and wildlife behavior. Fire can stimulate forest regrowth, improving ecosystem services and rangeland quality [16,24,25]. Post-fire environments often enhance regeneration by increasing soil nutrients and light availability, while also reducing herbivory through the activation of plant defense compounds [24,26]. However, fire can also negatively impact forest recovery and habitat quality [21,27]. Nutrient-rich regrowth tends to attract herbivores, particularly ungulates, whose overabundance may hinder regeneration [12,28]. Additionally, fire can increase surface albedo, raising ground temperatures and reducing shelter, which may displace wildlife unable to thermoregulate effectively [29].

Few long-term data sets exist to address pressing questions regarding post-fire regeneration patterns in megafire scars [12,30,31]. The 2018 Pole Creek megafire in central Utah is an ideal study system for looking at the legacy effects of fire on patterns of regeneration and herbivory. Three forest types across an elevation gradient were burned during the fire including *Populus tremuloides* (quaking aspen) and *Abies lasiocarpa*, *Abies concolor* (subalpine fir, white fir) referred to as aspen/fir forests at high elevation, *Quercus gambelii* (Gambel's oak) and *Acer glabrum*, *Acer grandidentatum* (mountain maple, bigtooth maple) referred to as oak/maple forests at mid elevation, and *Pinus edulis*, *Pinus monophylla* (pinyon, single-leaf pinyon) and *Juniperus osteosperma* (Utah juniper) referred to as pinyon/juniper forests at low elevation. This study system is ideal for testing patterns of herbivory on post-fire regeneration because ungulate populations dominated by elk, deer and cattle are high in the Pole Creek landscape. No previous studies that we are aware of have analyzed the multi-year regeneration and herbivory responses of multiple forest types burned during a megafire.

This study aimed to evaluate the effects of fire on tree regeneration and herbivory patterns across three forest types affected by a megafire. Specifically, it addressed the following questions: (1) How does fire influence regeneration patterns over time in different forest types? (2) Do forest types vary in their response to ungulate herbivory, and is this response modified by fire?

2. Materials and Methods

2.1. Study Area

The study was conducted in the Pole Creek megafire complex located within the Uinta-Wasatch-Cache and Manti-La Sal National Forests in northern Utah (40.0838° N,

111.5960° W). Elevation ranged from 1622 to 2693 m and slope was held constant across sites. The Coal Hollow fire, Bald Mountain fire, and Pole Creek fire were all lightning-ignited fires beginning on 4, 24 August and 6 September 2018. The three fires converged to create a 40,000 hectare burn scar referred to as the Pole Creek megafire that ended on 6 October 2018. Approximately, 40% of the study area within the fire perimeter was stand replacing (high burn severity) while 60% was a mosaic of unburned, low or moderate severity.

Dominant vegetation was characterized by three distinct forest types that varied along an ecotonal elevational gradient. Aspen/fir forests were dominant at the highest elevation, oak/maple forests at middle elevations, and pinyon/juniper forests at low elevations of the fires' extent. Of the key species in this study, aspen, maple, and oak saplings regenerate via clonal or vegetative regeneration, while the fir, pinyon, and juniper species regenerate via seeds. The soils within the Pole Creek Fire complex are primarily shallow, stony, and loamy soils derived from igneous and sedimentary parent materials. Ungulates common to the area include *Cervus canadensis* (elk) and *Odocoileus* spp. (deer). *Bos taurus* (domestic cattle) and *Ovis aries* (domestic sheep) grazing allotments exist within the study area as well.

2.2. Study Design

Study plots were chosen within each forest type by pairing adjacent high-severity burn (100% overstory tree mortality) with unburned patches (no overstory fire tree mortality) of comparable size within the fire perimeter. Burn severity maps were created in ArcGIS Pro 3.0 ESRI (Environmental Systems Research Institute, Redlands, CA, USA) using differenced normalized difference in vegetation indices (dNDVI) derived from Landsat-8 imagery courtesy of the United States Geological Survey (USGS). The derived maps were then used to identify patches of high burn severity, which were later ground-verified by visiting each location. Six transect pairs were identified for aspen/fir and pinyon/juniper forest types, and five pairs for oak/maple forests (Figure 1). Transects were installed across the entire megafire to the extent that species distribution, burn severity, and human access allowed.

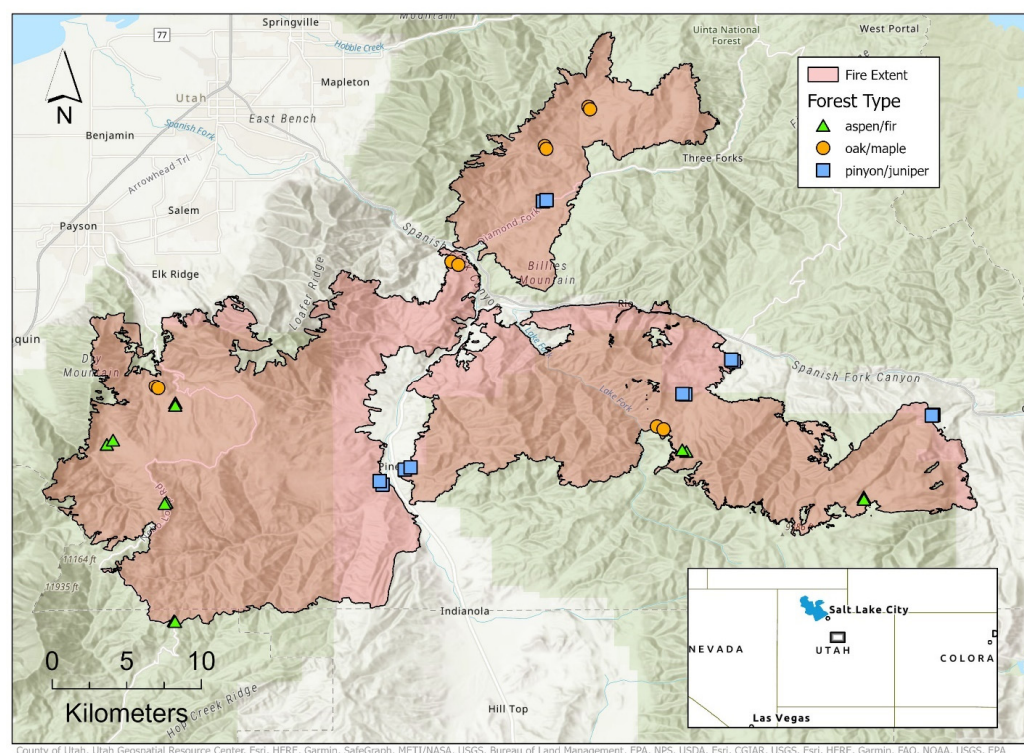


Figure 1. High-severity burn–unburned transect pair locations in aspen/fir, oak/maple, and pinyon/juniper forest types within the Pole Creek megafire burn scar in northern Utah, USA.

2.3. Stand Characterization and Field Measurements

Stand composition and structure of both burned and unburned stands were characterized using estimates of stand density and by identifying tree species. Forest regeneration responses were measured yearly from 2019 to 2021 in late July when ungulate browsing was heaviest [32]. Sapling density, browse, and height of key tree species (quaking aspen and *Abies* spp. in aspen/fir forests, Gambel oak and *Acer* spp. in oak/maple forests, Utah juniper and pinyon species in pinyon/juniper forests) were measured along 50×2 m belt transects run through each high-severity burn–unburned pair at each study site (Figure 2). Sapling density was measured by counting all saplings of each key species within the belt transect. Clumped individuals were treated as a single organism for density measurements because they self-thin over time [33]. The height of each sapling within the transect was determined using a measuring stick. The browse percentage of saplings was calculated by counting the missing and intact apical meristems after the manner of Rhodes et al. [32]. The average slope and aspect of sites were determined using topographical analysis of USGS Landsat data in ArcGIS Pro 3.0.



Figure 2. Paired unburned–high-severity burn transects in aspen–conifer (**top**), oak–maple (**middle**) and pinyon–juniper forests (**bottom**). Photos on the left show the unburned transects and photos on the right show high-severity burn transects.

2.4. Statistical Analysis

Data exploration was conducted according to the methods of Zuur [34] to test that all model assumptions were met. All response variables met equal variance assumptions. To assess the data, we compared the average density, browse percentage, and height for each tree species and year using a repeated measures analysis of variance (ANOVA) using JMP 17 software (SAS Institute Inc., Cary NC, USA). Tukey's HSD was used to test pairwise comparisons to test across year burn effects.

3. Results

3.1. Fire Effects on Regeneration Density

The density of stand sapling regeneration exhibited variable responses depending on species and year. Oak sapling density increased by 99% in burned areas compared to unburned areas when averaged across years ($p \leq 0.05$) (Figure 3). In contrast, maple, pinyon, and fir densities were reduced by 133%, 200% and 200% along burned transects compared to unburned transects when averaged across years ($p \leq 0.1$) (Figure 3). Fire did not significantly affect aspen or juniper densities ($p = 0.20$ and $p = 0.27$). Oak sapling density decreased by 19% from 2019 to 2021 while maple and fir sapling densities increased by 32% and 125% during the same three-year period when averaged across burn levels ($p \leq 0.1$) (Figure 3). Year did not significantly affect aspen, juniper, or pinyon densities ($p = 0.30$, $p = 0.39$, $p = 0.36$). The fire-by-year interaction term was only significant for fir sapling density ($p \leq 0.1$) (Figure 3).

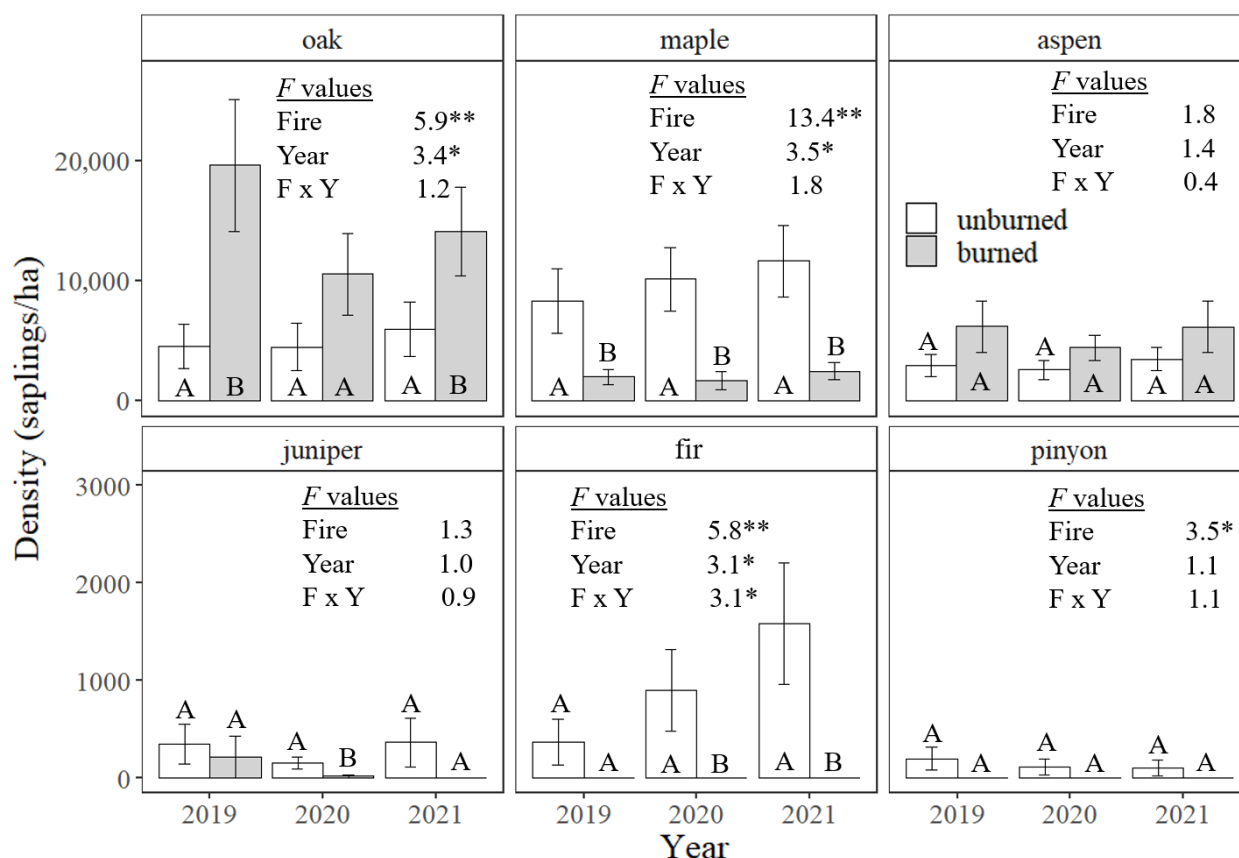


Figure 3. The effect of fire on density of aspen, fir, oak, maple, pinyon, and juniper saplings across years. Asterisks represent p -value significance: * $p \leq 0.1$, ** $p \leq 0.05$. Letters that are different between bars (within each year, for each species) indicate a significant difference between burned and unburned ($p \leq 0.1$).

3.2. Fire Effects on Browse Pressure on Deciduous Species

Deciduous saplings were browsed 66% more in burned areas compared to unburned areas when averaged across years ($p \leq 0.05$) (Figure 4). In 2019, deciduous sapling browse was 94% greater in burned areas than unburned areas ($p \leq 0.1$) (Figure 4). The main effect of year and the fire-by-year interaction term did not significantly affect browsing of deciduous species collectively or individually (Figures 4 and 5). Maple saplings were browsed 117% more in burned areas than in unburned areas when averaged across years ($p \leq 0.05$) (Figure 5). Fire did not significantly affect the browse of oak and aspen saplings ($p = 0.3$ and $p = 0.5$) (Figure 5). Coniferous species showed little evidence of browsing.

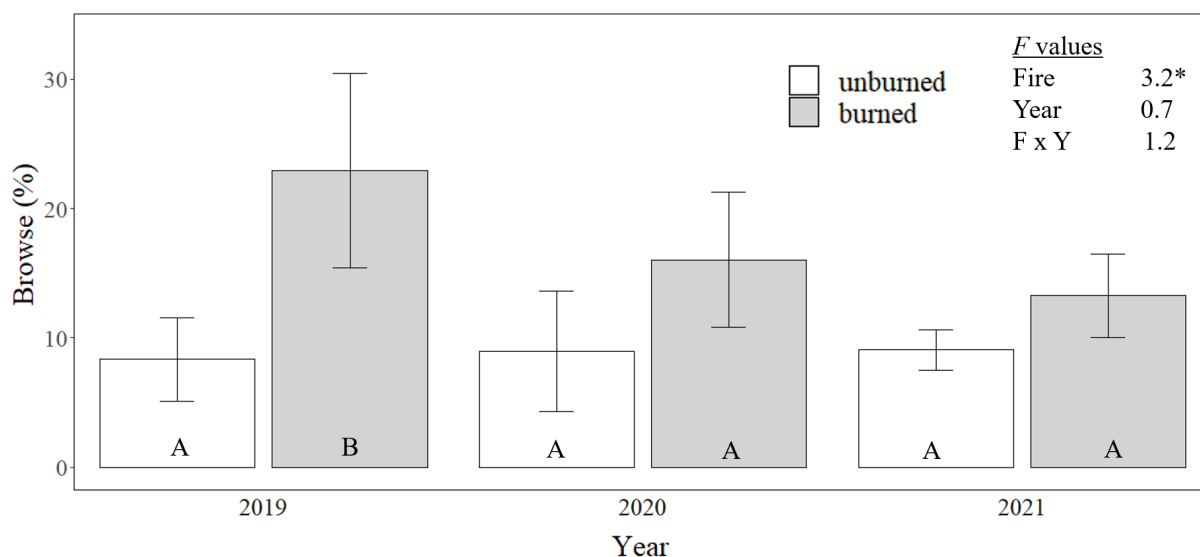


Figure 4. The effect of fire on browse levels of aspen, oak, and maple saplings across years. Asterisks represent p -value significance: * $p \leq 0.1$. Letters that are different between bars (within each year) indicate a significant difference between burned and unburned ($p \leq 0.1$).

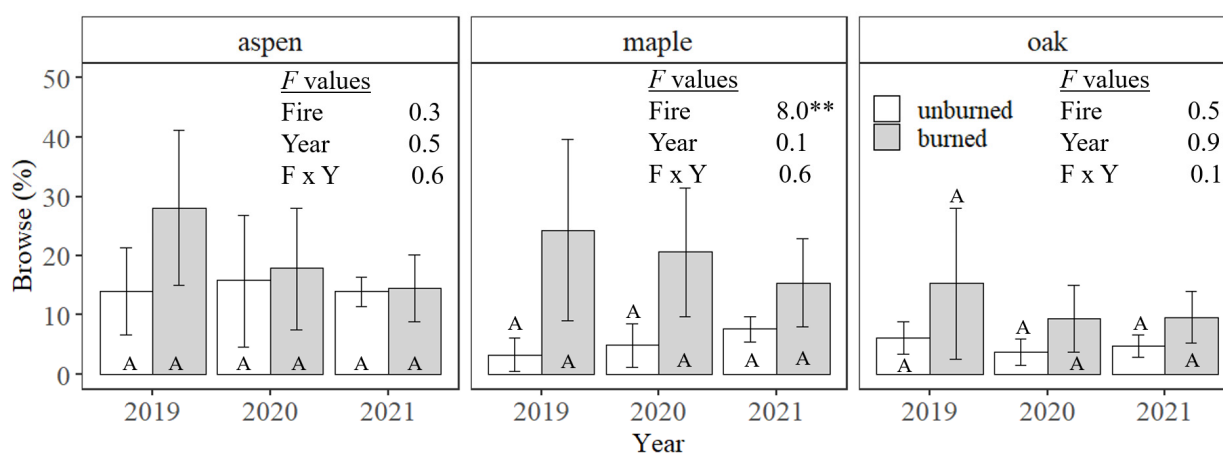


Figure 5. The effect of fire on browse levels of aspen, oak, and maple saplings across years. Asterisks represent p -value significance: ** $p \leq 0.05$. Letters that are different between bars (within each year, for each species) indicate a significant difference between burned and unburned ($p \leq 0.1$).

3.3. Fire Effects on Recruitment Potential

Sapling height averaged across species increased by 48% over three years from 2019 to 2021 ($p \leq 0.001$) (Figure 6). The main effect of fire and the fire-by-year interaction term did not significantly affect mean species sapling height over the course of the study ($p = 0.30$ and $p = 0.11$) (Figure 6). Over the three-year study period, the average height of

aspen, fir, juniper, and pinyon pine was significantly lower in burned stands compared to unburned stands ($p < 0.05$). In contrast, oak sucker height increased significantly following fire ($p = 0.03$), while maple height showed no significant difference between burned and unburned stands ($p = 0.30$) (Figure S1).

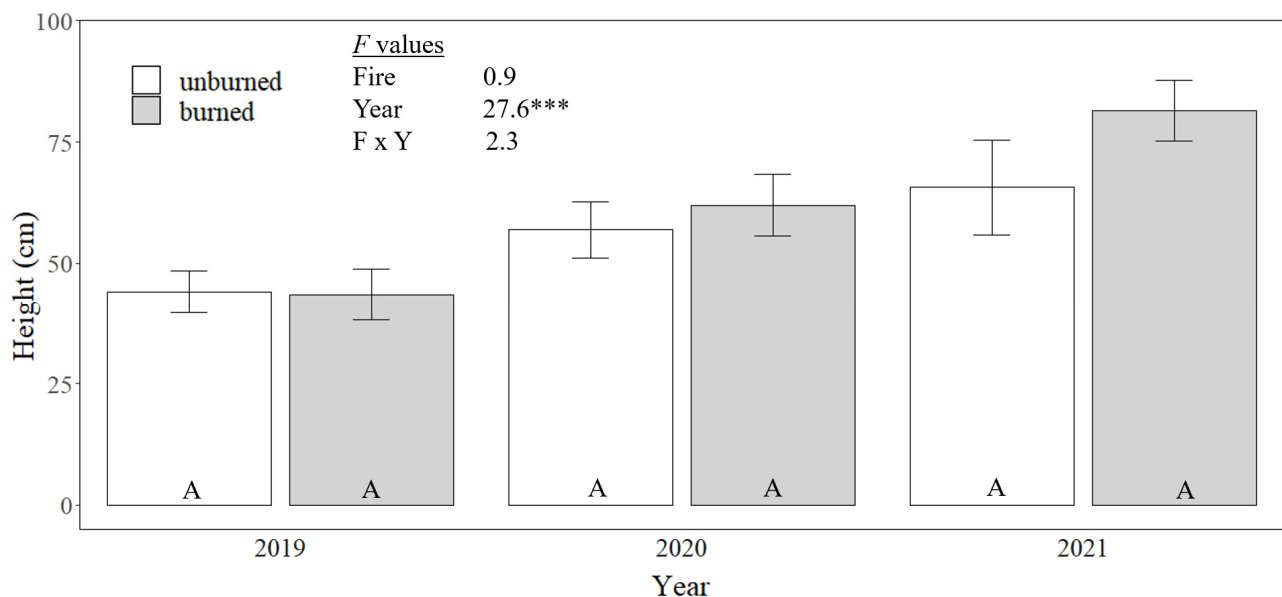


Figure 6. The effect of fire on the combined species height of aspen, fir, oak, maple, pinyon pine, and juniper over multiple years. Asterisks represent p -value significance: *** $p \leq 0.001$. Letters that are different between bars (within each year) indicate a significant difference between burned and unburned ($p \leq 0.1$).

4. Discussion

Assessing the regeneration responses of multiple forest types in the Pole Creek megafire provided insights into landscape-scale forest regeneration responses in the boundaries of a megafire scar three years post-fire. The results demonstrated that post-fire environments elicited highly variable forest regeneration responses depending on tree species during that time period (Figure 3). Ungulate herbivory that has been implicated in forest regeneration failure [32,35] was widespread across the forest landscape (Figures 4 and 5). Tree regeneration varied by species with quicker responses from root sprouting species (Figure 3). Ungulate browsing was moderately greater in post-fire environments and varied by tree species (Figures 4 and 5). While ungulate browsing was widespread across the study area, meristem removal did not exceed thresholds for forest regeneration failure [32] and attenuated over the three-year study period indicating that forest recruitment is likely to be successful.

4.1. Fire Effects on Regeneration by Species

Regeneration densities showed strong positive or negative responses to fire, that is likely tied to regeneration strategy (Figure 3). Sprouting species such as aspen and oak showed rapid and positive responses to fire, which is in line with previous research [26,36,37]. High-severity fires have been found to trigger strong suckering responses due to increased light availability, nutrient pulses, and reduced competition [24,38,39]. Tree species that primarily reproduce by seed, including maple, fir, pinyon, and juniper, showed negative density responses to fire during the three year study window (Figure 3), which is consistent with previous studies [40–42]. Post-fire seed regeneration is often slower than sprouting due to the added barriers of seed dormancy [43], reduction in nurse plants [40,44,45], and

long distance seed transport especially in large fire scars [11,22]. Bigtooth maple can regenerate through sprouting but is also heavily reliant on seed regeneration following high-severity fires [41]. Post-fire fir regeneration is primed by aspen facilitation that can take several decades after a fire [42,44,45]. As long as mature seed source trees exist within 5–10 km junipers can regenerate from seed relatively quickly under ideal weather conditions, while pinyon trees are more reliant on protective cover and can take much longer to establish [40,46].

4.2. Fire Effects on Browse

Browse pressure was greater in burned areas than in unburned areas for deciduous species but the effect diminished over the three-year study period (Figure 4). Ungulate herbivores can favor foraging in burned areas [47,48] because fire instigates sapling regeneration [38,49] with high nutrient and protein content [47,50]. However, high burn severity can elevate foliar defense chemistry [24,49] that deters ungulate herbivory [51]. Selective herbivory of palatable post-fire saplings leads to an increase in unpalatable saplings [50], which may explain the decrease in browse pressure over the three-year study period (Figure 4). Furthermore, increasing time since fire is inversely related to plant tissue nutrient concentrations that can affect ungulate herbivore browsing preferences [47,52]. As the vegetation regenerates, the burn scar “magnet effect” on herbivores diminishes over time [47,53] and the animals often return to pre-fire foraging behavior (Figure 4) [54].

4.3. Fire Effects on Recruitment Potential (In the Context of Browsing)

Sapling height for the majority of species was reduced by fire (Figure S1) but increased over the three-year study period, showing progression toward stand recruitment (Figure 6). Large fires remove plant-plant competition and can accelerate the vertical growth rate of saplings and alter herbivore behavior that would otherwise suppress vertical growth through selective overgrazing [16]. When herbivory levels drop below 30–40% meristem removal, vertical growth, and recruitment potential increase [32,55]. The average meristem removal in burned areas in this study remained below the critical browse threshold one-year post-fire and dropped to even lower levels in years two and three (Figures 4 and 5). Maintaining apical meristems which drive vertical sapling growth likely explains the increased sapling height over the three-year study period (Figure 6). Relatively low levels of meristem removal in this study are likely explained by the large size and high burn severity of the Pole Creek megafire. Both fire size and high burn severity are known to reduce meristem removal by ungulate herbivores by stimulating aspen regeneration vigor and defense and by changing animal foraging behavior [16,24].

5. Conclusions

Our results show that tree species burned within the same megafire event respond differently to fire, likely due to growth strategy, abiotic conditions, and palatability. Wildfires heavily influence regeneration in mixed aspen, oak/maple, and pinyon/juniper forests, with strong implications for herbivory. Our data show a decline in ungulate herbivory over time, and trends towards successful forest recruitment in the Pole Creek fire scar. Previous studies have found that forest regeneration can succeed even in areas with high ungulate populations, particularly when wildfires were large and burn severity was high. These conditions enhance plant defenses and alter ungulate behavior, increasing resilience to browsing. Where ungulate browsing pressure is high and forest regeneration is a management goal, we recommend prioritizing large wildfires that create a mosaic of burn severities.

Understanding the effect of megafires on forest ecosystems in North America is important as they become more common due to climate change. Our results provide insight into how forest regeneration strategies (seed vs. sprouting) may affect post-fire regeneration responses, but more research is needed to better understand these responses. A key strength of this three-year study is its ability to inform rapid and targeted management decisions by highlighting how three forest types respond differently to fire. However, future research is needed to determine how burn severity influences regeneration across various forest types affected by megafires. In addition, longer-term datasets are essential to better understand forest recruitment dynamics in megafire burn scars and to build a more comprehensive picture of ecosystem resilience under changing fire and herbivory regimes.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/fire8080323/s1>, Figure S1: The effect of fire on height of aspen, fir, oak, maple, pinyon, and juniper saplings across years.

Author Contributions: D.A.T.: Methodology, Formal Analysis, Investigation, Data Curation, Writing—Original Draft, Visualization, Project administration. K.K.: Investigation. N.Z.: Investigation. B.W.A.: Conceptualization, Methodology, Validation, Writing—Review and Editing, Supervision, Funding acquisition. N.H.: Conceptualization, Methodology, Validation, Writing—Review and Editing. R.A.G.: Conceptualization, Methodology, Validation, Writing—Review and Editing. S.B.S.C.: Conceptualization, Methodology, Validation, Resources, Writing—Review and Editing, Supervision, Funding acquisition. All authors have read and agreed to the published version of the manuscript.

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