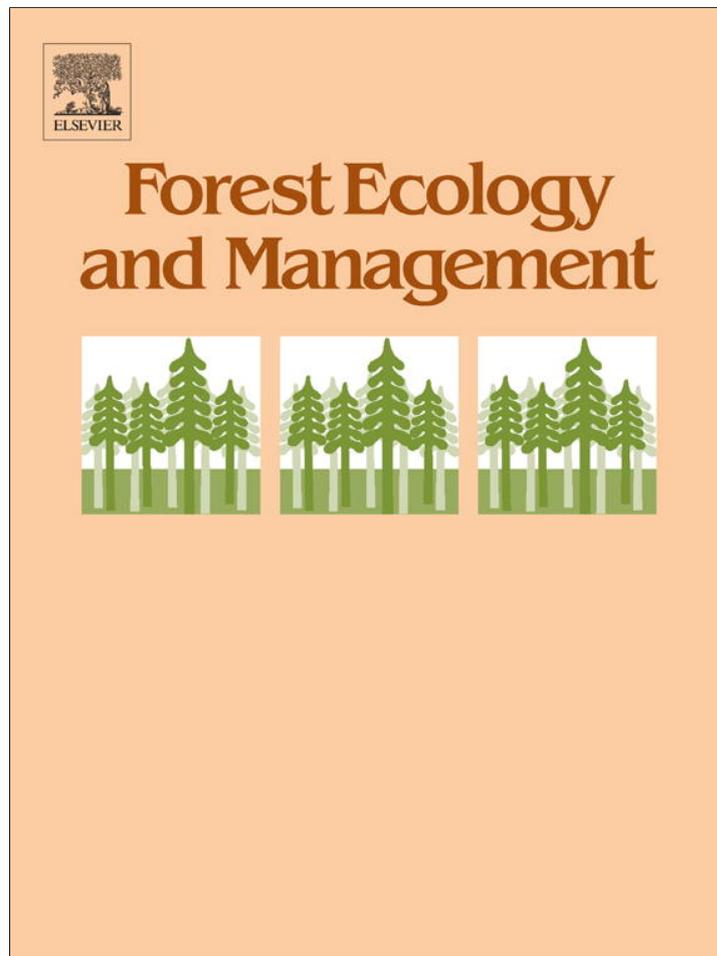


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Salvage harvest effects on advance tree regeneration, soil nitrogen, and fuels following mountain pine beetle outbreak in lodgepole pine

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ABSTRACT

The extent and severity of recent native bark beetle (*Dendroctonae*) outbreaks in western North America have created a pressing need for forest managers to understand potential consequences of post-disturbance management. For example, post-outbreak timber harvest (i.e., salvage harvest) could alter future forest development, productivity and susceptibility to subsequent disturbance. To assess the potential for such consequences, we measured first-year effects of post-outbreak timber harvest on tree regeneration, soil nitrogen (N) availability and fuels by using a paired and replicated before–after–control–impact (BACI) experimental design with eight pairs of 0.25-ha plots in beetle-killed lodgepole pine (*Pinus contorta* var. *latifolia*) in Greater Yellowstone (Wyoming, USA). Post-outbreak timber harvest reduced total (live + dead) lodgepole pine basal area by 90%. Total sapling density (advance regeneration) declined by about 50% following harvest, with tall (30–140 cm) saplings declining most, but mean post-harvest sapling density still exceeded 1600 stems ha⁻¹. Relative species density was unaffected and remained dominated by lodgepole pine. Soil temperature at the litter–soil interface was warmer during summer in harvested stands, and soil NO₃⁻ concentration increased with harvest relative to untreated plots. Soil NH₄⁺ concentration and resin bag N accumulation increased through time in all beetle-killed plots and were not affected by harvest. Following harvest, dead woody surface fuels in all size categories doubled, and canopy fuel load and canopy bulk density both were reduced; dead fuel depth, duff depth, and canopy base height did not differ between untreated and harvested plots. Harvest did reduce canopy fuels, but the natural progression of needle shedding after beetle-kill accounted for 25–40% of this total canopy fuel reduction. Salvage harvest seems unlikely to alter post-outbreak successional trajectories in these lodgepole pine forests. However, the altered fuel complex (immediate increase in dead woody surface fuels and expected long-term reduction in large-diameter fuels) in harvested plots could cause subsequent fire behavior and effects to differ between harvested and untreated stands.

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1. Introduction

Recent outbreaks of native bark beetles (*Dendroctonae*) have affected millions of hectares in western North America and killed up to 70–90% of large trees in some areas (Raffa et al., 2008). Because of their extent and severity, the outbreaks have created a pressing need for forest managers to understand how post-disturbance management may affect these ecosystems. Salvage harvest (the removal of disturbance-killed trees) is often conducted to recover economically valuable timber, reduce perceived risk of subsequent disturbance, and/or enhance recovery of disturbed areas (Dale

et al., 2001; Beschta et al., 2004; McIver and Ottmar, 2007). Across all land ownerships in the western US, over 3.5 million ha of forests affected by beetle outbreak have been identified for potential treatment (USFS, 2011). Although salvage harvest has been the focus of research following fire (e.g. Donato et al., 2006; Greene et al., 2006) and, to a lesser extent, windstorms (e.g. del Rio, 2006; Peterson and Leach, 2008b; Fraver et al., 2011), few studies consider salvage harvest in beetle-killed forests (but see Collins et al., 2010, 2011, 2012). Knowledge of whether salvage harvest changes future forest development, potential productivity, and susceptibility to subsequent disturbance is sparse but needed to guide post-outbreak forest management (e.g., D'Amato et al., 2011). To assess the potential for such consequences, we evaluated first-year ecological effects of salvage harvest on tree regeneration, soil nitrogen availability and fuels in lodgepole pine (*Pinus contorta* var. *latifolia*) forests recently attacked by the mountain pine beetle (*Dendroctonus ponderosae*).

Bark beetles are phloem-feeding specialists native to temperate and boreal coniferous forests (Bentz et al., 2009), and the effects of

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bark beetle outbreaks on stand structure have been well documented (e.g. Romme et al., 1986; Axelson et al., 2009). In lodgepole pine forests, successful mountain pine beetle attack is usually limited to canopy and large sub-canopy trees (Safranyik and Carroll, 2006). Thus, stand-level beetle-caused tree mortality is incomplete, and the disturbance is also gradual because tree mortality occurs over several years. Snags remain standing for years or decades (Lewis and Hartley, 2005). The forest floor and duff layer remain intact during an outbreak, although dead needles are gradually added to the litter layer as canopy trees die. A flush of understory vegetation is often observed, likely in response to increased light, water and soil nutrients (Griffin et al., 2011). However, sapling densities are largely unchanged and sufficient for stand replacement (Rocca and Romme, 2009; Vyse et al., 2009; Diskin et al., 2011; Kayes and Tinker, 2012). Release of these understory survivors is often a major mechanism of regeneration (Veblen et al., 1991; Boggs et al., 2008; Nigh et al., 2008).

Salvage timber harvest operations cut and remove the merchantable disturbance-killed trees (and some live trees as well, depending on prescription), thus reducing the density and basal area of standing-dead trees. Harvested trees are generally large, and post-logging slash can be treated in various ways (e.g., removed, scattered, or cut and piled). Salvage harvest could unintentionally reduce live sapling density and understory vegetation by physical damage and mortality, soil disturbance, or altered microsite conditions (Blouin et al., 2005; Bulmer and Simpson, 2005; Kamaluddin et al., 2005). For example, post-fire salvage harvest has reduced conifer seedling density (Martinez-Sanchez et al., 1999; Donato et al., 2006; Greene et al., 2006) and total vegetative cover (Stuart et al., 1993; Purdon et al., 2004; McIver and Ottmar, 2007). However, salvage operations following beetle outbreaks might also enhance establishment of post-outbreak tree seedlings in areas where soil disturbance exposes mineral soil (Collins et al., 2010).

Nitrogen (N) often limits productivity of lodgepole pine forests and can be a sensitive indicator of disturbance (Fahey et al., 1985), but the effect of post-outbreak salvage harvest on N availability is difficult to predict. During the first few years of a bark-beetle outbreak, soil temperature decreases because increased litter provides added insulation (Griffin et al., 2011; Simard et al., 2011); soil moisture also increases as trees die and evapotranspiration declines. However, salvage harvest can increase soil temperature (Smethurst and Nambiar, 1990; Fontaine et al., 2010), and logging machinery can compact forest soils, reducing porosity and water-holding capacity (Blouin et al., 2008). Thus, post-outbreak salvage harvest could lead to warmer, drier soils, which might reduce N availability, but data are inconclusive. Some studies report short-lived increases in N mineralization rates following compaction (Kranabetter et al., 2006) and others report no effect (e.g. Goodman and Hungate, 2006) or reductions in soil inorganic N pool sizes (Blouin et al., 2005; Choi et al., 2005; Kamaluddin et al., 2005). Inputs of litter and fine wood may further increase following salvage logging (Smethurst and Nambiar, 1990; Goodman and Hungate, 2006), and this material may serve as a temporary N sink if it remains on the forest floor (Remsburg and Turner, 2006). Thus, evidence for how post-outbreak salvage might affect soils and N cycling is inconclusive, and alternative expectations are plausible.

Reducing the likelihood and/or severity of subsequent fire is among the objectives of post-outbreak salvage logging in the western US (USFS, 2011), but the effectiveness of such treatments has not been evaluated. Bark beetle outbreaks initially (i.e., 1–4 years) change fuel abundance and distribution in lodgepole pine by thinning canopies and enhancing understory plant growth (Page and Jenkins, 2007b; Jenkins et al., 2008; Simard et al., 2011). Shortly after beetle attack, reduced canopy fuel moisture and altered foliar chemistry may increase fire hazard (Jolly et al., 2012; Page et al.,

2012), but the concurrent reduction in canopy fuels through needle fall may mitigate this effect (Simard et al., 2011; Schroeder and Mooney, 2012). Salvage harvest removes the large standing snags but may increase the quantity of dead surface fuels (Collins et al., 2012), as with post-fire salvage logging (Donato et al., 2006; McIver and Ottmar, 2007; McGinnis et al., 2010). However, the effects of salvage harvest may differ following fire and beetle outbreak because their disturbance legacies are very different; fires directly remove canopy and surface fuels and directly affect understory vegetation, whereas bark beetles do not consume canopy biomass or surface fuels and do not directly affect the forest understory.

In this study, we asked how post-outbreak salvage harvest in beetle-killed lodgepole pine affected tree regeneration potential, soil N availability, and fuels during the first year following harvest. We expected sapling density (and thus tree regeneration potential) to be reduced following harvest. For soils and N availability, expectations were less clear, as canopy opening would increase soil temperatures but added litter would insulate soils and reduce soil temperature. Soil N pools and N availability might increase, decrease or remain unchanged. Finally, we expected canopy fuels and live surface fuels to be reduced, but dead surface fuels to increase.

2. Materials and methods

2.1. Study region and experimental design

Study sites were located in a 4-km² area of the Green River Lakes region on the Bridger–Teton National Forest in northeastern Wyoming, USA (Fig. 1). The forests established following a fire in 1849 and were dominated by lodgepole pine, with minor components of subalpine fir (*Abies lasiocarpa* Hook.), Engelmann spruce (*Picea engelmannii* Parry), and whitebark pine (*Pinus albicaulis* Engelmann). Stands were approximately 160 years old at the time of this study and had not been harvested previously (M.A. Dasher, personal communication). Mean temperature for the nearest weather station (Cora, Wyoming) is 14.2 °C in July and –10.2 °C in January, with annual precipitation averaging 302 mm per year, mostly as snow (WRCC, 2012). Soils are nutrient poor and derived from andesitic substrates. Mountain pine beetle activity in the area peaked in 2005, but affected forests included a mix of unattacked live trees and beetle-killed trees in the red and gray stages of canopy decline when initially sampled in 2007. A tree's foliage turns red within a year (red stage) after successful beetle attack, and the needles are shed from the canopy within 1–3 years (by the gray stage). Because trees are attacked over several years and not all trees are killed, the infested stands included live and dead trees in varying stages of post-attack condition (Table 1). Stands were all in the gray stage when sampled in 2010, post-treatment.

We used a paired and replicated before-after-control-impact (BACI) experimental design (Underwood, 1994) consisting of eight pairs of 50-m × 50-m plots located in beetle-killed forests. In each pair, one plot was designated for salvage harvest (Bend in the River timber sale), and a similar plot <400 m away was unmanaged (untreated plots). The timber sale was developed in response to the mountain pine beetle epidemic and the perceived need to remove dead and infested trees to improve stand diversity and reduce fuel loading (M.A. Dasher, personal communication). Timing of salvage operations was not under investigator control, and harvest was delayed somewhat because of market forces. A commercial operator conducted the salvage harvest in summer 2009 using a feller-buncher, with lop-and-scatter slash treatments in all harvested plots. The harvest prescription was to remove dead and dying (beetle-infested) lodgepole pine and stipulated that young growth (advance regeneration) should be protected throughout the harvest;

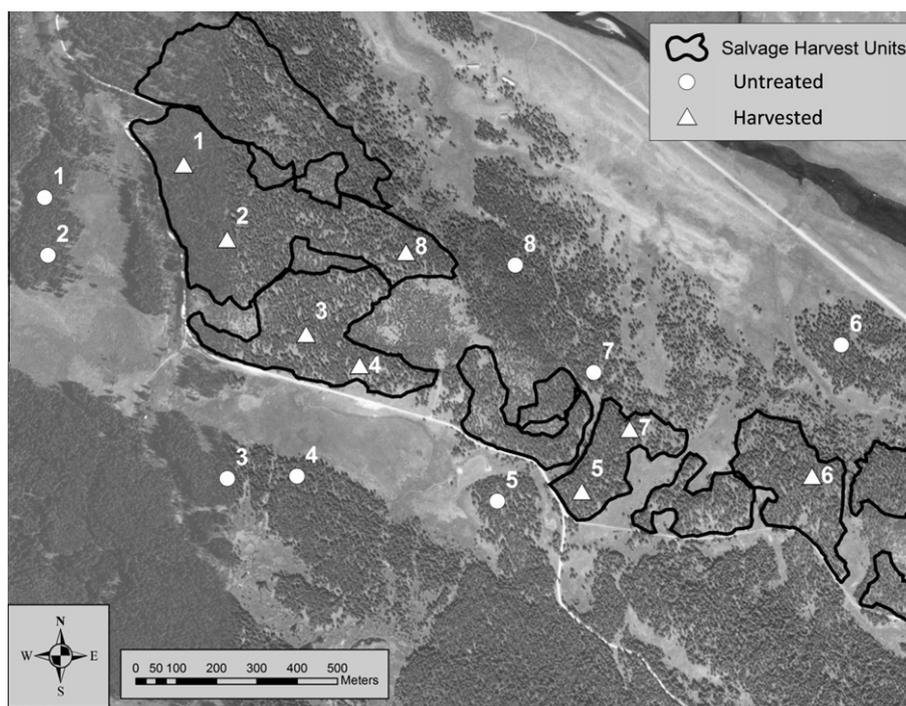


Fig. 1. Study area, Green River Lakes region of the Bridger–Teton National Forest. Eight plot pairs were established in summer 2007, with one plot inside a polygon designated for salvage harvest and the other untreated. Forests were dominated by lodgepole pine, and mountain pine beetle activity was extensive. Salvage harvests occurred in summer 2009.

no differential treatment among conifer species was specified. Approximately 90% of the basal area removed was beetle-killed, and because few large trees were unattacked, plots were essentially clearcut. Logs were limbed to a top diameter of 15.2 cm, and slash (tree top and all limbs cut from the tops and boles) was dispersed to a maximum depth of 60 cm. There was no broadcast burn after harvest operations, and no burning before post-treatment sampling. In all plots, vegetation, litter, soils, and fuel data were collected during summer 2007 (pre-salvage) and again in summer 2010 (post-salvage). With the exception of harvested plots during the summer 2009 treatment period, resin bag N was measured continuously from summer 2007 through summer 2010, and soil temperature was recorded hourly from summer 2008 through summer 2010.

2.2. Vegetation and fuel sampling

In each plot, trees (>1.4 m tall) were sampled within three 200-m² subplots: two rectangular 4 m × 50 m subplots along the eastern and western plot edges, and one 8-m radius circular subplot at the plot center. For each tree rooted in the subplots, we recorded tree species, diameter at breast height (DBH), status (live, dead standing, or dead downed), condition of foliage remaining in the tree canopy (100% green; 51–100% red needles, with the remainder fallen; 0–50% red needles, with the remainder fallen; no needles), presence of any serotinous cones, and signs of MPB presence (pitch tubes, J-shaped galleries, exit holes, and boring dust; see Simard et al., 2011). In 1/4 of each subplot, tree saplings (all stems <1.4 m in height) were described using the same variables as canopy trees, except that height (nearest 10 cm) was noted instead of DBH. In the west and east subplots, we recorded crown base height for each tree and sapling as the distance between the ground and the lowest green or red needles. Crown base height was recorded with a graduated pole (for heights ≤6 m) or an electronic clinom-

eter (for heights >6 m) with a 0.25-m precision from 0 to 1 m, a 0.5-m precision from 1 to 6 m, and a 1-m precision above 6 m.

Ground cover of litter, coarse wood, bare soil, and three plant functional groups (forbs, sedges, and graminoids) was visually estimated to the nearest 10% in twenty 0.25-m² circular microplots; total cover was allowed to exceed 100% to account for multiple vegetation strata. Ten microplots were located within the central subplot using a stratified random design, and five microplots were systematically distributed along the length of each rectangular subplot.

Surface fuels were sampled in ten 10-m long transects, five in each rectangular subplot, using Brown's planar intersect method (Brown, 1974). We recorded dead woody surface fuels that intersected a 2-m high plane in the following diameter classes: 0–0.64 cm (1-h timelag fuels; tallied over the first 2 m of each transect), 0.64–2.54 cm (10-h timelag fuels; tallied over the first 2 m of each transect), 2.54–7.62 cm (100-h timelag fuels; tallied over the first 3 m of each transect), and >7.62 cm (1000-h timelag fuels; diameter measured and decay class recorded over each 10-m transect). Duff (organic layer between the mineral soil surface and the litter layer, composed of the fermentation and humus layers) depth and dead fuel depth (distance between bottom of litter layer to top of highest dead surface fuel in plane) were recorded at two and three locations, respectively, within the first two meters of each transect. Fuel load per area was calculated for each diameter class following Brown (1974).

2.3. Litter and soil sampling

We sampled litter and soils in each plot to assess and interpret soil N availability. In each 0.25-m² microplot of the center subplot, litter depth was recorded at three locations, and a 400-cm² sample of the litter layer (Oi) was collected. The litter was oven-dried at 60 °C and the mass recorded. For chemical analysis, litter from each microplot was subsampled in three categories: fresh cur-

Table 1

Pre-salvage characteristics for untreated and to-be-harvested plots in beetle-killed *Pinus contorta* forests. Values are overall means \pm 2 SE ($N = 8$) by treatment category; P values are from paired t -tests ($N = 8$ plot pairs) and boldface indicates $P < 0.05$.

| Site characteristic | Planned post-beetle treatment category | | P |
|---|--|-----------------|---------------------|
| | Untreated | Salvage harvest | |
| <i>Topography</i> | | | |
| Elevation (m) | 2510 \pm 22 | 2526 \pm 12 | 0.0899 |
| Aspect (SW index) ^a | -0.7 \pm 0.4 | -0.1 \pm 0.6 | 0.2250 |
| Slope (°) | 14 \pm 6 | 15 \pm 5 | 0.7851 |
| <i>P. contorta</i> basal area ($m^2 ha^{-1}$) | | | |
| Live unattacked | 8.3 \pm 2.8 | 5.6 \pm 2.8 | 0.0978 |
| Live attacked | 2.1 \pm 2.2 | 0.6 \pm 1.2 | 0.3050 |
| Dead unattacked | 5.0 \pm 3.1 | 8.0 \pm 4.3 | 0.2290 |
| Dead attacked | 22.4 \pm 4.1 | 21.9 \pm 5.0 | 0.8156 |
| <i>Live sapling density (height \leq 140 cm, stems ha^{-1})</i> | | | |
| Total, all species | 7133 \pm 3380 | 3567 \pm 1855 | 0.1010 ^b |
| <i>Pinus contorta</i> | 4383 \pm 2854 | 2225 \pm 1326 | 0.2798 ^b |
| <i>Abies lasiocarpa</i> | 684 \pm 520 | 325 \pm 240 | 0.2502 ^b |
| <i>Picea engelmannii</i> | 808 \pm 699 | 328 \pm 324 | 0.1498 ^b |
| <i>Pinus albicaulis</i> | 1258 \pm 416 | 667 \pm 394 | 0.1372 ^b |
| <i>Ground cover (%)</i> | | | |
| Bare soil | 0.4 \pm 0.5 | 0.1 \pm 0.1 | 0.1705 |
| Litter | 42 \pm 9 | 41 \pm 10 | 0.7418 |
| Coarse wood | 2.6 \pm 3.2 | 2.3 \pm 1.7 | 0.8202 |
| Total biotic | 62 \pm 11 | 60 \pm 13 | 0.7322 |
| Graminoid | 16 \pm 6 | 7 \pm 4 | 0.0607 |
| Shrub | 7 \pm 6 | 3 \pm 3 | 0.0976 |
| Forb | 37 \pm 11 | 49 \pm 9 | 0.0664 |
| <i>Surface fuels</i> | | | |
| 1-h fuels (tonnes ha^{-1}) | 1.65 \pm 0.26 | 1.35 \pm 0.25 | 0.1712 |
| 10-h fuels (tonnes ha^{-1}) | 6.69 \pm 1.57 | 5.51 \pm 1.71 | 0.2928 |
| 100-h fuels (tonnes ha^{-1}) | 6.63 \pm 3.00 | 7.63 \pm 4.54 | 0.7169 |
| 1000-h fuels (tonnes ha^{-1}) | 36.0 \pm 13.5 | 27.6 \pm 17.2 | 0.4607 |
| Herbaceous fuels (tonnes ha^{-1}) | 0.92 \pm 0.19 | 0.91 \pm 0.08 | 0.8585 |
| Live woody fuels (tonnes ha^{-1}) | 1.59 \pm 1.21 | 0.82 \pm 0.84 | 0.1507 |
| Dead fuel depth (cm) | 19.1 \pm 7.1 | 14.6 \pm 7.8 | 0.4192 |
| Duff depth (cm) | 3.0 \pm 0.4 | 2.7 \pm 0.7 | 0.6300 |
| <i>Canopy fuels</i> | | | |
| Available canopy fuel load (tonnes ha^{-1}) | 9.05 \pm 0.94 | 8.58 \pm 1.39 | 0.8133 |
| Effective canopy bulk density ($kg m^{-3}$) | 0.07 \pm 0.01 | 0.07 \pm 0.02 | 0.8993 |
| Effective canopy base height (m) | 3.1 \pm 1.4 | 3.2 \pm 1.2 | 0.7315 |
| <i>Litter (Oi)</i> | | | |
| Mass ($g m^{-2}$) | 1614 \pm 236 | 1668 \pm 160 | 0.7698 |
| Depth (cm) | 2.7 \pm 0.4 | 2.3 \pm 0.4 | 0.1913 |
| N pool size ($g N m^{-2}$) | 12.6 \pm 2.2 | 13.9 \pm 1.8 | 0.3794 |
| <1 yr old needle %N | 0.73 \pm 0.07 | 0.69 \pm 0.05 | 0.3402 |
| All needles %N | 0.74 \pm 0.07 | 0.72 \pm 0.08 | 0.6538 |
| Total litter %N | 0.78 \pm 0.06 | 0.84 \pm 0.10 | 0.3030 |
| <i>Soils (Oe, A and B, to 15-cm depth)</i> | | | |
| <i>Texture & structure</i> | | | |
| Sand (%) | 61 \pm 5 | 57 \pm 5 | 0.3128 |
| Silt (%) | 26 \pm 4 | 29 \pm 3 | 0.1969 |
| Clay (%) | 13 \pm 2 | 14 \pm 2 | 0.8483 |
| Bulk density ($g cm^{-3}$) | 0.69 \pm 0.06 | 0.72 \pm 0.07 | 0.5277 |
| Organic soil depth (cm) | 3.2 \pm 0.3 | 2.7 \pm 0.2 | 0.0137 |
| Organic matter (%) | 4.3 \pm 0.8 | 4.7 \pm 1.0 | 0.5424 |
| <i>pH and cations</i> | | | |
| pH | 5.4 \pm 0.1 | 5.3 \pm 0.2 | 0.4905 |
| Ca ($\mu g g^{-1}$; exch.) | 1132 \pm 293 | 1251 \pm 361 | 0.5691 |
| Mg ($\mu g g^{-1}$; exch.) | 131 \pm 24 | 141 \pm 34 | 0.5415 |
| K ($\mu g g^{-1}$; exch.) | 187 \pm 37 | 185 \pm 25 | 0.8680 |
| P ($\mu g g^{-1}$; exch.) | 25 \pm 8 | 28 \pm 5 | 0.4172 |
| <i>Nitrogen</i> | | | |
| NH ₄ ⁺ ($\mu g N g^{-1}$) | 5.3 \pm 1.4 | 6.0 \pm 1.1 | 0.3769 |
| NO ₃ ⁻ ($\mu g N g^{-1}$) | 0.5 \pm 0.3 | 0.6 \pm 0.3 | 0.4116 |
| Organic N ($mg N g^{-1}$) | 0.86 \pm 0.25 | 0.94 \pm 0.28 | 0.6978 |

^a Calculated as: $\cos(\text{aspect}-225)$.

^b Paired t -test performed on \log_{10} transformed data.

rent-year needle litter, identified by bright red color and lack of mottling on surface (Morehouse et al., 2008); all-needle litter (readily identifiable needles of all ages, including current-year);

and total litter (all foliar litter and woody litter <1.0 cm wide). Sorted litter in each category was composited by plot and ground to powder for C:N analysis on a Leco CNS-2000 at the University

of Wisconsin Soil and Plant Analysis Laboratory (UWSPAL, 2010). The litter N pool for each plot was estimated from total litter N and litter mass.

Soil temperature was measured hourly in four randomly selected plot pairs from June 2008 through September 2010 using three pairs of iButton datalogger probes (Maxim Integrated Products Inc., Dallas Semiconductor, Sunnyvale, CA) per plot. Harvested plots were not instrumented during the salvage period in summer 2009. One of each iButton pair was installed at the litter–organic soil interface (Oi–Oe boundary), and the second was installed at 10-cm soil depth. Hourly data from the three probes at each depth were averaged to obtain hourly temperatures per plot. Daily mean temperatures for each depth were then calculated for each plot.

One soil core (Oe, A, B to 15-cm depth) was collected from each 0.25-m² microplot ($N = 10$) in the center subplot using a 5-cm diameter \times 15-cm long PVC corer. Soils were sieved (2 mm mesh), weighed, and divided into three subsamples: (1) 30 g oven-dried at 60 °C for gravimetric percent moisture (2007 and 2010); (2) 20 g extracted in 75 ml of 2 M KCl for 2 h, with the extract then filtered and frozen for later analysis of NH_4^+ and NO_3^- pools (2007 and 2010); (3) 20 g air-dried and bulked by plot for soil texture and chemical analyses (2007 only). Air-dried soil was analyzed for pH, total N, exchangeable Ca, Mg, and K, available P (Bray P1 extract), and organic matter at the University of Wisconsin Soil and Plant Analysis Laboratory (UWSPAL, 2010). Soil organic N was determined by difference using total N and inorganic N values, and soil texture was determined using the Bouyoucos hydrometer technique (Bouyoucos, 1962). KCl extractions were analyzed for $[\text{NH}_4^+]$ and $[\text{NO}_3^-]$ using colorimetric methods on an Astoria Pacific II segmented flow autoanalyzer.

Free resin bags were used as an index of soil N availability because they are effective in remote settings (Binkley et al., 1986; Binkley et al., 1992) and correlate well with more labor-intensive measurements of net N mineralization (Binkley and Matson, 1983; Binkley et al., 1986). Resin bags were constructed using 20 g of mixed bed ion exchange resin (J.T Baker #JT4631-1) tied inside a piece of un-dyed nylon stocking material (Binkley et al., 1992). One resin bag was incubated at 10-cm soil depth in each microplot ($N = 10$ bags per plot). Bags were deployed for sequential summer (ca. June–September) and winter (September–June) periods from June 2007 through September 2010, except that harvested plots were not measured during the summer 2009 salvage period. Upon retrieval, resins were removed from the nylon, extracted in 2 M KCl and analyzed as described above for soils. Resin bag data within each seasonal sampling period were calculated as the rate of N accumulation ($\mu\text{g N g resin}^{-1} \text{ day}^{-1}$).

2.4. Fuel calculations

2.4.1. Canopy fuels

Crown weight and the proportions of foliage and 1-h timelag fuels in the crown were estimated for individual stems using tree DBH measured in the field and allometric equations developed for Rocky Mountain conifers (Brown, 1978). To account for loss of foliage in recently killed trees (red and gray stages), foliage weight was multiplied by 0.25 and 0.75 for trees in the 0–50% and 51–100% red needle classes, respectively. Available canopy fuel load was computed for each stand as the sum of foliar biomass plus 50% of the 1-h timelag fuels, which are generally thought to be consumed during a crown fire (Reinhardt and Crookston, 2003; Reinhardt et al., 2006). Vertical profiles of canopy bulk density were then developed for each stand following Scott and Reinhardt (2001), Reinhardt et al. (2006) and Simard et al. (2011). Vertical profiles were used to calculate effective canopy bulk density (the maximum value of available canopy bulk density) and the effective canopy base height (the lowest height in the profile where canopy

bulk density exceeded 0.011 kg m⁻³) (Reinhardt and Crookston, 2003).

2.4.2. Surface fuels

Dry biomass of herbaceous and woody fuels were computed using percent cover data for each plot and previously published (Turner et al., 2004) or new allometric equations (*Shepherdia canadensis*, $R^2 = 0.97$). Equations for the dominant understory species were used to estimate biomass of each of the broad categories: *Calamagrostis canadensis* for grasses, *Carex geyeri* for sedges, *Arnica cordifolia* for forbs, *Vaccinium scoparium* for low shrubs, and *S. canadensis* for tall shrubs. Biomass of grasses, sedges, and forbs was then summed to obtain live herbaceous fuel load, and that of saplings and shrubs to obtain live woody fuel load.

2.5. Statistical analyses

To test for similarity in pre-salvage site conditions between the untreated and salvage harvested plots, we performed paired *t*-tests ($\alpha < 0.05$) on topographic (elevation, slope, aspect), soil (texture, N, organic matter (OM), pH, and cations), vegetation (basal area, density of <1.4 m stems, and ground cover), surface and canopy fuels, and litter characteristics measured in 2007. Potential effects of post-outbreak salvage logging on these variables were tested by calculating plot-level changes between 2007 and 2010, and performing paired *t*-tests ($\alpha < 0.05$) of this change in untreated vs. salvage harvested plots. Further, because some responses are changing through time in response to time-since-beetle outbreak, general linear models of the form $y = \text{year} + \text{treatment} + \text{year} * \text{treatment}$ were also used with these variables. The year * treatment term tested for the salvage effect.

Soil temperatures were analyzed using mid-summer (July 1–August 31) and mid-winter (January 1–February 28) data from before and after the salvage period. For each soil depth, we averaged the difference in mean daily temperature for each plot pair ($n = 4$ instrumented pairs) during each season, then performed paired *t*-tests at the plot level to compare the differences between harvested and untreated plots before salvage to the differences after treatment. We performed similar paired *t*-tests for the earlier (July 1–10) and later (August 22–31) summer time period. Potential effects of post-beetle salvage logging on resin bag N accumulation rates were tested using paired *t*-tests of the change over time in untreated vs. salvage harvested plots using only the years immediately before and after salvage (2010–2008). All variables were tested for normality and transformed when necessary to meet the assumptions of statistical methods. Unless otherwise noted, reported variance measures are two standard errors of the mean.

3. Results

3.1. Pre- and post-salvage stand conditions

Paired plots (untreated and salvage) were similar ($P > 0.05$) prior to treatment in all topographic, vegetation, cover, fuels, litter, and soil metrics except for organic soil depth, which was deeper by only 0.5 cm in untreated plots (Table 1). Most (97%) of the total basal area was lodgepole pine, and beetle-caused mortality in 2007 averaged 60% of lodgepole basal area (Table 1). An average of 11% of trees had serotinous cones present, which is an intermediate level of serotiny for the region (Tinker et al., 1994; Schoennagel et al., 2003). Sapling density (advance regeneration) was abundant, averaging >5000 stems ha⁻¹ with lodgepole pine representing approximately 60% of the saplings (Table 1). Saplings of whitebark pine, subalpine fir and Engelmann spruce were present at lower densities (<1000 stems ha⁻¹). Sapling densities did not differ

between paired plots (Table 1), nor did relative density by species (data not shown).

Following salvage harvest, total lodgepole pine basal area was 90% lower in the harvested plots but was unchanged in untreated plots (Fig. 2a). However, beetle-killed basal area increased in untreated plots from 2007 to 2010, and live unattacked basal area declined, because the bark beetle infestation continued during this time (Fig. 2a). Two of the eight untreated plots had substantial lodgepole pine basal area (5.9 and 7.8 m² ha⁻¹) that was green in 2007 but under attack by mountain pine beetle, and the attacked trees subsequently died. In the understory, forb cover and total biotic cover were reduced, and coarse wood cover (>7.6 cm diameter) increased by a factor of five in the harvested plots (Fig. 2b). Graminoid, shrub and bare soil cover did not differ between harvested and untreated plots (Fig. 2b).

Following salvage harvest, total tree sapling density (i.e., advance regeneration) was reduced by about 53% (from 3575 to 1688 stems ha⁻¹) in the treated plots compared to the untreated plots, which did not change. In treated plots, the significant reductions (~60%) were observed in the larger height class (30–140 cm; Fig. 2d). Density of smaller saplings (<30 cm) was not affected by harvest. Lodgepole pine sapling density did not differ between treated and untreated plots (Fig. 2d), and the relative density of each species did not change (paired *t*-tests, all *P* > 0.05). When tree species were considered individually, only Engelmann spruce saplings showed a significant post-treatment reduction (~20%) in density (paired *t*-test, *t* = 3.27, *P* = 0.0137). Post-treatment total sapling density averaged 1687 ± 1020 stems ha⁻¹ in the harvested plots in 2010, about half of which was lodgepole pine (888 ± 800 stems ha⁻¹). Pre-treatment lodgepole pine sapling density was <1000 stems ha⁻¹ in three plots and remained low following treatment. In the other five plots, pre-treatment lodgepole pine sapling density ranged from 2067 to 5066 stems ha⁻¹ and was reduced to 200–3300 stems ha⁻¹ following salvage harvest. In plots that received no treatment, the 2010 lodgepole pine sapling densities ranged from 1000 to 9200 stems ha⁻¹.

3.2. Litter, soil temperature and soil nitrogen availability

Several litter variables changed with time but did not respond to salvage harvest; the only litter variable that responded to salvage harvest was %N of all-needle litter, which increased by 31% in harvested plots but did not change in untreated plots (Fig. 3a). Variables that changed only with time included total litter %N (21% increase; *P* = 0.0002; Fig. 3b), total litter N pool (50% increase; *P* < 0.0001; Fig. 3c), and litter mass (37% increase, from 1600 to 2200 g m⁻²; *P* < 0.0001; Fig. 3d). The increase in litter mass over time was driven by two untreated plots in which basal area of green-attacked trees was high in 2007, and substantial canopy foliage was shed between 2007 and 2010 these two plots; in the other untreated plots, trees were in the red stage and had shed more of their needles prior to our initial sampling. With the two green but beetle-attacked plot pairs removed from the analysis, litter mass did not change between 2007 and 2010 in the untreated plots but increased by 52% (859 g m⁻²) in harvested plots. Litter depth and the %N of fresh (<1 year old) needle litter did not change over time or with salvage (Fig. 4e and f).

Following salvage harvest, summer soil temperatures at the litter–soil interface were about 1 °C warmer in treated plots (*t* = -3.81, *P* = 0.0318, d.f. = 3) but winter soil temperatures did not differ (*P* > 0.05) (Fig. 4). Within the summer season, the early summer litter–soil interface temperatures were 2.3 °C warmer in harvested plots (*t* = -10.61, *P* = 0.0018, d.f. = 3), whereas late-summer temperatures did not differ with treatment (*P* > 0.05). Soil temperatures at 10 cm depth were not affected by harvest during summer or winter.

Soil NH₄⁺ concentration tripled between 2007 and 2010 across all plots (from 5.7 ± 0.9 to 17.3 ± 0.9 μg N g soil⁻¹) with no additional effect of salvage harvest (Fig. 3g). In contrast, soil NO₃⁻ concentration did not change through time in untreated plots but almost tripled in harvested plots (from 0.6 ± 0.2 to 1.6 ± 0.5 μg N g soil⁻¹; Fig. 3h). Total extractable soil inorganic N was dominated by NH₄⁺ and increased in all plots between 2007

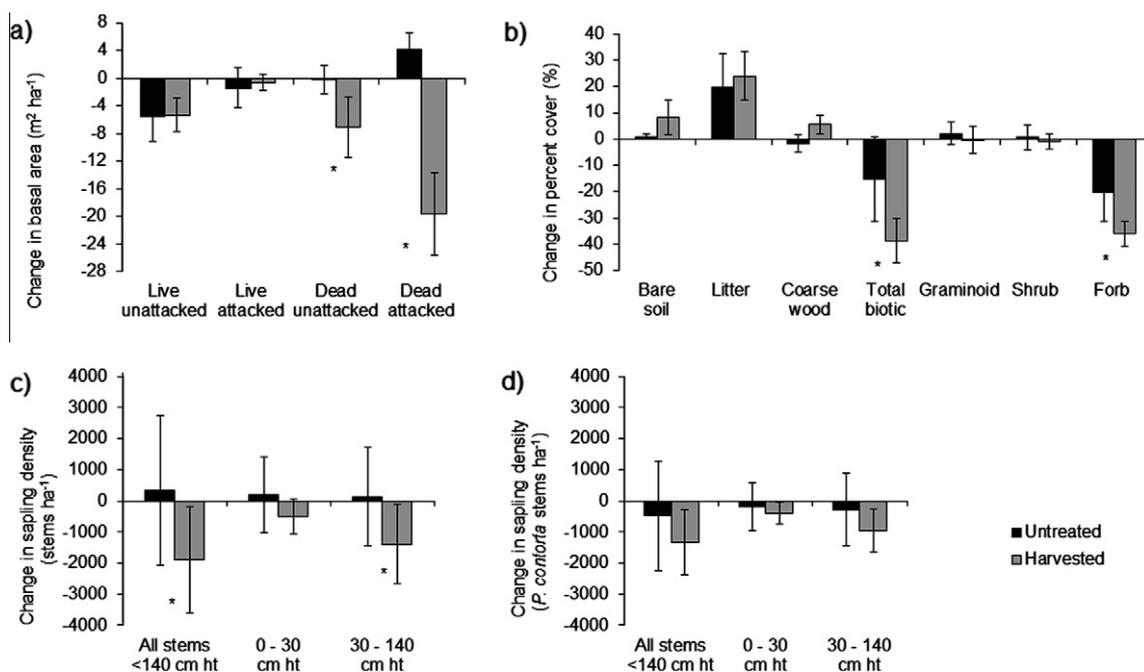


Fig. 2. Changes (2010 minus 2007) in stand structure, ground cover, and sapling density in untreated and harvested plots following the 2009 logging treatment: (a) live and dead basal area in attacked and unattacked lodgepole pine, (b) percent ground cover in abiotic (bare soil, litter, and coarse wood) and biotic (total and by plant functional group) classes, (c) density of all saplings < 140 cm tall, and (d) density of lodgepole pine saplings < 140 cm tall only. An asterisk indicates a significant difference at $\alpha = 0.05$. *N* = 8 pairs of plots. Error bars = 2 standard errors.

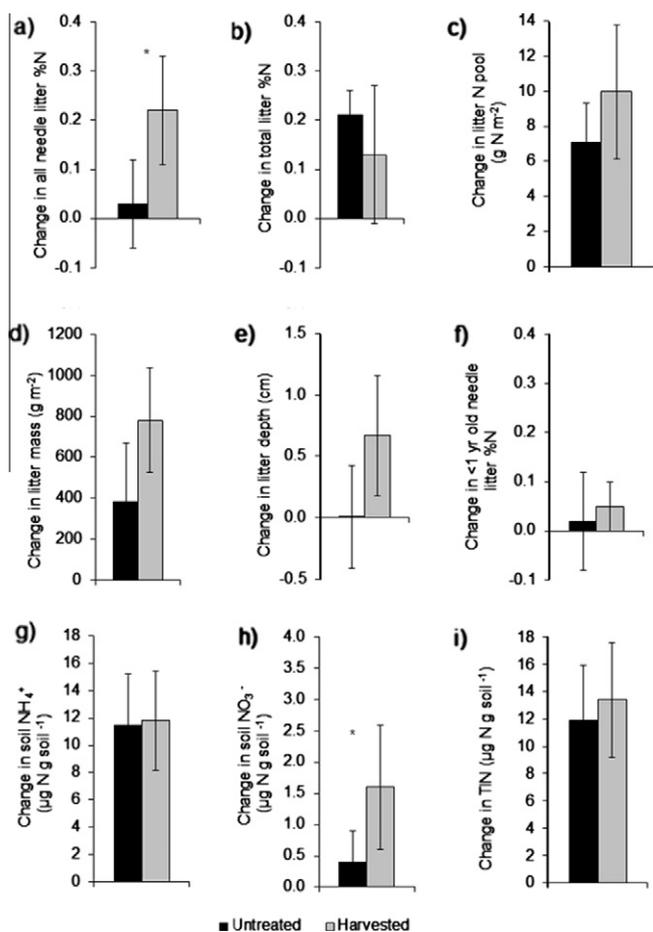


Fig. 3. Change in litter quantity and quality, and soil N in untreated and salvage-harvested plots following logging: (a) %N in all needle litter, (b) %N in total litter, (c) total litter N pool, (d) litter mass, (e) litter depth, (f) %N in < 1 yr old needle litter, (g) extractable soil NH_4^+ , (h) extractable soil NO_3^- , and (i) total extractable inorganic N (TIN). An asterisk indicates a significant difference at $\alpha = 0.05$. $N = 8$ pairs of plots. Error bars = 2 standard errors.

and 2010, but it was not affected by salvage harvest (Fig. 4i). Resin bag NH_4^+ accumulation rate increased about threefold between 2007 and 2010 in all plots and was always higher in summer than in winter (Fig. 5a). Resin bag NO_3^- accumulation rate was consistently low ($< 0.10 \mu\text{g N g resin}^{-1} \text{ day}^{-1}$) in summer and winter (Fig. 5b). There was no effect of salvage harvest on seasonal or annual accumulation rates of either NH_4^+ or NO_3^- in the paired comparisons ($P > 0.05$).

3.3. Fuel quantity and vertical distribution

Dead woody surface fuel loads in all size categories doubled in the treated plots following harvest, whereas these fuel loads did not change between 2007 and 2010 in untreated plots (Fig. 6a). Live herbaceous fuel load decreased in all plots, but the decrease was greater in harvested plots (-60%) than in untreated plots (-20% ; Fig. 6b). Live woody fuel load also decreased between 2007 and 2010 in all plots (-41%) but did not differ between harvested and untreated plots (Fig. 6b). Salvage harvest had no detectable effect on duff depth or dead fuel depth, which was highly variable (Fig. 6c).

Available canopy fuel load decreased between 2007 and 2010 in all plots, but the decrease was significantly greater in salvage-logged plots (-80%) than in untreated plots (-30% ; Fig. 6d). Similarly, effective canopy bulk density decreased in all plots, but the

decrease was greater in salvage-logged plots (-76%) than in beetle-only plots (-20%) (Fig. 6e). Canopy base height increased ($+54\%$) between 2007 and 2010, but among-plot variability was high, and canopy base height did not differ between harvested and untreated plots (Fig. 6f). However, in two sites, salvage logging reduced canopy bulk density below the generally accepted threshold (0.011 kg m^{-2}) used to define the effective canopy base height to carry fire (Scott and Reinhardt, 2001; Reinhardt et al., 2006).

4. Discussion

In this study, we found that post-outbreak timber harvest in beetle-killed lodgepole pine forests reduced advance regeneration by $\sim 50\%$ and substantially altered the amount and vertical distribution of fuels. Forb cover was reduced following salvage harvest, but graminoid, shrub and bare soil cover did not differ between untreated and harvested stands. Effects of salvage harvest on soil N availability were minimal relative to untreated stands. The results of the current study contribute to a growing understanding of post-disturbance timber harvest (McIver and Starr, 2001; Noss and Lindenmayer, 2006) and its consequences for future forest development, productivity and susceptibility to subsequent disturbance (Donato et al., 2006; Greene et al., 2006; McIver and McNeil, 2006).

4.1. Forest development

Salvage harvest operations in our study plots resulted in a net decline in total sapling density, consistent with several other studies of post-disturbance timber harvest (Jonasova and Prach, 2004, 2008; Donato et al., 2006; Greene et al., 2006; Keyser et al., 2009). The taller saplings were reduced, whereas small saplings ($< 30 \text{ cm}$) were not. The intact understory and forest floor in beetle-killed stands may protect smaller stems by physically buffering them from mechanical damage, whereas taller saplings may be more vulnerable (Vyse et al., 2009). Nonetheless, despite the significant reduction, total sapling densities remained $> 1600 \text{ stems ha}^{-1}$, which is considered sufficient for stand replacement (Vyse et al., 2009). Given substantial variability in pre-treatment sapling densities, salvage harvest did not appear to change the spatial pattern of advance regeneration. Lodgepole pine sapling density was $< 1000 \text{ stems ha}^{-1}$ in six of the eight salvaged plots, suggesting that these plots could potentially fall below the minimum density of full site occupancy (e.g., Lhotka and Loewenstein, 2008), but these plots were still within the range observed in other untreated post-outbreak lodgepole pine stands in Greater Yellowstone (Simard et al., 2011). Tree regeneration could be augmented by subsequent tree seedling establishment, which has been observed in other post-outbreak harvested stands (Collins et al., 2011). The warmer temperatures we observed during early summer in harvested plots also could lead to earlier seed germination in treated plots. However, the lack of change in bare soil cover following harvest in our study area suggests soil disturbance was minimal, and thus germination sites may not have been increased with salvage operations.

With respect to tree species composition, successional trajectories did not appear to be altered by salvage logging in our study area; lodgepole pine will likely continue to dominate in most stands. Lodgepole pine often dominates advance regeneration following beetle outbreak in unmanaged forests (e.g. Diskin et al., 2011; Kayes and Tinker, 2012). In our study, lodgepole pine remained dominant following harvest, with average densities $> 800 \text{ stems ha}^{-1}$, comparable to those observed in a time-since-outbreak chronosequence in Greater Yellowstone (Simard et al., 2012). We found no change in the relative abundance of tree species in the advance regeneration following salvage harvest, despite

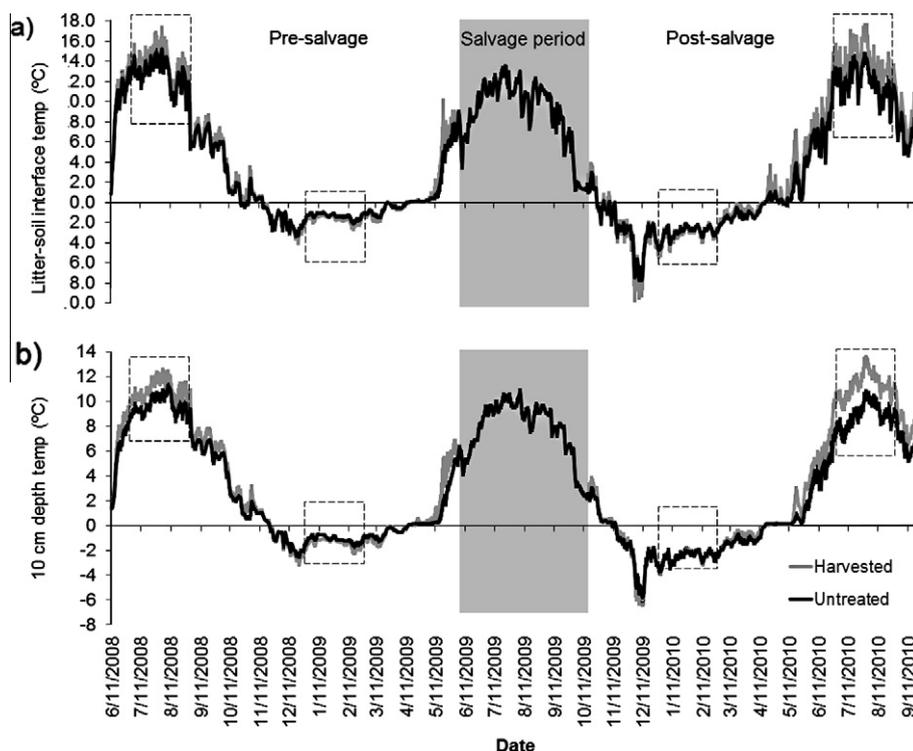


Fig. 4. Average \pm one standard error of daily soil temperature in untreated and salvage-harvested plots following logging. Harvested plots were not instrumented during the salvage period in summer 2009. Untreated plot data (black) are overlaid on harvested plot data (gray): (a) temperature at the litter–organic soil interface and (b) temperature at 10-cm soil depth. Time periods used in statistical analyses (see text) are shown in boxes.

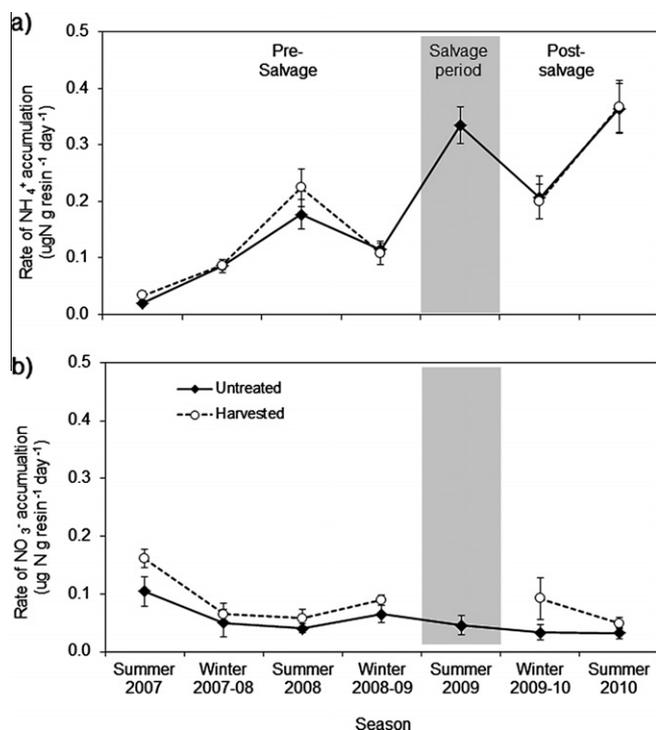


Fig. 5. Resin bag N accumulation rates in untreated and salvage-harvested plots following logging. Harvested plots were not measured during the salvage period in summer of 2009: (a) resin bag NH_4^+ accumulation rate and (b) resin bag NO_3^- accumulation rate. $N = 8$. Error bars = 2 standard errors.

a significant reduction in Engelmann spruce saplings. The lower density of advance spruce regeneration could, however, reduce interspecific competition and enhance growth of advance lodge-

pole pine regeneration. Among other studies, the consequences of salvage harvest for tree composition vary considerably. Successional trajectories were also unaltered by salvage harvest in loblolly pine (*Pinus taeda*) following an outbreak of the southern pine beetle (*Dendroctonus frontalis*) (Coleman et al., 2008) or windthrow (Peterson and Leach, 2008a). In contrast, a shift to subalpine fir appeared likely in post-outbreak lodgepole pine stands in Colorado that were untreated, whereas lodgepole pine dominance was maintained by post-outbreak salvage harvest (Collins et al., 2011). Post-beetle (*Ips typographus*) clear-cut salvage logging in a Norway spruce (*Picea abies*) forest also reduced the density of spruce saplings and instead promoted early-successional understory species (Jonasova and Prach, 2004, 2008). However, even when forest composition does not change, effects of initial differences in tree density on stand structure and biomass can last for decades and even centuries (Kashian et al., 2005a, b; Donato et al., 2012). Variation in disturbance severity and legacies, tree species characteristics, harvesting techniques, and season all likely play a role in determining whether post-disturbance harvest will shift forest composition.

4.2. Soil nitrogen availability

Inorganic N availability increased in all plots (untreated and harvested) as the beetle outbreak progressed. This is consistent with our time-since-outbreak chronosequence study of unmanaged lodgepole pine stands, which revealed modest increases in net N mineralization and nitrification (Griffin et al., 2011). With the exception of increased (but still low) soil NO_3^- and increased all-needle-litter %N, salvage had no additional effect on litter and soil N dynamics within the year after harvest relative to the changes already occurring in beetle-killed forests. Reduced forb cover in the post-outbreak salvage plots may have contributed to the increased NO_3^- , as forbs preferentially take up NO_3^- over NH_4^+

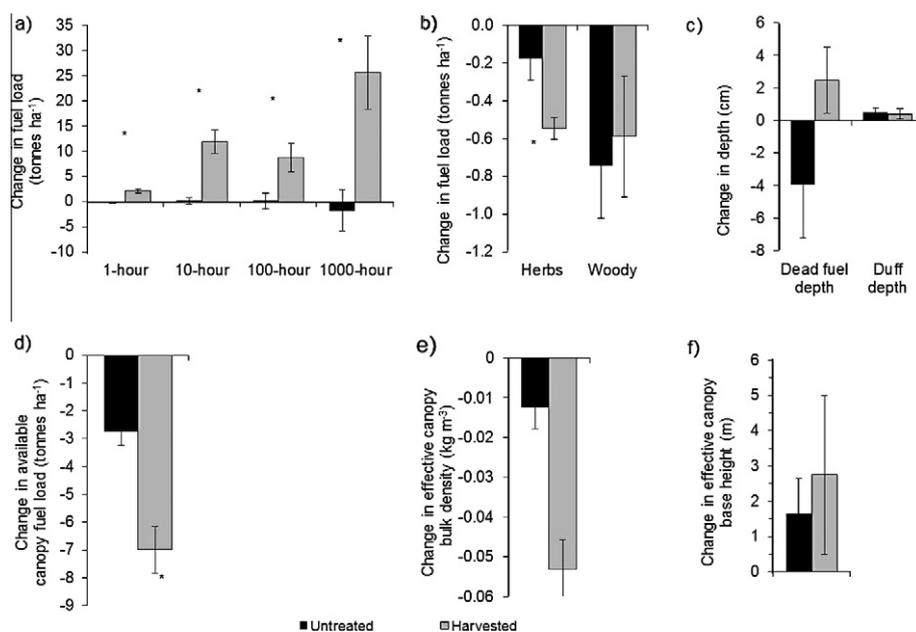


Fig. 6. Changes in surface and canopy fuels abundance in untreated and salvage-harvested plots following the 2009 logging treatment: (a) dead woody surface fuels, (b) live surface fuels, (c) dead fuels and duff depths, (d) available canopy fuel load, (e) effective canopy bulk density, and (f) effective canopy base height. An asterisk indicates a significant difference at $\alpha = 0.05$. $N = 8$ pairs of plots. Error bars = 2 standard errors.

(Miller and Bowman, 2002; Falkengren-Grerup et al., 2004). Although soil N availability often increases following disturbance, the potential for N leaching appears relatively low. Other studies in Rocky Mountain conifers have reported low NO_3^- production and export even after a majority of trees die or are removed (Knight et al., 1991; Parsons et al., 1994; Prescott et al., 2003; Thiel and Perakis, 2009). Because live tree basal area and litter mass were similar in harvested and untreated plots, salvage harvest may not have immediately altered the balance between plant uptake and litter input. Furthermore, post-outbreak litter inputs have high C:N ratios (Griffin et al., 2011) and may serve as N sinks in the early stages of decomposition (Fahey et al., 1985; Remsburg and Turner, 2006), limiting the accumulation of inorganic N in soils.

Soil temperature changes following bark beetle outbreaks (Griffin et al., 2011), and here we observed an increase in summer soil temperature at the litter–soil interface with salvage harvest. Increased soil temperature following post-outbreak salvage harvest has been reported elsewhere (Hais and Kucera, 2008) and probably occurs because the removal of tree boles and decline in understory vegetation reduces soil shading. Warmer soil temperatures may be associated with drier soils and fuels. In a study of post-fire salvage harvest, Fontaine et al. (2010) recorded lower nightly minimum temperatures and earlier daytime heating, but no increase in maximum daily surface air temperatures; they reported that temperature effects of salvage harvest were similar, but muted, compared to live-tree logging effects. The influence of post-beetle salvage on local temperature and moisture dynamics could be particularly important in topographic positions, such as south-facing aspects or lower treeline, where tree establishment or growth may be water limited.

4.3. Fuel quantity and vertical distribution

Post-outbreak salvage logging strongly affected the quantity and vertical distribution of canopy and surface fuels. Our prior chronosequence studies of mountain pine beetle outbreaks in unmanaged lodgepole pine stands in Greater Yellowstone found large declines in available canopy fuels, no initial changes in dead

woody surface fuels, and increases in large woody surface fuels by 30 years post-outbreak (Simard et al., 2011). As expected, salvage logging reduced total canopy fuel load and canopy bulk density by removing beetle-killed trees and some live trees. Part of these fuel reductions, however, was solely due to the temporal dynamics of the bark beetle outbreak. Beetle-killed trees were shedding their needles throughout the study period, reducing canopy fuel load by 30%, reducing canopy bulk density by 20%, and increasing canopy base height by 54%. Thus about 25–40% of the total reduction in canopy fuels in the salvage-logged plots would have occurred during the initial post-outbreak years, even in the absence of logging.

Salvage logging had variable effects on the vertical distribution of canopy fuels among plots. This variability, and the fact that canopy fuels were also being shed in untreated sites between 2007 and 2010, resulted in no net effect of salvage logging on effective canopy base height, except in the two plots where canopy bulk density was reduced below the threshold (0.011 kg ha^{-1}) needed to sustain a canopy fire. If salvage harvest is conducted to reduce canopy fuels, these results underscore the importance of carrying out salvage operations promptly to maximize their effectiveness. Implementing harvest during the red stage would produce the greatest reduction in canopy fuels; as stands progress to later post-outbreak stages, much of the canopy fuel has already been shed (Simard et al., 2011; Hicke et al., 2012; Schoennagel et al., 2012). Recent studies also indicate increased flammability of red needles from beetle-infested lodgepole pine (Jolly et al., 2012), although the extent to which the behavior of actual fires will differ in beetle-killed stands vs. unattacked stands remains to be empirically evaluated (e.g., Jenkins et al., 2012).

In contrast to canopy fuels, dead woody surface fuel loads roughly doubled with post-outbreak salvage harvest. Other studies have also reported increased dead surface fuel loads following post-disturbance timber harvest (e.g., McIver and Ottmar, 2007; Donato et al., 2006; McGinnis et al., 2010; Collins et al., 2012). In contrast, dead woody surface fuels did not change between 2007 and 2010 in the untreated plots, indicating little input of dead woody fuels from the canopy to the surface during the initial 3–4 years of an outbreak. These results, obtained from monitoring

the progression from red to gray stage in the same study plots, are consistent with the findings from our time-since-outbreak chronosequence (Simard et al., 2011) and other studies (Klutsch et al., 2009; Schoennagel et al., 2012; but see Page and Jenkins, 2007b).

When short-term changes and long-term implications are considered, we can summarize three key findings regarding the nature and dynamics of the fuels (Fig. 7). (1) Dead woody surface fuels did not change in unmanaged stands during the first several years following outbreak (Simard et al., 2011), but they increased immediately and substantially with post-outbreak timber harvest. We also observed that live herbaceous fuels were reduced (relative to the 2007 pre-harvest measures) in all plots during 2010 (the first year after salvage harvest) because a late snowmelt delayed plant phenology. However, the reduction in live herbaceous fuels was greater in the harvested plots, and the reduced herbaceous fuels might partly mitigate effects of the increased woody surface fuels on fire behavior. However, such ameliorating effects would likely be short-lived because herbaceous vegetation increases rapidly in response to canopy openings (McCambridge et al., 1982; McMillin and Allen, 2003). (2) Available canopy fuels declined substantially in salvage-logged stands, but part of the reduction was caused by the ongoing shedding of needles from beetle-killed trees; available canopy fuels also declined in untreated stands during the first few years after beetle outbreak. (3) Large dead woody surface fuels increased in untreated stands 25–30 years after beetle outbreak as beetle-killed trees fall to the ground (Simard et al., 2011), but this increase will not occur in harvested stands during this timeframe because the source of the large fuels was removed (Lewis, 2009). The timing of treefall in unmanaged stands is not known precisely, but most fire-killed lodgepole pine snags fall within 20 years in the study region (Romme et al., 2011). However, surface fuels in harvested and untreated plots will likely remain distinct for decades (Fig. 7; Collins et al., 2012). In the long term, lower coarse wood loads in harvested stands may increase fire suppression effectiveness by reducing the time needed for fireline construction, for snag mitigation for crew safety, and for mop up (Jenkins et al., 2012).

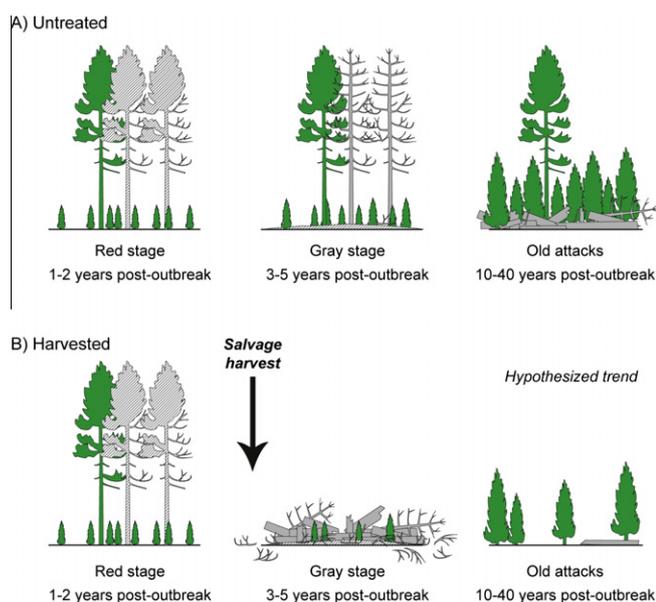


Fig. 7. Illustration of changes in fuels following high-severity beetle infestation (A) with no forestry treatment and (B) with salvage harvest during the red or gray stage. Top panel based on fuel profiles from a time-since-outbreak chronosequence study in Greater Yellowstone (Simard et al., 2011); lower panel based on fuel profiles reported from this study using a BACI experimental design. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4.4. Conclusions

This study suggests that merchantable trees can be harvested from some beetle-killed lodgepole pine forests without severely compromising potential tree regeneration and without large initial effects on soil N. It is important to note that our study plots were all on infertile sites with minimal topographic relief, and results may differ for more fertile sites or steep slopes, for different harvest timing or methods, and for different forest types. This study also suggests that the window of time in which salvage harvest could reduce post-outbreak canopy fuels compared to untreated stands is short. The longer salvage harvest is delayed after beetle attack, the less effective the treatment will be for reducing canopy fuels because the red stage is ephemeral, and available canopy fuels are progressively shed from beetle-killed trees (Page and Jenkins, 2007a; Derose and Long, 2009; Simard et al., 2011; Hicke et al., 2012).

Post-outbreak salvage harvest may increase the influence of surface fuels on fire occurrence and behavior in the early years and decrease the role of large downed woody fuels in the later years. The increased abundance of surface fuels in harvested plots could promote greater subsequent surface-fire activity, with potentially deleterious consequences for regenerating trees (e.g., greater mortality of advance regeneration) and for soils (e.g., more soil heating). Over the longer term, whether the prevalence of coarse woody fuels in untreated stands will make subsequent fires more intense and more difficult to manage relative to harvested stands remains an unresolved concern for many forest managers. The consequences of salvage operations on the fuel complex must be considered carefully, as fire behavior may differ in harvested and untreated stands for decades following treatment, especially if harvesting was to alter forest community composition (e.g. Diskin et al., 2011; Kayes and Tinker, 2012; Collins et al., 2012).

Post-disturbance salvage harvest does have persistent effects on structural legacies, such as snags and downed coarse wood (D'Amato et al., 2011), and structural differences may have lasting influences on ecosystem recovery and biodiversity (e.g., Lindenmayer and Noss, 2006). The long-term consequences of post-outbreak timber harvest on tree regeneration, soil fertility, the fuel complex and subsequent fire behavior remain to be evaluated. As post-outbreak treatment is considered throughout the western US, studies of varying site conditions, forest communities and harvest methods are needed to gain a more complete understanding of post-outbreak management options and efficacy.

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