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Regeneration of Quaking Aspen and Understory Vegetation Change After Fire Risk Reduction Treatment

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REGENERATION OF QUAKING ASPEN AND UNDERSTORY VEGETATION CHANGE AFTER FIRE RISK REDUCTION TREATMENT

by

Allison M. Trudgeon

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Ecology

Approved:

R. Justin DeRose, Ph.D. Major Professor	Larissa L. Yocom, Ph.D. Committee Member
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UTAH STATE UNIVERSITY
Logan, Utah

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ABSTRACT

Regeneration of quaking aspen and understory vegetation change
after fire risk reduction treatment

by

Allison M. Trudgeon

Utah State University, 2023

Major Professor: Dr. R. Justin DeRose
Department: Wildland Resources

Quaking aspen (*Populus tremuloides* Michx.) is a keystone species that, when coexisting with conifers (i.e., seral aspen), often undergoes stand-replacing disturbances to sustain long term vigor. Historically, mixed-to-high severity fire reduced fuels and regenerated aspen, but such disturbances have become less common in recent decades. This has often led to high fuel loading, and many seral aspen stands are at now risk of high-severity fire. The lack of a commercial market for aspen, and the risk of conducting prescribed fire, means there are few management options to regenerate aspen and reduce fuel loads. This has led to the development of a novel practice called roller-felling, a mechanical treatment method designed specifically to reduce fuel loading and restart succession of late seral-stage, now conifer-dominated, aspen communities. Further, such early successional aspen dominant communities are thought to mitigate fire spread across landscapes and near developed properties

This study assessed the short-term impacts (one- and two-year) of roller-felling on aspen regeneration and understory vegetation. We compared metrics of stand composition, structure, and aspen regeneration densities to determine treatment response. Roller-felling eliminated the overstory and resulted in prolific aspen suckering; this corresponded to changes in forb and shrub composition and ground covering of biotic functional groups. Decreased slash retention and/or scarification of mineral soil promoted aspen regeneration and higher densities of early-successional forbs. Greater slash retention and less machinery traffic reduced aspen regeneration and influenced understory composition, resulting in greater shrub cover and forbs species of mid- to late-successional status. Most early successional dynamics (e.g., greater aspen prior to disturbance or lessened slash retention promoting sucker densities) of aspen regeneration were observed, suggesting roller-felling acted as a stand-replacing disturbance and restarted succession. This study established a baseline for long-term monitoring of roller-felled areas, furthering the understanding early successional aspen ecology, which will have application to forest management regionally, where the goals are to reduce fire risk and maintain aspen communities across the western US.

(163 pages)

PUBLIC ABSTRACT

Regeneration of quaking aspen and understory vegetation change after fire risk reduction treatment

Allison M. Trudgeon

Quaking aspen (*Populus tremuloides* Michx.) is a keystone species that, when coexisting with conifers (i.e., seral aspen), often undergoes stand-replacing disturbances to sustain long term vigor. Historically, mixed-to-high severity fire reduced fuels and regenerated aspen, but such disturbances have become less common in recent decades. This has often led to high fuel loading, and many seral aspen stands are at now risk of an unpredictable, high-severity fire, posing a threat to development in the wildland-urban-interface. The lack of a commercial market for aspen, and the risk of conducting prescribed fire, means there are few alternate management options. This has led to the development of a novel method called roller-felling, a mechanical treatment designed specifically to reduce fuel loading and restart succession of late seral-stage, now conifer-dominated, aspen communities.

This study assessed the short-term impacts (one- and two-year) of roller-felling on aspen regeneration and understory vegetation. We compared metrics of stand composition, structure, and aspen regeneration densities to determine treatment response. Roller-felling eliminated the overstory and resulted in prolific aspen suckering; this corresponded to changes in forb and shrub composition and ground covering of biotic functional groups. Decreased slash retention and scarification of mineral soil promoted aspen regeneration and higher densities of early-successional forbs. Greater slash retention and less machinery traffic reduced aspen regeneration and influenced understory composition, resulting in greater shrub cover and forbs of mid- to late-successional status. Well-established dynamics (e.g., greater aspen prior to disturbance or lessened slash retention promoting sucker densities) of early-successional aspen regeneration were observed, suggesting roller-felling acted as a stand-replacing disturbance and restarted succession, effectively reducing the risk of high-severity fire. This study established a baseline for long-term monitoring of these areas, furthering the understanding early successional aspen ecology, which will have application to forest management regionally, where the goals are to reduce fire risk and promote aspen across western US.

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Allison M. Trudgeon

CONTENTS

LIST OF TABLES

Page

LIST OF FIGURES

Page

PREFACE

Because this thesis has been prepared in journal format, there is some redundancy between chapters. Chapters 2 and 3 will be submitted to peer-reviewed journals for publication in the near future. Each chapter has been or will be published with co-authors; as such, the pronoun “we” is used throughout the thesis.

CHAPTER I

INTRODUCTION

Quaking aspen (*Populus tremuloides* Michx.) is the most widespread broadleaf tree species in North America, coexisting with myriad understory and overstory associates, and supports a greater degree of biodiversity than their neighboring ecosystems (Little, 1971; Stohlgren et al, 1997; Chong et al, 2001; Kuhn et al, 2011). Historically, stand-replacing disturbances acted to reduce fuels and regenerate aspen, critical for community health and persistence. However, successful fire suppression efforts over the last several decades, coupled with a wetter climate, drastically reduced the occurrence high-severity fire in seral-aspen communities, resulting in a paucity of younger age classes on the western landscape (DeByle et al, 1987; Windmuller et al, 2021); many aspen stands are now at risk of high-severity fire due to increased fuel loading and climate change (e.g., warmer and drier conditions). Although fire remains a critical ecological process, alternate treatments may be needed if aging stands are in proximity to human development where high-severity fire is unfeasible. This perceived need for alternate treatments that regenerate aspen and reduce fire risk has led to development of a method called roller-felling.

Roller-felling involves pulling a large barrel drum connected via a chain or cable between two bulldozers. This could act as an alternative, more cost-efficient treatment to traditional silvicultural coppice regeneration system (i.e., clear-felling) or prescribed fire, that have similar stand-replacing objectives, (i.e., reset succession, regenerate aspen, or reduce fuel loading). Recently, roller-felling has been implemented in Utah, but the effect of treatment on total forest communities has yet to be quantified. Quantifying aspen regeneration is a common metric to determine treatment efficacy, but monitoring changes in understory composition provides another assessment of ecosystem condition. In this study, we assessed the short-term impacts (one- and two-year) of roller-felling on aspen regeneration and complementary changes in understory vegetation communities. This will provide insight into early successional dynamics of aspen communities post mechanical disturbance, with ramifications to forest management across the western US, where such a practice may be considered.

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CHAPTER II

REGENERATION OF QUAKING ASPEN AFTER FIRE RISK REDUCTION TREATMENT

Abstract

Quaking aspen (*Populus tremuloides* Michx.) is a keystone species throughout North America, valued for supporting increased vascular plant diversity and critical wildlife habitat. When coexisting with conifers (i.e., seral aspen), compositional shifts lead to decreased overstory aspen presence over time and stand-replacing disturbances are necessary to maintain aspen population health and persistence of this early-successional species. Mixed-to-high severity fires have traditionally reduced fuels and regenerated aspen, but with human intervention (e.g., fire suppression), such disturbances have become uncommon. This has led to large areas with little age class diversity and an abundance of fuels, and many seral aspen stands are overdue for stand-replacing disturbance. Limited treatments that regenerate aspen and reduce fuel loads remain available, due to the lack of a commercial market for aspen and the risk of conducting prescribed fire. This has led to the development of roller-felling, an alternative treatment developed specifically to reduce fuel loading and restart succession of late seral-stage aspen communities.

This study examined one component of post-disturbance forest recovery: short term (one- and two- year) aspen regeneration as a result of roller-felling. We compared metrics of stand composition, structure, and aspen regeneration densities to determine treatment impact. Roller-felling eliminated the overstory and resulted in prolific regeneration, while decreased slash retention, exposure of mineral soil, and less machinery traffic promoted higher stem densities. Regeneration was influenced by pre-treatment composition, but to a lesser extent than expected, and self-replacing densities were observed in areas with the low proportions of prior aspen. Our findings also suggest climate (e.g., precipitation in the year after treatment) can influence post-treatment regeneration success, and roller-felling may not unequivocally result in sufficient regeneration. When evaluating aspen's response to treatment as one metric of impact, we found roller-felling emulated aspects of stand-replacing disturbance (e.g., complete overstory removal) and restarted succession, as most well-established, early successional dynamics were observed during the short-term span of this study. Aspen's ability to recover in self-replacing densities after a mechanical disturbance of high severity, such as roller-felling, emphasizes this species' tolerance and resilience, contributing to greater understanding of this important early successional species in the Western US.

Introduction

Quaking aspen (*Populus tremuloides* Michx.) communities of North America are extensive and support a greater degree of biodiversity than their neighboring ecosystems (Little, 1971; Stohlgren et al, 1997; Chong et al, 2001; Kuhn et al, 2011). Our understanding of aspen's regeneration strategies, genetic diversity, and relationship with fire has improved within recent decades, challenging former assumptions about the ecology and management of this important species (Long and Mock, 2012; Kubitske et al, 2019; Kreider and Yocom, 2021a; 2021b). Historically, stand-replacing disturbances acted to reduce fuels and regenerate aspen, critical for community health and persistence. However, throughout the latter 20th century, successful fire suppression efforts (e.g., Grissino-Mayer and Swetnam, 2000) and a wetter climate (e.g., Millar et al, 2004) resulted in relative infrequency of such disturbances (i.e., high-severity fire) across the western US, including within seral aspen stands of late successional status that may have naturally burned (DeByle et al, 1987); conspicuous distribution of stand age on a landscape-level corroborates exclusion, as fewer stands were subject to stand-replacing during this time period (Windmuller et al, 2021). Recent climatic patterns (e.g., warmer and drier) conditions, combined with increased fuel loading via natural succession and fire suppression, have created conditions conducive for a high-severity fire in these communities (Pierce and Taylor, 2010; Strand et al, 2009; Kulakowski et al, 2013). However, with the expansion of urban interface into forested areas, critical fires that naturally restart succession become less feasible, and minimal alternatives that reduce fuel loading and regenerate aspen are available to landowners. Harvest is not feasible given the lack of a commercial market for aspen, and prescribed burns remain infrequent due to associated risk; the perceived need for alternate treatments that regenerate aspen and reduce fire risk has led to development of a method called roller-felling. In this study, we assessed the short-term impacts (one- and two-year) of roller-felling on post-treatment aspen regeneration and soil compaction.

Roller-felling involves pulling a large barrel drum between two bulldozers, connected via a large, industrial chain. The barrel elevates the cable so that it connects to standing trees at roughly breast height, thereby increasing the fulcrum at which the force of the cable is applied and decreasing the effort needed to topple the trees. This approach to toppling stands of aspen could serve as an alternative treatment to traditional silvicultural coppice (i.e., clear-felling) or prescribed fire, that have the similar objectives, (i.e., reset succession, regenerate aspen, or reduce fuel loading). Though such an active management alternative may be efficient, greater impacts to other forest components (e.g., soil structure and function) may result in undesirable outcomes. Recently, roller-felling has been implemented in Utah, but the effect of treatment has yet to be quantified. Understanding various impacts of roller-felling (e.g., soil compaction, residual slash density) on aspen regeneration will help determine the efficacy of treatment as an aspen regeneration technique, which could allow for informed application.

In the western US, aspen communities have been characterized as stable or seral, based on successional seres, geographic range, associated species, and historic disturbance regime (Rogers et al, 2014). Stable, or ‘pure,’ stands are occupied almost solely by aspen for multiple rotations. These stands have minimal overstory associates and are considered persistent, whereas seral stands are characterized by early aspen dominance, followed by conifer establishment in a classical successional sere (Rogers et al, 2014). Over time, more shade-tolerant conifer species, such as subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), Engelmann spruce (*Picea englemannii* Parry ex Engelm.), and Douglas fir (*Pseudotsuga menziesii* Franco) establish in the understory, and in the continued absence of disturbance, eventually outcompete aspen, resulting in a reduced percentage of aspen in the canopy.

The natural fire disturbance regime of seral aspen stands ranges from mixed- to high-severity (Shinneman et al, 2013); historic fire return data prior to European settlement suggested fire severity increased with higher conifer abundance, and decreased with higher aspen proportion (Morris et al, 2019). Fire suppression and wetter conditions during the last century have likely caused disturbance intervals to stray from their natural regimes, increasing fuel loads and abundance of more flammable conifers in many seral aspen stands (Strand et al, 2009; Pierce and Taylor, 2010; Shinneman et al, 2013; Millar et al, 2004). Although wildfire is a natural, critical process that promotes ecosystem health, the destructive and unpredictable nature of high-severity fire can be perceived as undesirable; continued fire exclusion will predictably result in increasing dominance of shade-tolerant conifers, increasing fuel loading and the probability of high-severity fire (Pierce and Taylor, 2010; Morris et al, 2019). Furthermore, in the prolonged absence of disturbance, the biodiversity and ecosystem function typically associated with aspen-dominated communities would decrease, as aspen become an increasingly minor component of the canopy

As an early successional species, quaking aspen easily dominates recently disturbed areas that have high light availability. Post-disturbance regeneration of aspen can be prolific, with upwards of 200,000 stems/ha having been reported (Peterson and Peterson, 1992), which is typically attributed to aspen's primary regeneration strategy of vegetative suckering. Resprouting of a genetically similar ramet (i.e., sucker) from a pre-existing aspen root system (i.e., suckering), allows aspen to quickly colonize disturbed areas, provided aspen was present prior to disturbance (Frey et al, 2011). Mature aspen stems produce suckers asexually throughout their life cycle, but the removal of aspen's main stem can stimulate a more robust response, as the interruption of auxin transport from leaves to roots stimulates suckering via intact root system (Frey et al, 2011; Wan et al, 2006). A secondary and less common regeneration strategy is the establishment of a new genet via sexual reproduction, which may be more frequent than formerly thought (Kreider and Yocom, 2021b; Kay 1993). Regardless of reproductive strategy, fire in seral aspen forests plays a rejuvenating role, creating conditions suitable for aspen establishment and persistence. However, where high-severity fire is not desirable from a management perspective, fuel reduction in seral aspen stands is a crucial management objective.

Management approaches to regenerating quaking aspen – a review

As development in wildland-urban-interface increases across the western US, treatments that reduce fuel loads and restart succession in late-stage, seral aspen stands have increased in popularity among land managers in an attempt to promote public safety and ecosystem health. Early successional aspen dominant communities are thought to mitigate fire spread across landscapes (Fechner and Barrows, 1976; Nesbit et al, 2023), making promotion especially desirable near developed areas. Although wildfire is the natural disturbance that promotes these communities, mixed-to-high severity fire is not always feasible, and alternate options for treatment are generally limited to prescribed fire or regeneration harvest.

Prescribed fires can create stand-replacing conditions resulting in aspen regeneration, but implementation in the Western US remains expensive, time consuming, and rare (Kolden, 2019). A primary concern among managers when conducting prescribed burns is maintaining control of the fire, which discourages application of higher severity burns that are challenging to manage (Ryan et al, 2013). Low-severity behavior is preferable, but costly fuel reduction treatments are often necessary to ensure this desired behavior in seral aspen stands, and without manipulation prior to burning, stands may amplify to crown fires (Shepperd, 2001). Social sentiment towards this management technique remains unsavory (e.g., Weir et al, 2019) due to inaccurate perception of increased danger (e.g., Twidwell et al, 2015), and is further perpetuated by infrequent prescribed burns that escape boundaries (e.g., Hermit's Peak Fire) and destroy human infrastructure. The seasonal window for prescribed burning has become more stringent in an attempt to mitigate this perceived risk, making implementation more challenging and increasingly rare (Quinn-Davidson and Varner, 2009; Twidwell et al, 2015; Kolden 2019).

The silvicultural treatment of aspen via the coppice system is a well-documented (e.g., Bartos and Mueggler, 1982; Sheppard, 1996) and reliable strategy to regenerate aspen that has the added benefit of reducing overstory fuels. This technique requires both established road infrastructure and a market demand for aspen, both of which are nonexistent in many regions across the western US. Furthermore, if an aspen regeneration harvest were implemented to reduce fuels, treatment of slash would likely be necessary to achieve additional fuels reduction.

In addition to typical fuel reduction treatments, less common techniques have been explored. Variations of bulldozing treatments (under different pseudonyms) have been applied with the objective of regenerating aspen and have been employed in a variety of management contexts. In 1973, the practice of "shearing," or cutting mature aspen stands with a sharp blade mounted to a tractor, was implemented in Wisconsin, with the intent of regenerating aspen and resulted in high sucker density, even in stands with minimal aspen prior (Perala, 1972). This same process, termed bulldozer "shearblading" in the 1990s, was employed in interior Alaska to reduce fire risk and promote wildlife habitat, which elicited aspen regeneration densities similar to adjacent harvested areas (Paragi and Haggstrom, 2007).

Scarification by heavy machinery can modify aspen regeneration by altering soil water holding capacity or reducing vegetative competition (Bella, 1989; Lavertu et al, 1994; Powers, 1999). Light damage to root systems via mechanical site preparation increased sucker densities following harvest, while severe damage reduced suckering (Fraser et al, 2003). For this reason, harsh site preparation techniques (e.g., "double-disking" per Ehrentraut and Branter, 1990; or "drum chopping" per Peltzer et al, 2000) were developed to excessively damage or fragment aspen root systems to reduce suckering, which typically resulted in lower densities. However, aspen have a high tolerance of root disturbance and damage; moderate soil disturbance or root damage can also stimulate a greater suckering response (Frey et al, 2011).

Soil disturbance via bulldozer has been explicitly linked to greater post-harvest suckering per Shepperd (1996). When mature trees were tipped over above the root collar with a bulldozer, which exposed bare soil where larger roots closer to the bole were established, higher aspen densities were observed than when traditional harvest was applied, consisting of cutting trees with a chainsaw above the bole and leaving soil undisturbed. However, excessive machinery traffic during logging operations reduces regeneration, and the negative relationship between increased soil compaction and decreased suckering density remains well-established (Navratil, 1991; Shepperd, 1993; Frey et al, 2011).

Recently, roller-felling has been applied on private land in Utah with the paired goals of regenerating aspen to increase wildlife habitat and reducing fuel loads. This treatment involves pulling a large barrel drum attached via cable between two, parallel bulldozers, after an initial cutline has been bulldozed around the pre-defined treatment unit. The roller is positioned centrally between the cables and suspended roughly ~1 m above the ground, giving the cable leverage to effectively topple trees. The felled trees are then windrowed, cured for several years, and subsequently pile-burned. This method allows for varying amounts of residual slash to be retained in treated areas for different management objectives. Roller-felling may prove to be more efficient than alternative treatments, given the amount of area the apparatus covers in a single operation.

Determinates of aspen regeneration

Aspen regeneration, regardless of disturbance type, is highly dependent on pre-disturbance species composition. Various metrics of aspen composition have been found to be correlated with greater regeneration densities (Graham et al, 1963; Frey et al, 2011; King and Landhäusser, 2018; Jean et al, 2019). Aspen basal area (total and percentage), overstory density (trees per hectare), and advance regeneration (e.g., <10 cm DBH) prior to treatment have been shown to positively influence regeneration (Smith et al, 2011; Frey et al, 2011; Britton et al, 2016). Conversely, the percent and absolute basal area occupied by conifer was observed to decrease regeneration potential (Smith et al, 2011; Margolis and Farris, 2014; Krasnow and Stephens, 2015; Clement et al, 2019). Time since disturbance (i.e., establishment) impacts regeneration not only via compositional species shifts, but regeneration potential fluctuates with age: maximum suckering potential occurs when aspen stems are ~ 20 years of age and can decline after stems reach > 80 years, and interconnected root systems break up and decay as stands age (Peterson and Peterson, 1992).

Establishment and survival of aspen after disturbance is contingent on edaphic and topographic variables. At higher elevations, warmer, southern facing areas are beneficial to establishment while northern facing sites favor aspen at lower elevations due to moisture holding capacity (Smith et al, 2011; Harvey et al, 2016; McIlroy and Shinneman, 2020). Although slope steepness is often associated with soil instability, greater post-disturbance aspen densities have been observed on steeper slopes (Johnston, 2001). Additionally, past studies indicate topography exerts only a weak influence on regeneration (Rogers et al, 2010; Smith et al, 2011); this relationship is complex and can vary on a site-specific basis, further complicated by aspen's extensive range.

Competition between aspen and other functional vegetation groups also affects early stem densities. Increased grass and shrub cover reduced regeneration after both harvest and fire (Peterson and Peterson, 1992; Landhäusser and Lieffers, 1998; Jean et al, 2020), and grass competition on scarified sites was correlated to reductions in aspen growth (Navratil, 1991; Landhausser and Lieffers, 1998; Bockstette et al, 2017). Large increases in shrub abundance after clear-cutting have been observed in aspen stands (Bartos and Mueggler, 1982), and summer harvesting has been specifically recommended to reduce shrub competition (Bella, 1989).

Ungulate browse is a common biotic agent of mortality in early succession, as reductions in stem densities and biomass are well known to correspond with greater ungulate densities, frequently resulting in severe understocking (Kaye et al, 2005; Rogers and Mittanck, 2014). Nutrient-dense apical meristems of young aspen suckers are browsed by a variety of ungulates throughout the growing season, the most common species of concern being Rocky Mountain Elk, (*Cervus elaphus*, L.), and to a lesser extent, Mule deer *(Odocoileus hemionus hemionus;* State of Utah, 2022). Sustainable thresholds of herbivory vary based on location and management objective, but a coarse maximum of 30% meristem removal via ungulate browse has been suggested as indicative of unsuccessful recruitment (Olmsted 1979; Rogers et al, 2014). Prior studies in this area suggest browse levels by both elk and cattle habitually exceed sustainable levels in mature aspen stands, leading to inadequate recruitment (Rogers and Mittanck, 2014). Reductions in ungulate browse are associated with intentional post-logging herbivore barriers, such as slash piles, fencing, “hinged” residual trees, and scattered coarse woody debris acting are well-documented (Grisez, 1960; Rumble et al, 1996; Larsen and Ripple, 2001; Kota and Bartos, 2010).

Although slash retention can promote regeneration by deterring browse, the increased shade and decreased surface area associated with slash can reduce suckering potential and negatively impact regeneration (Doucet, 1989; Shepperd, 1996, 2001; Paragi and Haggstrom, 2007). Increased slash can facilitate less favorable growing conditions for young aspen suckers, as the substrate beneath dense woody debris is subject to fewer growing degree days; this colder microclimate can also reduce juvenile growth rates by limiting water uptake (Landhausser and Leiffers, 1998; Wan et al, 2009). Nonetheless, a moderate amount of slash on the landscape doesn’t necessarily suppress a vigorous suckering response, and self-replacing densities among post-harvest slash is not uncommon (Shepperd, 1996, 2001).

The short-term (i.e., one- and two-year) effects of roller-felling on aspen regeneration was explored in this study; we compared metrics of stand composition, structure, and aspen regeneration densities to determine treatment impact. Broadly, high sucker densities were predicted following treatment, and well-established metrics of increased understory and overstory pre-treatment aspen (e.g., basal area, density) were expected to correlate with greater regeneration. We anticipated lower regeneration with increasing aspen age due to a reduction of suckering potential and via successional species shifts (i.e., increased conifer basal area). Increased shrub, forb, and grass ground cover after treatment was expected to reduce regeneration due to competitive mortality. Increased residual slash was hypothesized to decrease stem densities but deter ungulate browse, while overall levels of browse were predicted to exceed sustainable thresholds. A gradient of bulldozer traffic was present across the study, and areas subject to increased movement (i.e., initial bulldozer cutlines established at the beginning of the roller-felling process) were hypothesized to be more compacted and exhibit lower regeneration. Many mechanisms of soil disturbance were at play throughout the process of roller-felling, and it is unclear how and to what degree this will impact regeneration.

In this study, we determined the initial response of aspen to roller-felling and its associated attributes (i.e., increased soil disturbance), contributing to our understanding of aspen's resilience to severe disturbance and controls of early successional processes. Comparison of pre- and post-treatment metrics, along with differences across treated areas (e.g., slash), allowed for a conservative quantification of impact. Ultimately, most early successional dynamics of aspen regeneration were predicted to hold; if early succession follows a similar trajectory to other disturbances, this could indicate roller-felling has a similar effect on aspen, allowing for conservative assumptions that later successional dynamics may apply in this context as well.

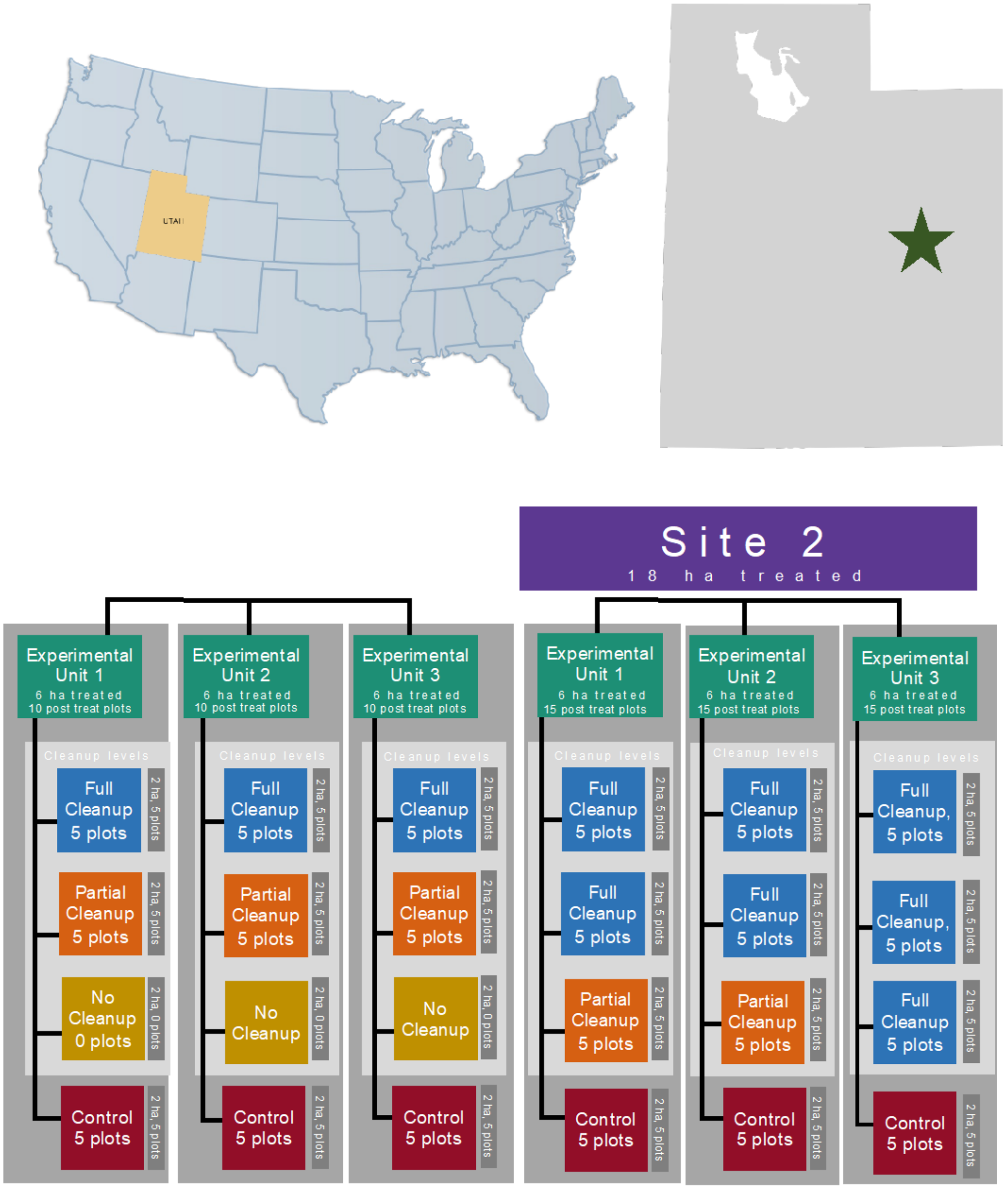
Methods

Study area

The Tavaputs Plateau in east-central Utah, USA, is a remote portion of the

Colorado Plateau, comprised of state, federal, and private land (Figure 1). This study included two sites located on private land: Site 1 (39.57, -110.26) was located roughly 15 km northwest of Site 2 (39.70, -110.37). Elevation at both sites was comparable and spanned a gradient of 2500 to 3040 m A.S.L. (above sea level). Thirty-year mean annual temperature for the study area was 4.7 ºC, with large variation by season: 30-year mean July temperature was 17.9 ºC, while January was 4.9 ºC (PRISM Climate Group, 2022). Annual precipitation in this area averaged 564 mm and exhibited a bimodal distribution, with winter and summer precipitation peaks. Synoptic weather patterns in this region are driven by westerly storm tracks, with summer precipitation delivered by the North America Monsoon (Mock, 1996).

Figure 1: Overview of experimental design; site 1 was treated in 2020 and site 2 was in 2022. Each site contained three units, consisting of three treatment blocks. Untreated areas, adjacent to the six units, were monitored for the duration of the study.



Soil types on wetter, north-facing slopes were primarily characterized as Mollisols, specifically Cryoborrols, followed by Inceptisols, and Andisols, while soil types on drier, south-facing slopes were largely categorized as calcareous Entisols (Web Soil Survey, 2022). However, soil types generally correlated to aspect, due to solar radiation and associated vegetation. Vegetation types in this area consisted of pure and seral aspen communities, mixed conifer, and sagebrush (*Artemisia* spp.) communities (McNab et al, 2007; Rogers et al, 2014). These vegetation types largely corresponded with aspect; seral aspen stands corresponded broadly to north-facing slopes with increased moisture holding capacity, while sagebrush communities were more common on drier, south-facing slopes. Study units at both sites coarsely favored north-facing aspects due to the treatment focus on mature, seral aspen stands (Table 1) and slopes were generally moderate, averaging 15% across both sites.

Table 1: Site and composition of stands prior to treatment. * indicates significant differences between treatment levels. Note a reduced sample size for aspen age and site index *n*; 39 of 75 plots contained no suitable aspen for age determination. Conifers were cored at the remaining 36 plots.

Site Characteristics					
	n	Mean	± S.D.	Range minimum	Range maximum
Elevation (m)	75	2906	46	2825	2991
Slope (%)	75	16	12	0	53
Aspect	75	N - NW	NA	NA	NA
Composition prior to treatment					
Total Basal Area (m^2/ha)	75	35	16	9	76
Aspen Basal Area (m^2/ha)	75	17	14	0	60
Conifer Basal Area (m^2/ha)	75	18	11	0	52
Aspen % of Basal Area	75	46	30	0	100
Dead Standing Aspen (m^2/ha)	75	3	4.5	0	20
Overstory aspen stems (trees per hectare, TPH)	75	120	133	0	843
Understory fuel loading (Mg/ha)	75	27	15	0.5	68
Total biomass (all overstory and understory, Mg/ha)	75	86	23	28	140
Aspen quadratic mean diameter (cm)	75	38	26	0	107
Aspen Age	39	131	43	61	223
Aspen Site Index	39	49	9	30	69
Composition 1 year after treatment					
Residual slash (Mg/ha) *	75	17	14	1.6	56.6
Ground covering % soil *	75	43.9	21.4	0.8	85.5
Ground covering % grass	75	1.6	1.8	0	7.3
Ground covering % forb	75	6.6	6.3	0	33.3
Ground covering % shrub *	75	2.0	3.5	0	22.5
Ground covering % coarse woody debris *	75	18.7	15.9	2.2	87.2
Aspen stems per hectare*	75	52,667	51,659	0	237,000

Tree species composition was dominated by aspen and subalpine fir, with minor overstory associates of Engelmann spruce and Douglas-fir in stands of later successional stages. Prior to roller-felling, overstory vegetation in these sites was generally unmanaged and characterized as late-stage, seral aspen stands (*sensu* Rogers et al, 2014), and characterized by very high surface fuel loadings (26.9-46.3 Mg/ha, across all size classes) and total biomass loading (i.e., all live and dead overstory combined with surface fuel) that averaged 86 Mg/ha (Table 1). Sites were similar in potential productivity (aspen site indices 47 to 51, Edminster et al, 1985) and comprised of units that spanned a late-stage, successional gradient with varying proportions of aspen and conifer, primarily subalpine fir (Table 1). Basal areas averaged 30 m^2/hectare across all treated units and aspen as a percent of basal area was similar at both sites and averaged 17 m^2/ha^{-1}. No overstory management had been employed at either site within the recent past.

Available wildlife population estimates from the State of Utah were aggregated over the area surrounding both study sites (215,000-hectare management unit); however, differing ungulate densities between sites were empirically detected (see below). Available estimates of elk density across the management area were 2,100 in both 2020 and 2021, and deer populations were estimated at 6,800 in 2020 and 6,500 during 2021. Additionally, wildlife management objectives between sites differed: site 1 maintained intentionally higher densities of elk and deer for recreational hunting, and minimal (< 50 across ~80,000 ha) domestic cattle. Management objectives at site 2 had no focus on fostering increased elk populations and contained greater densities of domestic cattle. To verify the state's coarse population estimates and get finer estimates of ungulates at each site, pellet counts, delineated by species, and browse levels were included in protocol before and after treatment (see below).

Study design

To capture the impact of roller-felling, we employed a triplicate, variable treatment design (Figures 1 and 2), sampled across two sites and growing seasons. Site 1 was treated in September 2020 and monitored for two growing seasons after treatment. Site 1 contained three experimental units, located within 3 km of each other (Figure 1). A total of 18 hectares, split among the three experimental units, were treated with a variable cleanup design. Each 6-hectare, experimental unit contained three, 2-hectare blocks, adjacent to one another, consisting of gradient densities of residual slash (Figure 1). Three, coarse cleanup levels were applied: 1) all slash pushed into a burn pile (full or total cleanup), 2) moderate residual densities of slash, with majority of slash pushed into burn pile (partial cleanup), and 3) no residual slash pushed into burn piles (no cleanup, Figure 2). Residual slash densities varied by cleanup level: full cleanup averaged roughly 9 Mg/ha outside of slash piles and 37 Mg/ha in partial cleanup areas (Figure 2). Additionally, the area occupied by slash pile varied cleanup level: slash piles averaged 17% of ground area in full cleanup areas and 11% in partial cleanup areas. Adjacent to treated units, 2-hectare, untreated, control areas were monitored for the duration of study. Site 1 was monitored for two years post-treatment (Figures 1 and 2).

Figure 2: Sampling design at each unit. Pink circles represent post-treatment sampling plots: five were collected in full cleanup areas (blue), five in partial (orange), and five in untreated areas (red). Plots at site 2 were not monumented and surveyed once in the year after treatment. At site 1, plots were monumented and measured for two years. In the second sampling season, five plots per unit were added in bulldozer cutlines (green perimeters), indicated by black circles. At site 1, three exclosures were constructed (yellow squares) in each full, partial, and untreated area, for a total of nine per unit.

Similar to Site 1, a total of 18 hectares was treated with a variable treatment design at site 2, and contained three experimental units within 1.5 km of each other. Site 2 was treated in July 2021 and monitored for one growing season after treatment. Each 6-hectare experimental unit was intended to be treated identical to site 1, with three adjacent blocks of gradient densities of residual slash. However, this design was not implemented as intended (Figure 2). Due to landowner preference, the three no cleanup areas were omitted. Additionally, one of the three experimental units was uniformly treated with full cleanup, omitting the partial cleanup area, due to concerns of slope steepness. The remaining two units were treated with two blocks as full cleanup and one partial cleanup. At site 2, a total of 14 hectares had full cleanup applied, while 4 hectares had partial cleanup applied (Figure 2). Three untreated, 2-hectare control areas were established near each experimental unit and monitored for the duration of study (Figures 1 and 2). Site 2 was monitored for one year after treatment.

Across both sites, 36 total hectares were roller-felled in 2020 and 2021 with this variable treatment design: 20 hectares with full cleanup, 10 with partial, and 6 hectares were treated with no cleanup. Sites had 18 hectares treated each, but disparity between treatment cleanup levels were present between and across sites. Site 1 contained equal proportions of full, partial and no cleanup areas, each 6 hectares. Site 2 contained disproportionate treatment areas: 20 hectares treated with full cleanup, 10 with partial, and 0 hectares with no cleanup (Figure 1).

Sampling methods and plot design

Prior to treatment, units at both sites were surveyed to quantify pre-treatment stand composition and forest characteristics. Pre-treatment data collection consisted of five, variable radius sampling plots within each cleanup area block and the adjacent untreated control area, for a total of 20 plots per experimental unit, and 120 plots across both sites (Figure 2). Plots were independent and spaced at a minimum of 45 meters apart to ensure no overlap and characterize the entirety of units. Basic plot-level attributes of elevation, slope, and aspect and fuel model, along with photos, were collected at each plot. To quantify stand structure and composition, a 4-m basal area factor prism was used to sample overstory trees, indicated by a diameter at breast height (DBH) of 10 cm or greater. At each plot, DBH, status of live or dead, and species of every overstory tree was recorded. The total tree height and height to crown base was measured for every other tree and the tallest tree was cored for site index determination. Pre-treatment overstory data was collected at five plots within each treatment block; compositional means were calculated for each of the 15 treatment blocks to determine various metrics of pre-treatment composition.

At the center of the variable radius plot, a fixed-area, nested understory plot of 1/1000th hectare (1.78m radius) measured seedlings and saplings less than 10 cm DBH. This subplot quantified advance regeneration, and understory trees were identified to species. The extent of wildlife browse was quantified by noting the number understory aspen stems with intact apical meristems (i.e., removal via browse by ungulate). To determine residual slash density, two standard Brown's transects were established at each plot, originating at plot center (Brown, 1974). The first transect extended 22.86 m (75 feet) at a 0-degree (North) azimuth, while the second transect was generated randomly by spinning the compass. Duff and litter measurements were collected at two locations along each transect, at 13.71 m (45 feet) and at the 22.86 m terminus. Understory fuel loading by size class was quantified along both transects and delineated by 1-hour (<0.6 cm), 10-hour (0.6 to 2.5 cm), 100-hour (2.5 to 7.6 cm), and 1000-hour (>7.62 cm) fuel classes. Along these transects, 10 overstory canopy densitometer readings were collected in meter increments, defined as canopy cover of aspen, conifer, both, or open/no cover.

Six ocular ground covering estimates were collected at each plot, with three estimates of 1m^2 quadrat covering along the two transects. Each quadrat survey was taken on the right side of transects at approximately 6.1 m (20 ft), 12.2 (40 ft), and 18.3 (60 ft) from plot center. Ground cover types were split into eight categories and the percentage of each functional plant group (biotic: grass, forb, shrub, and tree) and abiotic cover (bare soil, rock, litter, and coarse woody debris) was estimated. The area within these quadrats was surveyed for fecal pellets; if present, type was noted (e.g., deer, elk) and pellets were counted. Pellet counts were expanded to represent conditions on a hectare basis for analytical purposes. Pre-treatment ungulate use (i.e., pellet density), understory composition, and fuel loading data was collected for five plots per treatment block.

To determine the effect of ungulate herbivory on regeneration, permanent exclosures were constructed at site 1 in the three experimental units treated in 2020; construction began early in the 2021 growing season, prior to any response to treatment. This allowed for observation of regenerative growth and response to treatment across two full growing seasons. No browse exclosures were constructed at site 2. A total of 27 exclosures, each 1.22 m^2 in area, were constructed across all experimental units at site 1 (Figure 2, yellow squares). Each unit contained nine exclosures: three exclosures per area in partial and total cleanup treatment areas, along with adjacent control areas. The no cleanup treatment area was omitted for exclosure construction and subsequent sampling, as extremely high slash levels restricted access. Exclosures were created with 4-foot-tall T-posts and cattle fencing to restrict browse from ungulates. However, this coarse cattle fencing allowed for entry of smaller mammals and rodents. Exclosures were surveyed at the end of the 2022 field season and the entirety of each exclosure was sampled; ground cover percentages were estimated and delineated by eight categories: four functional plant types of grass, forb, shrub, tree, and four abiotic cover types of bare soil, litter, rock, and coarse woody debris (> 0.6 cm in diameter).

Regeneration data was collected for two years after treatment at site 1. Sampling took place in mid-August of 2021 and 2022, towards the end of the growing season to allow for adequate regeneration. Forty-five sampling points were monumented with rebar at site 1 in 2021 (Figure 2). Five sampling points were established per 2-hectare treatment: five in full cleanup, five partial cleanup treatments, and five within the adjacent control (Figure 2). A total of 15 plots per experimental unit were surveyed, as the no-cleanup treatment was omitted due to high slash levels that restricted sampling access. Post-treatment plots did not intersect slash piles and were stratified across the unit, ensuring adequate coverage within each treatment area. Fixed area (1/1000th ha) plots determined regeneration stem density. Understory trees were counted, identified to species, and broken up by height classes. Regeneration < 1 m was considered height class 1, and stems > 1 m were classified in height class 2. Browse was quantified by noting the number understory aspen stems with intact apical meristems (i.e., removal via browse by ungulate). Two standard Brown's transects, oriented at north and a random azimuth, were established at plot center (Brown, 1974). Transects captured slash loading, duff and litter depth, pellet counts, and functional plant group percentages, in the same design as pre-treatment plots. Residual slash densities within treatment areas were extrapolated from this point-count-intersect data collected along the two transects. A total of 30 plots in six treatment blocks were measured across site 1 in the first growing season after treatment and distributed equally, with 15 plots in the three full cleanup treatment areas and 15 plots in three partial treatment areas (Figure 2, pink circles).

At site 2, post-treatment regeneration data was collected in mid-August of 2022. Sixty plots were surveyed across treated areas and adjacent controls at the three experimental units (Figure 1) for a single growing season after treatment. Site 2 treatment design omitted the no cleanup areas and were replaced with full cleanup treatment. Regardless, experimental units were still divided into three cleanup areas and five plots were sampled within each 2-hectare area (Figure 2). Regeneration data from a total of 35 plots was collected across seven full cleanup and two partial cleanup treatment areas. Adjacent, untreated control areas were also sampled with five plots after treatment. Plots did not intersect slash piles and were stratified to ensure adequate coverage within each treatment area. Sampling protocol at site 2 was identical to site 1, but plot centers were not monumented. A total of 45 plots in treated areas were measured across site 2 in the first growing season: 35 in full cleanup areas and 10 in partial areas.

In the one-year post-treatment regeneration sampling there was a disparity of plots between treatment levels and sites. Of the 75 plots, 30 of 75 (40%) were at site 1, and 45 of 75 (60%) were at site 2. At site 1, 50% of plots (15 of 30) were sampled in partial and 50% in full cleanup areas, while at site 2, 22% of plots (10 of 45) were in partial cleanup areas and 78% (35 of 45) in full treatment areas. Of the 75 post-treatment plots sampled across both sites one year after roller-felling, 67% (50 of 75) were in full cleanup and

33% (25 of 75) in partial cleanup areas.

At site 1, regeneration data was collected for a second growing season in mid-August of 2022, two years after treatment. Monumented plots were revisited and surveyed with protocol identical to the previous growing season. A total of 30 monumented plots in treated areas were resampled: 15 in full cleanup areas and 15 in partial cleanup areas. Adjacent control areas were also revisited, and five plots were surveyed per unit.

During this second season of sampling at site 1, an additional 15 plots were surveyed using the post-treatment protocol, but outside the treatment areas in the initial bulldozer cutlines created on the outer perimeter of treatment areas (Figure 2, black points). Initial cutlines were assumed to be subjected to increased bulldozer traffic throughout the roller-felling process and were assessed to determine the influence that repeated movement of heavy machinery might have on regeneration via soil compaction. We collected soil samples to quantify soil bulk density, as a proxy for soil compaction. Two soil samples were taken at each of 15 plots within the bulldozer cutline. These two vertical soil core samples were collected at a depth of 10 cm from mineral surface; samples were 2.5 cm in width, for a total of 196 cm^3 in volume. Cores were extracted at approximately 2 m from plot center along the two fuels transects and soil core contents were placed in doubled paper bags. In this second sampling season, one soil sample was extracted from each monumented plot in full, partial, and control areas. This single core was taken approximately 2 m from plot center along the established north transect. A total of 30 soil core samples were collected from treated areas: 15 in full cleanup areas and 15 in partial, Fifteen cores were extracted from adjacent control areas. In total, 75 soil cores were collected across site 1: 30 in bulldozer cutlines, 15 in full cleanup, 15 in partial cleanup, and 15 in adjacent control areas. Samples were oven-dried at 105 ºC for two hours and then weighed to determine oven dry weight. Soil bulk density was calculated for each individual sample by dividing the core volume (180 cm^3) by the oven dry weight.

Analytical approach

A regression modeling approach was used to investigate possible variables that influenced aspen regeneration densities after roller-felling. In addition to factors of site, unit, and treatment level, a suite of hypothesized predictor variables were calculated from the pre-treatment overstory data and post-treatment data (Table 1). Because pre- and post-treatment plots (n = 75) were not spatially relocated, any predictor variables measured prior to treatment were averaged at the treatment block level (n = 15). A conservative, correlation analysis was performed at the treatment block level (n = 15) using Spearman's correlation coefficients to determine the possible influence, and direction, of explanatory variables (Table 1) on regeneration densities. Non-linear regression was used to characterize the relationship between regeneration and residual slash.

We further compared site and treatment levels individually using t-tests and F-tests. Full (n = 50) and partial (n = 25) treatment area regeneration densities were compared, and differences between site 1 (n = 30) and site 2 (n = 45) were assessed. Additionally, regeneration of the same treatment level was evaluated between sites: full cleanup at site 1 (n =15) was compared to site 2 (n = 35) and densities at partial cleanup of site 1 (n = 15) were assessed against site 2 (n = 10).

At site 1, changes in regeneration density and ungulate browsing effects were explored from year one to two. We used paired t-tests to determine if changes were equal between treatment levels and compared levels of ungulate browse outside and within exclosures. Residual slash, percent ground covering, and soil bulk density were compared by treatment level using t and F tests. ANOVA tests were used to explore differences in stem densities and treatment attributes across experimental units and by unique site/year x treatment level groups.

Linear regression was employed to determine if residual slash levels acted as a deterrent to ungulate browsing; browse percentages were compared by site and treatment level using t-tests. Densities of stems in height class 2 within exclosures were compared against regeneration outside of exclosures in full and partial cleanup areas.

All analyses were performed using R statistical software (RStudio team, 2020). Data manipulation utilized the *dplyr* and related *tidyverse* packages (Wickham et al, 2019), and non-linear modeling included the *aomisc* (Onofri, 2020) and *nlme* (Pinheiro, 2022) packages. Graphics were generated with the *ggplot2* package (Wickham et al, 2019).

Results

One year post treatment

Influences on regeneration densities

Aspen regenerated in relatively high densities one year after treatment. Approximately 92% of plots (69 of 75) had one or more stems present. Regeneration was highly variable across all sites and treatment levels, with a mean 52,000 stems/ha.

Distribution of regeneration was positively skewed: half of all plots did not exceed 35,000 stems/ha, and the fourth quartile range spanned 81,000 to 237,000 stems/ha.

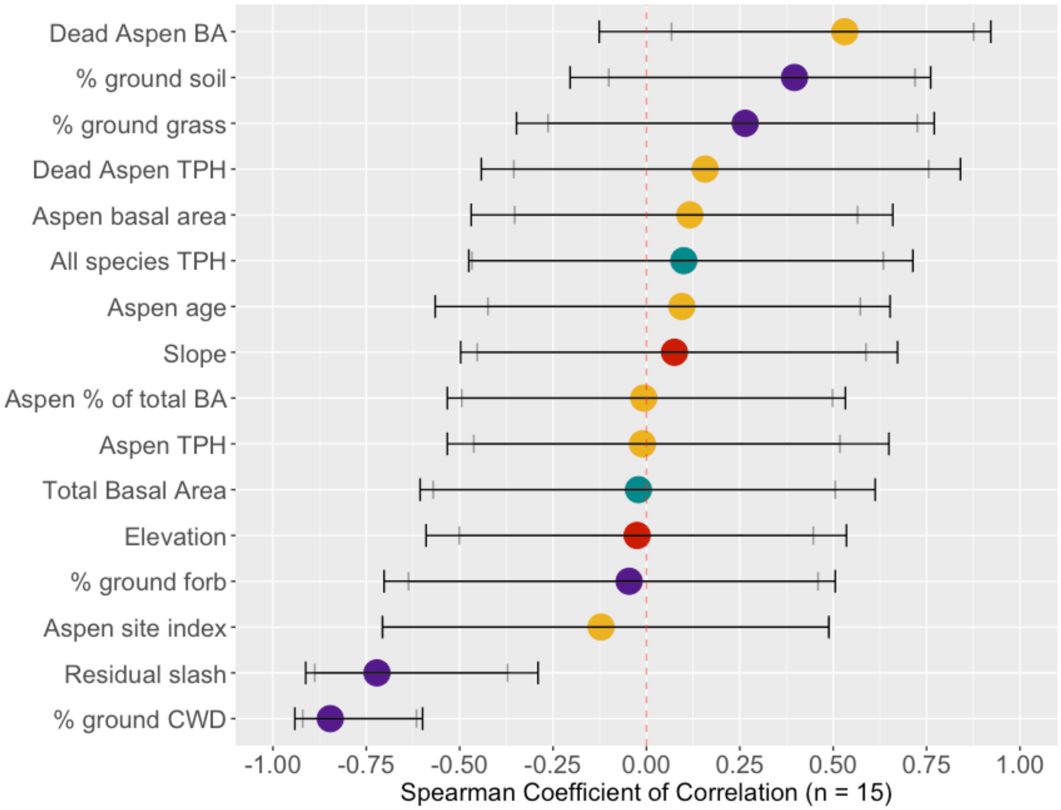
In the strongest model tested, treatment level, site, and pre-treatment overstory aspen density exerted the greatest influence on regeneration and explained 23% of variation in stem densities (Table 2). Of these variables, treatment level exhibited the strongest correlation, with significantly lower regeneration observed in partial cleanup areas ($p < 0.001$). A weaker correlation was observed for site, where site 1 exhibited higher regeneration ($p < 0.05$). A positive relationship between overstory aspen density and regeneration was also found to be significant ($p < 0.05$). Although residual slash decreased regeneration, this correlation was only marginally significant ($p = 0.096$).

Table 2: Summary of multiple linear model explaining the contribution of predictor variables to aspen regeneration (stems/ha). Significant predictor variables are noted in bold and * denotes a two-factor variable. Partial cleanup treatment was negatively correlated, and site 1 was positively correlated to regeneration.

Independent variable	Coefficient	Standard Error	*t*	*p*
Treatment level *	-52,017	31,474	-3.309	**0.002**
Site *	62,948	15,718	2.000	**0.049**
Aspen trees per hectare	314	163	1.917	**0.059**
Residual slash (Mg/ha)	-434	516	-0.842	0.403

Dead aspen basal area exhibited the strongest positive correlation to regeneration ($r = 0.53$, Figure 3), although this relationship was marginally significant at $p < 0.10$. No other variables that characterized pre-treatment stands were strongly correlated to regeneration densities (Figure 3). The strongest relationship observed was the negative correlation between residual slash and regeneration (r = 0.72, Figure 3). Percent coarse woody debris was also significantly correlated to regeneration (r = 0.85), but highly covaried with residual slash (r = 0.86).

Figure 3: Selected independent variables and their correlation to aspen regeneration, indicated by Spearman rank coefficients. The red dashed line indicates no correlation: greater distance from 0 represents stronger correlation. Colored points closer to 1 indicate positive correlation, and values closer to -1 indicate negative correlation. Color represents the type of variable: yellow corresponds to metrics of pre-treatment aspen, blue corresponds aspen and conifer composition, red corresponds to topographic variables, and purple corresponds to post-treatment variables. Smaller gray bars indicate the 90% confidence intervals, and outer black bars represent 95% confidence intervals.

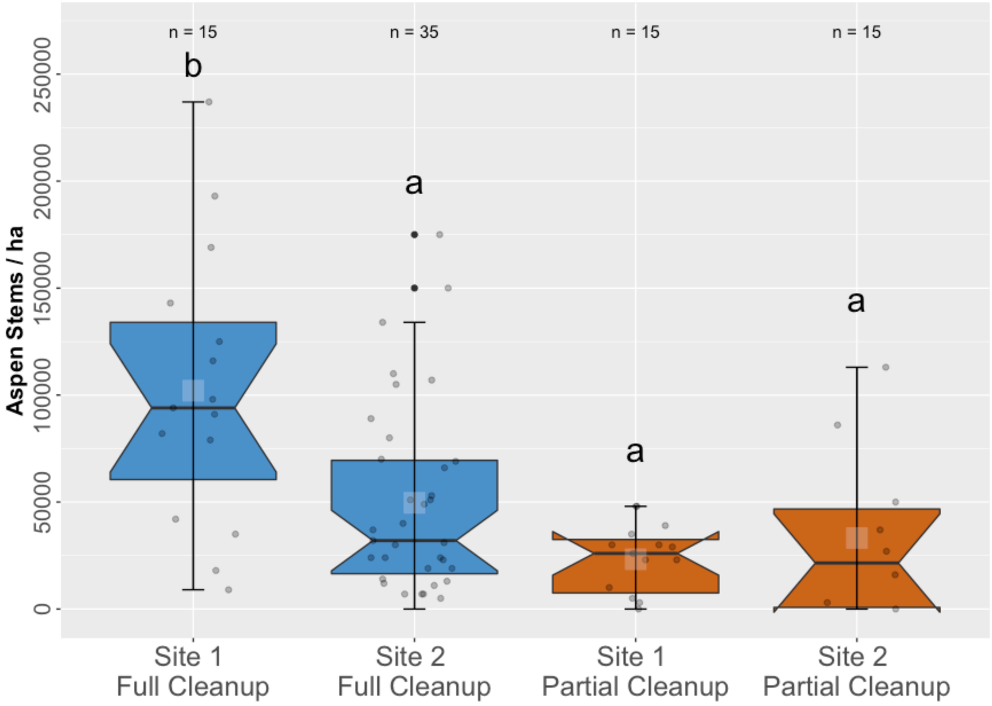


Site and treatment level effect on regeneration

Site and treatment level differences existed in aspen regeneration (Figure 4).

When assessed as four separate groups, mean regeneration density of site 1 full cleanup areas was significantly greater ($p < 0.001$) and more variable than the other three groups. Regeneration of partial cleanup areas at site 1, full cleanup areas at site 2, and partial cleanup areas at site 2 were not significantly different from one another.

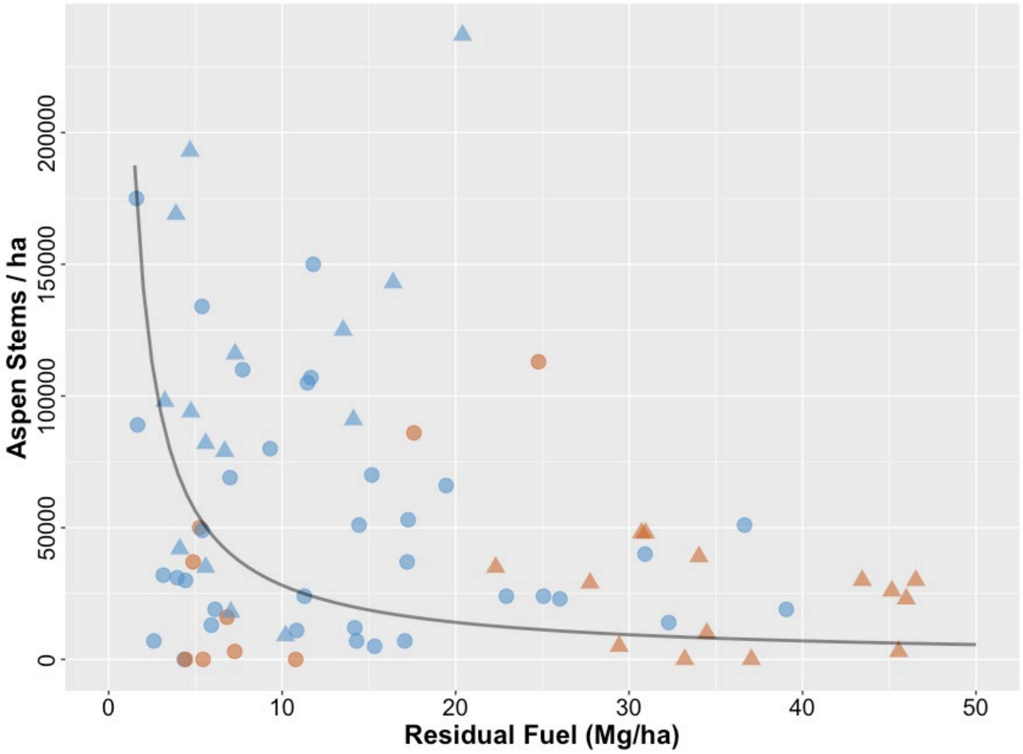
Figure 4: Regeneration one year after treatment, separated by site and treatment level. Full cleanup areas are represented in blue and partial in orange. Significant differences are indicated by lack of overlap within notches and different letters above boxplots. Transparent white boxes represent mean density of respective groups.



Mean stem density within full cleanup areas at site 1 was 102,000 stems/ha, approximately double than that of site 2 (~ 50,000 stems/ha). Partial cleanup areas at site 1 and 2 exhibited similar regeneration, with means 23,000 stems/ha and 32,000 stems/ha, respectively. Site 2 exhibited greater variability ($p < 0.001$) in partial areas, ranging from 0 to 113,000 stems/ha, while site 1 densities ranged from 0 to 48,000 stems/ha. When full and partial treatment areas were aggregated, greater regeneration was observed at site 1, with a mean density 63,000 stems/ha, and 46,000 stems/ha at site 2. This difference was not significant, although site 1 exhibited greater variability ($p < 0.05$).

A negative exponential relationship between regeneration densities and residual slash was observed (Figure 5). Plots with greater than 25 Mg/ha in residual slash never exceeded 50,000 stems/hectare, whereas plot with lower amounts of residual slash were substantially more variable, regardless of site or treatment level.

Figure 5: Relationship between regeneration and residual slash, shown by the gray line: stems ~ $1/(3.554e^{-06}$*Mg/ha). Plots in full cleanup areas are represented by blue points, and partial cleanup in orange. Triangle points indicate site 1 plots, and circles indicate site 2.



Ungulate browse effect on regeneration

One year after treatment, ungulate browse was observed on 51 of 75 (68%) plots and 24% of stems per plot were browsed. The percent of stems browsed exhibited no relationship to slash, and increased retention did not appear to deter browse. Percent of browse was less contingent on treatment level, and instead highly dependent on site. Browse levels were significantly higher ($p < 0.001$) at site 1, averaging 44%, while 11% of stems were browsed at site 2. At site 1, browse percentages between full and partial treatments were relatively similar (44% and 46%), with both groups exhibiting large variance. Site 2 exhibited minimal variance, and browse was also comparable between full and partial cleanup areas (11% and 12%). Pellet counts of elk and deer were also significantly higher ($p < 0.01$) at site 1. In the 270 m^2 surveyed, ~560 elk (~20,000/ha) and 300 deer (~11,000/ha) pellets were observed in total, and present in 17 of 45 (37%) plots in treated areas at site 1. Surveyed area at site 2 contained 0 elk and 87 (3,200/ha) deer pellets, present in one of 45 plots (2%). Cow dung was observed in one quadrat at site 2 and absent at site 1.

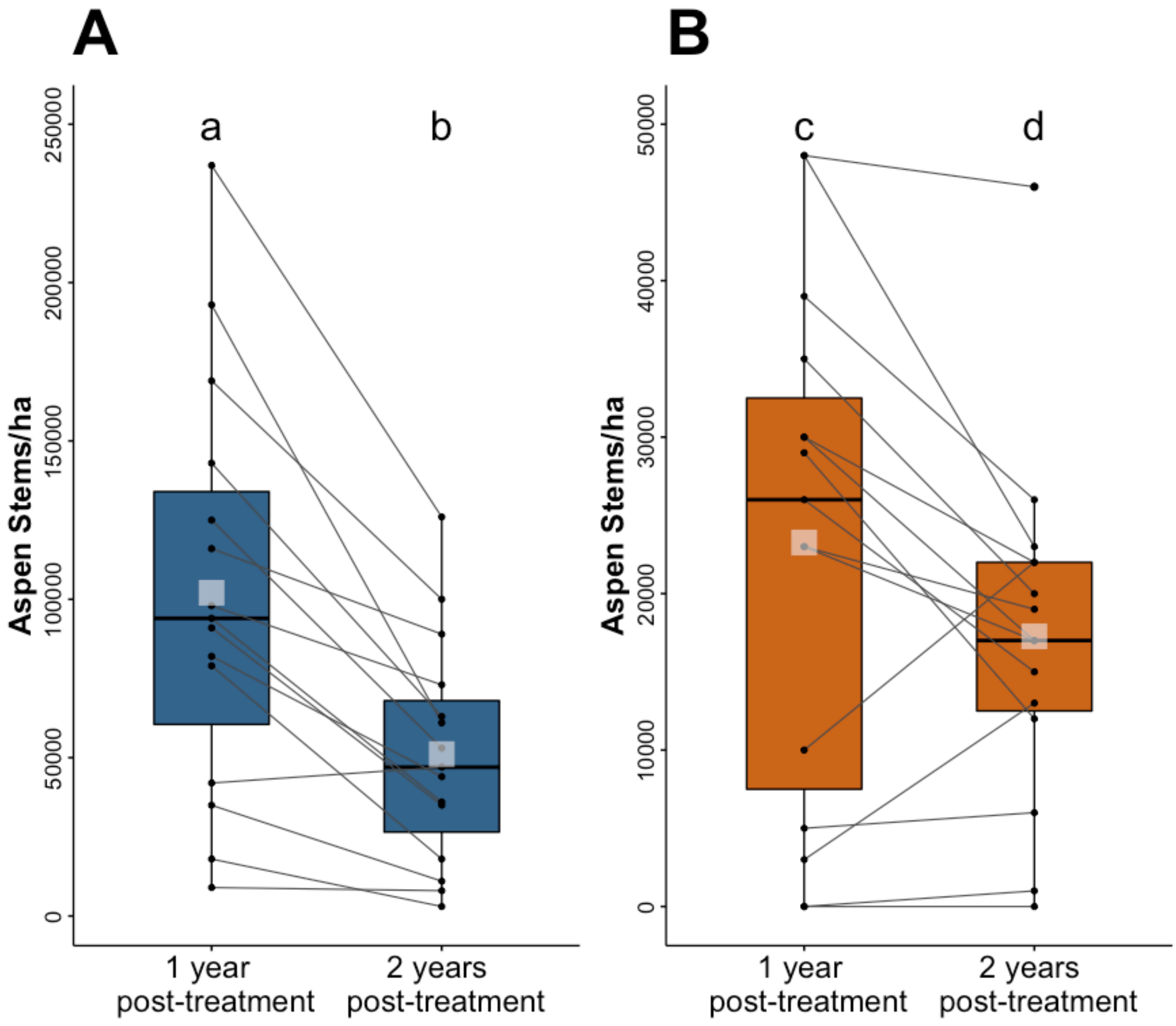
Two years post treatment

Influences on regeneration

Regeneration at site 1 decreased significantly ($p < 0.05$), from a mean 63,000 stems/ha in year one, to 34,000 stems/ha in year two (Figure 6). Second year densities remained highly dependent ($p < 0.05$) on treatment level. Higher regeneration was observed in full cleanup areas, despite a larger absolute reduction in density. Full cleanup areas exhibited a ~50% decrease ($p < 0.001$) in regeneration, from means of 102,000 to

51,000 stems/ha across paired plots; 14 of 15 full cleanup plots showed a decline in density, but all plots had one or more stem present. The most drastic decrease on the plot level was in full cleanup areas, exhibiting an 84% reduction. Partial cleanup areas experienced a lesser decline than full cleanup areas ($p < 0.001$), as density decreased by 25% (~ 6,000 stems/ha), with means decreasing from 23,000 to 17,000 stems/ha across paired plots ($p < 0.05$). Although mean stems declined, ~ 27% (4 of 15) plots experienced an increase. One of 15 plots had no aspen stems present.

Figure 6: Change in regeneration from one to two years after treatment; note different y axis between A and B. On the left, blue boxplots in figure A represent differences in density within full treatment areas. Orange boxplots on the right in B indicate changes in partial cleanup areas. Gray lines connect between paired black points, denoting change in density observed at each plot (*n* = 15 per treatment). Significant differences in regeneration are indicated by different letters above boxplots and transparent white boxes represent mean density.



Ungulate browse effect on regeneration

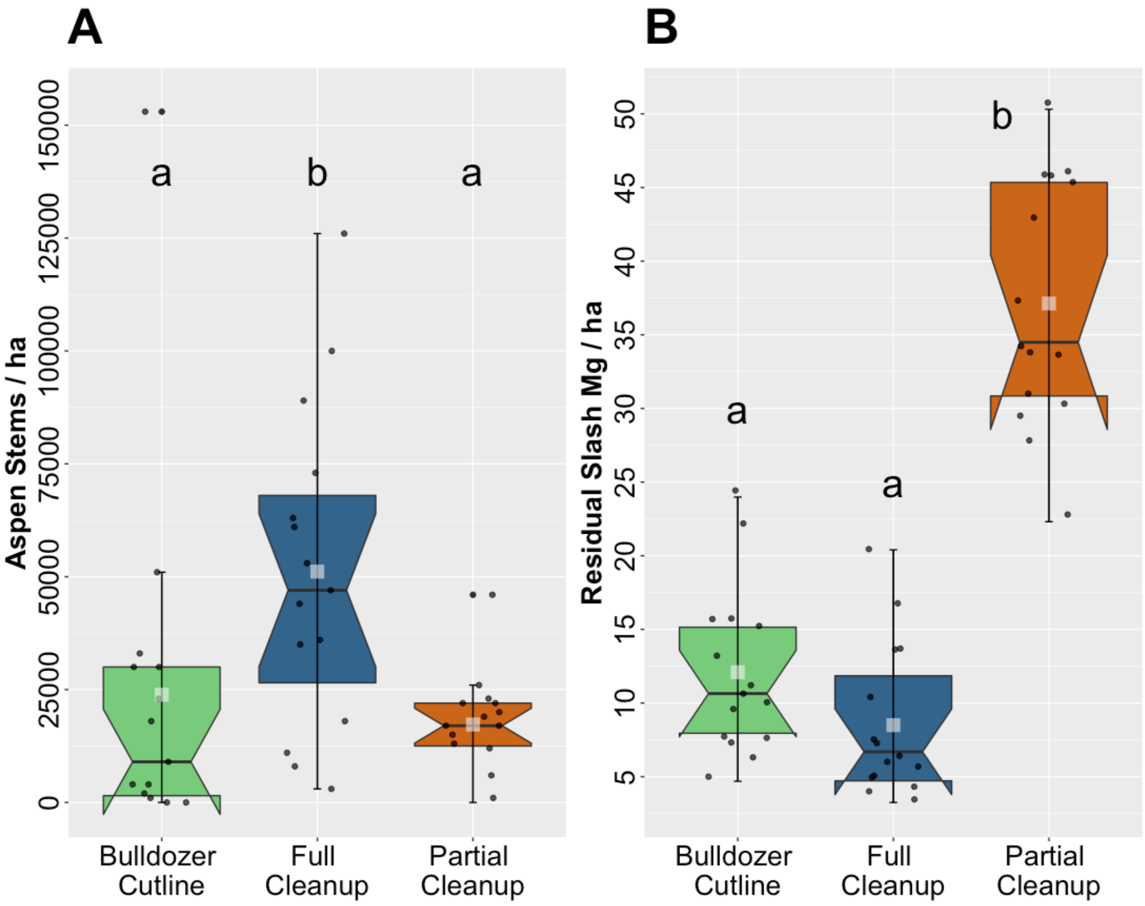
The percent of stems with browse detected in the second year of sampling increased significantly ($p < 0.01$) from ~45% to approximately 63%. Full cleanup areas experienced a larger increase ($p < 0.01$), from 42% to 71% of stems browsed. Partial cleanup areas experienced a lesser increase in browse ($p = 0.054$, from 46% in year one to 54% of stems in year two. Percentages of browse showed minimal linear correlation to residual slash ($r = 0.15$), but greater browse was observed in full cleanup areas.

Exclosures restricted ungulate browsing for two growing seasons and resulted in greater percentages and absolute numbers ($p < 0.05$) of class 2 stems across both treatment levels. Within the 18 exclosures, mean density of class 2 stems was 15,000 stems/ha, comprising 18% of total stems; outside of exclosures, mean density of class 2 stems was 4,000 stems/ha and 7% of all stems. Two of 18 exclosures had 0 stems present, both in partial cleanup areas. Full cleanup areas had similar percentages (10%) and absolute (~7,500 stems/ha) class 2 stems inside and outside of exclosures. In partial cleanup areas, exclosures contained a greater percent ($p < 0.01$) and number ($p < 0.05$) of class 2 stems, while mean density was only 666 stems/ha outside of exclosures.

Impact of increased compaction on regeneration

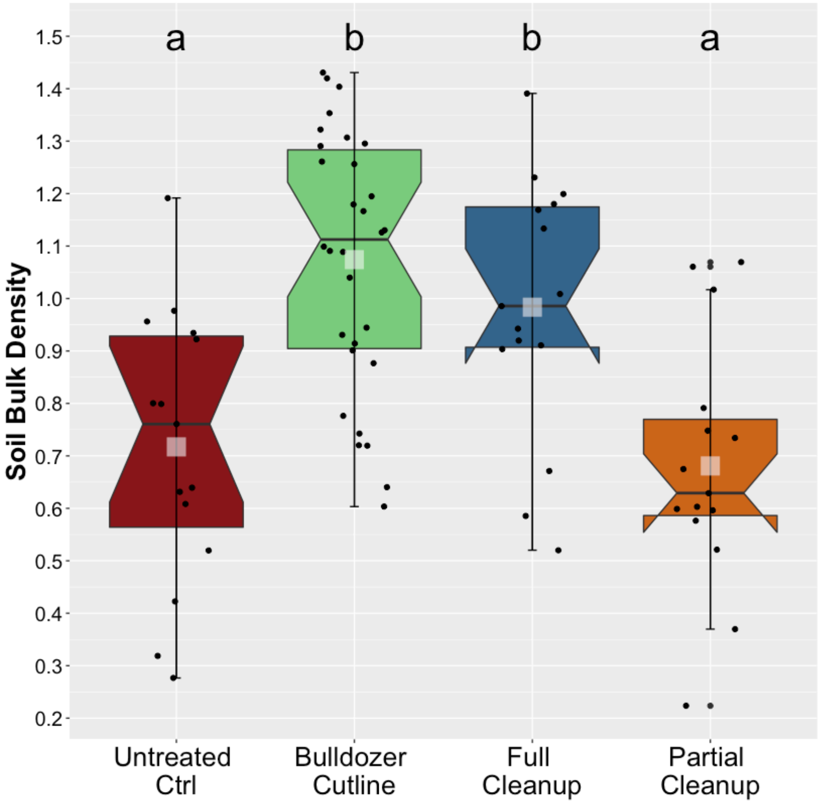
Initial bulldozer cutlines contained a mean density of 24,000 stems/ha (Figure 7a) and relatively low amounts of residual slash (~12 Mg/ha, Figure 7b). Stem densities were highly variable and ranged from 0 to 153,000 stems/ha, the highest observation in the second sampling season. Mean density of full cleanup areas was nearly double ($p < 0.05$) than cutline areas, averaging 51,000 stems/ha, but exhibited equally high variance (Figure 7). Amounts of residual slash were similar between cutline and full cleanup areas. Partial cleanup levels exhibited comparable regeneration mean density to bulldozer cutlines but contained significantly greater residual slash ($p < 0.001$, Figure 7b).

Figure 7: Differences in regeneration (A) and residual slash (B) between treatment types. Significant differences are indicated by different letters above boxplots and lack of overlap in notches. Transparent white boxes represent means of regeneration and slash.



Soil bulk density (BD) varied by treatment cleanup level: bulldozer cutlines and full treatment areas had similarly high bulk density, which was greater ($p < 0.001$) than the mean in partial and untreated control areas ($p < 0.001$, Figure 8). Soil BD did not correlate to regeneration when assessed on a plot level across all treatment areas or when assessed independently by distinct treatment level datasets. When regeneration was evaluated by groups of treatment level, results of linear regression indicated bulldozer cutline areas were significantly associated ($p < 0.05$) to decreased regeneration, to a similar degree as partial treatment (Figure 7a). Increased BD was strongly associated ($p < 0.01$) to full cleanup and bulldozer cutline areas ($p < 0.001$), and lower BD was correlated ($p < 0.001$) to untreated control areas. Partial cleanup areas contained lower BD that was more variable and not significantly correlated. Bulldozer cutlines exhibited the least variable BD, although not significantly, and high variance in BD was observed across all treatment areas. Soil bulk density appeared to have minimal to no impact on regeneration densities at a plot level, and no significant relationships were detected.

Figure 8: Soil bulk density of bulldozer cutlines, full cleanup, partial cleanup, and untreated areas. Significant differences are indicated by different letters above boxplots and lack of overlap in notches. Transparent white boxes represent soil bulk density mean of each treatment group.



Discussion

Aspen have the potential to regenerate in extremely high densities after roller-felling, but appeared to be most dependent on the amount of residual slash: more slash and less exposed soil greatly diminished the probability of prolific suckering. Site and aspen composition prior to treatment also impacted regeneration, but potentially to a lesser degree. The amount of machinery traffic reduced regeneration, but appeared to exhibit threshold behavior. Although high densities were generally observed after treatment, ungulate browse quickly exceeded sustainable levels, affecting future stand health and development. Greater stem densities were observed in the first year after treatment, suggesting the positive response of aspen to treatment decreases over time (in the short term). Many early successional dynamics known to apply after other stand-replacing disturbances were observed, which indicated that roller-felling can function as a stand-replacing disturbance and stimulate aspen's suckering response; this suggests treatment could contextually be applied to reduce fire risk and promote aspen regeneration.

Effect of treatment level on regeneration

The level of treatment cleanup exerted the greatest influence on regeneration. Differences between full and partial cleanup areas, specifically in amount of residual slash and proportion of exposed soil, appeared to be responsible for a muted suckering response in partial cleanup areas. Covering by forbs and grass did not vary by cleanup level, and contrary to previous work (e.g., Landhausser and Lieffers, 1998) did not seem to impact regeneration. Residual slash was significantly greater and more variable ($p < 0.001$) in partial cleanup areas (28 Mg/ha) than in full cleanup (12 Mg/ha), and bulldozer cutlines contained similar amounts of slash (12 Mg/ha); bare soil occupied 25% of ground cover in partial and 50% in full cleanup areas (all p-values < 0.001). Partial areas also exhibited greater ground covering of shrubs and litter/duff (p-values < 0.001). Competition with shrubs may have reduced regeneration, but this is difficult to disentangle with variables of treatment level and associated residual slash/bare soil, as shrubs occupied ~ 5% of total ground area in partial cleanup and <1% in full cleanup areas. Additionally, bare soil and slash showed a strong inverse correlation (-0.70), so it is unclear which mechanism exerted a greater influence on density. Discerning the individual impact of slash, bare soil, and shrubs on regeneration remained challenging, as different amounts across treatment types limited our ability to isolate these variables. However, it would appear increased levels of slash removal and soil scarification promoted greater regeneration.

Our observations were concurrent with studies of harvest and mechanical treatments that indicated regeneration declines with slash retention (Shoup, 1967; Steneker, 1976; Doucet, 1989; Shepperd 1996, 2001). However, patterns of decreased regeneration and slash can be driven by several mechanisms. Increased shade, less surface area, a cooler microclimate (i.e., fewer growing degree days), or a combination of these interactions may explain the lower densities observed in partial cleanup areas. Studies that cited slash as a temperature-mediated control on regeneration were conducted at higher latitudes (Bella 1989; Paragi and Haggstrom, 2007), while latitudes similar to our study attributed lower density to shading, and lacked temperature-related variables (Shepperd, 1996, 2001). The exact mechanisms behind increased slash and reductions in regeneration within our study remains unknown, as temperature was not monitored. Nonetheless, our study supports the breadth of literature (e.g., Steneker, 1976; Doucet, 1989; Shepperd 1996, 2001; Paragi and Haggstrom 2007) demonstrating the impact of slash on aspen regeneration and suggests light exposure and temperature also have a similar effect on regeneration after roller-felling.

Soil scarification after slash removal can stimulate regeneration (Maini and Horton, 1966; Fraser et al, 2003). Specifically, treatments that involve “root-ripping”, or separating roots from the base of stumps, can increase suckering (Shepperd, 1996, 2001). However, site preparation techniques remain cautiously applied, in an attempt to reduce soil disturbance, as gauging bulldozer blades beneath the surface can negatively impact suckering if roots are overly fragmented and destroyed (Perala, 1972; Shepperd, 1993, 1996; Frey et al, 2011), while severe site preparation techniques have been intentionally applied to decrease regeneration. Lower densities associated with “disk-trenching” and “drum-chopping” (per Ehrentraut and Brantner, 1990; Peltzer et al, 2000; Fraser et al, 2003) were not observed in our study, despite similarity to roller-felling. Frequent upending of root wads up to a depth of 1.5 m and repeated movement of machinery that excavated the soil profile caused severe disturbance, but it would appear roller-felling generally does not result in a level of root damage or fragmentation sufficient to limit regeneration. This suggests treatment severity falls below a theoretical threshold applied in other studies, and was similar to the degree applied by bulldozing in Shepperd (1996), which increased regeneration. These findings could also suggest a mechanism within the roller-felling process exerts a greater positive influence on regeneration, negating this soil disturbance component, or that aspen root systems are more tolerant to mechanical disturbance than previously thought.

Regeneration densities were greatest in the year after treatment, following established dynamics of early succession. Suckering is known to peak in the first or second year after disturbance, followed by a rapid decline via self-thinning and light competition (Peterson and Peterson, 1992; Frey et al, 2011). The percent and absolute number of class 2 stems increased from one to two years, indicating stand progression. Although a larger proportion and absolute reduction in density was observed in full cleanup areas (~ 50%), this is not cause for concern, as precipitous loss in density is not uncommon. Reductions of up to 80% have been observed in the first five years after establishment (Bartos and Mueggler, 1982; Crouch, 1983; Frey et al, 2011), and predictable stand development would constitute a large reduction in stems to reach a common successional threshold of ~ 20,000 stems/ha by year six (Peterson and Peterson, 1992). Furthermore, suckering tends to occur in clumps, and self-thinning is critical for healthy structure and growth habit, as subordinate stems are outcompeted and the most vigorous stem within each clump dominates (Shepperd, 1993). Considering the prolific densities year after treatment, a large reduction in stems and increases in height (e.g., increased percent and absolute density of stems in a taller size class) suggests conventional dynamics are at play, and this early successional trajectory indicates healthy development.

Full cleanup areas appeared to promote greater stem growth, suggested by 15% (~7500 stems/ha) of regeneration in class 2, as opposed to 3% of total stems in partial cleanup areas exceeding a height of 1 m. These growth rates are indicative of stand development, concurrent with height and stand progression of young aspen stands (Shepperd, 1993). Sucker growth tends to be greatest in the year after disturbance, and the slower growth rate in partial treatment areas may reveal a delay in future stand development, as slower growth has been correlated to lower sucker densities (Shepperd, 1993; Bartos et al, 1991). Additional benefits to increased sucker densities and subsequent leaf area include lessened mortality via disease (e.g., *Hypoxylon mammatum* (Wahl.); Ostry and Anderson, 1990) or competition (Landhausser and Lieffers, 1998), and overall greater biomass associated with insurance against loss to stressors of browse or insect damage (Peterson and Peterson, 1992; Desrochers and Lieffers, 2001b; Frey et al, 2011), making higher densities a generally desired outcome following disturbance.

Increased sucker densities can also have consequences: extremely high densities (>200,000 stems/ha) in the year after disturbance can reduce sucker height, growth, and biomass, stunting short term (i.e., < five-year) stand development (Stone and Elioff, 1998; Kabzems and Garcia, 2004). Longer-term, timber management guidelines suggest a lower density (>12,000 stems/ha) of well-distributed suckers can promote greater tree height and biomass than stands with > 80,000 stems/ha (Graham et al, 1963; Brinkman and Roe, 1975). The extremely high densities observed in full cleanup areas could delay short-term stand development, and with the lack of spatial distribution data, potential heterogeneity could lead to lessened growth. Although it is likely that initial densities will converge within the decade and develop on a similar trajectory (Peterson, Kabzems, and Peterson 1989), differences in density in combination with other ecological characteristics between full and partial cleanup areas may result in divergent stand development.

It is important to note that slash retention, and subsequent negative impact on suckering, varied slightly between sites, as each were treated by different bulldozer operators. The three partial cleanup areas at site 1 retained significantly more slash than at the two at site 2 ($p < 0.01$). Moreover, the entirety of area at site 1 contained more slash than site 2, which also had and a greater proportion of plots with lower slash retention (i.e., full cleanup). Despite this, lower regeneration was observed in at site 2. Since site and year are conflated, this could suggest that the temporal variable of treatment year and associated climactic dynamics (i.e., precipitation, Romme et al, 1995; McIlroy and Shinneman, 2020) are a large determinant of regeneration after roller-felling.

Effect of site

The influence of site proved to be significant in this study, and while the sites were only ~ 10 km apart, located on the same base geology and overall similar in elevation and species composition, they were treated in different years. Because of this, climactic differences between treatment years (2020 and 2021) and their subsequent growing seasons may partially explain the greater densities observed at site 1. Precipitation from January to August of 2021 totaled ~ 319 mm, roughly 92% of the 30-year mean (~ 346 mm) for this 8-month period, while precipitation in 2022 for the same time frame totaled ~ 203 mm, approximately 43% less than the 30-year mean (PRISM Climate Group, 2022). The 2022 season received substantially less precipitation than 2021, which could explain the decreased regeneration densities observed at site 2. Short-term regeneration studies that investigated climatic effects on suckering were mostly limited to a post-fire framework (e.g., Turner et al, 2003; Romme et al, 2005); nonetheless, higher annual precipitation and increased winter precipitation (i.e., snowpack), have been correlated to greater sucker densities and frequency (Hansen et al, 2016; McIlroy and Shinneman, 2020). Climatic variation could be one mechanism controlling regeneration densities, in addition to pre- and post-treatment site conditions. Unfortunately, it is impossible for us to differentiate the effect of site and year (climate).

Differences in composition prior to treatment were revealed between the 2 sites: paradoxically, site 2 exhibited composition more traditionally associated with increased suckering (i.e., total basal area, aspen basal area, and aspen stems, p-values < 0.05). Aspen and conifer were significantly older at site 1, which contained more dead and downed woody debris (p-values < 0.001), while aspen as a percent of basal area, dead aspen basal area, and site indices were similar between sites. Delineating by experimental unit revealed more substantial disparities, further complicating interpretation. Despite these differences, modelling indicated regeneration was not correlated to unit, and composition traditionally correlated with increased suckering did not influence regeneration, demonstrated by site 2. It is important to note the reduced explanatory power of composition prior to treatment, which was averaged across treatment blocks and not spatially paired to a distinct regeneration density. However, this could suggest weather (i.e., precipitation) exerts a larger influence on suckering in the year after disturbance than previously thought, or that regeneration after roller-felling is less contingent on prior composition than disturbances of fire or clear-cut harvest due to this treatment's unique characteristics.

Effect of pre-treatment composition

While we hypothesized aspen composition before roller-felling would exert a strong effect on post-treatment regeneration, as has been found by many previous works (Graham et al, 1963; Smith et al, 2011; Britton et al, 2016) the only metric found to be significant regarding this effect was overstory aspen stems. This builds on pre-existing knowledge of aspen ecology and corroborates the findings of Smith et al, (2011): a greater number of above-ground aspen stems, independent of basal area, increases regeneration potential, Smith et al, (2011) recommends > 200 aspen stems for adequate density, and only three of 15 treatment blocks in our study contained mean aspen stems > 200. This could suggest that mechanical disturbance applied beyond the recommended pre-fire compositional limit can still produce adequate regeneration. Additionally, Smith et al, (2011) was conducted in a post-fire framework, and the fact that these dynamics were mirrored in our study suggests successional principles can apply in the context of roller-felling.

Increased dead aspen basal area was not predicted to correlate with greater regeneration, and our hypotheses more closely resembled the inverse (i.e., increasing age of stand and/or aspen with stand reduces regeneration, e.g., Krasnow and Stephens, 2015). As composition shifts towards conifer over time, only decadent aspen stems with limited suckering capacity remain. Variables of conifer composition (e.g., lower regeneration with greater conifer presence prior to disturbance) known to influence regeneration proved inconclusive in this context (Smith et al, 2011; Margolis and Farris, 2014; Krasnow and Stephens, 2015; Clement et al, 2019), and our findings demonstrated the opposite: a compositional shift away from live overstory aspen may not invariably reduce post-treatment suckering. In this context, a decrease in live overstory aspen could increase regeneration, potentially by the persistence of root systems and their associated suckering ability. This finding is unexpected, and rather perplexing, and could be driven by an attribute unique to roller-felling process or mediated by a variety of ecological mechanisms.

As aspen trees grow and increase in mean tree size (or QMD as measured here), their mean root diameter decreases (Shepperd and Smith, 1993). Increased QMD is associated with a lower proportion of non-structural carbohydrates; and although these carbohydrates don’t stimulate sucker initiation, they are strongly correlated to growth (Shepperd and Smith, 1993; Frey et al, 2011). Moreover, larger roots near the base of mature aspen stems exhibit lower suckering than smaller lateral roots (< 2 cm in diameter) located at ends of parental root systems (Brown, 1935; Schier, 1981; Shepperd and Smith, 1993; DesRochers and Lieffers, 2001a) and lower density aspen stands can contain greater proportions of dead root biomass (Desrochers and Lieffers, 2001b). For these reasons, it is possible that the increased overstory aspen stems observed in this study (i.e., a greater number of smaller aspen stems), as opposed to basal area, may have reflected a greater density of live roots < 2 cm, with greater suckering capacity. Additionally, death of a mature aspen stem does not constitute mortality of its entire root system; in fact, remaining live aspen can be positively affected by the death of an adjacent stem by acquiring its dead roots and inheriting an established root system (DeByle, 1964; Desrochers and Lieffers, 2001b). These mechanisms below the soil surface could also explain our findings: although aspen have senesced from the overstory and declined in above ground live biomass, their root systems persist. Root age does not appear to reduce suckering (Schier and Campbell, 1980), and these residual root systems could have the ability to produce high sucker densities, especially if subject to a severe disturbance that causes root damage and stimulates suckering. Root system dynamics were not monitored in this study, but may help explain the lack of hypothesized correlation between regeneration and aspen basal area, along with the positive relationship between mature aspen stems, aspen dead basal area, and sucker density.

Another possible interpretation of these findings could be associated to the exact timing of disturbance in the seral-aspen successional trajectory, as increased standing dead aspen may serve as a harbinger of a compositional shift towards conifer dominance. Standing dead aspen generally falls and becomes downed woody debris within 10 years of death (Hogg and Michaelian, 2015), and treatment applied to stands in this specific successional stage could influence suckering potential. The correlation between standing dead aspen and more robust suckering may support a more nuanced view of regeneration in relation to pre-disturbance composition. Our findings may suggest that if disturbance takes place close to the terminus of aspen canopy presence (i.e., dead overstory), there is still great potential for prolific suckering, and conifer presence only decreases suckering only after crossing a certain compositional threshold. Similarly, a metric of < 80% overstory conifer was suggested in Smith et al, (2011) as sufficient for post-fire regeneration; our study corroborated this threshold, as the proportion of conifer prior to treatment did not exceed 75%. Although live overstory composition (i.e., conifer or aspen basal area, aspen stems) remains deterministic, other compositional attributes such as dead aspen (per this study) or advance regeneration (per Britton et al, 2016) and the finer timing of disturbance within the successional trajectory of seral aspen stands may also influence regeneration.

Ironically, Krasnow and Stephens (2015) found evidence that greater conifer and/or dead aspen basal area prior to fire decreased aspen regeneration in the Sierra Nevada region. However, increasing fire severity, quantified in part by remnant, uncombusted coarse woody debris, remained a stronger predictor within their model, and the authors argue that suckering potential increased with disturbance severity. This also relates to the findings in Smith et al, (2011), which indicated larger disturbance size can facilitate greater regeneration. Both studies, however, were conducted within the framework of natural wildfire. Our counterintuitive findings may suggest that prior composition is less deterministic of regeneration in the context of mechanical disturbance, specifically to more severe treatments such as roller-felling, or that disturbance severity plays a larger role promoting regeneration.

Although pre-treatment composition was influential, treated areas with minimal aspen still exhibited adequate, and even prolific, sucker densities. Although less ubiquitous, several studies noted aspen's ability to vegetatively regenerate in high densities despite minor overstory presence prior to disturbance, attributing this to the presence of few parent trees and their remaining root system (Mitton and Grant, 1980; Debyle and Winokur, 1985; Schier, 1985). Furthermore, Lavertu et al, (1994) observed stand age and successional composition to have no relationship to sucker production in the one to three years after harvest. This was situationally observed in our study: high densities were present after treatment in areas with few overstory aspen stems, low aspen basal area, and/or high conifer abundance. The regeneration patterns observed in this study support the theory that few remaining aspen trees in a stand prior to disturbance can support roots sufficient for suckering, even to a density of self-replacement, as these roots can extend up to 50 m from the main stem and likely spread into adjacent areas without aspen (Schier and Smith, 1979). Within the context of roller-felling, this suggests low aspen presence prior to treatment does not preclude prolific suckering, which could have implications for management application.

Impact of browse on regeneration

Ungulate browse can decrease sucker density by reducing growth rates and/or increasing susceptibility to stressors of disease or drought, predisposing stems to early mortality (Shepperd and Fairweather, 1985; Rhodes et al, 2019), and excessive herbivory can cause inadequate overstory recruitment. Browse levels consistently exceeded sustainable thresholds (e.g., 30%; Olmsted, 1979) at site 1, and were consistent across treatment levels. This implies residual slash does not deter browse, in contrast to our hypotheses. This could be due to the low height of slash, which generally did not exceed 0.5 m, and studies that cited slash as a deterrent indicated a height threshold of efficacy. Piles > 0.8 m were shown to reduce browse (Ripple and Larson, 2001) and "hinging" (cutting trees but leaving part the cambium attached so the fallen tree remains partially attached) trees at height of 1.5 m reduced browse to a greater degree than shorter slash piles (Kota and Bartos, 2010), while other studies have observed no browse protection from logging slash (Shepperd, 1996). Regardless, in areas with high ungulate populations, it would appear that retaining slash does not reduce the negative impact of herbivory on stand development. If roller-felling is to be applied, ungulate density needs to be considered, as treatment objectives of long-term aspen health, development, and persistence may not be feasible with an unsustainable population of ungulates.

Ungulate browse does not necessarily constitute mortality, but suckers that avoid mortality and are subject to repeated browse can experience lasting changes in growth pattern, rate, and chemical composition (Dieni et al, 2000; Rhodes et al, 2017, 2019). Re-establishment of the apical meristem after browse results in "bush-like" or "shrubby" growth structure with no central axis and decreases stem growth, instead allotting resources to the production of more lateral suckers. This repeated browse restricts overstory recruitment of aspen and promotes conifer dominance, accelerating succession (Shepperd, 2006; Rhodes et al, 2019). Over-browsing can encourage a negative feedback loop of poor stand health and development, detrimental to aspen persistence, emphasizing that the negative effects of browse should not be overlooked when considering implementation, and supplementary management actions that limit browse (e.g., fencing) may be needed in conjunction with roller-felling.

Estimation of browse in the second year after treatment may be less accurate than the year prior, as year two browse was solely determined by apical meristem removal at the time of sampling (e.g., August 2022). Stems with reinitiated, intact meristems were denoted as unbrowsed, and re-browse (i.e., stems browsed in year one and two) was not possible to differentiate visually, and therefore not quantified. If stems browsed in 2021 persisted and hadn't yet reestablished dominance by the following August, they would have been counted as browsed in 2022, possibly resulting in over-estimation. Although exact temporal (e.g., year) measurements are lacking, it is doubtful that browse varies substantially from our findings; if a sucker has not reestablished apical dominance within a year of removal, mortality is likely. Regardless, the amount of browse observed during the second sampling season was almost double (~ 63% across all treated areas) than the suggested annual threshold of 30% (Olmsted, 1979), which stresses the need for future monitoring to determine if these negative impacts pose long-term concerns on stand development.

Impact on soil properties

Initial bulldozer cutlines generally exhibited lower densities relative to full cleanup areas, despite similar attributes. The factors shown to limit suckering (i.e., slash, less exposed mineral soil) were not present in these areas, suggesting machinery traffic may limit aspen's suckering response. Although bulldozer cutlines exhibited the highest soil BD, full cleanup BD was not much lower and exhibited the greatest regeneration, suggesting aspen root systems can tolerate relatively high amounts of traffic and still sucker in high densities. This could also indicate a threshold of machinery traffic, independent of BD, can be tolerated: the degree of traffic in cutline areas exceeded this, while full cleanup area did not.

Post-harvest studies have noted a non-linear relationship between soil BD and traffic: soil BD increased with minimal (>10) machinery passes, then remains constant with increasing passes (Shepperd, 1993; Sealey and VanRees, 2019). Concurrent with Sealey and VanRees (2019), soil BD showed no correlation to regeneration, but low stem densities were observed with the highest level of traffic. Bulldozer cutline traffic resembled the increased levels in their study (> 50 passes), and also contained lower regeneration. Exact numbers of passes are not available in our study, but estimates (personal communication) indicate a gradient was applied, with bulldozer cutlines experiencing the greatest degree, followed by full, then partial cleanup areas. The number of passes in the full cleanup appeared to be substantial enough to increase soil BD but not limit regeneration, suggesting regeneration is only restricted by the bulldozer movement when applied past a certain threshold. This could also suggest that compaction (i.e., increased soil BD) may not be the mechanism limiting regeneration in these highly trafficked areas. Movement may damage the root itself and not just physically restrict suckering ability by compacting the surrounding substrate (Shepperd, 1993). Independent of the mechanism, bulldozer traffic beyond a threshold can decrease regeneration, and this effect of roller-felling should not be overlooked.

It is important to note that cutlines were only surveyed at site 1, which demonstrated overall higher densities. Site 2 bulldozer cutlines were not measured and could be understocked. The stressor of increased compaction at site 1 may have been surmountable with adequate soil moisture, but sufficient suckering may be less feasible if drier conditions follow in the year after treatment. Longer-term monitoring is needed to ascertain if heavy machinery movement has a lasting ecological impact.

While roller-felling largely functioned as a stand-replacing disturbance, processes of mechanical disturbance and natural wildfire have different impacts on soil properties. Fire functions as a critical nutrient cycling process, increasing nutrient availability and altering soil's chemical properties. Greater C, N, and P as a result of fire is correlated with more vigorous aspen regeneration (Smith et al, 2011), while burned soil is linked to increased defense compound production in leaves against herbivory (Wan et al, 2014) and greater probability of aspen establishment via seed (Kreider and Yocom, 2021a). Soil properties are also influenced by repeated movement of machinery; harvest and associated compaction followed by severe scarification reduced available N, P, and microbial biomass (Tan et al, 2008), while forest floor removal (i.e., scarification) alone reduced microbial biomass (Tan et al, 2005). In addition to edaphic differences, wildfire can leave behind legacy trees that function as wildlife refugia and create microclimate heterogeneity, while roller-felling indiscriminately removes all canopy trees. Although treatment emulates the stand-replacing nature of fire, it omits critical ecological processes that could alter stand development. Supplementary sampling and analysis of soil (e.g., nutrient content) and future monitoring is needed to determine the lasting impact of treatment on soil properties.

Fire is not entirely excluded from the roller-felling process, as slash piles are burned after years of curing. Despite ignition attempts at site 1 in 2021 and 2022, no piles have been burned as of spring 2023. Although this limits the scope of our study, pile burning is a common management technique, widely applied to reduce fire risk or dispose of post-harvest slash. The long- and short-term effects on soil properties (e.g., Korb et al, 2004; Rhoades et al, 2021), understory composition (e.g., Selmants and Knight, 2003; Dagley et al, 2020), and stand development (e.g., Adams, 1972; Rhoades and Fornwalt, 2015) remain well-documented, allowing for informed speculation. It is likely that exposure to abnormally high temperatures will produce a less hospitable substrate and foster composition dissimilar from that of roller-felled (i.e., unburned) areas.

Broadly, pile-burned areas are expected to have minimal, if any, aspen regeneration. Desolate burn scars will likely persist for decades, contrasting with adjacent roller-felled areas that support high sucker densities (Frey et al, 2011; Fornwalt and Rhoades, 2011; Rhoades and Fornwalt, 2015). Moderate heating of soil promotes regeneration, and most suckers originate from roots in the upper (i.e., 10 or 15 cm) soil profile, but extreme temperatures of sustained, high-severity fire causes root mortality, reducing or eliminating regeneration (Howard, 1996; Frey et al, 2011). Furthermore, slash piles are intended to promote total combustion; the fuel arrangement combined with low moisture content encourages burning, and the effects (e.g., temperature) are more severe in these concentrated areas (Wan et al, 2001). Additionally, piles dominated by fuel of larger size classes (i.e., 1000 -hour vs. 10-hour) generate higher temperatures that penetrate into soil deeper layers and persist for longer (Busse et al, 2013). In our study, pile composition could be coarsely derived from pre-treatment sampling, as biomass was simply redistributed via roller-felling. Piles were generally dominated by larger woody debris, likely increasing the probability of root mortality and lack of regeneration. Succession within burned areas is expected to be delayed and remain understocked for decades (Adams, 1972; Korb et al, 2004; Rhoades and Fornwalt, 2015).

Differences between pile-burned and unburned areas are not limited to aspen regeneration, and prolonged exposure to lethal (e.g., > 60°C, Busse et al, 2010) temperatures will have immediate effects of decreased soil microbial content and increased acidity (Korb et al, 2004; Jiménez Esquilín et al, 2007), while decreased water infiltration capacity and changes in nutrient content will likely persist for years (Rhoades and Fornwalt, 2015; Rhoades et al, 2021). Post-burn monitoring is warranted to verify these speculations, although it is unlikely that pile burning in the context of roller-felling will differ from that of other management practices.

Management implications

Although roller-felling stimulated aspen's suckering response, long-term stand health and persistence is contingent on a suite of environmental variables, in addition to sufficient regeneration. However, continuous stocking of adequate densities remains critical for overstory recruitment and development. Minimum thresholds of stocking are suggested to ensure adequate development, as failure is thought to lead to earlier succession of conifers (Kitchen et al, 2019), but a wide range of stem densities are considered acceptable, as variable densities tend to converge within the decade following disturbance (Peterson, Kabzems, and Peterson 1989). Additionally, the desired amount of regeneration following treatment varies by location and management objective. Management solely for wildlife tends to favor higher densities, as denser stands support more biomass and associated forage for ungulates (e.g., mule deer, moose; Peterson and Peterson, 1992; Gullion, 1984). Specifically, a minimum of 30,000 stems/ha in the second growing season has been recommended for ruffed grouse (*Bonasa umbellus*) habitat in the Great Lakes region (Gullion, 1984). Lower densities are preferable for silvicultural management: guidelines in eastern Canada suggest a preferred density of 15,000 stems/ha, independent of spacing, and a minimum of 2,500 *well-spaced* stems/ha (Hambly, 1985) for healthy stand development, while desired densities for pulp production are 6,000 stems/ha and 2,500 well-spaced stems/ha for optimum lumber output in western Canada (Steneker, 1976).

In the intermountain West, common guidelines suggest an absolute minimum of 2500 stems/ha as sufficiently restocked, or self-replacing (O'Brien et al, 2010; Kitchen et al, 2019). This more liberal metric is consistent with study objectives, and 92% of plots exceeded this coarse threshold in the short-term time frame (two years) of our study, while 75% of plots (56 of 75) met the more conservative metric of >15,000 stems/ha. Although regeneration densities are a common and simple metric to determine treatment "success", this alone does not indicate holistic, long-term stand health. Continued monitoring of understory vegetation, browse impact, and other metrics quantifying the effects of roller-felling, in addition to regeneration, are needed to confirm these areas maintain healthy stand development.

Although stems were present in almost all sampling plots, the area occupied by slash piles was omitted from sampling, and these areas are expected to support minimal regeneration, as lethal temperatures from burning will likely eliminate live roots and their suckering potential while facilitating irregular spacing. Piles occupied 17% of total ground area in full cleanup areas and 11% in partial; despite these surface area reductions, stem densities will still meet adequate stocking thresholds, even if burned areas contain minimal suckers. Aspen colonization within these areas will be reliant on encroachment from intact roots in adjacent, unburned (or lightly burned) areas, provided tolerance of soil conditions, or establishment via seed. Sexual reproduction is associated with burned soil (Krieder and Yocom, 2021a), but the substrate beneath burned piles subjected to extreme heat generally remains less hospitable for plant establishment (Korb et al, 2004; Fornwalt and Rhoades, 2011). Spatially, pile edges are subjected to decreased temperature and lessened burn duration (Busse et al, 2013), while changes to soil properties and composition are more pronounced in the pile interior (Korb et al, 2004; Jiménez Esquilín et al, 2007; Fornwalt and Rhoades, 2011; Hubbert et al, 2015) and take longer to recover. For these reason, burned areas, especially towards pile interiors, will likely experience a prolonged delay in regeneration. As aspen mature, this will create a mosaic of canopy gaps that negatively effects long-term stand development. Simple rehabilitation treatments, such as post-burn mulching, scarifying, or seeding, can ameliorate some of the negative impacts of pile burning has on plants and soil (Korb et al, 2004; Fornwalt and Rhoades, 2011). Long-term absence of aspen in burned areas could warrant amelioration treatments, and future monitoring is needed to determine trajectories of stand development.

It is important to note that many of the thresholds outlined above rely on antiquated literature derived from data collected under wetter conditions and lower atmospheric CO2 levels, which may necessitate revision. In the western US, climate projections indicate a continuation of drier and warmer conditions (Kim, 2005; IPCC, 2022). Drought stress can increase mortality (Worrall et al, 2008), while rising temperatures can promote insect populations (Oystershell scale, per Crouch et al, 2021). Increased atmospheric CO2 can increase plant productivity (e.g., Norby et al, 2005), and current stocking guides used for aspen management may underestimate a stand's maximum carrying capacity (Kubitske et al, 2019). Forest management remains dynamic (e.g., Long and Mock 2012; Nagel et al, 2017), and the metrics we observed that quantified roller-felling "success" may not be applicable or feasible in the future.

Although most plots the self-replacing threshold of 2,500 stems/ha, lower regeneration densities were present when slash densities exceeded ~ 25 Mg/ha, and when > 25 Mg/ha was retained, high variability and the potential for prolific regeneration was observed. This supports the findings of Shepperd (1996) and suggests that complete slash removal is not imperative for adequate regeneration, but heavy residual slash loading should be avoided to prevent insufficient sucker densities. Post-harvest studies have shown that thicker layers of soil organic matter (i.e., litter/duff) can also restrict regeneration, while the exposing of bare mineral soil can promote suckering (Peterson and Peterson, 1992; Lavertu, 1994; Paragi and Haggstrom, 2007; Lafleur et al, 2015). Our results indicated bare soil encourages suckering, but also demonstrated a threshold-based relationship. When bare soil occupied < 25% ground cover, invariably low densities were observed, indicating a minimum of 25% mineral soil exposure is needed for high sucker densities. This suggests that complete cleanup and scarification during the final stages of roller-felling is not imperative for adequate regeneration, which can improve efficiency and lower treatment costs, increasing economic feasibility. Regardless, the result of roller-felling largely mimicked other stand-replacing treatment options of harvest of prescribed burning, suggesting this method could be a contextually appropriate, and economically viable, alternative for land managers.

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CHAPTER III

UNDERSTORY VEGETATION CHANGE FOLLOWING STAND-REPLACING MECHANICAL TREATMENT

Abstract

Understory plant communities in quaking aspen (*Populus tremuloides* Michx.) dominated forests are characterized by high diversity, hosting multiple functional groups, and a broad suite of species, that contribute to increased ecosystem function (e.g., water yields) and greater plant productivity. While historical quaking aspen fire regimes would have created conditions for abundant aspen and associated vegetation communities, the policy of fire suppression has drastically reduced the amount of aspen regenerated by fire. Alternatives to aspen regeneration using silvicultural and mechanical approaches have been developed. This study assessed the short-term response (one- and two-year) of understory plant communities to one such treatment, called roller-felling. Understory plant composition was compared across a gradient of ecological conditions, pre- and post- treatment, in response to roller-felling. Forbs that may have been present in more diverse understories of earlier successional stages, and absent in later stages preceding treatment, were observed in treated areas. The introduction of native species that were either dormant or absent from the seedbank indicates treatment can initiate vigorous understory renewal. Conversely, non-native forbs that were formerly excluded can also be introduced, particularly where bare soil is exposed, emphasizing the importance of contextual knowledge prior to application. Composition varied across a gradient of ecological conditions within treated areas, suggesting that lessened severity (i.e.,

retaining slash, decreasing machinery traffic, and/or light scarification of soil) can promote persistence and/or establishment of mid-to-late successional species. The short-term, early successional trajectory observed after treatment was largely concurrent with our understanding of aspen community dynamics following other stand-replacing disturbances, suggesting roller-felling has a similar impact on understory composition.

Introduction

Quaking aspen (*Populus tremuloides* Michx.) is North America's most widespread deciduous tree species and is recognized as a keystone species across the western U.S. for supporting greater degrees of understory diversity (Little, 1971; Stohlgren et al, 1997; Chong et al, 2001; Kuhn et al, 2011). When coexisting with conifers (i.e., seral aspen), this early-successional species requires a stand-replacing disturbance to regenerate. Historically, mixed-to-high severity fires created stand-replacing conditions that regenerated aspen and reduced fuel loading. Wildfire is a common and critical disturbance in these systems, specifically in later successional stages; however, such events have become less frequent due to human intervention (i.e., fire suppression) and recent climatic patterns (i.e., relatively wet 20th century; DeByle et al, 1987; Grissino-Mayer and Swetnam 2000; Millar et al, 2004). High fuel loading puts many of these stands at risk of high severity fire. A perceived need for alternate treatments that reduce fire risk has led to the development of a mechanical treatment method, called roller-felling, designed specifically to regenerate aspen and reduce fuel loads in late-seral stage aspen communities. In this study, we assessed the short-term response (one- and two-year) of this method on understory vegetation composition.

Roller-felling is a stand-replacing treatment, accomplished by pulling a large barrel drum between two bulldozers; this drum is connected via an industrial cable, which remains lifted ~ 2 m above the ground. This cable knocks over intact trees as the barrel is dragged across the landscape, which increases the fulcrum at which the force of the cable is applied while decreasing the effort needed to topple the trees. Roller-felling was recently applied in central Utah, but environmental impact has yet to be quantified (Chapter 2). While aspen regeneration is a common metric to assess treatment efficacy, a broader understanding of roller-felling's impact on understory communities should provide an additional assessment of ecosystem condition and provide insight into early successional dynamics of aspen communities after mechanical disturbance.

Aspen-dominated canopies support a more productive understory than that of conifer, as dissimilarities in canopy structure and the chemical composition of foliage promote different understory conditions (St. Clair et al, 2013). Understory productivity can decrease by half when conifers occupy just 15% of the canopy (Mueggler, 1988), and it is well-established that diversity is greatest in aspen-dominated stands, decreasing as conifer presence increases (e.g., St. Clair et al, 2013; Morris et al, 2019). A canopy dominated by broad-leafed aspen is relatively sparse, and their leaves tend to "flicker" with a light breeze of wind; frequent vertical orientation of these leaves allows for increased light to reach the understory (Roden and Pierce, 1990, 1993). Conversely, conifer dominated canopies are denser, and contain evergreen needles with a higher leaf area index that restricts the passage of light and fosters a darker forest floor (Messier et al, 1998; Buck and St. Clair, 2012; St. Clair et el, 2013).

In addition to structural differences between aspen and conifer canopies, the chemical composition of canopy foliage also affects understory conditions. Nutrient-poor needles decompose more slowly than aspen leaves, reducing the rates of litter nutrient cycling and input (Preston et al, 2009), and increased conifer presence reduces soil moisture holding capacity (LaMalfa and Ryle, 2008). Soil properties can change significantly throughout centuries of seral-aspen succession (St. Clair et al, 2013): a formerly bright, fertile understory becomes favorable for species tolerant of nutrient-poor soil and shade, and species with these life history traits dominate in later successional stages (Mueggler, 1988), possibly reducing diversity (Stohlgren et al, 1999; Kuhn et al, 2011). This shift occurs on longer time scales, allowing for progressively different species to occupy this environment at various points along a successional gradient (McCloskey, 2006; Rogers and Ryel, 2008). When a stand-replacing disturbance removes the overstory and promotes aspen regeneration, there will also likely be a large change in understory composition and diversity.

The natural fire disturbance regime of seral aspen stands ranges from mixed- to high-severity (Shinneman et al, 2013), however, suppression and wetter conditions during the last century has likely caused fire intervals to stray from their natural regimes, increasing abundance of more flammable conifers in many seral aspen stands (Strand et al, 2009; Pierce and Taylor, 2010; Shinneman et al, 2013; Millar et al, 2014). Historic fire return data, prior to European settlement, suggested fire severity increased with higher conifer abundance, and decreased with higher aspen proportion; this transition also suggests a reduction in species diversity (Morris et al, 2019). Over time, natural overstory succession leads to a decrease in understory diversity associated with aspen-dominated communities (St. Clair et al, 2013; Morris et al, 2019), and disturbance is critical to initiate succession and promote aspen persistence and associated diversity.

Following disturbance, quaking aspen easily dominates landscapes as an early successional species. This is attributed to their primary regeneration strategy of vegetative suckering, or resprouting of a genetically similar ramet (i.e., sucker) from a pre-existing aspen root system. This asexual process allows aspen to quickly colonize disturbed areas, provided presence prior to disturbance (Frey et al, 2011). Mature aspen stems continuously produce a low number of suckers throughout their life, while a more robust suckering response is triggered by removal or mortality of the main stem, as the interruption of auxin transport from leaves to roots stimulates suckering via intact root system (Frey et al, 2011; Wan et al, 2006). Although uncommon, aspen can reproduce sexually and create new genets (i.e., genetically unique), which may be more frequent than formerly thought (Kreider and Yocom, 2021b; Kay 1993). Regardless of reproductive strategy, disturbance (i.e., fire) remains vital to promote aspen establishment and persistence.

Although aspen regeneration is critical for stand development, many ecosystem indicators can be employed to assess the impact of treatment, in addition to raw stem counts (e.g., Kitchen et al, 2019). Edaphic metrics, such as water retention (e.g., St. Clair and Buck, 2012), or lichen diversity (e.g., Rogers et al, 2009) have been studied in mature aspen stands, while indicators of soil compaction (e.g., Sealey and VanRees, 2019), soil nutrient composition (e.g., Bock and VanRees, 2002), and wildlife use (e.g., grouse, per Guillion, 1984) have been applied to quantify ecosystem function in early successional stages. Although it is impossible to measure all environmental responses, the ability to contrast pre- and post-disturbance conditions allows for conservative quantification of treatment impact.

Changes in understory vegetation (e.g., diversity, composition) are a common metric explored after treatment to evaluate stand progression and, ultimately, ecosystem function. Stand-replacing disturbance will increase light availability to the forest floor, and invariably shift understory composition. However, it is possible that metrics of diversity (e.g., the number of total species observed or diversity indices) will not experience a large increase or decrease with treatment, instead alternating in equally abundant constituents of late or early successional species. This is consistent with the intermediate disturbance hypothesis, which proposes that diversity is greatest at intermediate levels of disturbance, as species of early- and late- successional status can coexist (Connell, 1977). Although late successional species may decline drastically, levels of disturbance can promote short-term increases in richness due to an abundance of early successional species (Haeussler et al, 2002; Pykala, 2004), while higher intensities of disturbance, specifically to soil (i.e., logging followed by burning) are linked to greater compositional change (Halpern, 1989).

Previous studies have focused on aspen regeneration after fire or harvest, which allows for supplemental understory changes to be quantified. Prior to disturbance, understory diversity of late-stage seral understories remains low, especially in contrast with earlier successional stages. Early successional composition and subsequent diversity can increase following disturbance, but is dependent on characteristics (e.g., type, severity, frequency). Fire promoted greater forb abundance and decreased shrub cover (Bartos and Mueggler, 1981), while clear-cutting resulted in the inverse (Bartos and Mueggler, 1982; Peltzer et al, 2000; Haussler and Bergeron, 2004), and greater diversity was observed within clear-cut stands than adjacent burned areas (Haussler and Bergeron, 2004). Certain degrees of mechanical site preparation resulted in greater diversity of functional groups (Peltzer et al, 2000; Haeussler et al, 2002), and scarification can promote early successional diversity (Pykala, 2004). Greater degrees of disturbance (i.e., salvage logging post windthrow) altered species composition and was associated with greater presence of forbs and grasses, and less shrub cover (Peltzer et al, 2000; Rumbaitis, 2006; Shaefer et al, 2016). Understory species diversity increased with windthrow, supplemented by early and late successional species consistent with the intermediate disturbance hypothesis (Rumbaitis, 2006; Lain et al, 2008; Connell, 1978), but declined with increasing severity and the introduction of additional salvage logging (Rumbaitis, 2006; Schaefer et al, 2016). Interacting dynamics between disturbance type and severity determine early successional trajectories, shaping community composition and future stand development.

A severe, stand-replacing disturbance creates conditions favorable for early, pioneer species colonization, such as exposure of mineral soil, but has inherent potential to introduce or increase abundance of non-native species. Aspen stands can offer fertile ground for non-native plant invasion due to shared dependence on recently disturbed conditions for persistence (Shepperd, 2006), and have been shown to host greater amounts of non-natives, independent of successional sere, which could indicate a higher probability for invasion post-disturbance (Chong et al, 2001). Increased severity of mechanical disturbance has been observed to promote non-native species introduction (Haeussler et al, 2004), while higher intensity of harvest also increased biomass of non-native species (Hayes et al,2022), alongside introduction of high rates of aspen stem pathogens (Hinds, 1976).

Roller-felling can promote greater soil disturbance than other treatments (Chapter 2), and understory species may respond differently. During the initial felling stage, root-wads of mature stems are frequently uprooted, up to a depth of 1.5 m beneath the soil profile. Bulldozers then repeatedly push downed trees and debris into long windrows, scarifying the soil, removing surviving vegetation, and compacting the remaining substrate. This initial felling stage may mimic conditions of a severe windstorm that results in "pit and mound" microtopography. Similarly, blowdown events have been studied within these systems, mainly to quantify the compounding effect of salvage logging (e.g., Rumbaitis, 2006; D'Amato et al, 2011). Unlike roller-felling, past logging techniques have been developed specifically to minimize disruption of the soil profile; severe site preparation is typically avoided, as greater soil disturbance can damage and fragment root systems, reducing regeneration (Perala, 1972; Shepperd, 1993, 1996). Machinery traffic is also intentionally minimized, as compaction is widely recognized to diminish suckering (e.g., Navratil, 1991; Shepperd, 1993; Frey et al, 2011). Since aspen regeneration remains a primary objective, treatments promoting less soil disturbance are generally applied, and most studies are conducted in this framework.

Following disturbance, biotic and abiotic factors shift understory composition and determine vegetation that persists into later succession, and ungulate herbivory is a common biotic agent of mortality in early succession. Greater densities of Rocky Mountain Elk, (*Cervus elaphus*, L.), and Mule deer *(Odocoileus hemionus hemionus)* correspond with decreases in aspen regeneration biomass (Shepperd and Fairweather, 1985; Rogers and Mittanck, 2014), but nutrient-dense vegetation that coexists with aspen in early succession is also known to provide valuable forage (Beck and Peek, 2005). Prior studies in this area suggested elevated rates of ungulate browse on aspen regeneration (e.g., Rogers and Mittanck, 2014), indicating greater forage demand may be present. Diet preferences differ by ungulate species (e.g., elk versus deer) and vary temporally with season and successional stage (Beck and Peek, 2005; Hayes et al, 2022), influencing understory composition. Exposure to repeated browse can lead to disproportionate mortality or removal of palatable species, allowing less palatable species to dominate, which can reduce diversity and richness (Augustine and McNaughton, 1998) and negatively affect long-term understory development.

It cannot be assumed that traditional dynamics of early succession will apply after roller-felling, as studies of compositional change were conducted in different frameworks (e.g., fire, harvest). Attributes of treatment are more similar to harvest than fire, but roller-felling is generally more aggressive, and certain post-harvest dynamics may not hold as most studies induced less soil disturbance. Frequent tree uprooting, alongside soil compaction and exposure, could reveal different compositional responses or mechanisms of greater importance. The initial stages of roller-felling create conditions characterized by exposed mineral soil and high light availability, which could promote diversity, while later stages scarify and compact the soil surface, which removes the upper mineral layer and could reduce diversity; this may also reduce the viability of pre-treatment species or foster inhospitable conditions for establishment. Although roller-felling will influence composition, responses of vascular and woody species remained unclear.

Roller-felling was expected to alter understory conditions, promoting vegetation dissimilar from pre-treatment, or undisturbed, environments. A large shift in species composition and functional group was predicted, while the effect on diversity remained unknown. An abundance of early successional species of their respective functional groups was hypothesized in treated areas, in contrast with untreated areas exhibiting later-successional composition. We hypothesized conditions after roller-felling to be optimal for non-native species colonization, but it was unclear if non-native species would be introduced or increase with treatment. Composition was expected to differ by ecological setting, characterized by variable treatment attributes, (e.g., more slash retention or machinery traffic).

This study provided an assessment of the short-term (i.e., one- and two-year) impact of roller-felling on understory vegetation, and pre- and post-treatment understory composition was compared to determine treatment impact. Interactions of disturbance (e.g., soil disturbance, compaction) throughout the treatment process rendered understory composition unclear, but most early successional dynamics were predicted to hold. If early succession followed a similar trajectory to other disturbances, this could indicate roller-felling had a comparable effect on understory vegetation, allowing for conservative assumptions of later successional dynamics to also apply.

Methods

Study area

This study was conducted on private land on the Tavaputs Plateau, located in east-central Utah, USA. This remote, high-elevation area of the Colorado Plateau is comprised of state, federal, and private ownership. Our study area (Lat: 39.57, Long: -110.26) consisted of three units (Table 3), and elevation spanned a gradient of ~ 550 m, ranging from 2500 to 3040 m above sea level (A.S.L). Thirty-year mean annual temperature for the study area was 4.7 ºC, with large variation by season: 30-year mean July temperature was 17.9 ºC, while January was 4.9 ºC (PRISM Climate Group, 2022). Annual precipitation averaged 564 mm and exhibited a bimodal distribution, with winter and summer precipitation peaks. Synoptic weather patterns in this region are driven by westerly storm tracks, with summer precipitation delivered by the North America Monsoon (Mock, 1996).

Table 3: Site and composition of units prior to treatment. * Indicates significant differences between treatment levels. Sample sizes for site index varied as some plots contained no suitable aspen to core for age and site index determination. Conifers were cored at the remaining plots.

Site Characteristics													
		Unit 1				Unit 2				Unit 3			
	n	Mean	± S.D.	Range min	Range max	Mean	± S.D.	Range min	Range max	Mean	± S.D.	Range min	Range max
Elevation (m) *	15	2838	17	2815	2871	2858	35	2801	2903	2962	22	2895	2991
Slope (%) *	15	11.4	5.6	3	23	10.1	6.5	23	15	9.8	9.5	0	33
Aspect	15	NE - NW				NW				Variable			
Composition prior to treatment													
Total basal area (m^2/ha)	15	26	9	16	48	31	14	12	48	18	11		48
Aspen basal area (m^2/ha) *	15	15	10	0	28	19	13	0	40	5	7	0	20
Conifer basal area (m^2/ha) *	15	11	11	0	28	12	10	0	28	13	8	0	28
Aspen % total basal area *	15	58	42	0	100	61	34	0	100	24	28	0	75
Aspen site index	9-14	49	7.3	39	63	56	7.6	47	63	46	12	38	59
Understory surface fuel (Mg/ha)	15	37	20	10	68	33	13	15	54	36	12	23	62
Total biomass (Mg/ha)	15	84	20	49	127	85	26	28	133	73	21	31	124
Ground covering % forb	90	2.9	5	0	35	1.7	2.7	0	15	2.1	5.5	0	30
Ground covering % shrub	90	3.5	7.9	0	60	4.2	10	0	65	2.1	8.3	0	60
Ground covering % grass *	90	9.7	18.5	0	90	7	19	0	89	1.7	8.5	0	60
Ground covering % soil	90	1.7	6.1	0	48	1.9	7.0	0	63	1.0	5.3	0	40
Ground covering % litter/duff *	90	63.0	27.9	0	100	53	25.9	0	96	30.1	25.3	0	95
Ground % coarse woody debris *	90	9.1	14.1	0	100	19.8	20.5	0	85	33.0	25.3	0	100

Soil types generally correlated to aspect, due to solar radiation and associated vegetation: soil types on wetter, north-facing slopes were primarily characterized as Mollisols, specifically Cryoborrols, followed by Inceptisols, and Andisols, while soil types on drier, south-facing slopes were largely categorized as calcareous Entisols (Web Soil Survey, 2022). Vegetation types in this area consisted of pure and seral aspen communities, mixed conifer, and sagebrush (*Artemisia* spp.) communities (McNab et al, 2007; Rogers et al, 2014). Vegetation types within the study area largely corresponded with aspect; seral aspen stands corresponded broadly to north-facing slopes with increased moisture holding capacity, while sagebrush communities were more common on drier, south-facing slopes. Stable aspen communities were present in areas of indiscriminate slope and/or that of moderate moisture regimes. Study areas at two of three units coarsely favored north-facing aspects due to the treatment focus on mature, seral aspen stands, while one unit contained more variable aspects (Table 3). Slopes of the study units were generally moderate, with means of 10 – 12 % across the three units.

Units were similar in potential productivity, with mean site indices ranging from 46 to 56 across units. Prior to treatment, units were broadly within a late successional stage and contained high surface fuel loading across all size classes, averaging 35 Mg/ha (Table 3). Units contained varying proportions of aspen and conifer, primarily subalpine fir, and unit 3 contained lower percentages of aspen than units 1 and 2 (Table 3). Total basal area was within expected ranges, averaging 25 m^2/hectare across the three treated units. Mean total basal area of unit 1 and 2 was 26.4 and 30.8 m^2/hectare, respectively. Unit 3 exhibited lower basal area, containing a mean 18.4 m^2/hectare; differences in aspen basal area among units followed a similar trend. Ground covering percentages of forbs, shrubs, and grasses were generally low, not exceeding 15% of total ground cover, while the litter ground cover category was most common (Table 3). No management actions (including, but not limited to harvest, coppice, fuel reduction, or prescribed burns) had been employed within the recent past.

Available wildlife population estimates from the state of Utah were aggregated over the areas surrounding the study site (215,000-hectare management unit). However, we measured ungulate densities separately here (Chapter 2). Available estimates of elk density were 2,100 in both 2020 and 2021, and deer populations were estimated at 6,800 in 2020 and 6,500 during 2021 across the entire 215,000-hectare management area. Management objectives within this study area focused on wildlife: intentionally higher densities of elk and deer, and minimal (< 50) domestic cattle (*Bos* spp.), were maintained for recreational hunting purposes. To verify the state's coarse population estimates and get finer estimates of ungulates populations, pellet counts, delineated by species, and browse levels were included in protocol before and after treatment, outlined in Chapter 2.

Study design

This study area was treated in fall 2020 and sampled twice post-treatment, in August of 2021 and 2022. The study area contained three experimental units, located within 3 km of each other. A total of 18 hectares were treated with different cleanup levels; each 6-hectare, unit contained three treatment areas, adjacent to one another, consisting of a gradient of residual slash (Figure 2, Chapter 2). Three, coarse cleanup levels were applied: 1) all slash pushed into a burn pile (full or total cleanup), 2) moderate residual densities of slash, with majority of slash pushed into burn pile (partial cleanup), and 3) no residual slash pushed into burn piles (no cleanup). Vegetation sampling was omitted in no cleanup areas, due to restrictive slash levels. Initial bulldozer cutlines, surrounding the perimeters of treated units by roughly ~ 5 meters, were also monitored to determine potential impacts of heavy machinery traffic. Adjacent to treated units, 2-hectare, untreated, control areas were monitored for the duration of study.

Understory vegetation sampling was delineated by treatment levels across three units. Each unit contained four treatments: untreated, full cleanup, partial cleanup, and bulldozer cutlines. Treatments varied by ecological condition: untreated areas had intact overstories while treated areas (full, partial, and cutlines) were recently disturbed and lacked overstories. Full, partial, and cutline areas differed by post-treatment attributes, and residual slash densities varied by cleanup: full cleanup averaged roughly 9 Mg/ha outside of slash piles and 37 Mg/ha in partial cleanup areas (Chapter 2). Slash densities in cutlines most closely resembled full cleanup areas, with a mean of 12 Mg/ha, whereas dead and downed woody debris (e.g., slash) in untreated areas averaged 22 Mg/ha. Minor variance in residual slash was present across the three units (Figure 2, Chapter 2). The percent of ground occupied by plant functional types differed between untreated and treated areas, and additionally based on the treatment cleanup level (Chapter 2).

Sampling methods and plot design

A total of 630 vegetation surveys were collected at 45 plots in treated and untreated areas, with 15 plots in each of the three units. Plots were monumented and monitored for two years after treatment. At each plot, six 1 m^2 quadrats were surveyed, which quantified forb and shrub composition. Two transects were established, extending from plot center, and three quadrat surveys were conducted along each transect. The first transect extended 22.86 m (75 feet) at a 0-degree (north) azimuth and the second was generated randomly. Transects did not intersect slash piles and were stratified across the unit, ensuring adequate coverage. Each quadrat survey was taken on the right side of transects at approximately 6.1 m (20 ft), 12.2 (40 ft), and 18.3 (60 ft) from plot center. Within each quadrat, all forbs (vascular plants) and shrubs (woody plants) were identified to genus and marked as present or absent. Identification to species was included if distinguishable characteristics were present (according to Flora of North America, 1993). Grasses, sedges, and graminoids were not identified to species. Ocular estimates of functional groups were also collected within each quadrat and delineated by eight categories: four functional plant types of grass, forb, shrub, tree, and four abiotic cover types of bare soil, litter, rock, and coarse woody debris.

A total of 270 quadrats were surveyed in the first year after treatment across three units. At each unit, 90 quadrats were surveyed: 30 surveys were conducted in partial, full, and untreated areas at the five plots established in each treatment cleanup level and adjacent control area (e.g., Figure 2, Chapter 2). Across all units, a total of 90 quadrat surveys were taken in full cleanup, partial cleanup, and untreated areas. Two years after treatment, 360 quadrats were surveyed across three experimental units. An additional five plots were added per unit in original bulldozer cutlines, increasing the number of quadrats surveyed. Initial cutlines were assumed to be subjected to increased bulldozer traffic throughout the roller-felling process and were added to determine the influence of repeated movement of heavy machinery on vegetation composition. These plots were not monumented and only surveyed once, two years after treatment. The same protocol was implemented at these additional plots, with six quadrats per plot, adding 90 surveys to second year of sampling. In the second growing season, 360 quadrats were surveyed, and

270 were surveyed in the first. Across both years, a total of 630 quadrats were sampled within all treatment levels: full cleanup treatment (n = 180), partial cleanup (n = 180), bulldozer cutlines (n = 90), and untreated control areas (n = 180).

It is important to note that forb and shrub species composition was not collected prior to roller-felling, and adjacent, untreated areas were utilized as proxy for pre-treatment composition. Although controls were > 1 km from treated areas, the spatially explicit species prior to treatment remained unknown. Additionally, identification to the species level was challenging in the short-term, post-disturbance framework of this study. Many young, early pioneer forbs contained no identifiable characteristics, and some lacked leaves beyond cotyledons. If no distinct attributes were present, forbs were conservatively identified to genus to prevent incorrect classification.

Analytical Methods

Basic assessments of species frequency and diversity were compared across treatment cleanup levels and against untreated areas. Species frequency was quantified by the number of quadrats with that species present and allowed for inferences of basic relative abundance. Results were delineated by functional group (i.e., tree, forb, shrub, and grass) and compared spatially (i.e., three units) and across a gradient of ecological conditions (i.e., full, partial, bulldozer cutline, untreated areas).

Diversity was calculated at different scales using Shannon-Weiner diversity indices. This index considered both richness and evenness of species; the value produced (between 0 – 3.5) represented the level of certainty in which we can predict a given species would be a randomly chosen in a community. Uncertainty increases with diversity, and higher values indicated a more diverse, unpredictable community. This index was calculated on a plot level; the number of observations for each species were added across the six m^2 quadrats. Indices were then generated for each treatment block at the three units. At the landscape-level, indices were produced for groups with common spatial (i.e., three units) and environmental (i.e., treatment) attributes. All treatment types within one unit were aggregated to determine patterns in spatial diversity, while indices for treatment type were aggregated across the three units. Lastly, temporal indices were calculated, quantifying changes in one to two years following roller-felling.

Indicator species analysis (hereafter ISA; Dufrene and Legendre, 1997) was employed to determine differences in vegetation composition between and among treatments, accomplished by the statistical program Rstudio (Rstudio team, 2020) and the indispecies package (DeCaceres and Legendre, 2009). This analysis generated lists of species that were consistently faithful and exclusive to their respective group, which aided in determining the treatment affinity of a given species. With binary, presence-absence data and not abundance data, coefficients of association were produced for all observed species, which ranged from -1 (perfect negative indication) to 1 (perfect positive indication). The coefficient of each species was then tested for statistical significance by running a Monte Carlo randomization procedure (approximately 9,999 runs). P-values were given for each species, denoting the probability of encountering that species in a given group.

Separate ISA were performed for different functional groups (i.e., forbs and shrubs). Species that were identified only to the genus level and observations from 2021 were omitted, and ISA only included observations from two years after treatment. This allowed time for adequate species colonization and included the group of bulldozer cutline, which was not sampled in 2021. Four unique groups were employed for the separate analyses of forb and shrub indicators, with observations aggregated across the three units by four treatment levels: full cleanup (n = 90), partial cleanup (n = 90), bulldozer cutline (n = 90) and untreated (n = 90) areas. ISA requires at least one species present per observation (i.e., quadrat), and those with no forbs or shrubs present were omitted from their respective analyses, decreasing some sample sizes.

Results

Functional group: Forbs

Diversity and occurrence

Across the entire study, 37 forbs were identified in the two years following treatment; 27 were identified to species and 10 were unidentifiable beyond genus level. Nine species were unique to treated areas, four were present only in untreated areas, and 24 were common to treated and untreated areas. Of the 630 quadrats surveyed, 88 had no forbs present; 542 had one or more forbs present. The maximum unique species observed per m^2 was eight, which was observed in six quadrats. The distribution of total forb species peaked at two per m^2 quadrat, with 130 observations. The number of quadrats with zero to eight unique species varied slightly by treatment level, but generally followed a skewed positive distribution.

When all quadrats across the two years of sampling were assessed, nine forb species were unique to treated areas and four to untreated areas (Table 4). *Lappula occidentalis* was observed only in full cleanup, and *Urdica dioica* was detected once in cutline areas. Full cleanup and bulldozer cutline areas revealed more common species occurrences than partial or untreated areas. No species were unique to partial treatment areas, which contained more shared species occurrences with untreated areas. Untreated areas contained four unique forbs, one of which was *Orthilia secunda*, only present in untreated areas at unit 3.

Forb diversity varied temporally (i.e., one to two years after treatment) and spatially (i.e., units 1-3), but was less dependent on ecological condition (i.e., treated vs. untreated or among cleanup types); Shannon-Weiner indices were generally greater in units 1 and 2, and largely increased with time since treatment (Figure 9). When treated partial and full cleanup areas were aggregated and assessed by year, diversity indices increased ($p = 0.06$) from 1.37 to 1.66, and less variable indices ($p = 0.02$) were observed in the second season (Figure 9b). Mean diversity of full cleanup areas was 1.6 across both sampling years, increasing insignificantly ($p = 0.24$) from 1.47 in year one to 1.71 in year two. Partial cleanup areas exhibited slightly lower indices but increased ($p = 0.26$) by similar margins, from 1.29 to 1.57, with a mean of 1.4 across both years of sampling. Although indices were slightly lower in partial cleanup, no significant differences were observed when delineating by ecological condition (e.g., treated vs. untreated or among cleanup levels) when assessed separately as year one and year two, or when aggregated.

Despite similarities across ecological condition, indices varied spatially: when assessing composition data from both years, areas that generally favored northern aspects exhibited higher diversity indices than that of indiscriminate aspect (Figure 9). Slopes of unit 1 were broadly north facing (Table 3), exhibiting a forb diversity index of 1.84, while unit 2 favored a north-west aspect and contained a mean index of 1.83. These indices were significantly greater ($p < 0.001$) than unit 3, which exhibited a mean forb diversity index of 1.05. Unit 3 contained significantly lower forb diversity than units 1 and 2 when aggregated across all untreated and treated areas, when broken up by treatment type, and when assessed by year (all p-values < 0.001). Differences were more pronounced in year two (Figure 9b) than one (Figure 9a), and in full cleanup areas than partial or cutline areas.

Figure 9: Diversity of forbs one year (A) and two years (B) after treatment, delineated by unit and treatment level. The color of boxplot indicates treatment: full cleanup areas are represented in blue, partial is shown in orange, untreated areas are purple, and bulldozer areas are shown in green (only in Figure B, year two sampling). Significant differences in diversity between units are indicated by different letters above boxplots; the diversity of forbs across all treatments in unit 3 were significantly ($p < 0.001$) lower than those of units 1 and 2. Differences in diversity between units were less pronounced in year one (Figure A) and exhibited greater variance than year two (Figure B).

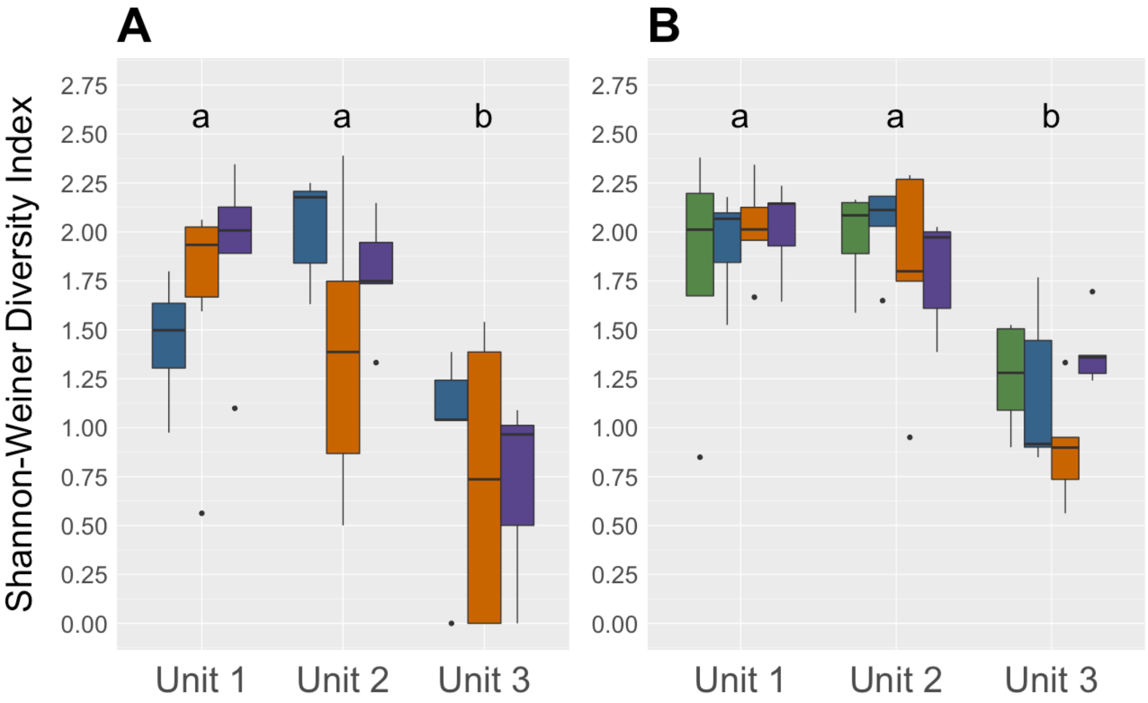


Table 4: Number of quadrats observations per forb and shrub species, delineated by treatment level and year. Lighter color indicates one year after treatment (*n* = 270), darker shading indicates two years after treatment (*n* = 360). Treatment levels differ by color: initial bulldozer cutlines are shown in green, full cleanup is blue, partial cleanup is orange, and untreated areas are shown in purple. ^ indicates forbs and shrubs identified to the genus level and * denotes non-native species. ◊ indicates updated scientific nomenclature. These species were noted by deprecated names in cited literature (e.g., Mueggler, 1988).

Functi-onal Group	Scientific Name	Treated					Untreated		Total
		Cutline	Full		Partial		Untreated		
		Year 2	Year 1	Year 2	Year 1	Year 2	Year 1	Year 2	
		n = 90	*n* = 90	*n* = 90	*n* = 90	*n* = 90	*n* = 90	*n* = 90	*n* = 630
Forb	*Achillea millefolium*	9	12	19	8	15	30	28	121
Forb	*Antennaria* spp. ^	2	0	0	1	2	0	0	5
Forb	*Aquilegia* spp. ^	4	0	0	0	2	0	0	6
Forb	*Arnica* spp. ^	0	0	0	0	0	21	21	42
Forb	*Astragalus miser*	5	12	10	9	11	20	24	91
Forb	*Chamerion angustifolium ◊*	4	4	5	7	9	2	0	31
Forb	*Chenopodium* spp. ^	65	36	71	14	38	1	1	226
Forb	*Collomia linearis*	7	7	5	0	0	0	0	19
Forb	*Cynoglossum officinale* *	1	4	1	3	0	0	0	9
Forb	*Descurania pinnata*	8	18	11	9	7	1	2	56
Forb	*Delphinium* spp. ^	0	0	0	0	0	0	2	2
Forb	*Dracocephalum parviflorum*	3	0	3	0	0	0	0	6
Forb	*Erigeron eatonii*	0	0	0	0	0	1	0	1
Forb	*Erigeron flagellaris*	3	0	2	1	1	0	1	8
Forb	*Frageria virginiana*	6	2	2	12	10	1	8	41
Forb	*Gentianella amarella*	1	0	2	0	1	0	4	8
Forb	*Geranium richardsonii*	1	1	2	3	7	5	3	22
Forb	*Hackelia patens*	0	4	0	2	1	0	0	7
Forb	*Lathyrus lanszwertii*	0	4	0	0	0	7	1	12
Forb	*Lappula occidentalis*	0	0	8	0	0	0	0	8
Forb	*Lupine* spp. ^	10	26	28	11	13	15	12	115
Forb	*Maianthemum stellatum ◊*	1	0	0	0	0	5	5	11
Forb	*Orthilia secunda ◊*	0	0	0	0	0	6	12	18
Forb	*Osmorhiza berteroi ◊*	1	2	1	12	13	12	19	60
Forb	*Phacelia* spp. ^	15	12	22	4	7	0	3	63
Forb	*Polygonum douglasii*	25	13	23	2	7	1	2	73
Forb	*Potentilla pulcherrima*	1	0	2	0	2	4	4	13
Forb	*Ranunculus* spp. ^	4	0	4	0	4	0	0	12
Forb	*Senecio integerrimus*	1	0	3	2	4	12	11	33
Forb	*Senecio* spp. ^	1	0	0	0	0	0	0	1
Forb	*Silene menziesii*	14	16	25	15	22	21	17	130
Forb	*Symphyotrichum ascendens*	3	5	5	7	2	6	8	36
Forb	*Taraxacum officinale* *	21	23	31	16	23	27	26	167
Forb	*Thalictrum fendleri*	5	0	2	0	2	6	10	25
Forb	*Thistle* spp. ^	1	0	2	0	1	1	1	6
Forb	*Urtica dioica*	1	0	0	0	0	0	0	1
Forb	*Viola* spp. ^	15	20	19	28	37	47	34	200
Shrub	*Amelanchier utahensis*	0	0	0	0	0	1	0	1
Shrub	*Artemisia tridentata*	2	0	2	0	1	0	0	5
Shrub	*Juniperus communis*	0	0	0	0	0	2	2	4
Shrub	*Mahonia repens ◊*	0	0	0	1	0	3	3	7
Shrub	*Paxistima myrsinites*	0	0	0	0	0	23	21	44
Shrub	*Physocarpus spp. ^*	0	0	0	0	0	0	1	1
Shrub	*Ribes* spp. ^	0	2	1	2	3	3	0	11
Shrub	*Rosa woodsii*	16	20	20	17	21	43	33	170
Shrub	*Rubus ideaus*	12	6	10	11	20	0	0	59
Shrub	*Sambucus racemosa*	1	0	0	0	2	0	0	3
Shrub	*Symphoricarpos oreophilus*	6	5	8	28	27	40	40	154

The number of species observed increased from 30 to 36 in the one to two years after treatment. One species (*Erigeron eatonii*) was only observed in the first sampling season, and seven additional, unique species were observed two years after treatment. The number of species observed per quadrat increased across treated areas from year one to two and remained constant in untreated areas.

The most frequently observed forbs (i.e., abundant) across the study area were *Chenopodium* spp. and *Viola* spp, present in 35% and 32% (226, 200 of 630) of quadrats in treated and untreated areas (Table 4). Other abundant forbs such as *Taraxacum officinale, Silene menziesii, Achillia millefolium,* and *Lupine* spp. were observed in > 100 of 630 quadrats (approximately 16% to 27%). Forbs varied in abundance when delineated by ecological condition or treatment (i.e., full, partial, bulldozer cutline, and untreated areas). Full cleanup and bulldozer cutline areas exhibited similar proportions of shared species. The genus *Chenopodium* remained the most abundant by a large margin, present in 60% (107 of 180) and 72% (65 of 90) of quadrats, respectively. Other common forbs such as *T. officinale, S. menziesii, A.millefolium,* and *Lupine* spp, *Viola* spp, and *Polygonum douglasii* were less abundant, but present in 10 – 30 % of quadrats in full cleanup (> 35 of 180) and cutline (> 10 of 90) areas. Partial cleanup areas contained abundant forbs such as *Chenopodium* spp, *T. officinale, S. menziesii*, and *Osmorhiza berteroi,* which were observed in > 25 of 180 quadrats (> 15%). Although less frequent ($p < 0.01$) than *Chenopodium* in full and cutline areas, *Viola* spp, was the most abundant forb in partial cleanup and untreated areas, present in 36% (65 of 180) and 45% (81 of 180) quadrats, respectively. Untreated areas contained other common forbs, including *A. millefolium*, *Arnica spp, T. officonale, S. menziesii*, and *O. berteroi*, which were present in roughly 20% - 30% of quadrats (18 to 58 of 180). *Chenopodium* spp, and *P. douglasii* were observed in ~1% (2 and 3 of 180) of quadrats in untreated areas.

Indicator species analysis

No forbs were present in 105 of 360 quadrats, and the remaining 255 observations were distributed uniformly across full, partial, cutline and untreated areas, ranging from 59 to 69 per group and contained 25 forbs identified to species. Twelve of 25 species were significantly ($p < 0.05$) associated with a particular group (Table 5). Untreated areas contained seven significant forb associations and five species were significantly correlated to treated areas; cutline and partial treatment groups each contained two significantly associated species, while full treatment areas revealed one. The strongest association was *O. secunda* to untreated areas, which generated the highest coefficient of correlation (0.38) but was only observed at unit 3.

Table 5: Indicator Species Analysis (ISA) depicts species preferences of forbs and shrubs two years after treatment; 12 of 25 species were significantly associated ($p < 0.05$) to a treatment group, indicted with shading and bolded *p*. Seven forbs were revealed as indicators of the untreated group, and five showed affinity for the treated groups. Full cleanup group contained one indicator forb, while partial and cutline groups each exhibited two forbs of indicator status. No shrubs were showed significant affinity for any treated group; two of eight shrub indicators were associated with untreated areas.

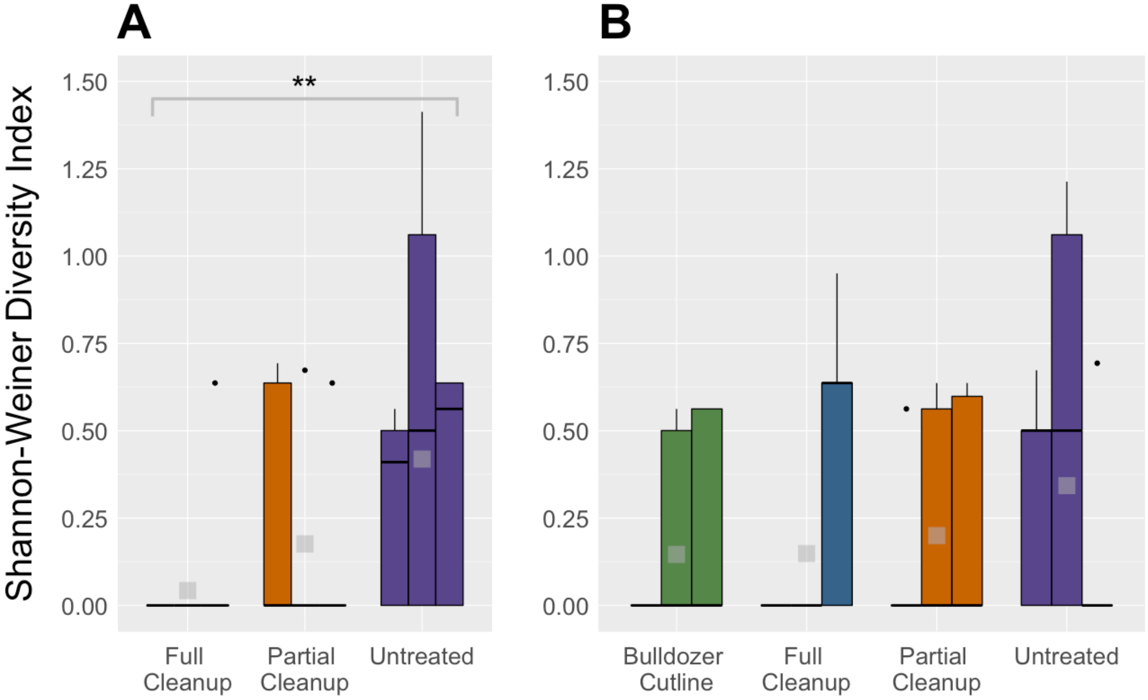
Indicator Species Analysis				
		12 of 25 forb species significantly associated		
Functional Group	Scientific Name	Treatment Groups (4)	Highest Coefficient of Association	*p*
Forb	*Achillea millefolium*	Untreated	0.18635899	**0.0071**
Forb	*Astragalus miser*	Untreated	0.24206986	**0.0009**
Forb	*Chamerion angustifolium*	Partial	0.17233383	**0.0293**
Forb	*Cynoglassum officionale* *	Cutline	0.05941953	0.3782
Forb	*Collomia linearis*	Cutline	0.19182513	**0.0113**
Forb	*Descurania pinnata*	Full	0.09034748	0.3346
Forb	*Dracocephalum parviflorum*	Cutline	0.10374285	0.1529
Forb	*Eridgeron flagellaris*	Cutline	0.08066303	0.3615
Forb	*Fragaria virginiana*	Partial	0.11807503	0.1599
Forb	*Gentianella amarella*	Untreated	0.0976724	0.2787
Forb	*Geranium richardsonii*	Partial	0.16880032	**0.0346**
Forb	*Hackelia patens*	Partial	0.11203705	0.4582
Forb	*Lathyrus lanszwertii*	Untreated	0.10599979	0.7264
Forb	*Lappula occidentalis*	Full	0.2992528	**0.0001**
Forb	*Maianthemum stellatum*	Untreated	0.1996982	**0.0123**
Forb	*Orthilia secunda*	Untreated	0.375	**0.0001**
Forb	*Osmorhiza berteroi*	Untreated	0.25621658	**0.0002**
Forb	*Polygonum douglasii*	Cutline	0.27314104	**0.0001**
Forb	*Potentilla pulcherrima*	Untreated	0.0786896	0.4336
Forb	*Senecio integerrimus*	Untreated	0.20300027	**0.0045**
Forb	*Silene menzesii*	Partial	0.07732826	0.4216
Forb	*Symphotrichum ascendens*	Untreated	0.11477814	0.1284
Forb	*Teraxicum officionale* *	Full	0.06512928	0.5325
Forb	*Thalictrum fendleri*	Untreated	0.1657188	**0.0229**
Forb	*Urtica dioica* *	Cutline	0.11298654	0.2276
		2 of 8 shrub species significantly associated		
Shrub	*Artemisia tridentata*	Cutline	0.08912639	0.6064
Shrub	*Juniperus communis*	Untreated	0.15132998	0.2684
Shrub	*Mahonia repens*	Untreated	0.15132998	0.264
Shrub	*Paxistima myrsinites*	Untreated	0.50917508	**0.0001**
Shrub	*Rosa woodsii*	Full	0.0979785	0.3733
Shrub	*Rubus idaeus*	Cutline	0.1597745	0.0837
Shrub	*Sambucus racemosa*	Partial	0.08537972	0.5264
Shrub	*Symphoricarpos oreophilus*	Untreated	0.27412579	**0.0013**

Functional group: Shrubs

Diversity and occurrence

A total of 11 shrubs were observed across the entire study; nine of 11 shrubs were identified to species and two were identifiable to the genus level. Diversity of shrubs was lower than that of forb but varied significantly ($p < 0.001$) by ecological condition: untreated areas exhibited the greatest shrub diversity, with a mean Shannon-Weiner index of 0.38, while indices across full, partial and cutline areas did not exceed 0.20 in the two years following treatment (Figure 10). Partial cleanup areas exhibited insignificantly ($p = 0.2$) greater shrub diversity than full and cutline areas. The distribution of total shrub species per quadrat followed a reverse-j distribution; the greatest number of quadrats contained zero shrubs (~ 47%, 293 of 630). The remaining 337 quadrats contained one or more shrubs species: cutline and full cleanup areas exhibited the lowest shrub presence, averaging ~35% (32 of 90, and 64 of 180) of quadrats, while partial cleanup areas contained one or more shrub in 58% (105 of 180) of quadrats. Untreated areas contained the greatest diversity and presence, with one or more shrub present in 77% (136 of 180) of quadrats. The maximum number of species in a single m^2 was four, observed in the untreated area at unit 2.

Figure 10: Diversity of shrubs one year (A) and two years (B) after treatment. The three boxplots per treatment represent the three units and colors indicate treatment: full cleanup areas are represented in blue, partial is shown in orange, and untreated areas in purple. Bulldozer cutline areas are shown in green, only sampled in year two (Figure B). The only significant difference (p = 0.008) is denoted with **, between full and untreated areas in year one (A). Transparent white boxes represent mean diversity across the three units within each treatment group.



Shrub diversity did not differ spatially, exhibiting similar indices across the three units. Temporally, diversity within treated areas increased by an insignificant (p = 0.37) margin, averaging 0.10 in year one and 0.16 in year two (Figure 10). Full cleanup areas experienced a greater proportional increase in shrub diversity (0.04 to 0.15), while partial cleanup areas showed a lesser increase (0.16 to 0.20). The number of species observed per quadrat increased across partial and full treatment areas and remained constant at untreated areas.

Shrub composition and abundance (i.e., number of observations) varied by treatment level (Table 4). Untreated areas contained four unique species; *Amelanchier* *utahensis* and *Physocarpus spp.* were both observed only once, and both in unit 2. *Juniperus communis* was uncommon and detected four times in the two sampling years. *Paxistima myrsinites* was both unique and abundant in untreated areas, present in ~25% of quadrats (44 of 180). *Rosa woodsii* and *Symphoricarpos oreophilus* were common, but not unique, to untreated areas, present in 44% and 42% (80 and 76 of 180) of quadrats.

Although untreated areas contained a greater absolute percentage of quadrats with *R. woodsii* and *S. oreophilus,* these two shrubs were the most frequently observed species in treated areas, present in 16% and 21% of quadrats (Table 4). Treated areas contained three unique shrubs, two of which were rarely observed. *Artemisia tridentata* and *Sambucus racemosa* were detected in > 3% of the total 450 treated quadrats, while *Rubus ideaus* was observed in 13% of quadrats. When delineating by treatment type, presence of *R. woodsii* and. *R. ideaus* was relatively uniform across full, partial, and cutline areas, not exceeding 10% of quadrats. Conversely, *S. oreophilus* was more common in partial cleanup areas, observed in 31% (55 of 180) of quadrats as opposed to ~ 7% in full cleanup and cutline areas.

Indicator species analysis

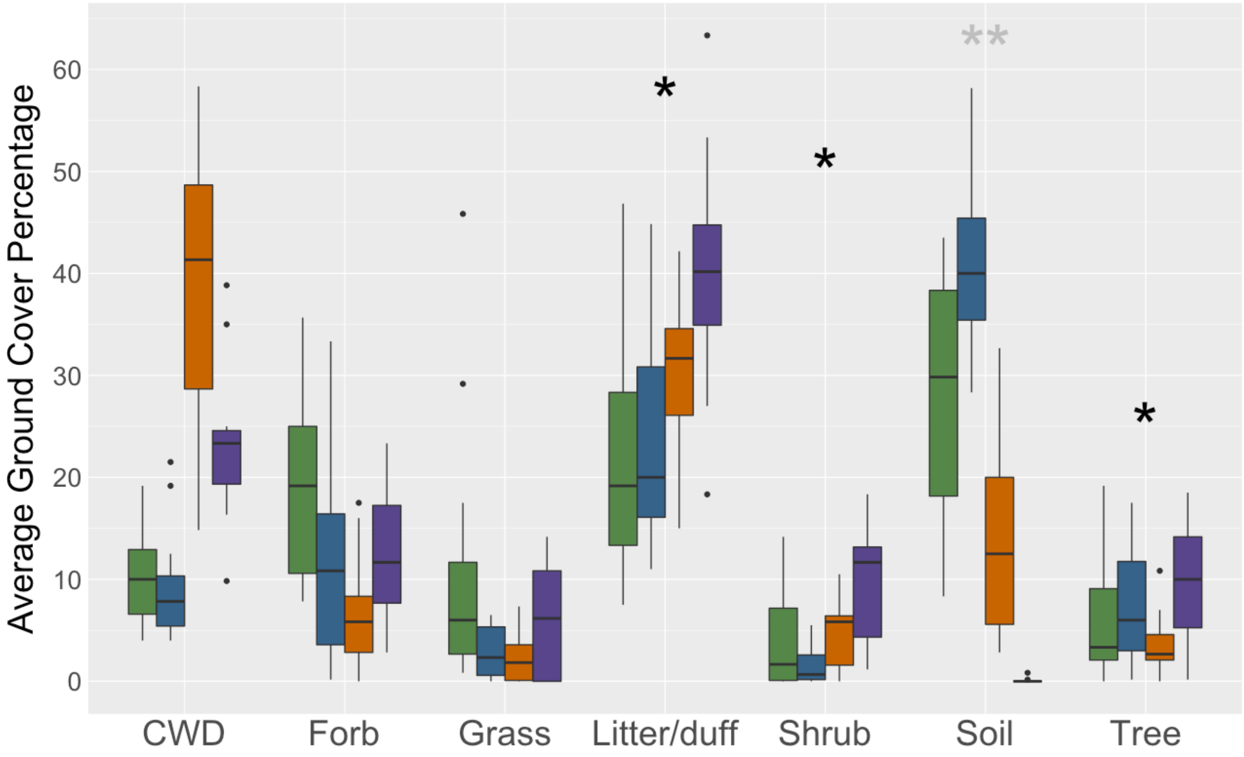
Approximately 189 of 360 quadrats contained one or more shrub identified to the species level in the second sampling season and were distributed unequally across groups. Treated areas contained more shrub-absent observations: cutline and full treatment areas contained 32 and 35 observations, respectively, and 56 of 90 quadrats in partial cleanup areas had one or more shrub present. Untreated areas exhibited the highest proportion of shrub-present quadrats (66 of 90). A total of eight species were included in analysis, and two generated significant ($p < 0.05$) associations, both to untreated areas

(Table 5). The correlation coefficient of *P. myrsinites* was 0.51, the strongest observed across the study. Association of *S. oreophilus* to untreated areas was weaker and exhibited a coefficient of 0.27. Spatially, these two shrubs demonstrated inverse patterns: *S. oreophilus* was abundant at unit 1 and infrequent in unit 3, while *P. myrsinites* was abundant at 3 and absent in 1. Unit 2 contained moderate amounts of both species. No indicator shrubs correlated to cutline, full, or partial cleanup areas, although *R. ideaus* was abundant in all treated areas and absent in untreated areas.

Ground covering percentage across functional groups

Ground cover percentages differed among cleanup levels and between untreated and treated areas (Figure 11). When both years were coarsely grouped as treated (i.e., full, partial, cutline areas) versus untreated, treated areas exhibited considerably less shrub ($p < 0.0001$) and tree ($p < 0.05$) ground cover, although disparities did not exceed 10%. Ground cover of litter/duff revealed a larger difference ($p < 0.0001$), averaging 40% in untreated areas and ~26% of treated areas. Conversely, bare soil occupied 28% of ground in treated and >1% bare soil in untreated areas, exhibiting the largest disparity ($p < 0.0001$) and illustrating the greatest ground cover change as a result of treatment. Similar amounts of coarse woody debris (20%), forb (12%), and grass (5%) ground cover were observed in treated (i.e., full, cutline, and partial combined) and untreated areas.

Figure 11: Differences in biotic and abiotic ground cover percentages in the second year after treatment. The color of boxplot corresponds to treatment level: bulldozer cutline areas are shown in green, full cleanup areas are represented in blue, partial is shown in orange, and untreated areas are purple. All functional groups contained significant differences when broken up by four treatments. When treated areas were aggregated as one group and compared against untreated areas, differences in litter/duff, shrub, and soil ground covering were observed; lighter ** indicates a significantly greater ground cover in treated areas, and a singular dark * corresponds to greater proportions in untreated areas.



When treated areas were broken down into three treatment levels (i.e., cutline, full and partial) and compared against untreated areas, significant differences were present among all functional ground cover types ($p < 0.0001$). Again, the greatest disparities manifested in litter/duff, and soil (Figure 11), but finer delineation revealed considerable differences in coarse woody debris. Generally, full and cutline areas were similar in ground cover percentages; both groups exhibited minimal (> 10%) coarse woody debris, less litter/duff, and increased mineral soil, while partial cleanup areas contained less bare soil and > 40% ground cover occupied by coarse woody debris. Shrub cover was similar between partial and cutline areas, averaging ~ 4%, but only comprised 1% in full cleanup areas. Forb, grass, and tree cover was generally lowest in partial treatment areas, differing significantly, but with less disparity (Figure 11).

Ground cover in untreated areas experienced minimal change across the two sampling seasons, while substantial temporal variability in biotic ground cover (all p-values < 0.001) was observed in treated areas. Forbs experienced the greatest increase, from 9% in year one to 16% of ground cover in year two, followed by grass (3% to 8%) and shrubs (3% to 7%). Conversely, abiotic ground cover types of bare soil and litter/duff experienced a significant decline, both averaging ~27% in the year after treatment and ~20% the following year (p-values < 0.001). Tree cover increased slightly ($p = 0.06$) from year one (5%) to two (7%), while coarse woody debris cover decreased insignificantly ($p = 0.3$), from 24% to 21% of ground cover. Forb and shrub ground cover increased by larger margins in partial than full cleanup areas. Predictably, partial cleanup areas experienced a greater decrease in coarse woody debris than full cleanup areas, while bare soil exhibited the inverse.

Discussion

Understory composition changed markedly following the roller-felling treatment; elimination of overstory resulted in prolific aspen suckering which corresponded to changes in forb and shrub composition. This would suggest roller-felling emulated stand-replacing disturbance and restarted succession. Among treatment types, variable levels of bulldozer traffic, soil scarification, and presumed compaction influenced species composition and ground cover of biotic and abiotic functional groups. Generally, scarification of mineral soil associated with treatment promoted a relatively high diversity of early successional species, primarily in the forb functional group (Figure 9). This contrasted with untreated and pre-treatment areas, as an intact canopy of aspen and conifer provided shade which fostered more forbs of late-successional status and greater shrub cover. Furthermore, these differences were reflected by a large proportion indicator species correlated to groups with these respective attributes: treated areas contained five forb and shrub species associated to early successional, disturbed conditions, while untreated areas contained nine species with affinity for later successional environments (Table 5). Despite substantial differences in composition, forb diversity across all groups remained relatively constant, as late successional species were proportionally replaced by fast-growing forbs of early successional status after treatment. Conversely, shrub diversity and ground cover were considerably higher in untreated areas (Figures 10 and 11); within treated areas, shrub cover and diversity varied by treatment types and associated attributes (i.e., the severity or level of cleanup).

Forbs

Contrasting forb composition between treated and untreated areas revealed preferences in ecological condition, demonstrated by a large proportion of forbs showing indicator status to a distinct group, and by differences in unique and abundant forbs and within groups. Time since stand-replacing disturbance determined composition: communities in recently disturbed (e.g., one or two years) areas differed from those that remained undisturbed for > 200 years. Severity (e.g., more machinery traffic, no residual slash and/or complete soil scarification) of roller-felling impacted composition, and greater severity increased divergence from pre-disturbance composition. Forbs that departed with disturbance appeared to have been proportionately replaced, reflected by similar diversity indices across groups (Figure 9). Shade tolerant (i.e., *O. secunda*, *O. berteroi*), browse resistant (i.e., *A. miser*, *A. millefolium*) forbs corresponded to untreated areas, and early-colonizing, light-favoring species (i.e., *P. douglasii*, *Chenopodium* spp.) preferred recently disturbed, roller-felled areas, which also contained unique native and non-native forbs.

Understory succession of montane, seral aspen communities (per Rogers et al, 2014) is not explicitly outlined, but remains best summarized in the habitat or community types compiled by Mueggler (1988). Generally, forbs that were abundant and/or indicators to untreated areas in our study have been correlated to late-stage seral aspen or conifer dominated stands (e.g., Mueggler, 1988; Mauk and Henderson, 1984). Many of these forbs are known to decline or depart after disturbance and were infrequently observed in post-fire (e.g., *T. fendleri,* per Mueggler and Bartos, 1981) or post-harvest studies (e.g., *M. stellatum,* per Crouch, 1983).This suggests treatment had a comparable, negative effect on many later-successional forbs. Although relatively predictable, the forb composition validates the successional status of stands prior to treatment and is suggestive of potential productivity. Furthermore, shifts in abundance of forb species that are common to pre- and post- treatment environments will indicate a given species' response to roller-felling.

ISA revealed seven species associated with untreated areas, six of which have been explicitly linked to undisturbed seral aspen communities of later-successional status (Table 5). Decline or departure of these species has been observed following fire, harvest, and/or windthrow, which allows for conservative comparison against roller-felling and more sound interpretation of impact. Decreases in *Thalictrum fendleri* and *Frageria virginia* after clear-cut harvest have been observed near our study site (Mueggler and Bartos, 1977), and *Astragalus miser* and *T. fendleri* declined following wildfire (Mueggler and Bartos, 1981); our study revealed both *A. miser* and *T. fendleri* as indicators of undisturbed, or untreated, areas. *Osmorhiza berteroi* and *A. millefolium* were correlated to untreated areas in our study, both of which are known to increase with greater conifer dominance in seral aspen forests (Mueggler, 1988). *Maianthemum stellatum* is known to decline following harvest (Crouch, 1983) and may leave the system entirely with the introduction of salvage logging (Rumbaitis, 2006), which is supported in our study by the association of *M. stellatum* with untreated areas. Presence of *Orthilia secunda* is associated with conifer dominance, and this forb is known to be intolerant of disturbance (Haussler et al, 2002), corroborating *O. secunda*'s indicator status in our study. *Senecio integerrimus* was the only indicator not explicitly linked to a later successional stage but has been observed in seral aspen understories (*sensu* Mueggler, 1988), although appearing somewhat infrequent. However, other members of the *Senecio* genus (e.g., *S. serra* or *S. triangularis*, per Mueggler, 1988) remain prevalent understory constituents throughout seral aspen stand succession.

Aside from *S. integerrimus*, the six understory species correlated to untreated areas are commonly associated with subalpine fir dominant stands with minimal, aging overstory aspen (Mauk and Henderson, 1984; Mueggler, 1988). Although treated stands were assumed to be of late-successional stages, this may suggest status closer to a successional climax. Understory conditions of untreated areas were characterized by an accumulation of dead and downed woody debris, a thick layer of conifer litter that is both nutrient-poor and slow to decompose, and limited soil moisture holding capacity (e.g., St. Clair et al, 2013), as suggested by the forbs revealed in ISA (Mauk and Henderson, 1984; Mueggler, 1988). Centuries of undisturbed succession created a less productive, dark understory that supported a unique community, comprised of fewer slow-growing, low-statured forbs, which can foster lower levels of diversity than prior successional stages (Mueggler, 1988; St. Clair et al, 2013), and was reflected by relatively low diversity indices observed in untreated areas. Variability in environmental condition (e.g., light availability, ground cover, soil quality) explained the differences in composition between untreated and treated areas, alongside the large proportion of indicator forbs observed in our study.

Fewer indicator forbs were associated to roller-felled areas, but differences in machinery traffic, scarification, and slash retention among full, partial, and cutline areas suggested these forbs exhibited an ecological preference (e.g., degree of soil scarification, residual slash), which alludes to various impacts of treatment attributes. Indicators of cutline areas were *P. douglasii* and *Collomia linearis* (Table 5), both of which are inconspicuous, short-statured, and favor disturbed soils (Mueggler, 1988). Abundance of

P. douglasii increased following clearcut harvest (Mueggler and Bartos, 1982), while establishment and persistence correlated to higher fire severity (Romme et al, 2016). *Polygonum douglasii* was observed in >25% of plots in cutline and full cleanup areas, in contrast with infrequent (~1%) presence in partial cleanup areas, suggesting higher severity of mechanical disturbance may also promote initial *P. douglasii* establishment. Forb composition in cutlines more closely resembled full cleanup areas (e.g., abundant *Chenopodium* spp. observed in > 60% quadrats), presumably due to similar amounts of residual slash and soil scarification (Figure 11). Full cleanup areas contained one indicator, *L. occidentalis*, known to colonize highly disturbed, drier environments (USDA, NRCS, 2022). Dynamics of *L. occidentalis* in our successional framework were limited (e.g., Harper et al, 1996), but lack of mention in relevant literature may suggest a short-lived role, relegated to earliest succession and followed by quick departure upon initial shading and/or competition.

Two native forbs were indicators of partial treatment areas (Table 5). As implied by the common name of fireweed, *Chamerion angustifolium* is a notorious colonizer of burned areas, while harvest promotes a lesser increase (Pavek, 1992; Haney et al, 2022). Presence will likely be ephemeral, as *C. angustifolium* is an early successional, shade-intolerant forb, and considered high value forage for mule deer (Haney et al, 2022). Despite shared observation in untreated areas, *Geranium richardsonii* was unexpectedly revealed as an indicator to a treated area. In contrast to *C. angustifolium, G. richardsonii* is commonly absent following fire and is typically associated with later-successional stages, sharing a guild with untreated indicators of *T. fendleri* and *O. berteroi* (Esser, 1994; Mueggler, 1988; Rumbaitis, 2006). It remains unclear if increased slash or decreased soil disturbance is the mechanism behind *G. richardsonii*'s persistence and/or establishment, but association to partial cleanup areas broadly suggests lower degrees of severity applied via roller-felling can promote a later successional forb.

Many of these findings may be explained by disturbance severity. Although challenging to define across disturbance types, increased severity is broadly understood as greater environmental impact. Partial cleanup areas were ameliorated by increased slash, less scarification, and reduced machinery traffic, resulting in lesser change (i.e., decreased severity), and supported later-successional composition. Greater relative abundance of mid- to late- successional forbs, such as *F. virginia, O. secunda,* and *G. richardsonii* (Table 4), in partial cleanup areas suggests lower severity decreased divergence from pre-disturbance conditions (Halpern, 1988). *Osmorhiza berteroi* and *F. virginia* persistence decreased with greater fire severity (Romme et al, 2016), while *G. richardsonii* has been correlated to blowdown events (i.e., moderate severity), and decreased with additional salvage logging (Rumbaitis, 2006). Composition of early successional species within partial cleanup areas may also suggests decreased severity: *C. angustifolium* is moderately tolerant of disturbance and declined with greater post-harvest site preparation (Haussler et al, 2002). This interpretation is speculative, and future monitoring is needed to determine if these later-succession species persist beyond the early successional stages examined in this study.

The second most frequent forb was *Viola* spp, observed in 32% of all quadrats across our study, but most common in untreated stands (Table 4). Characteristically low stature and few distinguishing qualities restricted identification to species, but classification to the genus is not uncommon (e.g.,Crouch, 1983; Romme et al, 2016).

This native forb of mid- to late- successional status occupies understories beneath both aspen and conifer (Crouch, 1983; Mauk and Henderson, 1984; Mueggler, 1988). Almost half (45%) of the quadrats in untreated understories contained *Viola* spp. followed by 28% in partial, 21% in full, and 17% in cutline areas, suggesting greater decline and divergence from pre-disturbance composition with increasing severity.

Conversely, increased severity of roller-felling promoted greater abundance of early successional forbs, especially species known to favor more disturbed conditions, such as *Descurania pinnata* and *Chenopodium* spp, both of which were more common in full cleanup and cutline areas than partial (Table 4). *Descurania pinnata* is a native, early post-fire colonizer that declines along a successional gradient and does not persist into late-seral stages (Howard, 2003), explaining minimal presence in untreated areas. Increased disturbance severity can delay or decrease colonization via seedbank mortality (Howard, 2003), but lack of fire and greater severity of mechanical disturbance appeared to promote *D. pinnata* establishment.

Although *Chenopodium* spp. was present in < 1% of all untreated quadrats, it was extremely prevalent in treated areas and remained the most observed forb in our study (Table 4). While generally low-statured, the growth habit of *Chenopodium* varies based on environment; when exposed to high light and bare soil following disturbance, this early-successional forb exhibits sprawling growth and creates a carpet-like covering across swaths of highly disturbed substrate. *Chenopodium* is also annual, making this expansive growth pattern increasingly advantageous and explaining presence in 50 % of all treated quadrats. Greater abundance of *Chenopodium* corresponded to increased treatment severity (i.e., 72% cutline, 60% full, and 29% partial quadrats), suggesting this genus is highly tolerant of machinery traffic and soil disturbance. Although unidentifiable beyond genus, literature (e.g., Mueggler, 1988; Debyle and Winokur, 1985) and regional vegetation data (i.e., State of Utah Big Game Range Trend Study, per Summers et al, 2006) suggested *Chenopodium fremontii*, which can increase slightly after fire, however, no studies corroborate a prolific post-disturbance colonization. Our findings suggest the dynamics associated with greater severity (e.g., soil scarification, compaction, decreased residual slash) of mechanical disturbance reduce competition and created conditions favorable for *Chenopodium* establishment.

Another common genus was *Lupine* spp, present in 18% of all quadrats, but more abundant in treated (20%) than untreated (15%) areas (Table 4). *Lupine* spp. is habitual resident of aspen dominated understories, and decreases with conifer presence (Mueggler, 1988; DeByle and Winokur, 1985), suggesting mid-successional status, and greater prevalence in treated areas suggests roller-felling promoted abundance of this native genus. Although less common, treatment appeared to promote the *Aquilegia* genus, which was observed in treated areas and absent in untreated stands. Lack of flowering limited identification, but speculation by regional vegetation data (i.e., State of Utah Big Game Range Trend Study, per Summers et al, 2006) suggests *Aquilegia coerulea,* which increased following disturbance of fire (Mueggler and Bartos, 1981) and is a notable forb in aspen dominated stands (Mueggler, 1988). Despite identification beyond genus, all *Aquilegia* species are native, suggesting this early successional forb was reintroduced with roller-felling.

Forb diversity was similar across the gradient of ecological conditions (i.e., untreated, full, partial, cutline areas), suggesting roller-felling exerted minimal impact on diversity. Early successional forbs were proportionately replaced by later-successional species, demonstrated by the suite of new, abundant forbs revealed via ISA. However, forb diversity varied spatially: unit 3 exhibited similarly low indices across all treatment types, while indices across treatments at units 1 and 2 were collectively higher (Figure 9). This could suggest diversity, regardless of successional status, is more contingent on inherent site quality; more specifically, early successional diversity may be less dependent on ecological conditions (e.g., density of slash or soil compaction) following disturbance.

Despite comparable indices, the components that comprised these similar levels of diversity differed greatly, and simply quantifying raw diversity omits the nuance associated with individual species. Generalists that are highly tolerant of a broad range of disturbed conditions were larger constituents of full and cutline areas (e.g., *P. douglasii, Chenopodium*), and increased severity of roller-felling may promote more generalist species composition. Consequently, post-treatment conditions may omit or lessen abundance of specialists that have evolved in these systems, as they require more narrow niches, such as specific post-fire substrate. Not only are specialists more susceptible to extinction when conditions are altered (Tilman, 1994), but replacement of specialist species by generalists can lead to functional homogenization and a decrease in diversity (Olden et al, 2004). Further investigation into the life history traits of the species observed, and those conspicuously absent, in treated areas could illuminate additional impacts of roller-felling on community composition.

Absence of *Cynoglossum officinale* and *U. diocia* in untreated areas suggests non-native forbs can be introduced with treatment (Table 4). *Urdica diocia* can produce large quantities of seed with long-term dormancy (Carey, 1995), and despite one quadrat detection, future monitoring is merited to determine persistence or potential expansion. Early successional presence of *C. officinale* in treated areas could have long-term consequences on understory development. Drought-resistance, shade-tolerance, and a thick, deep taproot gives *C. officinale* increased stress tolerance, allowing for decades of persistence after disturbance (Zouhar, 2002; Upadhyaya et al, 1988). Additionally, *C. officinale* prefers post-harvest substrate over burned soil (Dodson and Fiedler, 2006) and it would appear the bare, unburned soil exposed via roller-felling created conditions preferable for introduction.

Although we quantified the short-term (< two years) effect of treatment, early composition will influence long-term understory succession. The annuals *C. linearis* and *P. douglasii* are correlated to chronic browse exposure (Mueggler, 1988), and early establishment of these forbs in treated areas would indicate a decline is unlikely. Speculation of increased ungulate densities within this area, as suggested by Rogers and Mittanck (2014), was corroborated by disproportionate rates of apical stem removal and increased pellet observations (Chapter 2), and was further validated by an abundance of less palatable forbs (e.g., *A. millefolium, A. miser, T. officinale*) in untreated areas. The compounding effects of ungulate browse could reduce ecosystem function over time: browse of aspen suckers reduces overstory recruitment potential, and browse of more palatable forbs (e.g., *C. angustifolium, Lupine* spp.), can decrease understory diversity and richness (Bartos and Mueggler, 1977; Augustine and McNaughton, 1998). Further monitoring of these sites is needed to determine the interaction between roller-felling, browse, and understory community development.

The impact of ungulates is not limited to herbivory, and their role as seed dispersal agents has been widely documented (e.g., Bartuszevige and Endress, 2008; Parks et al, 2008; Albert et al, 2015). Ungulates function as vectors of dispersal mainly via consumption and defecation of seeds, or endozoochory (Janzen, 1984; Baltzinger et al, 2020), which alters understory structure and composition (Hobbs, 1996). At our study site, increased elk density for hunting remains the primary landowner objective, and minimal presence of domestic cattle is maintained (< 50 across > 80,000 ha) to encourage ungulate forage. Management actions were applied successfully, putatively observed by the contrast of minimal elk evidence (i.e., browse, scat) in adjacent landowner areas (Chapter 2). While cattle favor grass as forage, diet preferences of elk and deer facilitate greater dispersal of forbs, both native and non-native (Bartuszevige and Endress, 2008; Parks et al, 2008). Our study site is private and remote, and the forb composition at present contains a relatively few (i.e., two) non-native species. Fortunately, both are unpalatable (i.e., *C. officinale*, *T. officinale*) and less likely to be browsed and dispersed. However, potential relationships between ungulate populations and non-native species at a given site must be explored if roller-felling is to be considered.

Additionally, ungulates can alter understory composition by facilitating seed dispersal through fur-epizoochory, as adhesive seeds can attach to hair and fall off as they move across landscapes (Janzen, 1984; Baltzinger et al, 2020). This is largely dictated by life history traits: seeds with elongated or hooked appendages have increased probability of movement (Kulbaba et al, 2009; Albert et al, 2015; Baltzinger et al, 2020), and the barbed seeds, or burrs, of the genus *Cynoglossum* are particularly adhesive. Domestic cattle were identified as major vectors of non-native *C. officinale* dispersal in North

America, as burrs attach to the face when grazing (De Clerck-Floate, 1997). Although low cattle densities at our site may limit dispersal, this could be negated by high densities of other ungulates. Deer are known vectors of *Cynoglossum* (i.e., *C. virginianum* and *C. germanicum*) in its native range, and prolific expansion of the once rare *C. germanicum* was attributed to traits of epichory, toxicity, and the ability to colonize highly disturbed environments (Shiponeni and Milton, 2006; Boulanger et al, 2011; Baltzinger et al, 2020). Though not explicitly linked to *C. officinale* dispersal, elk and deer could theoretically function as vectors as they move across treated areas and browse on aspen stems. While speculative, this again emphasizes importance of context: increased ungulate populations (i.e., high cattle density) combined with non-native (i.e., *C. officinale*) presence and/or proximity must be considered prior to roller-felling.

The short-term, post-disturbance framework of this study posed challenges for forb identification, as many young forbs lacked leaves beyond cotyledons. With no distinguishing attributes, ten forbs were only identified to the genus level. Although this limits our findings, the genera observed across our study had similar life history traits, and at least one species per genus was known in proximity to our site. This allowed for conservative speculation of a genus' progression and role in understory species succession. Although our findings were not unimportant, the two-year frame limits the understanding to the short-term impact, illustrating the necessity for long-term monitoring of these areas if this treatment is to be applied.

Shrubs

Untreated areas contained two indicator species and greater shrub presence (Table 5, Figure 11), indicating treatment decreased shrub cover. Increasing severity of roller-felling appeared to reduce shrub cover: partial areas experienced a lesser change in ground cover and species composition than full or cutline areas, demonstrated greater abundance species shared with untreated areas (e.g., *S. oreophilus*). Increased slash and/or less mineral soil exposure may foster favorable conditions for establishment, as shown by species unique to treated areas, but the increased height of shrubs common to untreated areas would anecdotally suggest less machinery traffic allowed for persistence throughout the roller-felling process.

Most late-stage seral stands contain a sparse shrub layer, especially less productive stands in our region (Warner and Harper, 1972), and although untreated areas contained greater diversity and abundance, shrubs only comprised ~ 10% ground cover. Despite minimal detection in quadrats (Table 4), *A. utahensis, J. communis,* and *Physocarpus* spp. were observed visually throughout untreated stands. These shrubs are relatively shade-intolerant and slow-growing, explaining absence in treated areas. These species occupy understories beneath mature aspen and conifer, indicating mid- to late-seral successional status, and infrequency could suggest senescence and exclusion via seral stand development (Mauk and Henderson, 1984; Debyle and Winokur, 1985; Mueggler, 1988). *Amelanchier utahensis* and*, J. communis* reproduce primarily by seed, while *Physocarpus* spp. sprouts vegetatively from intact rhizomes and is considered a pioneer following fire in its northern range (Habeck, 1992). Disturbance to the soil profile throughout the roller-felling process may have damaged or removed *Physocarpus* spp. roots, delaying regeneration, and future monitoring is needed to determine if absence is ephemeral.

Untreated areas contained two indicator shrubs and several unique species that are common in early- and late- stage seral aspen, along with conifer dominated understories (Mauk and Henderson, 1984; Debyle and Winokur, 1985; Mueggler, 1988). *Paxistima myrsinites* and *Mahonia repens* are characteristic of later-successional status (Debyle and Winokur, 1985; Snyder, 1991; Ulev, 2006), and *P. myrsinites* was an indicator of untreated areas, exhibiting the strongest correlation coefficient (0.51, Table 5) across our study, while *M. repens* was present, but less frequent. *Symphocarpus oreophilus* was correlated with untreated areas, but observed in treated areas as well, and is known to occupy understories of both early successional aspen and conifer stands. Similar to forb indicators, *P. myrsinites* and *S. oreophilus* confirm the successional status of stands prior to treatment, allowing for roller-felling to be assessed against other disturbances.

Patterns of occurrence suggest decreased severity promoted persistence and/or establishment of *S. oreophilus*, as this shrub was observed in almost 50% of untreated area quadrats, 31% of partial, and > 7% in full cleanup and cutline area (Table 4). *Sympocarpus oreophilus* establishes in early stages and can coexist with seral species, but rarely occupies densely shaded conifer understories (Aleksoff, 1999; Mauk and Henderson, 1984; Mueggler, 1988), and exhibits a variable response to disturbance. Greater fire severity can reduce *S. oreophilus*, while low severity can promote vegetative sprouting if roots remain undamaged (Aleksoff, 1999; Bartos and Mueggler, 1981). Harvest can initially reduce presence, followed by abundance that exceeds pre-treatment levels within > five years (Crouch, 1983), or have no effect (Bartos and Mueggler, 1982). It would appear *S. oreophilus* is moderately tolerant of soil disturbance, but patterns of abundance would suggest the dynamics associated with increased roller-felling severity (e.g., increased scarification) reduced vegetative reproduction potential and subsequent abundance.

Rosa woodsii was present in 42% of untreated quadrats, suggesting an overarching affinity for undisturbed conditions. Furthermore, equal abundance (~20%) across treated groups would suggest minimal discretion in post-disturbance condition (Table 4). This early-successional shrub reproduces vegetatively, but its response to mechanical disturbance remained unclear. Clear-cutting can have minor impact (Bartos and Mueggler, 1982; Crouch 1983; Selmants, 2003) on *R.woodsii*, while greater degrees of site preparation (e.g., removing slash and duff to exposed mineral soil) can increase presence (Wilson, 2014; Haussler et al, 1990), while additional salvage logging activities can negatively affect this shrub*,* which showed preference for blowdown or undisturbed stands (Rumbaitis, 2006). Uniform abundance across treatment types suggests *R. woodsii* is relatively unaffected by varying residual slash or heavy machinery traffic and is generally tolerant of severe mechanical disturbance.

Since ISA generated species that were faithful and exclusive to a single group, species that were common in more than one treatment group (e.g., full and partial areas) were not detected as indicators, despite prevalence. *Rubus ideaus* was insignificantly (p = 0.08, Table 5) associated with cutline areas, but present in 11% of treated quadrats and absent in untreated areas (Table 4). When cutline, full, and partial cleanup areas were aggregated, *R. ideaus* was strongly correlated to this singular treated group, indicating roller-felling introduced an early successional shrub. *Rubus ideaus* reproduces vegetatively and colonizes burned sites but can respond positively to salvage logging with a high tolerance of soil disturbance (Tirmenstein, 1990; Lain et al, 2008), and presence in bulldozer cutlines and full cleanup area confirmed an increased tolerance.

Since dominance is short-lived (> 10 years), absence of *R. ideaus* in untreated areas was unsurprising, as many studies note little to no presence pre-disturbance (Peltzer et al, 2000; Selmants et al, 2003). Conversely, presence of *Sambucus racemosa* was rare, but also unique to treated areas (Table 4). Reproduction of *S. racemosa* post-disturbance is primarily vegetative; shade-intolerance and lack of establishment by seed explains absence in untreated areas. Presence of a native, early successional shrub may suggest healthy development, but infrequency warrants future monitoring to determine if this species will increase or persist. Abundance of *R. ideaus* and presence of *S. racemosa* suggests treatment can introduce shrubs excluded from later-successional stages, reinitiating understory succession.

The five observations of *A. tridentata* were limited to treated areas at unit 3. Aspen and *A. tridentata* are known to coexist, as their ecotones converge on an elevational gradient (Debyle and Winokur, 1985; Mueggler, 1988), and topography may explain patterns of *A. tridentata* occurrence. Vegetation of this plateau is determined by aspect: forested, seral aspen stands occupy northern, wetter slopes, while south and/or more indiscriminate, gradual slopes are drier and common hosts for sagebrush (e.g., *Artemisia* spp.) communities. Units 1 and 2 favored north facing slopes, while unit 3 was relatively flat and exhibited variable aspect (Table 3), with *Artemisia* communities immediately adjacent to treated areas. This suggests roller-felling could promote introduction of nearby shrub species, which highlights the importance of assessing neighboring composition prior to treatment. Mature aspen stands with > 10% *A. tridentata* can be at risk for decline or conversion away from aspen cover (Bartos and Campbell, 1998), and long-term monitoring is needed to determine *A. tridentata* persistence or expansion. It is important to note that adjacent, untreated stands served as a proxy for pre-treatment composition, and data on the spatially explicit species in roller-felled areas was not collected, limiting this interpretation.

Residual slash densities were greatest in partial cleanup areas, and slash retention is known to promote shrub cover (Rumble et al, 1996). Despite similarly low slash densities, cutline areas exhibited greater shrub cover and diversity than full cleanup areas (Figure 10). This could be due to location, as most cutlines were located on the perimeter of treated areas and adjacent to intact stands. Surrounding canopies could provide shade similar to that of slash, while proximity to a mature stand could increase the likelihood of seed dispersal. However, lower shrub height within cutlines (as opposed to partial areas) was anecdotally observed, and these areas contained a decreased proportion of late-successional shrubs (e.g., *S. oreophilus*) and slightly lower diversity. This suggests machinery traffic could reduce diversity and persistence, while less soil disturbance can facilitate shrubs of mid- to late- successional stages.

Woody species (i.e., shrubs) grow slower than vascular plants (i.e., forbs), and the relatively low covering of shrubs in treated areas was unsurprising. Slow growth also explains the difference in diversity across treatment types, as roller-felling removed all overstory vegetation, and in full and cutline areas, further scarified the ground which limited the persistence of pre-treatment species. Although metrics of diversity did not vary by unit, composition differed; unit 3 contained greater proportions of shrubs typically associated with less productive sites (e.g., *P. myrsinites*, per Warner and Harper, 1972), and corresponded to decreased forb diversity. The faster growth rate of forbs may have revealed an immediate difference in site quality, while differences in shrub diversity of could experience a delay and manifest in later successional stages. The two-year frame limits interpretation, but long-term monitoring of may elucidate relationships between diversity of different functional groups across roller-felled units.

The percentage of shrub cover within treated areas increased in the one to two years after treatment. However, partial cleanup areas experienced a greater increase, which may indicate a longer recovery in full cleanup areas. Complete elimination of pre-existing vegetation via scarification and/or increased machinery traffic could delay understory succession, and future monitoring of temporal differences in ground cover among treated areas is warranted to explore relationships between severity and recovery. An increase shrub cover was accompanied by decreases in abiotic cover groups of bare soil and coarse woody debris, while other biotic cover groups of grass, tree, and forb increased in the one to two years after treatment. These patterns are indicative of recovery, and the successional trajectories of roller-felled areas appears to be in accordance with other disturbances, but the short-term nature of this study warrants additional monitoring to understand the long-term impacts of treatment.

Management implications

The changes in understory composition observed after roller-felling would indicate that treatment functioned as a stand-replacing disturbance that effectively restarted succession. High densities of aspen suckers (Chapter 2) and colonization by early successional native forbs and shrubs across disturbed areas emulate the dynamics observed after traditional treatment (e.g., clearcut harvest). However, certain attributes of roller-felling emphasize the necessity for contextual understanding prior to application. Increased soil disturbance and lack of burning associated with roller-felling can promote non-native species (e.g., *C. officinale*); less remote areas or those with increased non-native presence slated for treatment could be subject to greater densities of non-native establishment. High densities of ungulate can negatively alter understory composition, succession, and structure; sustainable densities must be maintained on the landscape if treatment is to be considered.

Additionally, inherent differences between roller-felling and other disturbances cannot be overlooked. Although mechanical disturbances (e.g., harvest, roller-felling) can function as a stand-replacing proxy for fire, these methods omit heat and combustion, subsequently excluding a critical process of nutrient cycling that increases the availability of C, N, and P (Debano, 1991; Song, 2002). Post-fire soils differ from that of mechanical disturbance, and numerous studies (e.g., Hart and Chen, 2008; Haussler and Bergeron, 2004) explicitly contrast community composition in aspen systems following fire and harvest. Composition can differ initially (e.g., varying abundance of early post-fire specialists, per Haussler et al, 2007), which can encourage alternate successional pathways and lead to long-term divergence (Hart and Chen, 2008). The compositional differences observed between treated areas may impact long-term understory development, and future monitoring combined with supplementary analysis (e.g., ordination) is needed to determine if roller-felling poses a long-term concern for understory development.

Mechanical disturbance also induces changes to soil's physical properties, and the increased disturbance associated with roller-felling could have additional consequences that we were unable to quantify in this study. Harvest and associated compaction followed by severe scarification reduced available N, P, and microbial biomass (Tan et al, 2008), while forest floor removal (i.e., scarification) alone also reduced microbial biomass (Tan et al, 2005). Additionally, the constant movement of heavy machinery throughout roller-felling can mix and displace soil to a greater degree than traditional harvest, concurrently altering biotic components (e.g., fine roots or bacteria) within the upper layer and potentially removing them from the system completely. Additional soil sampling (i.e., soil nutrient composition) could more comprehensively quantify treatment's effect on soil and subsequent vegetation, and differences between treatment types could indicate attributes of roller-felling that are most consequential.

Composition varied across a gradient of ecological conditions within treated areas, and our results suggest that greater severity can increase divergence from initial composition (per Halpern, 1988). Retaining slash, decreasing machinery traffic, and/or reducing soil scarification can promote persistence and/or establishment of mid-to-late successional species by causing a lesser change from pre-treatment conditions. This allows for greater understory diversity, healthy stand progression, and subsequent ecosystem function. Furthermore, this influences the economic feasibility of implementation, and suggests that complete cleanup is not imperative to accomplish treatment objectives. Retaining low densities of slash on the landscape has minimal negative impact on aspen regeneration (Chapter 2), while encouraging healthy understory composition and recovery.

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CHAPTER IV

CONCLUSION

The effects of roller-felling were nuanced, but were generally in accordance with our hypotheses, as high densities of young aspen suckers and early successional vegetation quickly colonized treated areas. This is concurrent with the understanding of early-successional aspen ecology and associated understory dynamics, suggesting roller-felling largely emulated other stand-replacing disturbances and could be applied contextually as an alternative treatment to regenerate aspen, restart succession, and reduce fuel loading. The high densities of regeneration observed may suggest aspen root systems are more tolerant of severe soil disturbance than initially thought and indicate that low proportions of aspen prior to roller-felling can still constitute self-replacing densities. Our findings also suggest that regeneration is dependent on the amount of residual slash and the stochastic variable of precipitation in the year after treatment, emphasizing that high densities and self-replacement should not be unequivocally assumed after treatment. Initial densities are one of many criteria dictating stand progression, and the unsustainable levels of browse observed at one of two sites will likely hinder overstory recruitment, highlighting the importance of context in management application.

Regeneration was accompanied by a suite of early-successional species characteristic of recently disturbed aspen stands. Understory composition in the two years after treatment indicated a successional trajectory concurrent with other stand-replacing disturbances, suggesting reinitiation of understory succession. Early successional forbs that may have been present in more diverse understories of earlier successional stages, and absent in later stages preceding treatment, were observed following treatment, suggesting roller-felling may introduce native species that were dormant or removed from the seedbank. Conversely, formerly excluded non-native forbs can also be introduced following treatment. Composition was also dependent on roller-felling severity: less machinery traffic, scarification, and increased residual slash allowed for the persistence of some pre-existing vegetation, while the inverse promoted a more pronounced compositional change. Nonetheless, our findings suggest most well-established principles of early aspen succession apply in the context of roller-felling, and treatment could promote healthy stand progression of seral aspen communities. Although the short-term (i.e., two years) nature limits interpretation, this study set the groundwork for long-term monitoring of roller-felled sites, which furthers our understanding of regeneration dynamics and early successional aspen ecology, applying to forest and fire management across the western US.