

Are soil changes responsible for persistent slash pile burn scars in lodgepole pine forests?

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ABSTRACT

Pile burning is the most common method of logging residue disposal in Rocky Mountain forests. Though the high temperatures reached during burning affect numerous soil properties in the short term, the longer-term effects of the practice are less clear. We previously identified a 50-year time series of burn scars created after clear cut harvesting in lodgepole pine stands where we reported sparse tree colonization across the entire chronosequence. Here we analyzed soil nutrients and chemistry and conducted *in situ* and greenhouse seedling bioassays to determine whether edaphic factors or poor seedling performance explain the pattern. Pile burning had a lasting effect on soil pH, but nutrient availability was 2–3 times higher in burn scars compared to unburned forest soils for many constituents and planted pine seedlings had good survival and growth. However, seedling growth was slightly less in burn scars compared to unburned soils indicating suboptimal soil pH or other belowground factors may contribute to sparse tree colonization of the openings. For example, seedling survival and ectomycorrhizal fungi colonization were both lowest in the most recently created scars where soils were alkaline and improved with time as pH declined, suggesting gradual amelioration of post-fire growing conditions. Survival in burn scars was comparable for unprotected trees and those in protective mesh tubes, indicating that herbivory was not a significant impediment to seedling establishment. However, a preliminary study suggests that seed predation may have contributed to the low tree colonization into the openings. Though large burn pile scars may require soil rehabilitation, and soil changes may have a lasting effect on understory plant composition, we found that they were not a significant barrier to tree establishment in these moderate-size burn scars.

1. Introduction

Removal of logging slash through pile burning has long been used to reduce post-harvest wildfire risk and to promote tree regeneration in North American forests (Zon and Cunningham, 1931; Isaac and Hopkins, 1937). The influence of slash pile burning on soil temperature (Roberts, 1965) and soil chemical and physical properties (Tarrant, 1956; Dyrness and Youngberg, 1957) have been researched for more than 50 years. The extreme heating often has immediate effects on soil microbes, acidity, organic matter and plant-available nutrients (Covington et al., 1991; Wan et al., 2001; Rhoades et al., 2015). Recent growth of biomass energy markets that utilize small-diameter material (Fahey et al., 2010; Hartsough et al., 2008) broaden options for disposing of woody residue, but pile burning remains a common, cost-effective slash disposal method.

Federal regulations (National Forest Management Act of 1976; US P.

L. 94-588) stipulate that management activities on US Forest Service land must not permanently degrade the productive capacity of soils. Where severe soil damage (defined by severe burning, compaction, erosion, or topsoil displacement) occurs on >15% of a harvest treatment unit, rehabilitation may be warranted (US Forest Service, 2012). The negative consequences of pile burning are most severe for large, mechanically built piles (i.e., >20 m diameter) constructed at log landing and processing areas, where soils are influenced by a combination of displacement, compaction, and fire effects. These areas are high priority for rehabilitation treatments that typically involve mechanical decompaction and seeding of herbaceous plants (US Forest Service, 2012). In contrast, scars resulting from smaller, mechanically or hand-built (<20 m diameter) pile burns may be numerous but are rarely considered priorities for rehabilitation (Busse et al., 2014; Rhoades et al., 2015).

Salvage and hazard tree removal operations associated with recent bark beetle outbreaks (Griffin et al., 2013; Rhoades et al., 2020) spurred

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a large increase in pile burning and prompted questions about the long-term influence of the practice on forest and watershed resources. For example, at the peak of the beetle outbreak there were >140,000 piles on US Forest Service lands in northern Colorado (US Forest Service, 2012; R2 unpublished records). Pile burning has been used for post-harvest slash reduction and site preparation on subalpine forests of the region for more than a half century, and previously we documented pile burning and the resulting burn scars (i.e., non-forested openings) along a 50-year chronosequence of regenerating lodgepole pine forests (Rhoades and Fornwalt, 2015). Visible evidence of severe fire effects (e.g., soil char layers, fire-hardened and reddened soil) was ubiquitous in the openings though so were understory plants, and it is unknown whether post-fire changes in soils may be responsible for scarce tree colonization of the scars.

Land managers require information about the long-term consequences of pile burning to evaluate potential rehabilitation needs and alternative practices. Owing to the uniform size and arrangement of fuels and similar forest type, these burn scars create a well-replicated experimental design that permits study of soil changes following high severity burning, as well as an opportunity to compare scars to unburned forests that regenerated after clear cutting. In an attempt to disentangle the ecological processes responsible for maintaining the non-forested openings (Callaham et al., 2008; Heneghan et al., 2008), we evaluated growth and survival of trees planted into burn scars and in greenhouse trials that compared scar and forest soils under controlled moisture, herbivory and competition.

2. Methods

2.1. Site description

The pile burn scar chronosequence was located on land administered by the Medicine Bow-Routt National Forests in northern Colorado (Rhoades and Fornwalt, 2015). Study sites span 500 km² at a mean elevation of 2900 m. Total annual precipitation averages 65 cm (1981–2010; PRISM, 2016). Mean annual temperature is 2 °C with January and July means of –8 and 13 °C, respectively. Soils are formed in sandstone, siltstone and conglomerate residuum and colluvium and are moderately deep and well-drained to excessively well-drained. The most abundant soil types are loamy-skeletal, Typic Cryoboralfs and sandy-skeletal, Typic Cryochrepts. The area is part of the Southern Rocky Mountain Steppe ecoregion (Bailey, 1998). Lodgepole pine (*Pinus contorta* var. *latifolia*), the dominant tree species in the area, grows in relatively pure, even-aged stands on southerly aspects, lower elevations, and flatter slopes. It grows in association with subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*) and quaking aspen (*Populus tremuloides*) on northerly aspects and higher elevations.

2.2. Pile burn scar chronosequence

Lodgepole pine forests in this region are typically regenerated with clear cut harvests (Lotan and Critchfield, 1990). Post-harvest site preparation activities, consisting of piling and burning logging debris, aim to reduce surface fuel loads and create a seedbed to stimulate tree recruitment (Lotan and Perry, 1983). Slash piling and burning is conducted during site preparation operations with a tractor-mounted brush rake, blade or grapple hook and typically occurs within a few years of harvesting when there is adequate snow cover in order to reduce the risk of unintended ignition.

In our original study (Rhoades and Fornwalt, 2015), we randomly selected 10 clear cut harvest units per decade created during the 1960s through the 2000s, for a total of 50 units. In each unit we characterized five randomly selected scars per unit for the original study ($n = 250$), and we randomly selected 50 of the original scars for our current work. The harvest units were 15 ha on average with 2.2 scars ha⁻¹. Pile burn scars spanned from 10 to 15 m in diameter. Based on mean scar width

and height ($w = 12.5$ m; $h = 2.5$ m) and half-ellipsoid shape of local machine piles, we calculated a mean pile volume ($V = \pi h w^2 / 6$; Hardy 1996) of 204 m³. For comparison, in other lodgepole and ponderosa pine forests the volume of 3, 6 and 9 m diameter burn piles were 6, 64, and 170 m³, respectively (Busse et al., 2013; Finkral et al., 2012; Korb et al., 2004). At our sites, the mass of an average pile estimated based on typical dry wood density and packing ratios for short-needle pines (Hardy, 1996) would fall between 12 and 16 Mg pile⁻¹.

2.3. In situ and greenhouse seedling trials

To evaluate lodgepole pine seedling survival and growth with time since pile burning *in situ*, we planted lodgepole pine seedlings in the center of 10 burn scars per decade ($n = 10$ seedlings per scar and 100 per decade). The one-year old seedlings were grown from locally collected seed in 15.2 cm long containers (Stuewe and Sons, Tangent, OR) by the Colorado State Forest Service nursery. At the time of planting, trees averaged 13.9 and 0.3 cm in height and stem diameter. To evaluate herbivory, planted trees were either unprotected or planted within plastic mesh tree tubes (Quadel Industries, Coos Bay, OR). In August 2019, after two growing seasons, we tallied tree survival and measured total height, annual height increment, stem diameter, and root colonization by ectomycorrhizal fungi (see details below).

We also conducted a greenhouse trial with lodgepole pine seeds grown in soils collected from burn scars described above and adjacent regenerating forest across the chronosequence. Mineral soil (upper 15 cm) was sampled from 10 scars per decade and 20 m from scar edge in the surrounding regenerating forest. We composited forest and scar soils separately by decade, passed through a 2 mm mesh sieve to remove rocks and roots and packed into planting containers as above ($n = 20$ per decade). Lodgepole pine seeds used in the greenhouse trial were collected by the US Forest Service on the Medicine Bow-Routt National Forest at a similar elevation as the burn piles. Seeds were pre-germinated for 48 h under refrigeration in wetted, paper towels. Replicate seeds were planted in each container, then thinned to leave one seedling per container after two weeks. Seedlings were watered 2–3 times per week and grown for 12 months. Air temperature fluctuated widely within the greenhouse (10–32 °C) and the trial was conducted with a 16-hour photoperiod with 300 $\mu\text{mol m}^{-2} \text{sec}^{-1}$ average light intensity. Seedling mortality, associated with wilt or damping-off pathogens and other agents, was noted throughout the trial.

The height and stem diameter of *in situ* and greenhouse bioassay trees were measured at the time of harvest. Tree root systems were washed carefully to remove soil and above- and belowground tissues were divided. For greenhouse seedlings, above- and belowground tissues were oven dried at 60 °C for 48 h and weighed, tree needles were ground to a fine powder, and analyzed for N and C content by dry combustion (LECO 1000 CHN analyzer, LECO Corporation, St. Joseph, MI, USA).

We also quantified ectomycorrhizal fungi (EMF) on tree root tips of both bioassays. Following harvest, all roots were stored moist at 5 °C prior to EMF root-tip counts. Ten, 3-cm long sections of fine root (1-mm diameter) were clipped from the center portion of each root system and then suspended in deionized water and distributed evenly across a gridded Petri dish. The presence or absence of EMF root tips was recorded using a line intercept method to observe 100 live root tips per seedling under a dissecting microscope using 20 $\times$ magnification (McGonigle et al., 1990). In the greenhouse trial, the percent of root tips with EMF denotes the initial colonization of the seeded trees. In contrast, the roots of *in situ* trees were inoculated with EMF in the nursery prior to out-planting, so our root survey quantified net EMF infection rates after two years growing in burn scar soils. Following determination of EMF colonization, greenhouse seedling roots were dried, weighed, and analyzed for N and C content as described above.

2.4. Soil analyses

To determine the long-term effect of pile burning on soil nutrients, we analyzed plant-available soil N and other nutrients in burn scar and regenerating forest soils across the treatment chronosequence. We measured the supply of inorganic forms of soil N ($\text{NO}_3\text{-N}$ and $\text{NH}_4\text{-N}$) using net mineralization and nitrification incubations of mineral soils. Mineral soils (0–15 cm depth) were collected with a hand corer from the burn scar interior and 20 m beyond the edge of the burn scars in the regenerating forest ($n = 10$ per decade), immediately placed in coolers and stored at 4 °C. Samples were passed through a 4 mm mesh sieve and 10-g subsamples were extracted with 50 mL of 2 M KCl within 24 h. Extracts were analyzed for $\text{NO}_3\text{-N}$ and $\text{NH}_4\text{-N}$ by colorimetric spectrophotometry (Bundy and Meisinger, 1994; Lachat Company, Loveland, CO). A second set of subsamples was oven dried at 105 °C for 24 h to determine soil water content. A third subset was incubated for 28 d at 24 °C and 60% of field capacity (Binkley and Hart, 1989). Field capacity was approximated as the gravimetric water content of a subsample wetted to saturation then allowed to drain for 12 h. The incubated subsamples were extracted and analyzed as described above. Net mineralization was calculated as the change in $\text{NO}_3\text{-N}$ plus $\text{NH}_4\text{-N}$ between initial and incubated extracts and net nitrification as the change in $\text{NO}_3\text{-N}$. Mineral soil samples were dried for 48 h at 60 °C, ground and analyzed for total C and N by dry combustion (LECO 1000 CHN analyzer, LECO Corporation, St. Joseph, MI, USA).

Soil pH was analyzed in a 1:1 soil to deionized water ($<1.0 \mu\text{S cm}^{-1}$) slurry after one hour of agitation (Thomas, 1996). Soil pH was also measured in a weak salt solution (0.1 M CaCl_2) to evaluate the potential effect of ionic strength differences on soil acidity (Thomas, 1996). Exchangeable P and cations were extracted with Mehlich-III reagents (0.2 M CH_3COOH , 0.25 M NH_4NO_3 , 0.015 M NH_4F , 0.013 M HNO_3 , and 0.001 M EDTA; Mehlich, 1984) and analyzed by inductively coupled plasma mass-spectroscopy (NexIon 7300DV, Perkins Elmer Waltham, WA, USA).

Potential differences in soil properties and seedling biomass between scars and forests within decades or across decades were evaluated using one-way analysis of variance (SPSS Inc., V. 25 IBM, Chicago, IL, USA). We also used a generalized linear mixed model analysis of variance with location (scar or forest) and decade since treatment as fixed effects to examine differences between scars and the surrounding regenerating forest across time. Data were checked for homogeneity of variance and log transformed if necessary. Significance is reported at the $\alpha = 0.05$ critical value unless noted otherwise. Percent root colonization and root wilt data were analyzed using Mann-Whitney U tests. We used least-squares regression to evaluate changes in the burn scars and regenerating forests and openings with time since treatment.

3. Results

3.1. Tree seedlings

Overall, 62% of the *in-situ* pines survived and remained healthy the first two growing seasons in the burn scars (Fig. 1a). Survival was lowest for trees planted in the most recent burn scars (40% in 2000s scars) and highest for the oldest scars (90% in 1960s scars) and increased by about 13% per decade since treatment ($r^2 = 0.94$; $p = 0.003$). Survival did not differ between trees protected from herbivory by mesh tubes and unprotected trees. Annual height increment also increased with time since treatment (Fig. 1b), by 0.7 cm per decade on average. Total tree height was significantly higher in the 1960s compared to the 2000s scars (18.0 vs 14.8 cm) and the other age classes were intermediate (data not shown).

In the greenhouse trial, seedlings grown in scar soils had higher incidence of germinant wilt, lower height, stem diameter, and above and belowground biomass than those grown in unburned forest soils (Table 1; Fig. 2). Wilt-related seedling die-off was 1.8 times higher in

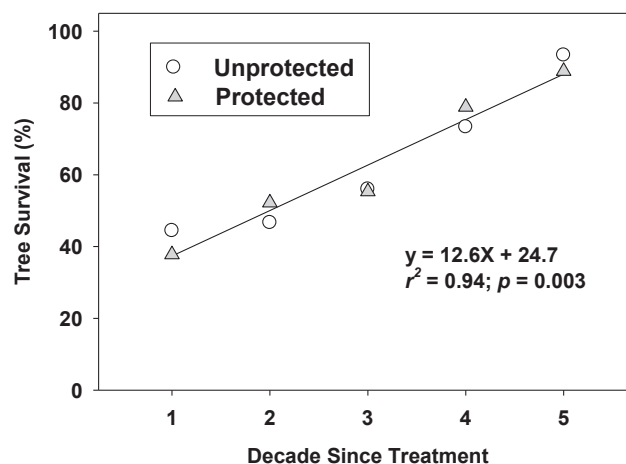


Fig. 1a. Survival of lodgepole pine seedlings planted *in situ* within pile burn scar soils. Planted trees were Unprotected or Protected inside plastic mesh tree tubes to reduce herbivory. Survival is based on 100 trees per decade for each planting treatment. Linear relation is fitted for all trees.

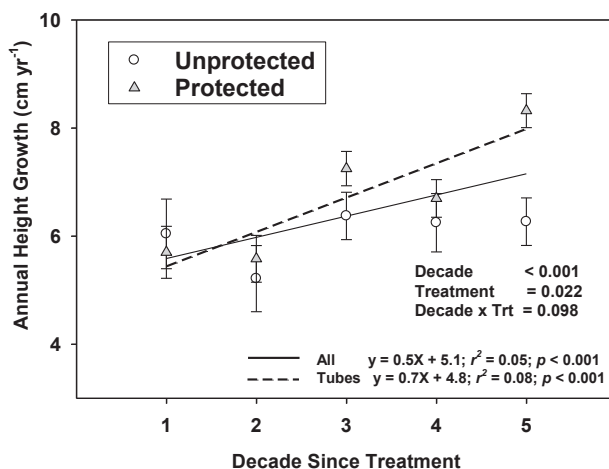


Fig. 1b. Annual height growth of lodgepole pine seedlings planted within burn scars. Height data are means with standard error bars in 2019 after two growing seasons. Individual linear relations are fitted for all trees and for trees planted within tree tubes. Decade, treatment and interaction effects were analyzed using mixed-effects, two-way analysis of variance.

scar soils the first month after germination. In forest soils, wilt was highest in recently treated areas (25% in 2000s harvests) and declined with time ($y = -4X + 26$; $r^2 = 0.64$; $p = 0.066$). There was no relationship between the incidence of seedling wilt and time since burning for the scar soils (range: 20–35% across decades). Roots comprised about 70% of total seedling mass at the end of the one-year greenhouse bioassay, and biomass partitioning between roots and shoots was similar among the treatments. Foliar and root N concentrations were marginally (2.1 vs 2.0%; $p = 0.097$) and significantly (1.1 vs 1.0%; $p = 0.014$) higher in burn scar soil, respectively (data not shown). However, due to the lower mass of seedlings grown in burn scar soils those trees had 25% lower total N stock than those grown in forest soils.

The lower greenhouse seedling biomass in scar soils was consistent across the chronosequence (Fig. 2), but both biomass and N stock increased with time since treatment in both locations (Table 2). Decade since treatment explained more of the variability (adjusted r^2) in above and belowground biomass and N stock in scar compared to forest soils. Similarly, the improvement in seedling biomass and N stock with time (slope of linear relation) was twice as high in the scar soils. Quadratic fits

Table 1

Characteristics of lodgepole pine seeded in burn scar and forest soil locations and grown for 1 year under greenhouse conditions. Data are mean and standard error for all decades (n = 100 tree pots per soil location). Germinant wilt is the proportion of seedlings that wilted and died within one month of emergence. Shoots (aboveground tissues) include stems and needles.

Seedling Response	Scar		Forest		p =
Germinant Wilt (%) [§]	26.0	(2.9)	14.0	(3.3)	**
Tree Height (cm)	4.3	(0.13)	4.9	(0.11)	***
Stem Caliper (mm)	1.4	(0.03)	1.6	(0.02)	***
Root Colonization (%) [§]	88.8	(1.0)	93.4	(0.6)	***
Oven Dry Mass (g tree ⁻¹)					
Shoots	0.2	(0.01)	0.3	(0.01)	***
Roots	0.4	(0.02)	0.6	(0.02)	***
Total Plant	0.7	(0.02)	0.9	(0.03)	***
Root : Shoot	2.1	(0.05)	2.1	(0.04)	
Nitrogen Stock (mg tree ⁻¹)					
Needles	4.5	(0.16)	5.9	(0.17)	***
Roots	4.8	(0.19)	5.7	(0.18)	***

***p < 0.001; **p < 0.01; §Mann-Whitney U test.

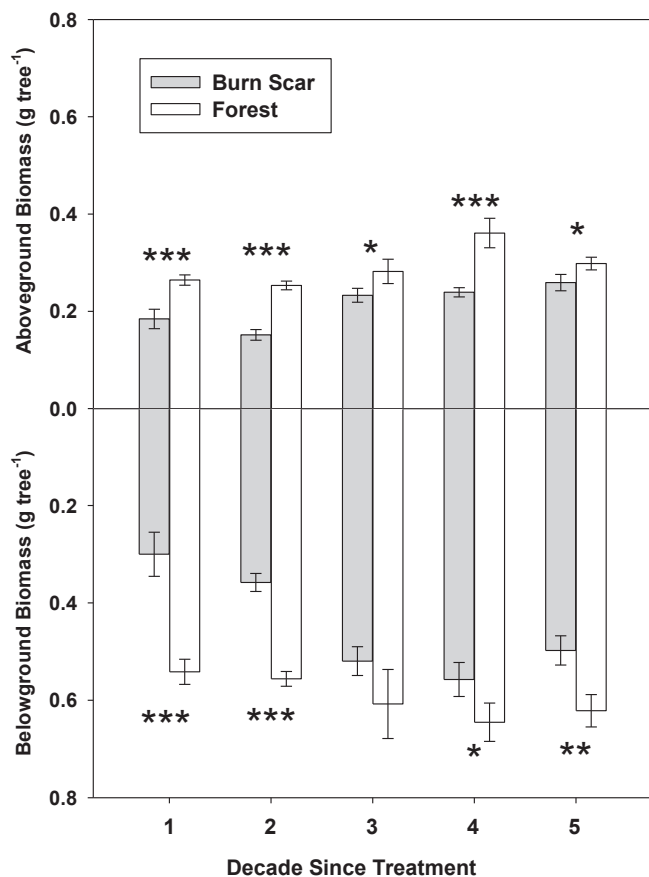


Fig. 2. Above and belowground biomass of lodgepole pine seedling after a one-year greenhouse bioassay. Data are means and standard error for 100 trees per decade and treatment. Treatment differences within decade are identified as follows: *** p < 0.001; ** p < 0.05; * p < 0.1.

explained slightly more of the temporal pattern but did not alter its general interpretation (data not shown).

Overall, we observed EMF on 91% of greenhouse seedling root tips (Fig. 3). Greenhouse trees grown in forest soils had higher colonization rates than those in burn scar soils (Table 1). The greatest difference in EMF colonization occurred the first decade after treatment when seedlings grown in scars had 18% lower colonization than forest soils (75 vs

94%). Colonization rates were relatively similar between scar and forest soils across the rest of the time series. In contrast, on seedlings grown *in situ* in burn scar soils, 45% of root tips were ectomycorrhizal (data not shown), and there were no significant differences with decade since treatment. However, infection rates on individual trees were highest in 1960s (93%) and lowest in 1990s and 2000s (79 and 72%) scars.

3.2. Soils

Soil pH was elevated in burn scars (Fig. 4a; Table 3), and the effect was greatest the first decade after treatment (8.0 vs 6.6). It then declined by 0.2 pH units per decade, remaining 0.4 higher than in the forest soils 50 years after pile burning. In the forest soils, pH increased slightly with time since clear cutting. Overall, pH was 0.7 units higher in scar than forest soils across the time series (7.4 vs 6.7). Soil pH measured in a weak salt solution was 0.9 units lower compared to pH in a deionized water slurry. The difference between scar and forest soils was similar for the two pH measurement types, indicating that post-fire changes in ionic strength did not influence the soil pH pattern.

On average, plant-available P and cations were 2- to 4-times higher in burn scar compared to forest soils (Table 3). All soil cations, except Ca, declined significantly with time since treatment. In contrast, plant-available soil P increased with time since treatment (1.3 mg P L⁻¹ per decade; Fig. 4b; Table 3).

In general, total soil N, C and inorganic N were higher in scar soils (Table 3), though plant available N supplied through net mineralization was lower (Fig. 5b). Total soil N and C were double and extractable NO₃-N was 1.8-times higher (p < 0.1) in scar soils. Soil C:N was also higher in the scar soils (26.3 vs 23.3). Gravimetric soil water was 38% lower in scar soils across the time series (data not shown). Immobilization of inorganic N was 4-times higher in scar soils (i.e., negative net mineralization), and this reduced net N supply was driven by NH₄-N rather than NO₃-N immobilization. Plant available NO₃-N and NH₄-N declined within time since treatment in both scar and forest soils (Fig. 5a). Conversely, net N transformations became less negative indicating declining immobilization and increasing N supply with time since treatment (Fig. 5b).

4. Discussion

4.1. Obstacles to tree regeneration

In our previous study (Rhoades and Fornwalt, 2015), we documented sparse tree colonization along a 50-year chronosequence of medium-sized (10–15 m diameter) slash pile burn scars in clear cut lodgepole pine forests. We also found indicators of severe fire effects due to high combustion temperatures (i.e., reddened and hardened soil, char). In this study, we set out to determine whether soil conditions form a major obstacle to tree regeneration within these burn scars. We found no conclusive evidence that they do. Though burn scars cover <5% of the area within regenerating clear cuts (Rhoades and Fornwalt, 2015), the decades-long vegetation cover type change they create is a poorly understood outcome of forest harvesting and site preparation activities that justified this investigation.

Lodgepole pine seedlings planted in burn scars had good survival (~60%) and growth (~6 cm yr⁻¹), and scar soils had higher, not lower, levels of soil nutrients. Like most pines, lodgepole pine tolerate or prefer acidic soils (Danielson and Visser, 1989; Erland and Söderström, 1991), so the neutral to slightly alkaline scars soils (7.2–8.0; Fig. 4a) may not have been optimal. Liming and wood ash addition are known to increase EMF colonization of pines growing in acidic soils (pH < 4.0), but to decrease it in neutral pH soils (Borja and Nilsson, 2009; Erland and Söderström, 1991). Though lower soil N supply, plant N uptake and EMF colonization may have contributed to reduced tree growth in scar soils (Table 1), that reduction was not sufficient to prevent trees from becoming established in the scars (Fig. 1). The improved tree growth we

Table 2
Relations between seedling biomass and nitrogen content and decade since treatment after a 1-year greenhouse bioassay in burn scar and regenerating forest soils. Linear regression parameters: adjusted r^2 , slope, y-intercept (y0), significance. Shoots (aboveground tissues) include stems and needles.

		Dry Mass						N Stock			
		r^2	slope	y0	p =			r^2	slope	y0	p =
Shoots	Scar	0.18	0.024	0.14	***	Needles	Scar	0.15	0.455	3.16	***
	Forest	0.06	0.018	0.24	**		Forest	0.03	0.261	5.11	**
Roots	Scar	0.21	0.060	0.27	***	Roots	Scar	0.12	0.504	3.23	***
	Forest	0.03	0.025	0.52	**		Forest	0.03	0.240	5.01	*
Total	Scar	0.22	0.083	0.41	***	Total	Scar	0.15	0.958	6.40	***
	Forest	0.02	0.034	0.78	*		Forest	0.03	0.478	10.22	**

*** p < 0.005; ** p < 0.05; * p < 0.1.

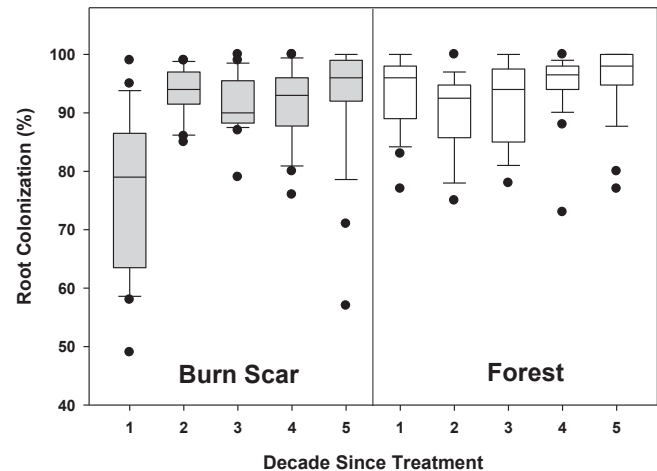


Fig. 3. Percent of lodgepole pine roots colonized by ectomycorrhizal fungi at the end of a one-year greenhouse bioassay. Boxes denote the 25th, 50th, 75th percentiles, bars denote the 5th and 95th percentiles, and dots denote outliers (100 root tips on 20 trees per decade).

observed in the older burn scars in both *in situ* and greenhouse trials (Figs. 1 and 2) suggests progressive amelioration of the burn scar growing environment.

Higher incidence of wilt and lower EMF colonization and seedling survival in the most recently treated sites suggests that interacting soil microbial processes may be responsible for poorer initial seedling performance (Table 1; Fig. 3). Incidence of damping-off can increase with pH in forest nursery soils (Kacprzak et al., 2001) and has been shown to cause >25% seedling losses in lodgepole pine seedlings above pH 7.0 (Griffin, 1958). Soil heating influences the composition of soil microbes and can reduce tree root symbionts after wildfire (Douglas et al., 2005; Martín-Pinto et al., 2006; Twieg et al., 2009; Glassman et al., 2016), pile burning (Pilz and Perry, 1984; Korb et al., 2004; Jiménez-Esquilín et al., 2007) and prescribed broadcast burning (Herr et al., 1994; Stendell et al., 1999; Taudière et al., 2017). However, the magnitude and duration of these effects vary with fire severity, forest types and site characteristics (Cairney and Bastias, 2007; Taudière et al., 2017). For example, pile burning eliminated most arbuscular mycorrhizal symbionts and native plant seeds from ponderosa pine forest soils (Korb et al., 2004; Jiménez-Esquilín et al., 2007). In contrast, a large, stand-replacing wildfire reduced the overall EMF spore density and the abundance of some rare species, but the soil spore bank remained functionally intact, so both *in situ* and greenhouse bioassay seedlings were colonized by EMF (Glassman et al., 2016). Residual mycobiont pools associated with residual root systems and deeper soil layers create ecosystem resilience (Perry et al., 1989) that influences the pace and composition of post-fire ecosystem recovery. Given the small size of the pile burn scars relative to wildfires or clear cut units (Parsons et al., 1994), it was not surprising that EMF inoculum was not a serious

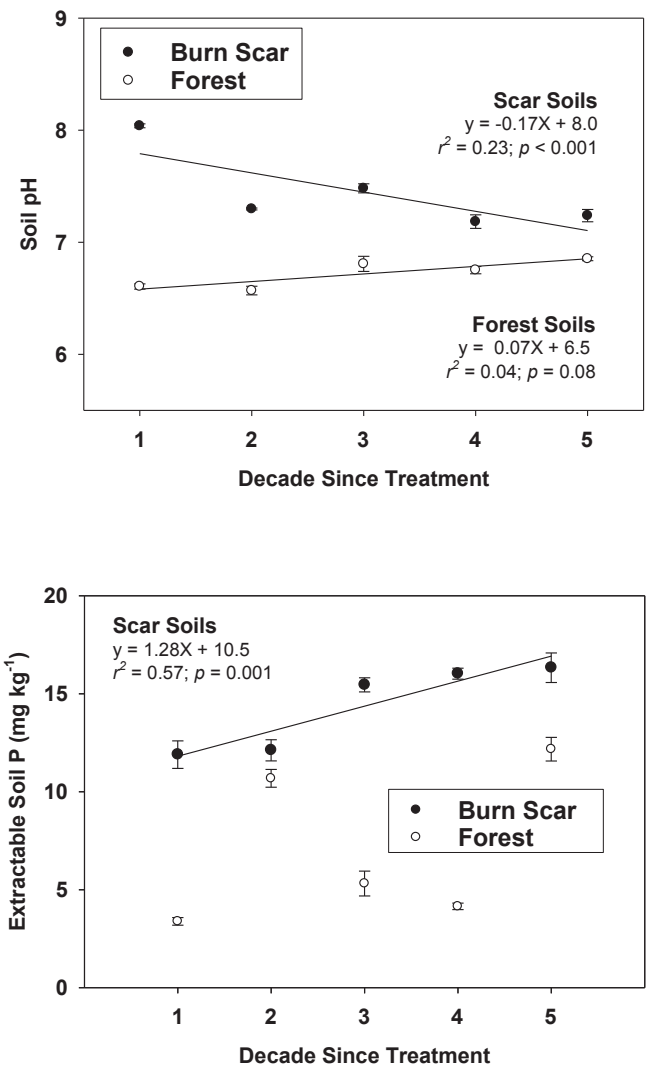


Fig. 4. a and b: Soil pH (4a) and extractable soil P (4b) in the mineral soil (0–10 cm depth) in pile burn scars and adjacent unburned forest soils. Data are means and standard error for 10 burn scars and forest sites per decade.

obstacle to tree regeneration.

Belowground root symbionts and EMF fungi specifically are known to promote survival and growth of lodgepole pine (Pedersen et al., 1999) and other species (Branzanti et al., 1999), and EMF inoculants alone or in conjunction with antipathogen biocontrol agents are common soil amendments in forestry nurseries (Qureshi and Khasa, 2008; Oliveira et al., 2010; Sousa et al., 2011, 2014). In addition to increasing host nutrient and water uptake, some EMF fungi have direct and indirect effects on plant pathogens (Hwang et al., 1995; Lladó et al., 2017) by

Table 3

Soil pH, extractable soil nutrients and total soil N and C in burn scar and regenerating forest soils (0–15 cm). Data are mean plant-available N (KCl-extractable), P and cations (Mehlich-extractable) with standard error in parentheses for all decades and oneway analysis of variance significance. Linear relation between soil concentrations and time since treatment in burn scar and forest soils.

			Scar	Forest	<i>p</i> =	Relation with decade since treatment					
						Scar			Forest		
						<i>r</i> ²	slope	<i>p</i> =	<i>r</i> ²	slope	<i>p</i> =
Soil pH	water		7.4	(0.07)	6.7	(0.06)	***	0.25	−0.17	***	
	weak salt		6.8	(0.08)	5.9	(0.06)	***	0.32	−0.21	***	
Extractable	NO ₃	(mg kg ^{−1})	0.7	(0.15)	0.4	(0.08)	*	0.13	−0.26	**	0.16
	NH ₄	“	1.3	(0.09)	1.1	(0.10)	NS			NS	0.23
	Sum	“	2.0	(0.19)	1.5	(0.16)	*	0.14	−0.34	**	0.25
	P	“	14.4	(0.6)	7.1	(1.0)	***	0.57	1.28	***	
	K	“	20.5	(2.3)	6.3	(0.9)	***	0.23	−2.88	*	
	Mg	“	7.6	(1.3)	3.5	(0.7)	**	0.18	−1.40	*	0.38
	Ca	“	2.6	(0.7)	0.8	(0.3)	**			NS	0.44
	Mn	“	8.1	(1.2)	1.9	(0.2)	***	0.46	−2.12	***	
	Zn	“	0.7	(0.1)	0.2	(0.04)	***	0.36	−0.16	**	
Total	N	(%)	0.08	(0.004)	0.04	(0.002)	***				0.36
	C	“	2.11	(0.15)	1.01	(0.07)	**			NS	0.32
	C:N		26.3	(0.94)	23.3	(0.95)	***			NS	0.10

*** *p* < 0.005; ** *p* < 0.05; * *p* < 0.1.

competing with or inhibiting pathogenic fungi, by enhancing plant growth and formation of defense compounds, and by altering root morphology (Whipps, 2004). The pattern of low EMF and high wilt we observed on greenhouse seedlings in 2000s pile scar soils may be evidence of microbial conditions that negatively affects post-fire pine survival and recovery. It is unclear if the lower overall EMF colonization of the *in-situ* seedlings (e.g., 48 vs 91% for *in situ* vs greenhouse trees) resulted from lower host investment in fungal symbionts in the relatively fertile scar soils or some other factor. It is also unknown how the EMF infection rate changed since out-planting. Recently initiated research using microbiome approaches will help determine what factors regulate soil symbiont and pathogen abundance and will help evaluate the relative importance of changes in plant composition and abundance and soil chemistry and nutrition with time since pile burning (Douglas et al., 2005; Twieg et al., 2009; Baldrian, 2017).

Although tree colonization was uniformly low across the 50-year chronosequence, planted seedlings performed well in burn scar soils both *in situ* and under controlled greenhouse conditions, suggesting that non-soil factors may be responsible the persistent forest openings. Moreover, similar survival and growth of protected and unprotected seedlings indicated that herbivory was not a major contributor to seedling damage in the burn scars. However, during a 14-day pilot study, we documented >50% losses of lodgepole pine seed to pine squirrel (*Tamiasciurus hudsonicus*) and least chipmunk (*Neotamias minimus*) in scar openings across all chronosequence age classes, indicating that seed predation may constrain tree establishment. Tree squirrels are known to consume entire seed crops (Steele and Yi, 2020) and reduce regeneration of lodgepole (Elliott, 1974; Gurnell, 1984) and other pine species (Siepielski and Benkman, 2008). Seedling herbivory and seed predation by voles (*Microtus* sp.) and mice (*Peromyscus* sp.) are known to cause economically significant tree losses in western Canada lodgepole pine plantations (Sullivan and Sullivan, 1982; Sullivan et al., 2001). Pile burning consumes the seed contained in post-harvest slash, and we hypothesize that in subsequent decades that seed predation combined with scanty seed inputs from the adjacent forest may create an additional obstacle that limits tree establishment within the scars. An evaluation of seed predation within the burn scars and surrounding forests is planned.

4.2. Forest management and conservation implications

Pile burning caused changes in soil chemistry and nutrients that have persisted since the 1960s, but our greenhouse and *in situ* trials demonstrated that soil conditions are not primarily responsible for the scarcity of tree regeneration within the scars. A combination of low seed availability from young trees and high seed predation appears more likely to explain the low pine density. Elsewhere in Colorado, limited seed availability contributes to slow post-fire tree colonization after extensive, severe wildfire (Chambers et al., 2016), resulting in low plant nutrient demand and elevated nutrient export from watersheds (Rhoades et al., 2019). This study demonstrated that planted pines survive and grow well in burn scars across the chronosequence, and that tree performance improved with time since burning (Fig. 1).

Though lodgepole pine has not been able to recolonize the burn scars, native understory vegetation thrives in them (Rhoades and Fornwalt, 2015). Within these lodgepole pine-dominated landscapes, the burn scar openings diversify forest stand structure, understory plant composition and wildlife habitat. Animals are known to influence post-fire plant diversity through their impacts on seed predation, herbivory, pollination, decomposition and seed dispersal (Kelly et al., 2018) and our pilot study suggests they may also contribute to maintaining these non-forested burn scar openings. Overall, our findings suggest the need for a more integrated appreciation of how the spatial extent and arrangement of vegetation type conversions caused by severe burning may alter ecosystem function and biodiversity (Bowman et al., 2016).

As reported elsewhere (Busse et al., 2013, 2014; Rhoades et al., 2015), the moderate size and low density of these burn scars and the enhanced fertility of their soils should not warrant rehabilitation in most cases. However, this is not the case for larger burn piles common to log processing areas where higher, prolonged and deeper soil heating causes significant chemical, biological and physical soil changes (USDA-FS, 2012; Johnson et al., 2011). Such areas are also subject to damage from heavy equipment traffic and active rehabilitation may be needed to reverse soil compaction, loss of soil organic matter and microbes and elevated soil alkalinity and nutrient levels. Lodgepole pine is relatively tolerant of the near-neutral to slightly alkaline pH (Anderson, 2003) we measured in the burn scars (Fig. 4a). However, grouse whortleberry (*V. scoparium*), the most common local understory shrub, has narrower and more acidic optimal pH range (4.3–5.2; Johnson, 2001) as does

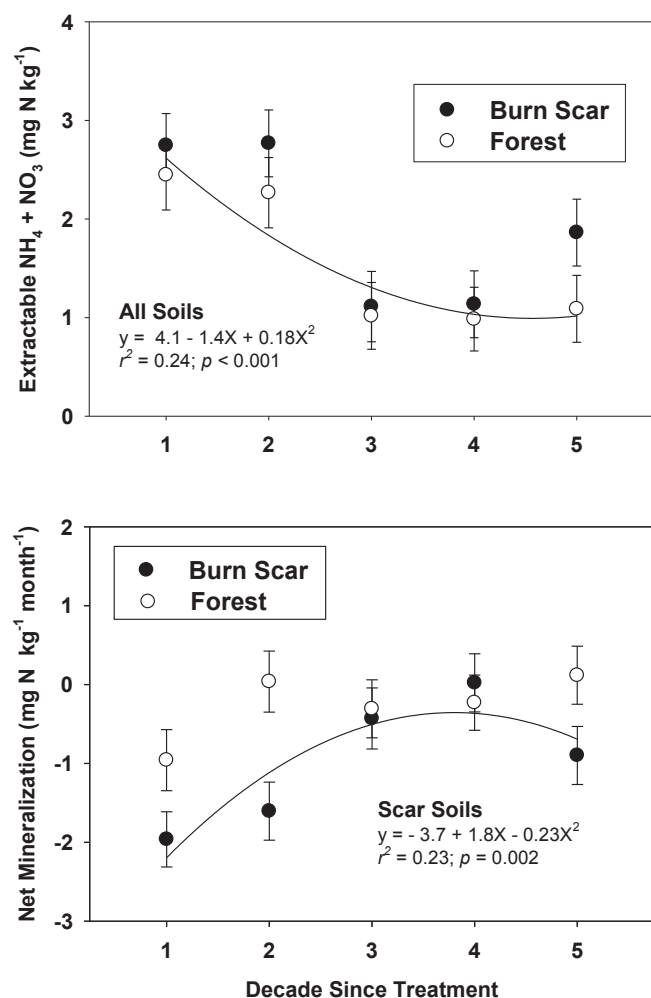


Fig. 5. a and b: Extractable inorganic N ($\text{NH}_4\text{-N} + \text{NO}_3\text{-N}$; 5a) and net mineralization (5b) in the mineral soil (0–10 cm depth) in pile burn scars and adjacent unburned forest soils. Data are means and standard error for 10 burn scars and forest sites per decade.

kinnikinnick (*Arctostaphylos uva-ursi*), another acid-loving understory plant common in these forests (Crane, 1991). The cover of these and a number of other woody understory species, were significantly reduced compared to the surrounding regenerating forest (Rhoades and Fornwalt 2015), and the soil pH effects of pile burning may have greater consequences for the understory plant strata. Rehabilitating moderate-size pile burn scars is mostly likely to be justified to favor native plants with acid soil requirements, and on sensitive, compactable soils, or near surface water, riparian or wetland areas and existing invasive plant populations.

CRediT authorship contribution statement

Charles C. Rhoades: Conceptualization, Project administration, Writing - original draft, Writing - review & editing. **Timothy S. Fegel:** Conceptualization, Methodology, supervision, Writing - review & editing. **Tahir Zaman:** Conceptualization, Methodology. **Paula J. Fornwalt:** Conceptualization, Writing - review & editing. **Susan P. Miller:** Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence

the work reported in this paper.

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