



Article

Overlapping Bark Beetle Outbreaks, Salvage Logging and Wildfire Restructure a Lodgepole Pine Ecosystem

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Abstract: The 2010 Church’s Park Fire burned beetle-killed lodgepole pine stands in Colorado, including recently salvage-logged areas, creating a fortuitous opportunity to compare the effects of salvage logging, wildfire and the combination of logging followed by wildfire. Here, we examine tree regeneration, surface fuels, understory plants, inorganic soil nitrogen and water infiltration in uncut and logged stands, outside and inside the fire perimeter. Subalpine fir recruitment was abundant in uncut, unburned, beetle-killed stands, whereas lodgepole pine recruitment was abundant in cut stands. Logging roughly doubled woody fuel cover and halved forb and shrub cover. Wildfire consumed all conifer seedlings in uncut and cut stands and did not stimulate new conifer regeneration within four years of the fire. Aspen regeneration, in contrast, was relatively unaffected by logging or burning, alone or combined. Wildfire also drastically reduced cover of soil organic horizons, fine woody fuels, graminoids and shrubs relative to unburned, uncut areas; moreover, the compound effect of logging and wildfire was generally similar to wildfire alone. This case study documents scarce conifer regeneration but ample aspen regeneration after a wildfire that occurred in the later stage of a severe beetle outbreak. Salvage logging had mixed effects on tree regeneration, understory plant and surface cover and soil nitrogen, but neither exacerbated nor ameliorated wildfire effects on those resources.

Keywords: disturbance; forest management; mountain pine beetle; subalpine ecosystem; Colorado; Rocky Mountains

1. Introduction

Lodgepole pine (*Pinus contorta* Dougl. ex. Loud. var. *latifolia*)-dominated ecosystems are adapted to periods of rapid post-disturbance change, as evidenced by the dense, even-aged forests that regenerate after wildfire and timber harvest [1,2]. New cohorts of lodgepole also establish readily after bark beetles (*Dendroctonus ponderosae* Hopkins) kill overstory pine [3,4]. The response of tree regeneration and understory plants following such disturbances determines forest vegetation dynamics and biodiversity [5–9] and has implications for ecosystem productivity and the biogeochemical processes that regulate soil nutrient retention and export [10–12]. For the 13,800 km² of forests infested by bark beetles since the early 2000s in Colorado, USA [13], the likelihood of overlapping disturbances increases with time as these forests are salvage logged or affected by wildfire [14]. However, the outcomes of compounding salvage logging and wildfire in beetle-killed lodgepole pine forests remain relatively poorly understood [15,16].

Site conditions and pre-disturbance forest composition and structure influence how individual and compound disturbance events affect forest ecosystem dynamics [17,18]. For example, while lodgepole

pine typically regenerates densely after wildfire, seedling densities often vary by orders of magnitude even across a single wildfire [2,19], reflecting spatial patterns of fire behavior, fuel load, slope and other site attributes [15,20,21]. The implications of bark beetle outbreaks on wildfire probability and severity are mixed [22,23]. For example, flammability of canopy fuels increases following beetle infestation at stand scales [24], whereas bark beetle activity is not well related to wildfire severity [23] or extent at regional scales [25]. The severity, specific order and timing of consecutive disturbances determine their ecological outcomes, with greater impacts expected when initial disturbance severity is relatively high and time between disturbances is relatively short [14,16,26]. Wildfires occurring during the initial green-attack stage of beetle outbreaks—when needle flammability is highest—and the red-needle stage—when foliage begins to fall but serotinous cones remain unopened—are likely to have different effects than those occurring in gray-stage forests after needles have fallen and cones have opened [21,24,27–30].

Forest management activities prompted by recent severe beetle outbreaks in lodgepole pine forests of Colorado and elsewhere in the southern Rocky Mountains aim primarily to regenerate forests and to reduce short-term crown fire risk and longer-term risk of severe wildfire effects associated with heavy fuel accumulation after tree fall [31,32]. However, like other types of disturbance, the consequences of post-beetle management vary with forest composition, stand structure and time elapsed since the outbreak [18,33], and such factors have likely consequences for potential fire risk and behavior and other ecosystem attributes. The process of removing the forest canopy during salvage logging, for example, increases the mass of surface fuels and alters their moisture dynamics [3,34], but it also affects light, moisture and soil nutrients that influence plant responses [35]. The initial understory plant response to post-beetle salvage logging can differ between woody and non-woody plants and be affected by logging slash retention [8]. The cohort of trees that regenerate beneath the beetle-killed overstory and following salvage logging can form a new stratum of fuels and a future management concern [3,28,36]. In spite of the continental scale of recent bark beetle outbreaks [37] and the ensuing management response, it is uncertain whether post-beetle logging will aggravate wildfire effects.

In October 2010, the Church's Park Fire burned lodgepole pine forests where bark beetle infestation killed >85% of overstory basal area in the early 2000s. Portions of the burned area were salvage logged one year prior to the fire. The Church's Park Fire provides a fortuitous opportunity to evaluate overlapping effects of salvage logging and wildfire within severely-infested, gray-phase, beetle-killed forests. Our assessment included tree regeneration, surface fuels, understory plants, soil nitrogen and water infiltration under these conditions. All individual and overlapping disturbance events are unique, but in the absence of well-replicated experimental trials, this case study increases understanding of post-fire ecosystem dynamics in gray-stage beetle-impacted forests.

2. Materials and Methods

2.1. Study Area

This research was conducted on the Arapaho-Roosevelt National Forest near Fraser, Colorado, USA, in forests burned by the Church's Park Fire (39°56'25" N; 105°57'00" W) and surrounding unburned areas. The study area lies on the western edge of Colorado's Front Range between 2438–3200 m elevation. The area receives ~700 mm of precipitation annually, 75% as snow. Soils are gravelly, sandy-loam Alfisols derived from colluvium and alluvium of granitic gneiss and schist parent material [38].

Forests of the study area are a mix of lodgepole pine, subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) and Engelmann spruce (*Picea engelmannii* Parry ex. Engelm.) with scattered patches of quaking aspen (*Populus tremuloides* Michx.), and are part of the temperate steppe mountain ecoregion that extends from New Mexico, USA to southwestern Canada [39]. Bark beetles reached epidemic levels around 2000 and their activity peaked around 2006 in this part of Colorado [40,41]. Overstory pine mortality commonly exceeded 70% in mature, pine-dominated stands in this region of Colorado [3,42]. At Church's Park, lodgepole pine comprised 69% of total stand basal area before the outbreak, 89% of

which was killed by beetles [43]. Lodgepole pine stands in the area typically contain a mixture of serotinous and non-serotinous cones [29].

Salvage logging occurred in 2009, several years after peak beetle activity. Harvested stands were clear cut and whole-tree yarded to central processing and loading areas (Figure 1) using tracked feller-bunchers and rubber-tired skidders. All harvest areas were on moderate (<35%), south-facing slopes.



Figure 1. Paired photos taken (a) one year pre-fire (October 2009) and (b) one year post-fire (September 2011) within the Church's Park Fire perimeter, near Fraser, Colorado. The photos are oriented northeast (20–30° azimuth) across an operational-scale Cut + Burn study site centered near 39°56'16.96" N; 105°56'33.43" W (See arrow in Figure 2). The log deck visible in photo (a) had been removed before the fire.

The Church's Park Fire began on 3 October 2010 and grew rapidly due to a combination of moderate wind speed, unseasonably high temperature, low relative humidity (16–32%), and very low fuel moisture (5%; [44,45]). The following three days were cooler with increasing humidity and the fire was 100% contained on 7 October. A cold front on 8 October effectively terminated the fire.

The fire burned a total of 200 ha of predominantly south-facing, beetle-killed, pine-dominated slopes, interspersed with meadows and aspen (Figure 2). Fire spread was pushed both across and upslope by down-valley winds. Observers noted very active to extreme fire behavior when the fire was burning in beetle-killed lodgepole pine stands, including active crown fire behavior, high rates of spread and flame lengths, and spotting of up to 0.4 km [46]. The crown fires burning through beetle-killed lodgepole pine stands and surface fires burning in salvaged logged units were classified as high- and moderate-severity based on complete or near complete combustion of organic soil layers and tree crowns and attached cones, and 100% mortality of residual live trees (Figure 2) [47]. According to burn-severity maps developed from remotely-sensed imagery and adjusted by on-site visual assessments, these areas comprised roughly half of the Church's Park Fire area (17% high- and 30% moderate-severity) [48]. Low-severity burning occurred primarily within meadow and aspen vegetation. Owing to the small size of and low risk for high intensity rainstorms after this October fire, post-fire mulch treatments were not applied [48].

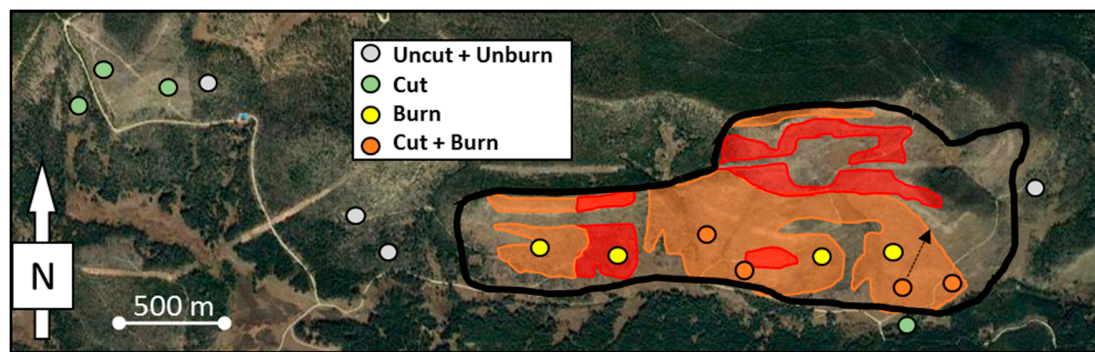


Figure 2. Perimeter of the Church's Park Fire and surroundings, near Fraser, Colorado, denoting areas mapped with moderate- (orange) and high- (red) burn severity and centers of operational-scale study sites. Unshaded areas within the fire perimeter were burned at low-severity. The dashed arrow is oriented with the general views in Figure 1. Aerial photo image date is 9 October 2015, five years after the fire. Image Citation: Google Earth Pro V7.3.1.4505 (Google LLC, Mountain View, CA, USA); accessed 2 February 2018.

2.2. Sampling and Analysis

We compared tree regeneration, surface fuel and understory plant cover and soil properties among the following ecosystem conditions: (1) Uncut + Unburned (UU); (2) Cut (C); (3) Burned (B) and (4) Cut + Burned (CB) (Figure 2). We established four operational-scale study sites (3–10 ha) for each ecosystem condition with three stand-scale sampling areas in each (~1 ha), then established one randomly-oriented 50-m long transect per sampling area. All study areas were dominated by gray-phase lodgepole pine prior to salvage logging and the fire. Burned study areas were located in high- and moderate-severity patches. All study areas were located on south-facing hillslopes with moderate slope (mean: 34%). Unburned study areas, both cut and uncut, were within 3 km of the fire perimeter.

We examined understory plant and surface cover, tree regeneration, and plant-available soil nitrogen (N) over the course of three years. We measured understory plant and surface cover in August 2012, 2013, 2014 with a gridded point-intercept method in five 1-m² quadrats per transect. Common understory plants were identified to genus or species while others were identified to growth form (graminoid, forb, shrub). Surface cover elements included organic horizon (O) soil (litter and duff), mineral soil, 1- to 10-h woody fuels (<2.5 cm diameter), 100-h woody fuels (2.5–7.6 cm diameter), and 1000-h woody fuels (>7.6 cm diameter). Regenerating trees were tallied within the quadrats by species and height classes (1–15 cm, 15–75 cm, ≥75 cm but <2.5 cm diameter). We used ion exchange resin (IER) bags to measure plant-available soil N and potential nitrate (NO₃-N) leached in spring snowmelt [49]. We inserted 10 resin bags per transect, 5–10 cm into mineral soil each fall and exchanged them the following spring during 2011/2012, 2012/2013, and 2013/2014. Resin bags consisted of a 1:1 mixture of cation (Sybron Ionic C-249, Type 1 Strong Acid, Na⁺ form, Gel Type) and anion (Sybron Ionic ASB-1P Type 1, Strong Base OH[−] form, Gel Type) exchange resin beads. After removal from the field, resins were extracted with a 2 M KCl solution, shaken for 60 min, filtered and frozen until analysis. Nitrate (NO₃-N) and ammonium (NH₄-N) concentrations were measured by spectrophotometry using a flow injection analyzer (Lachat Company, Loveland, CO, USA).

As an indicator of post-fire soil hydrologic conditions, in 2012 we also measured soil water infiltration rate with a field infiltrometer designed to assess wildfire effects (Decagon Devices, Pullman, WA, USA). We recorded the volume of water infiltrating into the mineral soil (2 cm depth) during triplicate 60-s subsample periods at five locations per sample transect. We evaluated soil hydrophobicity [50] at a similar sampling intensity by measuring the time that a water drop remained on the soil surface (e.g., water drop penetration resistance) using the following time periods: none (<10 s); weak (10–40 s); moderate (40–180 s); strong (>180 s).

Data were composited within the three stand-scale sampling areas in each of the four study sites ($n = 12$). Given the close proximity and consistent topographic position, forest composition and degree of beetle-related mortality of the study sites, we assume they are comparable for statistical analysis. The four ecosystem conditions were compared using analysis of variance with Cut, Burn, and a Cut \times Burn interaction as fixed effects and stand-scale sampling areas nested within study sites as random effects (SPSS version 22, IBM Co., Chicago, IL, USA). We added a repeated measures term for analysis of tree regeneration, surface and understory plant cover and plant-available soil N. Each water drop penetration measure was placed into a resistance class, plot and transect-scale replicates were averaged then analyzed as a continuous variable. Where fixed effects were significant, we used pairwise, Tukey-adjusted comparisons to identify differences among the four ecosystem conditions. Levene's statistic was used to test assumptions of homogeneity of variance; ion exchange resin data violated this assumption and were log-transformed prior to analyses. Statistical significance is reported where $\alpha \leq 0.05$, unless otherwise stated.

3. Results

Tree seedling density varied among the four ecosystem conditions (Figure 3). Total seedling density in 2014 was highest ($\sim 13,000$ trees ha^{-1}) in the UU areas, consisting almost entirely of subalpine fir (90% of all seedlings) in the smaller two size classes. Aspen and the other conifer species occurred at much lower densities in UU areas.

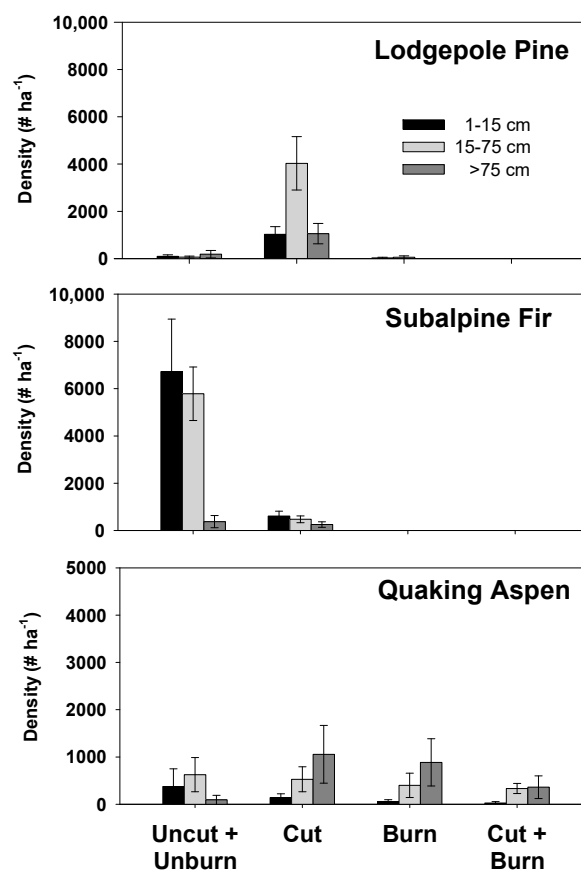


Figure 3. Tree seedling density in August 2014, four growing seasons after the Church's Park Fire and five years after harvesting of the bark beetle-infested lodgepole pine overstory. Data are means with standard error bars for twelve stand-scale sampling areas per ecosystem condition, by seedling height class. Spruce seedlings were absent from both burned conditions (Burn and Cut + Burn) and represented <56 tree ha^{-1} in both unburned conditions (Unburn + Uncut and Cut). Note: The y axis of the bottom panel is half that of the upper two panels.

Fir seedling density was 90% lower in harvested (C) compared to UU areas. Conversely, total lodgepole pine density was 6100 trees ha⁻¹ in C areas and 340 trees ha⁻¹ in UU areas. Cutting stimulated a 10-fold increase in the density of the tallest class of aspen via sprouting compared to the UU treatment. Burning had a dramatic and lasting effect on conifer seedling density (Figure 3). Pine seedlings were extremely rare (<100 trees ha⁻¹ in B; 0 trees ha⁻¹ in CB) and there were no fir or spruce [43] tallied in either burned condition (B or CB) during the study. Aspen was the only tree species found both in the B and CB areas. From 2012 to 2014, aspen sprout density increased 6-fold in B and 3-fold in CB areas, but changed little in the other conditions [43]. Conifer density did not increase in UU and C areas during the study.

Soil organic (O) horizon cover was 29% lower in the cut (C) areas compared to UU areas, averaged over all sample years (Table 1). Conversely, fine (1 and 10 h), 100 h, and total woody fuel cover was 1.7-, 4.0 and 1.9 times higher in C compared to UU areas. Burning (B) had greater effects than harvesting on surface cover (Table 1). Soil O horizon extent was 55% lower in B compared to UU areas on average, whereas mineral soil cover was about 30 times higher. Fine woody fuel cover was 73% lower in B areas overall; larger fuel classes and total woody fuel cover did not differ from UU areas. Organic horizon and mineral soil cover for CB treatments were intermediate relative to the UU and B treatments. However, woody fuel cover in the CB combination did not differ from burning (B) alone. Soil and wood cover changed little in UU areas over the course of the study (Table 1). There was no return of O horizon cover in the C, B or CB conditions over the course of the study or decline in mineral soil cover.

Table 1. Surface cover (%) after salvage logging and wildfire in bark beetle-infested lodgepole pine forests. Data are means with standard error for twelve stand-scale sampling areas per ecosystem condition per date. Different letters within columns denote differences within years based on Tukey's pairwise adjusted comparisons.

		Soil Surface Cover							Woody Fuel Cover											
Year	Condition/Label	Organic			Mineral			1 and 10-h			100-h			1000-h			Total Fuel			
2012	Uncut + Unburn (UU)	86.9	2.3	a	2.4	0.8	c	15.0	1.9	a	1.5	0.4	b	5.8	1.5	ab	22.5	2.5	b	
	Cut (C)	71.4	3.5	ab	12.5	2.4	c	24.8	4.8	a	6.5	0.9	a	11.2	2.8	a	43.9	6.6	a	
	Burn (B)	36.6	5.7	c	52.6	5.3	a	3.1	1.6	b	0.9	0.2	b	2.9	1.5	b	8.8	1.7	b	
	Cut + Burn (CB)	55.5	5.7	b	31.9	5.4	b	4.1	1.6	b	1.2	0.3	b	5.4	1.4	ab	10.9	2.4	b	
2013	Uncut + Unburn (UU)	87.2	2.3	a	1.5	0.3	c	9.5	1.8	ab	0.9	0.3	b	7.3	1.5	a	18.4	1.8	ab	
	Cut (C)	59.0	4.2	bc	14.8	3.7	bc	15.1	2.6	a	4.5	0.7	a	10.7	3.2	a	31.2	5.3	a	
	Burn (B)	47.8	4.9	c	44.6	5.5	a	3.0	1.2	b	1.2	0.3	b	3.1	1.4	a	9.6	1.5	b	
	Cut + Burn (CB)	64.9	4.9	bc	27.1	5.5	ab	4.0	1.0	b	1.8	0.4	b	4.0	1.0	a	10.9	2.1	b	
2014	Uncut + Unburn (UU)	85.3	0.9	a	2.0	0.6	c	11.5	1.8	b	2.2	0.5	b	4.2	1.4	ab	20.1	1.9	b	
	Cut (C)	53.2	4.8	b	15.3	2.6	c	21.8	3.5	a	5.7	1.2	a	10.8	2.5	a	42.3	5.8	a	
	Burn (B)	31.8	3.3	c	60.8	3.8	a	3.4	0.4	c	1.1	0.3	b	2.6	0.7	b	11.4	1.4	b	
	Cut + Burn (CB)	44.3	4.9	bc	46.6	5.1	b	3.6	0.6	c	1.4	0.6	b	4.8	1.7	ab	10.7	2.2	b	
Effects		F	p		F	p		F	p		F	p		F	p		F	p		
Cut		4.9	0.029		1.0	0.317		13.8	<0.001		53.7	<0.001		14.5	<0.001		27.4	<0.001		
Burn		123.0	<0.001		270.3	<0.001		101.9	<0.001		47.5	<0.001		19.5	<0.001		102.8	<0.001		
Cut * Burn		72.7	<0.001		42.7	<0.001		9.9	0.002		35.1	<0.001		3.3	0.071		23.6	<0.001		
Date		8.5	<0.001		6.0	0.004		3.1	0.051		1.01	0.368		0.2	0.800		1.9	0.151		

Graminoid cover was similar between C and UU conditions, and forb cover was only marginally lower, but shrub cover was considerably lower in the C conditions (Table 2). Averaged over the three-year study, shrub cover was 66% lower in C than UU areas. Total understory plant cover was 46% lower overall in C compared to UU areas. Graminoid and shrub covers were both 89% lower in B relative to UU areas, though forb cover was similar. Graminoid cover was intermediate for cutting followed by burning (CB) and was from 3 to 11 times higher than B. Understory plant cover was relatively stable over the course of the study in the UU and C areas. In contrast, total plant cover doubled between 2012 and 2014 in B areas. In the B treatment, graminoid, forb and shrub cover

increased 5-, 2- and 3-fold during the study. Shrub cover was also 5 times higher in the CB treatment in 2014 compared to 2012.

Table 2. Understory plant cover (%) after salvage logging and wildfire in bark beetle-infested lodgepole pine forests. Data are means with standard error for twelve stand-scale sampling areas per ecosystem condition per year. The sum of plant growth forms may exceed 100% within treatment due to overlapping plant canopy layers. Different letters within columns denote differences within single years based on Tukey's pairwise adjusted comparisons.

Year	Condition	Graminoid			Forb			Shrub			Total		
2012	Uncut + Unburn	43.7	4.7	a	34.8	4.3	a	39.7	3.7	a	118.2	5.9	a
	Cut	33.6	4.2	a	16.8	5.6	a	12.9	2.4	b	63.2	7.4	b
	Burn	1.2	0.3	b	20.0	3.1	a	2.3	0.4	c	23.6	3.1	c
	Cut + Burn	13.9	3.4	b	35.3	7.4	a	0.7	0.3	c	49.8	9.2	bc
2013	Uncut + Unburn	32.8	5.8	a	20.8	3.9	ab	38.2	3.0	a	91.8	8.5	a
	Cut	26.2	3.5	ab	13.1	3.5	b	11.7	2.1	b	51.0	5.5	b
	Burn	3.9	1.2	c	28.9	4.4	a	4.6	0.9	c	37.5	3.9	b
	Cut + Burn	13.9	2.5	bc	30.0	4.3	a	1.8	0.6	c	45.6	4.5	b
2014	Uncut + Unburn	33.3	3.9	a	37.5	5.1	a	39.8	3.2	a	110.5	7.4	a
	Cut	27.1	4.3	ab	16.0	5.0	b	15.7	2.6	b	58.7	6.2	b
	Burn	6.1	1.3	c	39.0	4.7	a	6.3	1.1	c	51.3	5.4	b
	Cut + Burn	18.5	3.4	bc	32.7	3.6	ab	3.3	0.9	c	54.5	5.4	b
<i>Effects</i>		<i>F</i>	<i>p</i>		<i>F</i>	<i>p</i>		<i>F</i>	<i>p</i>		<i>F</i>	<i>p</i>	
	Cut	1.0	0.331		6.2	0.014		179.0	<0.001		30.2	<0.001	
	Burn	150.4	<0.001		11.2	0.001		466.2	<0.001		111.5	<0.001	
	Cut * Burn	27.2	<0.001		11.1	0.001		120.4	<0.001		70.3	<0.001	
	Date	1.2	0.308		3.4	0.038		2.0	0.145		4.7	0.011	

As of 2014, cover of the most common species in each plant growth form remained low in both C and B treatments (Figure 4). The forb, heartleaf arnica (*Arnica cordifolia* Hook.) was 12% in UU areas and 3% and 1.5% in C and B areas. Fireweed (*Chamerion angustifolium* (L.) Holub.) cover was nearly 2.5 times higher in B relative to UU areas. The dominant shrub, grouse whortleberry (*Vaccinium scoparium* Leiberg ex. Coville), averaged 33% in UU areas compared to 12 and 2% after cutting and burning, respectively. Both arnica and whortleberry were nearly absent where cutting was followed by burning (CB), but the combined treatment more than doubled sedge cover (*Carex* spp., predominately *C. rossii* Boott. and *C. geyeri* Boott.) in areas that were only burned.

Plant available soil N (IER-N) was lowest in UU areas and generally increased with additional disturbance (Figure 5). Cut areas had significantly higher nitrate and total IER-N overall, though C and UU treatments did not differ statistically within individual years. Burned areas had elevated nitrate, ammonium and total IER-N relative to UU stands throughout the study. Averaged across three years, there were 5.4 and 3.5 times more nitrate and total IER-N in B compared to UU areas. The burn effect on IER-ammonium was statistically significant in 2012, when it was 2.2 times higher than in UU areas. Significant cut-by-burn interactions for nitrate and total IER-N indicate an additive effect of burning in salvage-logged areas (CB). Overall, CB areas had 10 and 6 times more nitrate IER-N and total IER-N, respectively, than UU areas. In 2012, CB areas had 14 times more IER-nitrate than UU areas and roughly double that measured in B areas. In the subsequent two years, IER-nitrate was similar in CB and B areas. On average, nitrate represented 76% of total IER-N in BC compared to 48% in UU areas.

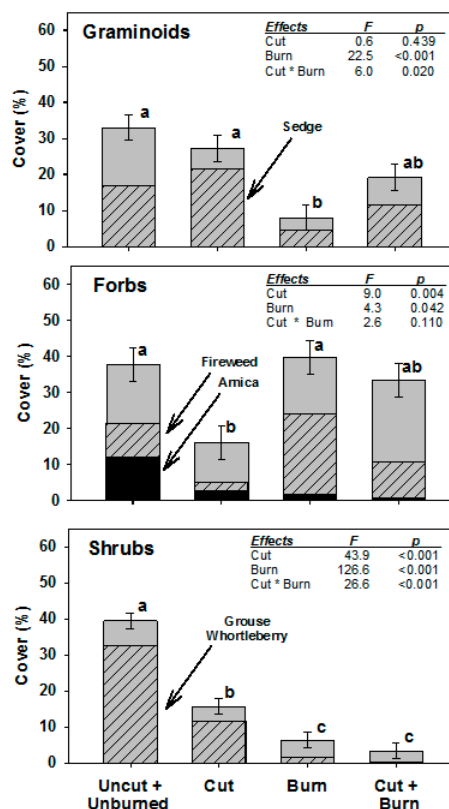


Figure 4. Understory plant cover in bark beetle-infested, cut and burned forest combinations at the Church's Park Fire, Colorado during August 2014. Data are means of total plant cover (gray bar) by plant growth form with standard error bars for twelve stand-scale sampling areas per ecosystem condition. The sum of plant growth forms may exceed 100% within treatment due to overlapping plant canopy layers. Different letters indicate that treatment values differ based on Tukey's pairwise adjusted comparisons. Cover of the most abundant (hatched) or second-most abundant (blackened) species in each growth form are displayed and identified by arrows.

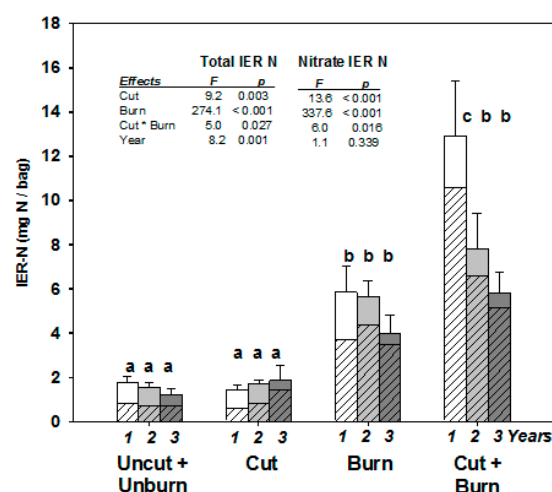


Figure 5. Plant-available soil N in bark beetle-infested, cut and burned forest conditions at the Church's Park Fire, Colorado. Bars are the average total IER-N and nitrate IER-N (hatched) with standard error bars. The three years denote the 2011/2012, 2012/2013 and 2013/2014 overwinter sampling periods. Different letters denote differences within years based on Tukey's pairwise adjusted comparisons of log-transformed total IER-N data.

In 2012, water infiltration in the B and CB areas (1.5 and 1.9 mL min^{-1}) was half the rate measured in UU areas (3.4 mL min^{-1}) (Figure 6a). Wildfire also inhibited water drop penetration, indicating moderate levels of hydrophobicity (Figure 6b) with highest resistance in B areas. Cutting decreased infiltration, though to a marginally lesser extent than burning, and it had no effect on hydrophobicity.

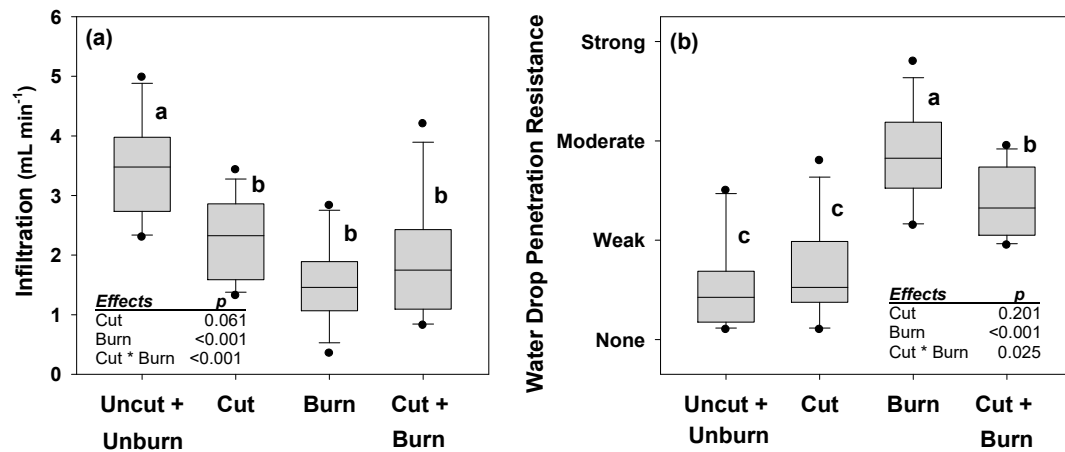


Figure 6. Water infiltration rate (a) and water drop penetration resistance (b) measured in 2012 after logging and the Church's Park Fire in mountain pine beetle-infested stands. Plots show 25th, 50th and 75th percentiles (box), 10th and 90th percentiles (whiskers) and outliers (filled circles). Different letters indicate that treatment values differ based on Tukey's pairwise adjusted comparisons. Water drop resistance ratings as follows: none <10 s; weak 10–40 s; moderate 40–180 s; strong >180 s.

4. Discussion

4.1. Overlapping Disturbances

The Church's Park Fire concluded a series of disturbances that started with bark beetle infestation and was followed by salvage logging in some stands. The lack of lodgepole pine recruitment for four years after the fire contrasted with dense post-fire seedling establishment that is typical within two to three years of harvesting and burning [2,20,31,51,52]. It also differed from fires in beetle-affected lodgepole stands that occurred during green-attack or red-needle stage [21,53] or gray-stage stands with lower outbreak severity (0–56% beetle-killed basal area) [15]. Cone serotiny is a critical determinant of post-fire and post-bark beetle lodgepole recruitment [15,54–56], and is prevalent in Church's Park area stands. Lodgepole pine seeds remain viable in serotinous cones for over 25 years after trees are infested by bark beetles [29], so there would have been a canopy seed source at the time of the fire. However, the fire scorched and consumed nearly all cones remaining on standing dead pine trees and in logging slash as well as any advance regeneration or seedlings established since the outbreak.

The absence of conifer regeneration within the Church's Park Fire contrasts with surrounding unburned areas as well, where bark beetle mortality alone or salvage logging of beetle-infested stands stimulated conifer recruitment. Observations of stand development 20–30 years after a 1980s-era beetle outbreak [17] confirm projections of stand dynamics based on inventory of seedling establishment after the recent outbreak [3]. Both of these Colorado studies along with those conducted elsewhere [57,58] suggest that (1) uncut beetle-infested stands will develop into well-stocked, conifer-dominated forests with more subalpine fir than prior to the beetle outbreak and that (2) salvage-logged, beetle-infested stands will regenerate into pine-dominated stands, similar to those that existed at the time of the outbreak. In our study, aspen was the only tree species observed regenerating via sprouting in significant numbers after the Church's Park Fire. Aspen density was relatively insensitive to cutting and burning compared to the conifers (Figure 3). Long-term forest development within the Church's Park Fire perimeter is uncertain, but based on our findings it appears likely that aspen will increase and

conifers will decline relative to pre-fire conditions and surrounding unburned areas; similar patterns have been reported elsewhere [18].

The outcome of individual disturbances is determined by unique combinations of site conditions, disturbance characteristics and post-disturbance ecological interactions [7]. At Church's Park, overlap of the beetle outbreak and salvage logging or wildfire disturbances are likely to produce even more complexity. The high levels of beetle-induced mortality (>85% of overstory basal area), time elapsed since the outbreak (~8 year post-infestation) and steep slopes were features of the site and wildfire that resulted in crown fire behavior with near-complete crown and cone consumption [16]. Though post-fire regeneration was generally adequate in beetle-infested northwestern Wyoming lodgepole stands, regeneration was nonetheless lowest under conditions such as those we studied, where crown fire in gray-stage beetle kill scorched crowns and consumed cones [15]. Our findings are specific to the site, pre-fire stand structure and fire behavior at Church's Park, but the compositional changes we documented after the fire are likely to be repeated where wildfires burn similar gray-stage, beetle-killed stands with extensive overstory mortality [18,37,59].

4.2. Implications of Post-Bark Beetle Salvage Logging on Wildfire Effects

Widespread overstory mortality associated with severe bark beetle outbreaks increased concerns about fire risk and prompted post-outbreak timber harvesting in Colorado after decades of public opposition [31]. Salvage logging is prescribed to address numerous objectives [60,61] and in response to recent insect outbreaks it has been used to reduce canopy fuels and crown fire potential, capture the value of dead timber, regenerate forests, protect infrastructure and humans from falling trees, and facilitate fire suppression [62]. However, as observed here and elsewhere, logging increases surface fuel loads [34,63], and in the event of a post-harvest wildfire, has the potential to exacerbate fire behavior and effects [64]. Salvage harvesting is controversial where it fails to meet intended objectives [60,65] and at Church's Park there was potential that logging in conjunction with the overlapping beetle and wildfire disturbances would have unintended negative consequences for biodiversity, ecosystem function and delivery of ecosystem services [61]. Regional concerns for management of federal forest lands include regenerating well-stocked forests, retaining native plant diversity and cover, maintaining soil and ecosystem productivity and protecting clean water supply.

At the time of the fire (<two years after harvesting), residual fine fuels likely altered fire spread and large fuels may have increased the duration of combustion in BC areas. Both graminoids and shrubs were negatively impacted by burning. Grouse whortleberry, the shrub that formed >30% cover in UU areas, was reduced to ~2% in B areas and was almost eliminated from BC areas (Figure 4). However, with that exception, other responses we measured suggest that fire effects were no more severe in areas that were logged prior to the fire. Conversely, while salvage logging removed the forest canopy and thus eliminated the risk of crown fire, the surface fire that burned through the harvested areas had similar effects to crown fire in uncut areas.

After the fire, BC areas had less exposed mineral soil and greater O horizon cover than solely burned (B) areas. The higher residual O horizon cover is likely to have contributed to the marginally higher water infiltration (Figure 6) and plant-available N in those areas (Figure 5) relative to B areas. The initial pulse of soil N in BC areas may have resulted from the combustion of accumulated post-harvest fuels; similar to N dynamics after pile burning, it began to recede after one year [66]. After the first year of sampling, soil nitrate was similar between B and BC areas relative to UU and C areas (Figure 5). Both bark beetles and salvage logging are known to increase soil N in unburned lodgepole pine forests [35,67]. In spite of post-bark beetle increases in soil N, and unlike beetle outbreaks in parts of Europe that receive high atmospheric N deposition [68], Colorado beetle outbreaks have not threatened surface water with high N loading [69]. Research in Europe and the US highlights the role of nutrient demand and compensatory growth by recruiting and residual vegetation for intercepting surplus soil nutrients after tree mortality [11,12,68,69]. At Church's Park, post-fire IER-N levels and the risk of nitrate leaching will recede as understory plant cover increases.

The marginally higher understory cover of BC compared to B areas suggests that salvage logging did not exacerbate these concerns at Church's Park.

The US Forest Service is required by the National Forest Management Act of 1976 (United States Public Law 94-588) to monitor and rectify tree regeneration failure associated with management activities. In all stand-level study areas affected by the Church's Park Fire (both B and BC), conifer regeneration fell below US Forest Service density thresholds aimed at ensuring the development of acceptably stocked forests (370 tree ha^{-1}) [70]. Though fire eliminated virtually all conifer regeneration in the B and BC areas (Figure 3), it did not reduce regenerating aspen density relative to unburned areas. Owing to the small spatial extent of the Church's Park Fire and establishment of conifer cohorts in beetle-infested and salvage-logged forests surrounding the burn, scarce regeneration within the fire is not likely to have negative effects on local biodiversity. Limited conifer recruitment into the Church's Park Fire, in fact, should interrupt landscape continuity and thus reduce the spread of future wildfires [19].

Nonetheless, the Church's Park Fire appears to have had a potentially lasting effect on forest species composition relative to pre-outbreak, pre-fire conditions. Aspen was present throughout the Church's Park area prior to the series of disturbances, and sprouts were stimulated or retained within salvage logged (C), burned (B) and combined cut, then burned areas (CB). Post-fire expansion of aspen is common in the Colorado subalpine forest zone and is associated with benefits for floral and faunal biodiversity, fire resistance, and landscape aesthetics [71,72]. Aspen regeneration was abundant across all our study conditions and our findings suggest that the species could play an increasingly important role in similar post-beetle outbreak forests across the Rocky Mountain West.

5. Conclusions

After four years of post-fire recovery, it appears that the overlapping disturbances culminating with the Church's Park Fire will have a long-term effect on forest development. The severe level of bark beetle-related overstory mortality, followed by crown fire in gray-stage stands, virtually eliminated conifer regeneration. In contrast to the conifers, the density of aspen in 2014 was similar inside and outside of the fire (Figure 3) and it has increased more than three-fold in burned areas since the fire. Shrubs were greatly reduced by burning alone and burning in previously-logged areas, though their cover has also begun to increase since the fire. The impacts of the Church's Park Fire on forest regeneration were consistent with patterns documented in northwestern Wyoming where crown fire consumed serotinous cones in gray-stage beetle-killed lodgepole pine [15]. Recent studies suggest that projected increases in drought and associated fire frequency and behavior may detract from the resilience of lodgepole and other forest types of the Rocky Mountain West [73,74]. However, low precipitation did not contribute to the scarce conifer regeneration following the Church's Park Fire [75]. Summer season precipitation in the year of the fire (2010) and the following year were above average. In fact, 2011 received the highest total precipitation during the past 30 years. Complete canopy, cone and seedbank consumption was the probable cause of the scant conifer regeneration following the wildfire. As beetle-killed lodgepole pine forests transition to the gray-stage, the conditions we documented after the Church's Park Fire are likely to become more common, especially throughout portions of Colorado, Wyoming and Montana with concentrated beetle activity and high levels of overstory mortality [41,59]. Future research should take advantage of these expanded possibilities and conduct well-replicated studies to advance understanding and provide critical knowledge for managing and conserving forest processes and biodiversity under changing climatic conditions.

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