BARK BEETLE DISTURBANCE AND
NITROGEN CYCLING IN CONIFER FORESTS
OF GREATER YELLOWSTONE

by

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Disturbance has long been considered an important driver of ecosystem dynamics (Bormann and Likens 1979, Pickett and White 1985, Chapin et al. 2002), influencing a wide range of key ecosystem functions such as carbon storage (Li et al. 2003, Kashian et al. 2006), nutrient retention (Pardo et al. 1995), and biodiversity (Connell 1978). The influence of disturbance on ecosystem function may be manifested through several key mechanisms, including the redistribution of biomass, nutrients, and energy among ecosystem pools, the alteration of spatial pattern (Hadley 1994, Turner et al. 1999, Turner et al. 2004), and changes in species composition (Chapin et al. 2002, Ellison et al. 2005). Effects of disturbance on ecosystem function have been quantified for a wide range of spatial scales from small gaps (Scharenbroch and Bockheim 2008) to whole continents (e.g. Potter et al. 2005), and often exhibit threshold spatial extents or severities where qualitative shifts in ecosystem response occur (Parsons et al. 1994). Temporal scale is also a key consideration, as many disturbance types have either long-lived or delayed effects on ecosystem function (Foster et al. 1998, Compton and Boone 2000, DeLuca and Aplet 2008). Disturbance interactions, often crossing multiple scales, will be key to predicting future ecosystem consequences and have been demonstrated in several systems (Paine et al. 1998, Throop and Lerdau 2004, Allen 2007, Raffa et al. 2008).

Insect activity and insect-induced tree mortality can be significant components of the disturbance regime in many temperate forests with substantial consequences for elemental nutrient cycling. Mechanisms of insect disturbance involve both direct influence of herbivory and insect-induced mortality on biomass stocks, growth rates, and ecosystem fluxes such as litterfall and decomposition, as well as indirect effects through altered abiotic conditions or shifts
in plant community composition (Mattson and Addy 1975, Schowalter 1985, Schowalter et al. 1986, Haack and Byler 1993, Hunter 2001). The great majority of studies regarding insect disturbance and nutrient cycling have focused on folivorous insects as the study system (e.g. Lovett and Ruesink 1995, Eshleman et al. 1998, Kosola et al. 2001, Christenson et al. 2002, Townsend et al. 2004). Significantly less attention has been given to potential nutrient cycling changes following outbreaks of non-folivorous insects, with notable exceptions (Huber et al. 2004, Huber 2005, Morehouse et al. 2008). By targeting specific tissues of host plants, various insect guilds can have widely differing effects on host mortality and the transfer of materials among ecosystem pools (Feller 2002, Lovett et al. 2006)

Even less studied is the role of forest type in determining ecosystem response to outbreaks of the same insect guild. This knowledge gap is particularly important when considering foundation species, whose characteristics largely determine ecosystem function (Ellison et al. 2005) and whose dominance in forests often increases susceptibility to insect attack (Safranyik and Carroll 2006). Variability in the baseline biogeochemistry of pure stands of different tree species (Prescott et al. 1992, Thomas and Prescott 2000, Giardina et al. 2001, Lovett et al. 2004) may lead to unique ecosystem responses following the same disturbance type. Furthermore, additional compound disturbances following insect attack such as fire or salvage logging may lead to qualitatively different effects on nutrient cycling compared to insects alone (Paine et al. 1998, Peters et al. 2004). This is particularly important if insect outbreak affects the probability or severity of other subsequent disturbances (Lindenmayer and Noss 2006, Page and Jenkins 2007, Simard et al. 2011). Disturbance types vary in the specific ecosystem components that are directly affected. For example, direct effects of bark beetles are limited to canopy vegetation, and can be contrasted with other disturbance types such as forest fire, windstorm, or
logging which cause immediate change in a wider range of ecosystem components including
understory vegetation and soils (Figure 1).

Figure 1. Impacts of bark beetle outbreak and other disturbance types on forest ecosystem components.
Beetles remove large portions of the canopy, but direct impacts are limited to this component. Other disturbances including salvage logging cause additional canopy disturbance, but also may have direct impacts understory vegetation and soil. Adapted from Roberts (2004).

Throughout western North America, several species of native bark beetles of the genus *Dendroctonus* (Coleoptera: Curculionidae: Scolytinae) have been in outbreak phase over the past decade (Raffa et al. 2008). The impacts of this disturbance type on some aspects of ecosystem function such as carbon sequestration (Kurz et al. 2008) and hydrology (Boon 2009) are beginning to be understood, but the consequences for nitrogen (N) cycling are less well-known. In the Greater Yellowstone Ecosystem of WY, MT, and ID, USA, current bark beetle outbreaks have occurred in multiple conifer forest types including lodgepole pine (*Pinus contorta* Dougl.), Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), Englemann spruce (*Picea engelmannii* Parry), and whitebark pine (*Pinus albicaulis* Engelmann). Outbreaks are allowed to progress naturally within the National Park lands of the region, however salvage logging is being applied as a management technique on National Forest lands to recover usable forest products and reduce a perceived risk of increased forest fire.
For my dissertation I will address three general questions related to the issues described above. (1) **How do forest structure, soil microclimate, and N cycling through the litter, soil, and vegetation change during and decades after beetle outbreak?** (2) **How does host tree forest type moderate the response of these ecosystem parameters to similar bark beetle outbreaks?** and (3) **How do forest structure, microclimate, and nitrogen cycling following post-beetle salvage logging differ from bark beetle outbreak alone**? I will approach these questions by taking advantage of concurrent outbreaks of two *Dendroctonus* bark beetle species in the Greater Yellowstone Ecosystem. First, I will use a replicated chronosequence approach to measure the effects of mountain pine beetle (*Dendroctonus ponderosae* Hopkins) disturbance over a thirty year time span in lodgepole pine forests. Second, I will explore the influence of forest type on ecosystem response to bark beetles by comparing changes in the mountain pine beetle/lodgepole pine system to those resulting from Douglas-fir beetle (*Dendroctonus pseudotsugae* Hopkins) outbreak in Douglas-fir forests over a shorter 5 year time scale. Thirdly, I will use a paired and replicated before-after-control-impact (BACI) experimental design in lodgepole pine forests to compare the combined effects of mountain pine beetle outbreak and salvage logging to the effects of bark beetles alone (Figure 2).

**Figure 2.** Three dissertation chapters on the influence of bark beetle disturbance on N cycling in conifer forests using multiple approaches. Chapter 1 *describes* a single beetle/host system over decadal scales. Chapter two *compares* two beetle/host systems over shorter time scales. Chapter three is an *experiment* testing short-term effects of the compound disturbances of beetles and salvage logging.
REFERENCES


CHAPTER 1

Nitrogen cycling following mountain pine beetle disturbance in
lodgepole pine forests of Greater Yellowstone

ABSTRACT

Widespread bark beetle outbreaks are currently affecting multiple conifer forest types throughout western North America, yet many ecosystem-level consequences of this disturbance are poorly understood. We quantified the effect of mountain pine beetle (Dendroctonus ponderosae) outbreak on nitrogen (N) cycling through litter, soil, and vegetation in lodgepole pine (Pinus contorta var. latifolia) forests of the Greater Yellowstone Ecosystem (Wyoming, USA) across a 0-30 year chronosequence of time-since-beetle disturbance. Recent (1-4 years) bark beetle disturbance increased total litter depth and N concentration in needle litter relative to undisturbed stands, and soils in recently disturbed stands were cooler with greater rates of net N mineralization and nitrification than undisturbed sites. Thirty years after beetle outbreak, needle litter N concentration remained elevated; however total litter N concentration, total litter mass, and soil N pools and fluxes were not different from undisturbed stands. Canopy N pool size declined 58% in recent outbreaks, and remained 48% lower than undisturbed in 30-year old outbreaks. Foliar N concentrations in unattacked lodgepole pine trees and an understory sedge were positively correlated with net N mineralization in soils across the chronosequence. Bark beetle disturbance altered N cycling through the litter, soil, and vegetation of lodgepole pine forests, but changes in soil N cycling were less severe than those observed following stand replacing fire. Several lines of evidence suggest the potential for N leaching is low following bark beetle disturbance in lodgepole pine.
INTRODUCTION

Bark beetle disturbance and nitrogen cycling

Disturbance regulates a wide range of ecosystem properties (Bormann and Likens 1979, Pickett and White 1985, Chapin et al. 2002), and in forests, disturbance-induced tree mortality can change stand structure, productivity, and nutrient cycling (Lodge et al. 1994, Ostertag et al. 2003). Because canopy foliage stores nutrients, determines litter quantity and quality, and moderates litter-soil microclimate (Prescott 2002), canopy disturbance may influence soil nutrient availability (Chapin et al. 2002). Previous studies of disturbance and nutrient cycling in forest ecosystems have provided insight into the magnitude, timing and mechanisms of response (e.g. Vitousek et al. 1979). However, disturbances vary spatially and temporally in both pattern and severity, and ecosystem response varies among disturbance types and forest communities.

Insect outbreaks are common disturbances in forest ecosystems, though most studies of insect herbivores and nutrient cycling have addressed Lepidopteran (e.g. Lovett and Ruesink 1995, Kosola et al. 2001, Christenson et al. 2002, Houle et al. 2009) and Homopteran (e.g. Kizlinski et al. 2002, Stadler et al. 2006) insects. Few studies have focused on stem phloem-feeding insects, such as *Dendroctonus* and *Ips* bark beetle species (Coleoptera: Curculionidae-Scolytinae). In contrast to folivores, bark beetles kill trees by consuming cambium and disrupting phloem flow, thereby acting as agents of selective mortality within a forest. Because bark beetle outbreaks have reached unprecedented levels throughout western North America (Raffa et al. 2008), understanding the ecological effects of widespread beetle-induced tree mortality has become increasingly important.

Bark beetles are native to temperate and boreal coniferous forests and intermittent outbreaks typically recur at decadal-scale intervals (Raffa et al. 2008). Successful beetle attack in
summer causes tree death by the following spring, when needles turn red and begin to fall; the stand progresses from this “red stage” to the “gray stage” as all needles are shed (Safranyik and Carroll 2006). Large trees are most susceptible to bark beetle attack, and mortality of large trees can reach 100% (Safranyik and Carroll 2006). When the outbreak subsides, release of subcanopy surviving trees is often the major mechanism of regeneration (Romme et al. 1986, Nigh et al. 2008, Vyse et al. 2009). Herbaceous species and shrubs also increase presumably in response to light and water availability (McCambridge et al. 1982, Stone and Wolfe 1996), but increased nitrogen availability may play a role. The effects of bark beetles on stand structure (tree density, basal area, and species composition) have been well documented (Shore et al. 2006, Dordel et al. 2008, Klutsch et al. 2009). However, the consequences of bark beetle outbreaks for nitrogen (N) cycling have not been widely studied.

The effect of bark beetle outbreak on N pools and fluxes depends on the balance between factors that enhance or limit nutrient supply. Stand-level transpiration declines as trees within the stand begin to die, and soil moisture increases. Nutrient uptake by trees also declines, but soil nutrient pools will increase only if the rate of nutrient supply via mineralization exceeds the rate of nutrient removal via uptake and leaching. A post-outbreak pulse of litter could increase soil inorganic N pools (Cullings et al. 2003), but conifer litter can also immobilize soil N (Fahey et al. 1985). Canopy and litter changes also affect incident radiation (Hais and Kucera 2008), air flow (Boon 2009) and soil insulation (Byers 1984), and experimental additions of lodgepole pine litter have been shown to modify litter-soil microclimate and soil N availability (Cullings et al 2003). In an N-saturated Norway spruce (Picea abies (L.) Karst.) forest in Bavaria, Germany, soil nitrate concentrations were elevated for 7 years after an outbreak of Ips typographus, but returned to pre-outbreak levels after 17 years (Huber 2005). In soils of southwestern US Pinus
ponderosa forests, disturbance by *Ips* and *Dendroctonus* bark beetle species increased soil ammonium and laboratory net nitrification rates, but did not affect soil nitrate or laboratory net mineralization rates (Morehouse et al. 2008). Additional studies that compare a broader range of N pools and fluxes, both during and after an outbreak, with unaffected stands are needed to understand how bark beetle disturbance alters N flow through the litter, soil, and vegetation over time.

**Approach and hypotheses**

We studied a 0-30 year chronosequence of mountain pine beetle (MPB; *Dendroctonus ponderosae* Hopkins) disturbance in lodgepole pine (*Pinus contorta* var. *latifolia* Dougl.) forests of the Greater Yellowstone Ecosystem. Specifically, we asked how litter quantity and quality, soil nitrogen pool and fluxes, and foliar nitrogen varied with time-since-beetle outbreak and evaluated several hypotheses. We expected litter depth, litter mass, and total litter N concentration to increase during an outbreak and decrease to below undisturbed levels 30 years after an outbreak. As observed by Morehouse et al. (2008) for *Pinus ponderosa*, we expected N concentrations in fresh needle litter to be elevated during the outbreak due to lack of N resorption prior to litterfall. For soil inorganic N, we expected nitrate and ammonium pools to increase during an outbreak but not differ from undisturbed stands by 30 years after an outbreak. Expectations for net N mineralization and net nitrification during the outbreak were less clear; abiotic changes may stimulate mineralization rates, but microbial populations, surviving vegetation and a pulse of needle litter could also act to immobilize soil N. By 30 years after an outbreak, however, we expected N mineralization to be lower than undisturbed stands because soils would likely be warmer and drier under an open canopy, and litter inputs would be diminished relative to undisturbed stands since canopy biomass is not yet recovered. Falling
beetle-killed snags may also reduce soil N availability and turnover during this period because coarse wood may be a net N sink (Fahey et al. 1985, Busse 1994, Laiho and Prescott 1999) and can reduce decomposition and mineralization by altering microsite conditions (Remsburg and Turner 2006, Metzger et al. 2008). For foliar nitrogen in lodgepole pine, we expected the foliar N concentration of surviving trees to increase during an outbreak and be positively correlated with net N mineralization, but total foliar N pool to decline with tree mortality. We further expected that these differences would persist 30 years after an outbreak because canopy biomass would still be greatly reduced relative to undisturbed stands, increasing resource availability per tree even if soil N pools and fluxes return to or fall below undisturbed levels. In the understory sedge Carex geyerii, we similarly predicted foliar N concentration to increase during an outbreak and be positively correlated with N mineralization.

METHODS

Study area

This study was conducted in subalpine forests of the Greater Yellowstone Ecosystem within Yellowstone National Park and Bridger-Teton National Forest in northwestern Wyoming, USA. Lodgepole pine is a common forest type of the region, and most soils are nutrient-poor and derived from volcanic rhyolitic and andesitic deposits. Climate is characterized by cool winters and dry summers, with mean July temperatures of 12.8 °C and mean January temperatures of -11.7 °C at Yellowstone Lake (WRCC 2010b). Mean annual precipitation is 563 mm, mostly occurring as snow, and increases with elevation (Dirks and Martner 1982). Extensive outbreaks of the MPB occurred in southern and western Yellowstone National Park in the 1970s and 1980s (Lynch et al. 2006). Since 2003, large areas of forest in the eastern and southern portions of
Greater Yellowstone have been affected by outbreaks of MPB in lodgepole pine and whitebark pine (*Pinus albicaulis* Engelmann), Douglas-fir beetle (*Dendroctonus pseudotsugae* Hopkins) in Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), and spruce beetle (*Dendroctonus rufipennis* Kirby) in Engelmann spruce (*Picea engelmannii* Parry). This study focused on lodgepole pine forests affected by MPB in both the current outbreak and previous outbreaks of the 1970’s and 1980’s.

**Sampling design**

We sampled a time-since-beetle (TSB) chronosequence including four classes with five replicates each (*N* = 20 plots). TSB classes included undisturbed stands; stands within the current outbreak, both red stage (2 years post-outbreak) and gray stage (4 years post-outbreak); and stands attacked by bark beetles approximately 30 years ago. Potential sites were identified using maps of current (USFS 2006) and historic (Lynch et al. 2006) mountain pine beetle outbreaks, soil type, and forest age. Field inspection assured selection of stands with comparable species composition, basal area, soils, and bark beetle mortality. Undisturbed and 30-year TSB stands were located in Yellowstone National Park, while red and gray stands were located within the current outbreak on the Bridger Teton National Forest (Figure 1). Disturbed plots were located within stands (0.25 ha) of homogenous structure and beetle disturbance intensity; undisturbed sites were located in comparable beetle-susceptible stands. In lodgepole pine, both beetle susceptibility (Safranyik and Carroll 2006) and ecosystem N status (Smithwick et al. 2009) are largely determined by stand structure and age. Thus, site selection based upon stand structure, age, and substrate largely controlled for pre-disturbance differences in these factors among classes. To validate the chronosequence, dendrochronological analyses were used to determine post-fire stand age for all plots and to reconstruct pre-outbreak stand structure and MPB outbreak.
severity for the 30 year TSB plots (Simard et al. 2011). An 8-m radius plot (201 m$^2$) was established at each site in summer 2007, and slope and aspect were recorded at the plot center.

**Microclimate**

To evaluate variation in growing-season microclimate, soil and air temperature were measured hourly in three of the five plots within each TSB class ($N = 12$ instrumented plots) from June 18 through August 7, 2008, using three pairs of iButton datalogger probes (Maxim Integrated Products Inc., Dallas Semiconductor, Sunnyvale, CA) per plot. One iButton of each pair was installed at the litter-organic soil interface, and the second was installed 10 cm below this interface. Air temperature was recorded using another temperature probe hung inside a covered but well-ventilated and open-bottomed white PVC housing attached to a tree at breast height near the plot center.

For each soil depth, temperature probe data were summarized as follows. First, plot-level hourly temperatures were determined by averaging data from the three probes per plot. To account for geographic variation and normalize comparisons among plots, hourly differences between air and soil temperature were calculated (difference = soil – air). Plot-level daily mean temperatures, temperature ranges, and soil-air temperature differences were then calculated from the hourly data, and averaged by class to determine class-level daily means. Plot-level growing season mean temperatures, ranges, and soil-air temperature differences were calculated by averaging daily means across the sampling period, and class-level growing season means were then calculated from these plot-level data.

**Vegetation**

All live and dead standing trees > 1.4 m tall were identified to species and measured for diameter at breast height (DBH). MPB-killed trees were identified by the presence of pitch tubes.
(tree resin accumulation at boring hole entrances), boring dust, and J-shaped galleries under the bark (diagnostic of *Dendroctonus* (Safranyik and Carroll 2006)). Downed logs rooted in the plot were also measured for DBH, identified to species, and scored as MPB-killed if J-shaped galleries were visible. Trees < 1.4 m tall were measured by 10 cm height classes in the northeast quadrant of the plot (50m²). Pre-outbreak basal area for red and gray stands was calculated by summing the basal area of live and beetle-killed trees. In the 30-year TSB stands post-outbreak growth of survivors was substantial, so pre-outbreak basal area was determined from dendrochronology using stand reconstruction techniques (Simard et al 2011). Beetle-killed basal area in the 30-year TSB stands was determined by summing the basal area of downed logs with evidence of MPB galleries. Lodgepole pine canopy biomass was calculated for each plot using allometrics developed for this region (Brown 1978). Ground cover was visually estimated to the nearest 10% by plant functional groups (forbs, sedges, grasses, and seedlings) in ten 0.25-m² circular microplots. The microplots were located within the inner 5-m plot radius using a stratified random design of fixed distances (one at 0.5-m; two at 1.5-m, 2.5-m and 3.5-m; and three at 4.5-m) and random bearings (in 10° increments) from the plot center, and averaged by plot. Biomass of the sedge *Carex geyerii* was calculated from allometrics previously reported for Yellowstone National Park (Turner et al. 2004).

**Litter quantity and quality**

In each 0.25-m² microplot, litter depth was recorded at three locations and a 400-cm² sample of the litter layer was collected and oven-dried at 60 °C. Plot-level litter depth and mass were obtained by averaging values from the 10 microplots. Litter from each microplot was sorted into three categories: fresh current-year needle litter, identified by bright red color and lack of mottling on surface (Morehouse et al. 2008); all-needle litter (all ages of needles combined); and
total litter (all foliar litter components and woody litter components < 1.0 cm wide). Sorted litter was composited by plot for each litter category, 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)

**Soil chemistry, N pools, and N fluxes**

One soil core was collected from each 0.25-m² microplot using a 5-cm diameter x 15-cm long PVC corer. Soils were sieved (2 mm), weighed, and divided into three subsamples: 30 g oven-dried at 60 °C for gravimetric percent moisture; 20 g extracted in 75 ml of 2M KCl for 2 hours, with the extract then filtered and frozen for later analysis of NH₄⁺ and NO₃⁻ pools; and 20 g air-dried and bulked by plot for soil texture and chemical analyses. Air-dried soil was analyzed for pH, total N, exchangeable Ca, Mg, and K, available P (Bray P1 extract), and organic matter content 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).

Net N mineralization and net nitrification were measured using ion-exchange resin cores (Binkley et al. 1992), with one core incubated in situ for approximately one year (July 2007 - June 2008) in each 0.25-m² microplot. Incubated cores consisted of a 5-cm diameter x 15-cm long PVC tube of soil with an ion-exchange resin bag placed at the bottom. 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. Upon retrieval in summer 2008, core soils were sieved (2 mm) and core soils and resin bags were extracted separately in 2M KCl in the same manner as the 2007 initial soil samples described above. All KCl extractions were analyzed for [NH₄⁺] and
[NO$_3^-$] using colorimetric methods on an Astoria Pacific II continuous flow autoanalyzer. For each microplot, mineralization and nitrification rates were calculated as:

$$\text{rate} = \frac{\text{(final soil N} + \text{resin bag N) – initial soil N}}{\text{incubation time}}$$

and expressed in units of $\mu$g N g soil$^{-1}$ year$^{-1}$. Values were then averaged by plot. Atmospheric N inputs in the region are low (~ 1 kg N ha$^{-1}$ year$^{-1}$; and were not factored into the soil N calculations. (www.epa.gov/castnet/charts/YEL408_totn.png)

**Foliar N**

In each plot, pole pruners were used to collect canopy foliage from three live mature lodgepole pines unattacked by MPB. Two fully sunlit branches (0.5-m long) were clipped from each tree and separated into two subsamples: current-year foliage (from one branch per tree), and all-years foliage (from the second branch per tree). Understory sedge (*Carex geyerii* Boott) foliage was collected by clipping 15-20 pieces from each quadrant of the plot. For both lodgepole and sedge foliar N, samples from two of the five undisturbed sites were excluded from the analyses reported here because they were sampled much earlier in the growing-season than the remaining eighteen sites. All foliar samples were oven-dried at 60°C and ground to powder for C and N analysis on a Leco CNS-2000 analyzer at the University of Wisconsin Soil and Plant Analysis Lab. Tree-level canopy data ($N=3$ per sample type) and quadrant-level sedge data ($N=4$) were averaged by plot. To compute canopy and *Carex geyerii* N pool sizes, the mean foliar N concentration for each plot was multiplied by biomass values derived from the allometrics cited above.

**Statistical analyses**

All statistical analyses were performed in SAS (SAS Institute Inc. 2003), and unless otherwise noted all reported variance values are two standard errors. ANOVA was used to test
for differences among TSB classes in stand basal area, site characteristics (slope, elevation, aspect, and soil chemistry), understory cover, soil temperatures, litter depth, litter quantity and quality, soil N pools, foliar N concentrations, and foliar N pools. When ANOVAs were significant, Tukey’s HSD test ($\alpha = 0.05$) was used to identify differences among means. Because variability in soil characteristics of $P. contorta$ forests in this region is known to influence nitrogen transformations irrespective of bark beetle outbreaks (Smithwick et al. 2005), we used general linear models to account for potential covariate effects (soil cations, C, OM, pH, bulk density, and C:N ratio) when testing for differences in net mineralization and net nitrification rates among TSB classes. To explore which beetle-induced changes were related to differences in soil N cycling rates among TSB classes, we used linear regression to identify relationships among litter, soil temperature, and N mineralization variables. Because only three out of five plots per TSB class were instrumented with soil temperature probes, regressions including soil temperature variables have $N = 12$ rather than $N = 20$. We also used linear regression to test whether foliar N concentrations in unattacked $P. contorta$ and $C. geyerii$ were positively related to N net mineralization rates.

RESULTS

Stand structure and site characteristics

Pre-disturbance stand structure and disturbance severity were similar across the chronosequence. There were no significant differences among TSB classes in pre-outbreak post-fire stand age ($168 \pm 18$ years), pre-outbreak $P. contorta$ basal area ($43.4 \pm 2.4$ m$^2$ ha$^{-1}$), background $P. contorta$ mortality ($7.2 \pm 1.1$ m$^2$ ha$^{-1}$), or beetle-killed $P. contorta$ basal area
(disturbed classes only; 33.7 ± 3.2 m² ha⁻¹) (Simard et al. 2011). In the 30-year TSB sites, peak mortality occurred 29 ± 2 years prior to sampling (Simard et al. 2011).

Topographic position (elevation, aspect, and slope) did not vary among undisturbed, red, and gray stands (Table 1). However, the 30-year TSB sites were on average 260 m lower in elevation than other classes and had shallower slopes than gray sites (Table 1). Soil texture was similar among TSB classes, with only percent sand and bulk density being slightly lower in the 30-year TSB compared to gray stands (Table 1). Soil K (average 160 ± 9 ppm), P (average 18 ± 2 ppm), and percent organic matter (average 4.5 ± 0.5) did not differ among TSB classes (Table 1). Soil pH, calcium and magnesium differed with the regional distribution of sites, with slightly higher pH (0.5 pH units) and 2-3 fold higher [Ca] and [Mg] in the Bridger Teton National Forest sites (red and gray) than in the Yellowstone National Park sites (undisturbed and 30-year TSB) (Table 1).

Total percent cover of understory vegetation ($F = 4.49$, $R^2 = 0.46$, $P = 0.02$) and percent cover of forbs ($F = 7.06$, $R^2 = 0.57$, $P = 0.003$) varied with TSB class (Figure 2). Total understory cover in the red class averaged 60%, approximately double that of undisturbed forest; understory cover in the gray and 30-year TSB classes was intermediate (Figure 2). Forb cover averaged 25% in the red class, approximately 2.5x greater than in undisturbed forest (Figure 2). Grass, sedge and shrub cover did not vary with TSB class ($P > 0.05$).

**Microclimate**

Air and soil temperatures during the 2008 growing season differed among TSB classes, and the 30-year TSB class was both the warmest and the most variable (Table 2). Mean daily air temperature in the 30-year TSB class was ~1 °C warmer than undisturbed, red, and gray classes, and the mean daily range of temperature extremes was greater (Table 2). Temperatures at the
litter-soil interface varied more among classes than did air temperatures, and were 4-6 °C warmer in the 30-year TSB class compared to undisturbed, red, and gray. Temperatures at the litter-soil interface did not differ from air temperature in the undisturbed class, but were ~2°C cooler than air temperature in the red and gray classes, and 3°C warmer than air temperature in the 30-year TSB class (Table 2). At 10 cm soil depth, temperatures were 3-4°C warmer in the 30-year TSB class compared to the undisturbed, red, and gray. Soil temperatures at 10 cm depth were always cooler than air temperatures but were 5.3 ± 0.2 °C less than air in undisturbed, red, and gray sites, and only 2.5 ± 0.9°C less than air in the 30-year TSB class (Table 2). There were no differences among classes in the slope or aspect of instrumented sites (Table 2). Mean elevation of the instrumented undisturbed sites was not significantly different from the instrumented sites in any other class (Table 2). Thus, differences in soil temperature between undisturbed and any disturbance class suggest an effect of TSB rather than topographic differences among classes.

**Litter quantity and quality**

Total litter depth was approximately 3 cm in red and gray stands, about twice that of undisturbed and 30-year TSB stands (Figure 3a). However, total litter mass averaged 1577 ± 149 g m⁻² and did not vary with TSB class (Figure 3b). The N concentration in fresh current-year-needle litter (Figure 3c) and all-needle litter (Figure 3d) varied with TSB class, with the highest values (~0.75%) observed in the red and gray classes and lower concentrations (~0.4-0.5%) in the undisturbed and 30-year TSB classes. However, N concentration of total litter averaged 0.78 ± 0.02% and did not vary with TSB class (Figure 3e). Litter N pool size averaged 13.8 ± 1.2 g N m⁻² in undisturbed, red and gray stands and was significantly lower (7.4 ± 2.5 g N m⁻²) in the 30-year TSB class compared to the gray (Figure 3f).
Among soil N pools, only soil ammonium pool size varied with TSB class (Figure 4a). Extractable \( \text{NH}_4^+ \) was six times greater in the red stands (4.75 \( \mu \text{g N g soil}^{-1} \)) compared to the undisturbed stands (0.74 \( \mu \text{g N g soil}^{-1} \)) and intermediate in the gray and 30-year TSB stands. Extractable \( \text{NO}_3^- \) was low (averaging 0.63 ± 0.20 \( \mu \text{g N g soil}^{-1} \)) and did not vary with TSB class (Figure 4b). Total extractable inorganic N averaged 3.11 ± 0.63 \( \mu \text{g N g soil}^{-1} \) (data not shown) and also did not vary with TSB class, nor did soil C:N ratio, total percent soil N, or soil organic N pool (Table 1).

Annual net N mineralization rate was approximately double (21 ± 7 \( \mu \text{g N g soil}^{-1} \text{ year}^{-1} \)) in the red and gray stages relative to the undisturbed and 30-year TSB classes (Figure 4c). After accounting for variation due to soil bulk density, pH and C:N ratio, the effect of TSB class on net N mineralization was significant; collectively, these variables explained 70% of the variation in net N mineralization (Table 3). Similar to annual net N mineralization, annual net nitrification rate was highest in the red stage (8.2 ± 4.2 \( \mu \text{g N g soil}^{-1} \text{ year}^{-1} \)) and about three times greater than in the undisturbed and 30-year TSB stages (Figure 4d). After accounting for soil bulk density, there was a significant effect of TSB class on annual net nitrification (Table 3). Net N mineralization and net nitrification were positively correlated \( (R^2 = 0.66, P < 0.0001) \), and nitrification fraction (ratio of nitrification to mineralization) averaged 0.32 ± 0.05 and did not vary among TSB classes (data not shown). In post-incubation soils, neither nitrate concentration (average 2.23 ± 0.67 \( \mu \text{g N g soil}^{-1} \)) nor the ratio of nitrate to total inorganic N (average 0.29 ± 0.07) differed among classes \( (P = 0.1314 \text{ and } P = 0.1710, \text{ respectively; data not shown}) \).

Net nitrogen mineralization rates were more strongly correlated with soil temperature (Figure 5b; \( R^2 = 0.39 \)) than with litter quality variables (Figure 5c-f; \( R^2 < 0.19 \)). Increased litter
depth in the red and gray classes corresponded to decreased soil temperatures, and shallow litter layers in the 30-year TSB class were associated higher soil temperatures (Figure 5a). Net N mineralization rates declined with increasing soil temperature across the TSB chronosequence (Figure 5b). Net N mineralization was weakly related to the nitrogen concentration in fresh needlefall (Figure 5c), but showed no relationship to the nitrogen concentration in all-needle litter or total litter, or to the total litter N pool size (Figures 5d-f).

**Foliar biomass and N**

Foliar biomass of live lodgepole pines was 69% lower in the current outbreak (red and gray sites) relative to undisturbed sites, and 48% lower in the 30-year TSB class (Table 4). Pre-outbreak foliar biomass of beetle-killed trees in the red and gray classes averaged 687 ± 49 g m^-2 (data not shown), which also represents the total mass of needle litterfall induced by the outbreak. The N concentration in current year foliage of unattacked *P. contorta* averaged 0.99 ± 0.02% in the red, gray and 30-year TSB classes compared to 0.82% in the undisturbed, and foliar C:N was concomitantly lower in the disturbed classes compared to undisturbed forest (Table 4).

The N concentration in all-age foliage of unattacked *P. contorta* was highest in the red and gray classes and lower in the undisturbed and 30-year TSB classes (Table 4). *P. contorta* foliar N pool averaged 8.3 g N m^-2 in undisturbed forest, was about 64% lower in the red and gray classes, and 48% lower in the 30-year TSB class (Table 4). Across all TSB classes, the N concentration of current year *P. contorta* foliage was positively related to soil N mineralization (Figure 6a).

Biomass of the understory sedge *Carex geyerii* did not differ across the chronosequence (Table 4), but foliar N concentration of *C. geyerii* was 50% greater (1.5-1.6% N) in red and gray stands compared to undisturbed and 30-year TSB stands. Foliar N concentration of *Carex geyerii* was also positively related to annual net N mineralization across all TSB classes (Figure 6b).
DISCUSSION

This study demonstrates the substantial effects of MPB outbreak on N cycling through the litter, soils, and vegetation of lodgepole pine forests across a replicated chronosequence of time-since-beetle disturbance. Beetle-induced tree mortality triggered a cascade of effects through increased needlefall and reduced N uptake, which in turn altered soil microclimate, increased soil N availability, and increased N concentration of surviving vegetation in recent outbreaks. Thirty years after the disturbance soil N parameters returned to undisturbed levels, though changes in soil temperature, %N of new foliage, canopy biomass, canopy N pool size; and the % N of needle litter were still evident. Our results also suggest several mechanisms that contribute to N retention in beetle-affected lodgepole pine forests and make N loss from the system unlikely.

Microclimate

A strong and persistent effect of bark beetle outbreak was observed on soil microclimate during the growing season. Within the current outbreak, soils were notably cooler than in undisturbed sites, most likely in response to increased litter depth. Though soil moisture was not measured in this study, soil moisture probably increased due to deeper litter and reduced transpiration caused by tree mortality (Stottlemyer and Troendle 1999, Tan et al. 2008, Griffiths et al. 2010). Experimental additions of needle litter have been shown to increase soil moisture in lodgepole pine forests even in the absence of tree mortality (Cullings et al. 2003). In the 30-year TSB sites soils were warmer and likely drier than in undisturbed forest, which can decrease decomposition (Remsburg and Turner 2006) and net N mineralization (Metzger et al. 2008) rates in post-fire lodgepole pine forests. Though we did not measure soil moisture or decomposition
directly, our results suggest similar mechanisms may be important in beetle-disturbed lodgepole pine forests as well.

**Litter quantity and quality**

The elevated N concentration of fresh needle litter in the current outbreak was consistent with our hypothesis and prior studies, and is likely due to a lack of N resorption prior to needle drop (Morehouse et al. 2008). However, we were surprised that the mass, N concentration, and N pool size of the total litter layer did not differ as expected. Gradual inputs of litterfall over several years combined with ongoing litter decomposition may explain why litter mass did not increase significantly. Foliar mass of beetle-killed trees in red and gray stands was estimated to be $687 \pm 49$ g m$^{-2}$ (data not shown), which is approximately half the mass of litter observed in undisturbed stands. Thus, if all beetle-killed foliage fell at once one may expect a 50% increase in the litter mass of attacked stands. However, beetle-induced litterfall extends over 3–4 years, and *P. contorta* litter can lose 30% of its mass after two years (Remsburg and Turner 2006). These processes may explain why the mass gained in the litter layer is smaller than the mass lost from the canopy by $\sim 200$ g m$^{-2}$, and why increases in litter mass following beetle outbreak (498 g m$^{-2}$) are small relative to the amount of litter already present on the forest floor prior to outbreak ($1512 \pm 457$ g m$^{-2}$).

Thirty years following outbreak, we also did not see the hypothesized declines in total litter biomass, N concentration or N pool size relative to undisturbed forest, even though stand basal area and therefore fresh litter inputs had not yet recovered. We suggest that persistent warming and drying of the forest floor and drier soil conditions under elevated coarse wood (Remsburg and Turner 2006) may have reduced decomposition rates during the post-outbreak period enabling more litter accumulation despite reduced input rates. The elevated N
concentration in all-aged needle litter also may represent a legacy effect of outbreak-induced litterfall undergoing an extended period of decomposition and N immobilization.

**Soil N pools and fluxes**

Although we expected both soil NH$_4^+$ and NO$_3^-$ to increase during the outbreak, only soil NH$_4^+$ was elevated despite observed increases both net N mineralization and net nitrification. Increased soil NO$_3^-$ has been observed following bark beetle outbreaks in other forest types (Huber 2005), however several studies of lodgepole pine have shown that mortality must be extensive before soil NO$_3^-$ increases. Parsons et al. (1994) found elevated NO$_3^-$ only in large experimental root gaps in which 30 trees were killed, and Knight et al. (1991) found no elevated NO$_3^-$ in soil solution following a 60% thinning but a 10-40 fold increase following clearcut. Plot-level tree mortality in this study averaged 76%, but surviving trees were intermixed with beetle-killed trees. Thus, undisturbed vegetation and microbial biomass were likely able to assimilate the products of increased nitrification yielding no change in NO$_3^-$ pool size. In contrast to many N-saturated forests of Europe and Eastern North America where atmospheric N deposition is high and nitrate levels can rise dramatically following disturbance (Huber 2005; Bormann and Likens 1979), conifer forests of western North America receive little N deposition and often show little response of nitrate following disturbance (Prescott et al. 2003; Titus et al. 2006).

Observed rates of net N mineralization and net nitrification in the undisturbed stands are within ranges reported by other studies from Greater Yellowstone for both mature (Turner et al. 2007) and 15 year-old post-fire (Metzger et al. 2008) lodgepole pine forests. Nitrification is typically low ($<2$ µg N g soil$^{-1}$ year$^{-1}$) in undisturbed lodgepole pine (Turner et al. 2007), and despite a significant increase in the red stage, net nitrification was never above 8.2 µg N g soil$^{-1}$
year\(^{-1}\) in any class. The magnitude of increased mineralization in the current outbreak is comparable to that reported by Parsons et al. (1994) for artificial root gaps of 15 lodgepole pine trees two years after disturbance, but less than increases reported for silvicultural gaps in Douglas-fir forests 6-8 years after disturbance (Thiel and Perakis 2009). Though we did not see any change in net N mineralization in the 30-year TSB stands relative to the undisturbed stands, decadal-scale effects of lodgepole pine mortality on net N mineralization have been documented in other studies. Twenty-four years following treatment, Tan et al. (2008) observed twice the rate of N mineralization in lodgepole stands thinned to 1600 stems ha\(^{-1}\), compared to unthinned stands. However, stands in that study were much younger (22 years) at the time of disturbance than ours (average 168 years), soils were generally more fertile (e.g., soil C:N ratios in control and thinned plots ranged from 20-33), and thinning residues were removed.

**Foliar N and biomass**

Nitrogen concentration of new lodgepole pine foliage demonstrated a rapid response of unattacked trees to increased nutrient availability. The foliar N concentration of current-year needles was positively correlated with net N mineralization, and lodgepole pine is known to take up both \(\text{NH}_4^+\) and \(\text{NO}_3^-\) (Hawkins et al. 2008). Fertilization studies in lodgepole pine have also demonstrated rapid response of foliar N to increased soil N availability, though this may attenuate after several years as foliage biomass increases (Blevins et al. 2005). Increased foliar N concentration in unattacked trees provided a mechanism for N retention in the canopy following bark beetle disturbance. Between the undisturbed and gray classes, beetle outbreak caused a 68% reduction in foliar biomass but only a 58% reduction in canopy N pool size.

The canopy N pool is an important regulator of ecosystem N cycling (Prescott 2002), and declines in canopy N pool size paralleled declines in live foliar biomass during the current
outbreak. Foliar N concentrations for undisturbed stands were similar to values previously reported for the Yellowstone region (Litton et al. 2004) and elsewhere (Binkley et al. 1995, Blevins et al. 2005). However, we were surprised to observe that foliar N concentration in current-year needles remained elevated in the 30-year TSB stands, although N concentration of composite foliage returned to undisturbed levels. Net N mineralization rates were comparable in undisturbed and 30-year TSB stands but foliage biomass remained substantially lower; thus, the availability of N per unit of foliage biomass was likely greater in the 30-year stands.

A flush of understory growth has been observed in many post-beetle conifer forest types, including lodgepole pine (Stone and Wolfe 1996), Douglas-fir (McMillin and Allen 2003), Engelmann spruce (Picea engelmannii) (Schmid and Frye 1977), subalpine fir (Abies lasiocarpa) (McMillin et al. 2003), and ponderosa pine (McCamanhoe et al. 1982). Reduced competition and increased light, moisture and nutrients are likely stimulants of this growth. As forbs prefer NO\textsubscript{3}\textsuperscript{-} uptake over NH\textsubscript{4}\textsuperscript{+} in deciduous woodland (Falkengren-Gerup et al. 2004) and alpine meadow (Miller and Bowman 2002) systems, increased forb cover observed in this study may be related to increased net nitrification. The positive relationship between N mineralization and Carex geyerii %N also suggests that herbaceous species benefit from increased N availability during bark beetle outbreak. Foliar %N of Carex geyeri can increase after fertilization in ponderosa pine forests (VanderSchaaf et al. 2004), and in lodgepole pine C. geyerii %N can increase following fire-induced changes in soil N availability. Interestingly, the increased N concentration we observed in C. geyerii is comparable to the increase observed two years after stand-replacing fire in lodgepole pine forests of the same region (Metzger et al. 2006).
Interpretations and comparison to post-fire lodgepole pine forests

Multiple lines of reasoning suggest that increased rates of net N mineralization and net nitrification during the current outbreak are likely not due to a pulse of litter N associated with beetle-killed trees. Beetle outbreak did not significantly change the mass or N pool size of total litter, and neither was correlated with N mineralization rates—a pattern that has been noted across a wide range of North American forests (Scott and Binkley 1997). Furthermore, fresh lodgepole pine litter immobilizes N for several years, acting as a net sink of N during this period rather than a source (Fahey 1983, Remsburg and Turner 2006). Thirdly, increases in net N mineralization following tree mortality are often limited to mineral soil horizons and not found in the forest floor (Morehouse et al. 2008, Tan et al. 2008, Thiel and Perakis 2009), which suggests belowground processes and abiotic changes may be more important than litter N inputs. Labile C leaching from fresh litter or decaying roots could play a role in stimulating gross N production and N consumption if microbial communities were C limited, although Giardina et al. (2001) found lodgepole pine soils of the intermountain West to have relatively large amounts of high quality soil C, with no relationship between C and N mineralization rates. Alternatively, declines in belowground C transfer beyond the rhizosphere (Högberg et al. 2010) following beetle-induced mortality could lead to decreased N demand by microbes and thus greater net N mineralization rates and extractable N pools. Further study is needed to understand the role of C availability on N transformations following bark beetle disturbance.

Despite the increases in available soil N associated with the current beetle disturbance, surviving lodgepole pine did not appear to have an excess of available N. Reduced competition and increased net N mineralization increased nutrient availability for surviving unattacked trees, as evidenced by a 20-30% increase in foliar N concentration. However, N concentrations in
current year foliage remained < 1.2%, suggesting N may still be limiting (Moore et al. 2004). When foliar N concentrations are considered along with the lack of elevated soil nitrate pools, our results also suggest that the risk of nitrogen loss via NO₃⁻ leaching following bark beetle outbreak is low.

The effects of bark beetle disturbance on soil and canopy N were substantially less than observed following fire in Greater Yellowstone. In two-year post-fire lodgepole pine forests, NH₄⁺ and NO₃⁻ pools were four times greater than in the red stage of a bark beetle outbreak (20 vs 5 µg NH₄⁺-N g soil⁻¹, 2 vs. 0.5 µg NO₃⁻-N g soil⁻¹), and net N mineralization and net nitrification rates were twice as great (18 vs. 9 µg N g soil⁻¹ year⁻¹ for mineralization, 16 vs. 8 µg N g soil⁻¹ year⁻¹ for nitrification) (Turner et al. 2007). Several studies also show that foliar N concentration of lodgepole pine is higher after fire than after bark beetle disturbance. Romme et al. (2009) found very high (1.87%) foliar N in 3 to 5-year old post-fire lodgepole pine seedlings, and Turner et al. (2009) found current-year foliage averaged 1.38% N and composite foliage 1.08% N in 17-year old post-fire lodgepole pine. Contrary to fire, bark beetles typically affect large mature trees with no direct disturbance to the understory or soils. Observed changes in soil N following bark beetle outbreak are similar to those following other selective agents of mortality in forests. In eastern hemlock (Tsuga canadensis) forests affected by the hemlock wooly adlegid (Adelges tsugae Annand), Orwig et al.(2008) documented increased mineralization, nitrification, and N pool sizes relative to undisturbed stands. Generally, the consequences of bark beetle outbreak for ecosystem processes are likely similar to any agent of mortality that selectively kills canopy trees and does not disturb soils or understory directly.

Though our chronosequence approach is strengthened by replication and by validation from companion dendrochronological analyses (Simard 2011), there were some noteworthy
differences among classes. Current outbreak sites had greater soil pH, Ca, and Mg which may have contributed directly to greater understory cover of forbs. The influence of soil cations on soil N transformations, however, is considered to be indirect through control on species composition and subsequent litter quality (Page and Mitchel 2008). Since all sites were dominated by lodgepole pine, differences in soil cations were unlikely to influence soil N parameters. Though not significant, thirty year old outbreak sites tended toward greater soil organic matter and total soil N, which may have resulted from organic N inputs during the outbreak rather than inherent pre-disturbance site differences.

CONCLUSIONS

Bark beetle disturbance significantly altered N cycling through the litter, soil, and vegetation of lodgepole pine forests. Beetle-induced litterfall increased litter depth and altered soil microclimate. Increased soil N in recently disturbed sites was more closely related to cooler soil temperatures than to litter quality, and was positively correlated with increased foliar N in unattacked vegetation. Effects of bark beetle disturbance on needle litter %N, soil temperature, and canopy N pool size persisted 30 years following outbreak. However, changes in soil N cycling during the outbreak were of lesser magnitude than those observed following stand replacing fire. Although significant, the net effects of bark beetle disturbance on N cycling in lodgepole pine were surprisingly minor given the extent of beetle-caused tree mortality.

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REFERENCES


USFS, 2006. Forest Insect and Disease Survey, regions 1, 2, & 4. USDA Forest Service.


## TABLES

**Table 1. Site characteristics across a chronosequence of mountain pine beetle disturbance in *P. contorta* forests.** Superscript letters next to values denote significant differences among classes (Tukey’s test, \( \alpha = 0.05 \)). \( N = 5 \) per class. Error ranges = 2 SE.

<table>
<thead>
<tr>
<th>Site variable</th>
<th>Undisturbed</th>
<th>Red</th>
<th>Gray</th>
<th>30 years</th>
<th>( P^w )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stand age (^x) (year)</td>
<td>179 ± 46 (^a)</td>
<td>164 ± 32 (^a)</td>
<td>176 ± 43 (^a)</td>
<td>152 ± 28 (^a)</td>
<td>n.s.</td>
</tr>
<tr>
<td><em>P. contorta</em> basal area (m(^2)ha(^{-1}))</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pre-outbreak live (^y)</td>
<td>42.7 ± 10.0 (^a)</td>
<td>48.3 ± 11.9 (^a)</td>
<td>40.2 ± 7.7 (^a)</td>
<td>42.4 ± 9.4 (^a)</td>
<td>n.s.</td>
</tr>
<tr>
<td>Beetle-killed</td>
<td>----</td>
<td>41.7 ± 10.5 (^a)</td>
<td>26.6 ± 6.5 (^a)</td>
<td>33.0 ± 12.7 (^a)</td>
<td>n.s.</td>
</tr>
<tr>
<td>Dead, non-beetle killed</td>
<td>5.6 ± 2.4 (^a)</td>
<td>6.0 ± 2.9 (^a)</td>
<td>10.9 ± 3.0 (^a)</td>
<td>6.5 ± 7.2 (^a)</td>
<td>n.s.</td>
</tr>
<tr>
<td><strong>Topography</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Elevation (m)</td>
<td>2400 ± 17 (^a)</td>
<td>2487 ± 34 (^a)</td>
<td>2476 ± 48 (^a)</td>
<td>2218 ± 160 (^b)</td>
<td>0.001</td>
</tr>
<tr>
<td>Slope (º)</td>
<td>8 ± 7 (^ab)</td>
<td>10 ± 9 (^ab)</td>
<td>21 ± 11 (^a)</td>
<td>2 ± 2 (^b)</td>
<td>0.025</td>
</tr>
<tr>
<td>Aspect (^z)</td>
<td>0.10 ± 0.94 (^a)</td>
<td>0.30 ± 0.66 (^a)</td>
<td>0.56 ± 0.26 (^a)</td>
<td>0.04 ± 0.81 (^a)</td>
<td>n.s.</td>
</tr>
<tr>
<td><strong>General Soil Characteristics</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sand (%)</td>
<td>62 ± 6 (^ab)</td>
<td>58 ± 5 (^ab)</td>
<td>69 ± 7 (^a)</td>
<td>55 ± 6 (^b)</td>
<td>0.034</td>
</tr>
<tr>
<td>Silt (%)</td>
<td>26 ± 6 (^a)</td>
<td>27 ± 5 (^a)</td>
<td>20 ± 6 (^a)</td>
<td>31 ± 5 (^a)</td>
<td>n.s.</td>
</tr>
<tr>
<td>Clay (%)</td>
<td>13 ± 1 (^a)</td>
<td>15 ± 2 (^a)</td>
<td>11 ± 2 (^a)</td>
<td>13 ± 2 (^a)</td>
<td>n.s.</td>
</tr>
<tr>
<td>Bulk density (g cm(^{-3}))</td>
<td>0.7 ± 0.1 (^ab)</td>
<td>0.7 ± 0.2 (^ab)</td>
<td>0.9 ± 0.2 (^a)</td>
<td>0.6 ± 0.1 (^a)</td>
<td>0.042</td>
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<tr>
<td>pH</td>
<td>4.9 ± 0.1 (^b)</td>
<td>5.4 ± 0.1 (^a)</td>
<td>5.2 ± 0.1 (^a)</td>
<td>4.9 ± 0.2 (^b)</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Ca (ppm; exchangeable)</td>
<td>452 ± 63 (^b)</td>
<td>1192 ± 651 (^a)</td>
<td>857 ± 244 (^ab)</td>
<td>322 ± 182 (^b)</td>
<td>0.014</td>
</tr>
<tr>
<td>Mg (ppm; exchangeable)</td>
<td>67 ± 12 (^b)</td>
<td>143 ± 54 (^a)</td>
<td>117 ± 35 (^ab)</td>
<td>71 ± 21 (^b)</td>
<td>0.018</td>
</tr>
<tr>
<td>K (ppm; exchangeable)</td>
<td>162 ± 22 (^a)</td>
<td>186 ± 60 (^a)</td>
<td>149 ± 29 (^a)</td>
<td>145 ± 23 (^a)</td>
<td>n.s.</td>
</tr>
<tr>
<td>P (ppm; Bray P1)</td>
<td>17 ± 4 (^a)</td>
<td>25 ± 12 (^a)</td>
<td>20 ± 9 (^a)</td>
<td>11 ± 3 (^a)</td>
<td>n.s.</td>
</tr>
<tr>
<td>OM (%)</td>
<td>3.9 ± 0.8 (^a)</td>
<td>5.3 ± 3.9 (^a)</td>
<td>3.3 ± 0.4 (^a)</td>
<td>5.3 ± 1.4 (^a)</td>
<td>n.s.</td>
</tr>
<tr>
<td>C:N</td>
<td>72 ± 23 (^a)</td>
<td>42 ± 26 (^a)</td>
<td>41 ± 7 (^a)</td>
<td>42 ± 11 (^a)</td>
<td>n.s.</td>
</tr>
<tr>
<td>Total N (%)</td>
<td>0.04 ± 0.03 (^a)</td>
<td>0.05 ± 0.03 (^a)</td>
<td>0.04 ± 0.01 (^a)</td>
<td>0.08 ± 0.04 (^a)</td>
<td>n.s.</td>
</tr>
<tr>
<td>Organic N (µg N g soil(^{-1}))</td>
<td>368 ± 271 (^a)</td>
<td>509 ± 306 (^a)</td>
<td>446 ± 109 (^a)</td>
<td>759 ± 416 (^a)</td>
<td>n.s.</td>
</tr>
</tbody>
</table>

\( ^w \) ANOVA \( P \) value; n.s. = non significant

\( ^x \) Post-fire stand age at time of mountain pine beetle disturbance.

\( ^y \) Data for 30 year TSB sites are from Simard (2011).

\( ^z \) Values are an index of southwest-ness ranging from -1 to 1, calculated as: cosine(aspect-225)
Table 2. Air and soil temperatures across a chronosequence of mountain pine beetle disturbance. Superscript letters next to values denote significant differences among classes (Tukey’s test, α = 0.05). N = 3 per class. Error ranges = 2SE.

<table>
<thead>
<tr>
<th>Variable</th>
<th>TSB Class</th>
<th>P *</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Undisturbed Red Gray 30 years</td>
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</tr>
<tr>
<td>Air temperature (°C)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean daily temperature</td>
<td>15.3 ± 0.4 b 15.1 ± 0.3 b 15.0 ± 0.5 b 16.3 ± 0.5 a</td>
<td></td>
</tr>
<tr>
<td>Mean daily range</td>
<td>19.4 ± 1.4 b 21.8 ± 0.8 ab 20.5 ± 1.6 b 25.1 ± 2.8 a</td>
<td></td>
</tr>
<tr>
<td>Litter-soil temperature (°C)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean daily temperature</td>
<td>15.4 ± 1.0 b 13.3 ± 0.8 bc 13.0 ± 0.6 c 19.2 ± 1.4 a</td>
<td></td>
</tr>
<tr>
<td>Mean daily range</td>
<td>27.4 ± 3.5 b 21.8 ± 3.6 b 19.3 ± 1.0 b 38.0 ± 7.0 a</td>
<td></td>
</tr>
<tr>
<td>Mean daily difference from air</td>
<td>0.1 ± 0.8 b -1.8 ± 1.0 b -2.0 ± 0.2 b 2.8 ± 1.4 a</td>
<td></td>
</tr>
<tr>
<td>10 cm soil depth temperature (°C)</td>
<td></td>
<td></td>
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<tr>
<td>Mean daily temperature</td>
<td>10.5 ± 0.3 b 9.4 ± 0.1 b 9.7± 0.4 b 13.8 ± 1.3 a</td>
<td></td>
</tr>
<tr>
<td>Mean daily range</td>
<td>2.4 ± 0.2 a 2.9 ± 0.8 a 2.8 ± 0.6 a 4.6 ± 1.8 a</td>
<td></td>
</tr>
<tr>
<td>Mean daily difference from air</td>
<td>-4.8 ± 0.1 b -5.6 ± 0.3 b -5.3 ± 0.8 b -2.5 ± 0.9 a</td>
<td></td>
</tr>
<tr>
<td>Topography of instrumented sites</td>
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<td></td>
</tr>
<tr>
<td>Elevation (m)</td>
<td>2401 ± 4 ab 2471 ± 40 a 2494 ± 68 a 2198 ± 227 b</td>
<td></td>
</tr>
<tr>
<td>Slope (°)</td>
<td>10.8 ± 10.6 a 6.2 ± 3.4 a 13.7 ± 5.5 a 2.5 ± 3.2 a</td>
<td></td>
</tr>
<tr>
<td>Aspect x</td>
<td>0.26 ± 1.25 a 0.42 ± 0.70 a 0.55 ± 1.34 a -0.09 ± 0.67 a</td>
<td></td>
</tr>
</tbody>
</table>

w ANOVA P value; n.s. = non significant
x Values are an index of southwest-ness ranging from -1 to 1, calculated as: cosine (aspect°-225)
Table 3. General linear models of net N mineralization and net nitrification across a chronosequence of mountain pine beetle disturbance in *P. contorta* forests. *N* = 5 per class.

<table>
<thead>
<tr>
<th>Response variable</th>
<th>Model Fit ($R^2$, $F$, $P$)</th>
<th>Parameter</th>
<th>Estimate</th>
<th>$F$</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Net N mineralization</td>
<td>0.70, 5.04, 0.007</td>
<td>TSB class</td>
<td>--</td>
<td>5.30</td>
<td>0.01</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Undisturbed</td>
<td>--</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Red</td>
<td>18.2</td>
<td>--</td>
<td>0.02</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Gray</td>
<td>16.2</td>
<td>--</td>
<td>0.03</td>
</tr>
<tr>
<td></td>
<td></td>
<td>30 years</td>
<td>-8.6</td>
<td>--</td>
<td>0.09</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Bulk density</td>
<td>-32.02</td>
<td>7.68</td>
<td>0.02</td>
</tr>
<tr>
<td></td>
<td></td>
<td>pH</td>
<td>-22.17</td>
<td>4.37</td>
<td>0.06</td>
</tr>
<tr>
<td></td>
<td></td>
<td>C:N</td>
<td>-0.19</td>
<td>5.66</td>
<td>0.03</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Intercept</td>
<td>153.9</td>
<td>--</td>
<td>0.02</td>
</tr>
<tr>
<td>Net nitrification</td>
<td>0.52, 4.06, 0.02</td>
<td>TSB class</td>
<td>--</td>
<td>4.58</td>
<td>0.02</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Undisturbed</td>
<td>--</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Red</td>
<td>1.3</td>
<td>--</td>
<td>0.01</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Gray</td>
<td>1.2</td>
<td>--</td>
<td>0.04</td>
</tr>
<tr>
<td></td>
<td></td>
<td>30 years</td>
<td>-0.31</td>
<td>--</td>
<td>0.53</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Bulk density</td>
<td>-3.56</td>
<td>8.52</td>
<td>0.01</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Intercept</td>
<td>4.01</td>
<td>--</td>
<td>0.0005</td>
</tr>
</tbody>
</table>
Table 4. Foliar N in unattacked lodgepole pine (*P. contorta*) and an understory sedge (*C. geyerii*) across a chronosequence of mountain pine beetle disturbance in *P. contorta* forests. Superscript letters denote significant differences among classes (Tukey’s HSD test, $\alpha = 0.05$). Error ranges = 2SE.

<table>
<thead>
<tr>
<th>TSB Class</th>
<th>Foliage variable</th>
<th>Undisturbed</th>
<th>Red</th>
<th>Gray</th>
<th>30 years</th>
<th>$P^*$</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Pinus contorta</strong></td>
<td><strong>New foliage</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>N (%)</td>
<td>$0.82 \pm 0.03$ b</td>
<td>$1.05 \pm 0.12$ a</td>
<td>$1.00 \pm 0.06$ a</td>
<td>$0.94 \pm 0.05$ a</td>
<td>0.016</td>
</tr>
<tr>
<td></td>
<td>C:N</td>
<td>$59 \pm 4$ a</td>
<td>$49 \pm 6$ b</td>
<td>$50 \pm 2$ b</td>
<td>$53 \pm 2$ ab</td>
<td>0.022</td>
</tr>
<tr>
<td></td>
<td><strong>All foliage</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>N (%)</td>
<td>$0.75 \pm 0.04$ b</td>
<td>$0.91 \pm 0.08$ a</td>
<td>$0.91 \pm 0.09$ a</td>
<td>$0.75 \pm 0.12$ b</td>
<td>0.014</td>
</tr>
<tr>
<td></td>
<td>C:N</td>
<td>$63 \pm 3$ a</td>
<td>$52 \pm 3$ b</td>
<td>$53 \pm 5$ b</td>
<td>$64 \pm 10$ ab</td>
<td>0.017</td>
</tr>
<tr>
<td></td>
<td>Biomass (g m$^{-2}$)</td>
<td>$1107 \pm 214$ a</td>
<td>$331 \pm 88$ b</td>
<td>$358 \pm 169$ b</td>
<td>$571 \pm 78$ b</td>
<td>$&lt;$0.0001</td>
</tr>
<tr>
<td></td>
<td>N pool size (g N m$^{-2}$)</td>
<td>$8.3 \pm 1.7$ a</td>
<td>$3.0 \pm 0.9$ b</td>
<td>$3.5 \pm 1.5$ b</td>
<td>$4.3 \pm 0.8$ b</td>
<td>$&lt;$0.0001</td>
</tr>
<tr>
<td><strong>Carex geyerii</strong></td>
<td><strong>N (%)</strong></td>
<td>$1.1 \pm 0.2$ b</td>
<td>$1.6 \pm 0.4$ a</td>
<td>$1.5 \pm 0.1$ ab</td>
<td>$1.1 \pm 0.1$ b</td>
<td>0.016</td>
</tr>
<tr>
<td></td>
<td>C:N</td>
<td>$43 \pm 9$ a</td>
<td>$28 \pm 7$ b</td>
<td>$29 \pm 2$ ab</td>
<td>$41 \pm 4$ ab</td>
<td>0.024</td>
</tr>
<tr>
<td></td>
<td>Biomass (g m$^{-2}$)</td>
<td>$46 \pm 46$ a</td>
<td>$32 \pm 42$ a</td>
<td>$52 \pm 42$ a</td>
<td>$179 \pm 129$ a</td>
<td>n.s.</td>
</tr>
<tr>
<td></td>
<td>N pool size (g N m$^{-2}$)</td>
<td>$0.5 \pm 0.5$ a</td>
<td>$0.5 \pm 0.8$ a</td>
<td>$0.6 \pm 0.8$ a</td>
<td>$2.1 \pm 1.7$ a</td>
<td>n.s.</td>
</tr>
</tbody>
</table>
FIGURE LEGENDS

**Figure 1.** Location of chronosequence sites in the Greater Yellowstone region. A) All sites; B) Undisturbed and 30 yr TSB (time-since-beetle) sites in Yellowstone National Park; C) Red and Gray sites in the Green River Lakes region of Bridger-Teton National Forest.

**Figure 2.** Understory cover by plant functional group across a chronosequence of mountain pine beetle disturbance in lodgepole pine forest.

**Figure 3.** Litter variables across a chronosequence of mountain pine beetle disturbance in lodgepole pine. A) litter depth, B) litter mass, C) fresh needle litter %N, D) all-needle litter %N, E) total litter %N, F) litter N pool. $P$ values are from ANOVA, and class differences were determined using Tukey’s HSD test ($\alpha = 0.05$). $N = 5$/class, error bars = 2 standard errors. Values within the same panel with the same letter are not significantly different.

**Figure 4.** Soil N pools and fluxes across a chronosequence of mountain pine beetle disturbance in lodgepole pine. For extractable NH$_4^+$ pool size (panel A), and extractable NO$_3^-$ pool size (panel B), significance levels are from ANOVA and Tukey’s HSD test ($\alpha = 0.05$). For net mineralization rate (panel C), and net nitrification rate (panel D), significance levels were determined from general linear models reported in Table 3. Summary statistics in each panel are for the class terms in each respective mode, and values within the same panel with the same letter are not significantly different. Error bars = 2 standard errors.
Figure 5. Relationships between litter depth and N content, soil temperatures, and net N mineralization rates across a chronosequence of mountain pine beetle disturbance in lodgepole pine. ● = undisturbed, ■ = red stage, ▲ = gray stage, ♦ = 30 year after outbreak. A) Soil temperature vs. litter depth. Solid symbols = litter-soil interface temperatures, open symbols = 10-cm soil depth temperatures; B) Net N mineralization vs. litter-soil interface temperature; C-E) Net N mineralization vs. fresh needle litter %N (C), all needle litter %N (D), and total litter %N (E); F) Net N mineralization vs. litter N pool. In panels A and B, n = 12 as only three plots per class were instrumented with temperature probes; All plots are included in panels C-F (n = 20). Summary statistics and regression lines in each panel are for significant linear regressions.

Figure 6. Foliar %N of unattacked lodgepole pine (A) and %N of the sedge Carex geyerii (B) vs. soil N mineralization rate in a chronosequence of mountain pine beetle disturbance in lodgepole pine. ● = undisturbed, ■ = red stage, ▲ = gray stage, ♦ = 30 year after outbreak. Summary statistics are from linear regression.
FIGURES

Figure 1
Figure 2

The figure shows a bar graph representing the ground cover in different conditions: Undisturbed, Red, Gray, and 30 yr. The graph indicates the percentage of cover by different vegetation types: Seedlings, Forb, Shrub, Sedge, and Grass. The Red condition has the highest percentage of cover among the Seedlings, Forb, and Shrub categories.
Figure 3

A) Litter depth (cm) 

B) Litter mass (g m$^{-2}$) 

C) Fresh needle litter %N 

D) All needle litter %N 

E) Total litter %N 

F) Litter N pool (g N m$^{-2}$)
Figure 4

A) $P = 0.05$

Extractable NH$_4^+$ (µg N g soil$^{-1}$)

B) $P = \text{n.s.}$

Extractable NO$_3^-$ (µg N g soil$^{-1}$)

C) $P = 0.01$

Net N mineralization (µg N g soil$^{-1}$ yr$^{-1}$)

D) $P = 0.02$

Net nitrification (µg N g soil$^{-1}$ yr$^{-1}$)

Legend:

- Undisturbed Red Gray 30 yr

A, B, C, D indicate statistical significance.
Figure 5

A) Adj. $R^2 = 0.31; P = 0.04$

B) Adj. $R^2 = 0.39; P = 0.02$

C) Adj. $R^2 = 0.19; P = 0.03$

D) $P = n.s.$

E) $P = n.s.$

F) $P = n.s.$
Figure 6

A) Adj. $R^2 = 0.41; P = 0.003$

P. contorta fresh foliar % N

B) Adj. $R^2 = 0.48; P = 0.007$

C. geyeri % N

Net N mineralization ($\mu$g N g soil$^{-1}$ yr$^{-1}$)
CHAPTER 2

Forest type influences ecosystem response to bark beetle disturbance

ABSTRACT

Outbreaks of native Dendroctonus bark beetles are causing extensive tree mortality in conifer forests throughout western North America, yet consequences for nitrogen (N) cycling in different forest types are not well known. We quantified beetle-induced changes in forest structure, soil microclimate, and N cycling through litter, soils, and vegetation in Douglas-fir (Pseudotsuga menziesii) and lodgepole pine (Pinus contorta var. latifolia) forests of Greater Yellowstone (WY, USA). We hypothesized N cycling responses would be greater in Douglas-fir, which generally has higher overall N capital. Undisturbed Douglas-fir stands had larger litter and soil N pools, and greater net N mineralization rates than lodgepole pine. However, responses to disturbance were similar and included a pulse of N-enriched litter, a doubling of soil N availability, a 30-50% increase in understory cover, and a 20% increase in N concentration of composite foliage in unattacked trees. Soil temperature did not vary in Douglas-fir, but was cooler in beetle-disturbed lodgepole pine. N concentration in fresh foliage was uncorrelated with N mineralization in Douglas-fir, but positively correlated in lodgepole pine. Though pools and fluxes of soil inorganic N doubled, they remained low in both forest types (< 6 µg N g soil⁻¹ NH₄⁺-N or NO₃⁻-N; < 25 µg N g soil⁻¹ yr⁻¹ net N mineralization; < 8 µg N g soil⁻¹ yr⁻¹ net nitrification). Our results suggest that bark beetle disturbance affects N cycling similarly in Douglas-fir and lodgepole pine, and both systems appear to have mechanisms that could enhance N retention following beetle outbreak.
INTRODUCTION

Insect outbreaks contribute significantly to many disturbance regimes, and can be strong drivers of change in forest ecosystems (Haack and Byler 1993). Insect-induced mortality alters ecosystem structure by redistributing biomass among ecosystem pools, often via the selective mortality of mature canopy trees. In turn, vegetation-driven aspects of ecosystem function such as primary production and elemental cycling may be affected from local to regional scales (Schowalter 1981). Widespread outbreaks of native *Dendroctonus* bark beetles are occurring within multiple conifer forest types of western North America, yet the consequences of this disturbance type for many ecosystem functions are not well known. Furthermore, the pre-outbreak condition and biogeochemical characteristics of infested stands can vary substantially among forests dominated by different host tree species (Thomas and Prescott 2000, Giardina et al. 2001, Lovett et al. 2004). In turn, ecosystems organized around such foundational species (Ellison et al. 2005) could have unique responses to similar bark beetle disturbance (Lovett et al. 2006). This variation may arise from specific biogeochemical properties of the host (e.g. nutrient uptake rates; nutrient allocation among tissues), host landscape position (e.g. elevation, slope, soil type), or post-disturbance successional trajectory (Schowalter 1981).

Extensive outbreaks of the Douglas-fir beetle (DFB; *Dendroctonus pseudotsugae* Hopkins) and mountain pine beetle (MPB; *Dendroctonus ponderosae* Hopkins) have affected Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), and lodgepole pine (*Pinus contorta* Dougl.) forests of Greater Yellowstone (Wyoming, USA) since 2003. At epidemic population levels, these closely related *Dendroctonus* species utilize pheromone-mediated mass attack strategies to overcome host trees (Raffa and Berryman 1987) and produce similar patterns of tree mortality, litterfall, and canopy decay across host forest types. Both beetle species tend to attack large
canopy-dominant trees. Stand-level mortality rates frequently exceed 50% (Negron 1998, Safranyik and Wilson 2006), leaving post-outbreak stands with decreased live stem density and mean stem diameter (McMillin and Allen 2003, Shore et al. 2006). Foliage of beetle-killed trees of both species turns red in the year following successful attack (red stage), and is shed to the forest floor within two or three years (gray stage) (Negron 1998, McMillin and Allen 2003). Canopy opening and subsequent inputs of needle litter to the forest floor induced by bark beetles may influence soil microclimate (Griffin et al. 2011) by increasing soil insulation (Byers 1984), incident radiation (Hais and Kucera 2008), and air flow through the stand (Boon 2009).

Despite the similar mortality, litterfall, and structural changes induced by both the MPB and DFB in their respective host forest types, subsequent effects on nitrogen (N) cycling may differ. Although lodgepole pine litter has a slightly higher N content than Douglas-fir, the concentration of lignin in lodgepole pine litter is twice that of Douglas-fir, resulting in a greater lignin:N ratio (Thomas and Prescott 2000). Lignin:N ratio is a strong control on litter decomposition (Scott and Binkley 1997) and subsequent return of N to the soil profile (Prescott 2005). Higher decay constant ($k$) values of Douglas-fir litter relative to lodgepole pine support this relationship (Keane 2008). Thus, in undisturbed systems N may be retained in the litter layer longer in lodgepole pine forests than in Douglas-fir. Insect-induced changes in needle senescence and nutrient content are known to influence litter decomposition rates in conifers (Koukol et al. 2008, Przybyl et al. 2008), and bark beetle mortality has been shown to increase fresh needle litter N concentration in both ponderosa pine ($Pinus ponderosa$ Laws.) and lodgepole pine (Morehouse et al. 2008, Griffin et al. 2011). Furthermore, in undisturbed forests Douglas-fir generally has greater pool sizes of soil inorganic N and greater rates of net N mineralization relative to lodgepole pine (Thomas and Prescott 2000). Greater baseline N capital of soils is
correlated with accelerated N cycling between soil, foliage, and litter N pools (Prescott et al. 2000), and may increase the potential for nutrient loss following disturbance. Laboratory studies show uptake rates of inorganic N in Douglas-fir roots are 73% greater for NO$_3^-$ and 35% greater for NH$_4^+$ than in lodgepole pine (Hawkins et al. 2008). These differences suggest that declines in stand-level nutrient uptake following bark beetle outbreak may be greater in Douglas-fir forests relative to lodgepole pine, leading to greater accumulation of inorganic N in soils and thus a greater potential for N leaching. Differences in N uptake rates may also contribute to variable responses of foliar N content in unattacked or surviving trees following disturbance.

In this study we address two overarching questions: (1) *How does DFB disturbance alter forest structure, soil microclimate, and N cycling through litter, soils, and vegetation in Douglas-fir forests?* (2) *Are the patterns of change observed in beetle-disturbed Douglas-fir forests similar to those in mountain pine beetle-disturbed lodgepole pine forests?* Forest structure, soil microclimate, and nitrogen pools and fluxes were measured in both undisturbed and gray stage beetle-killed forests. Hypothesized bark beetle effects and suggested mechanisms are summarized in Figure 1. We expected beetle disturbance to decrease live canopy biomass and initiate a pulse of N-enriched litter to the forest floor. Shading by litter and growth of understory vegetation was expected to cool soil temperatures, while soil N cycling rates and pools of inorganic N were predicted to increase resulting in increased foliar %N of surviving unattacked trees. When comparing forest types, we expected the absolute magnitude of increases in soil N pools and fluxes to be larger in Douglas-fir. However, proportional increases were predicted to be larger in lodgepole pine and therefore potentially more ecologically significant. Foliar N response to changing soil N availability could also vary among forest type, with more N-limited stands showing larger increases in foliar N. Bark beetle disturbance may also influence
the cycling of micronutrients in conifer forests, which can be important controls on macronutrient cycles.

**METHODS**

Lodgepole pine study area, site characteristics, and data used for our comparisons of forest type were reported in Griffin et al. (2011), with the exception of foliar micronutrients. Vegetation, litter, and soil sampling methods in Douglas-fir were identical to those used by Griffin et al. (2011) in mountain pine beetle-disturbed lodgepole pine stands.

**Douglas-fir study area and sampling design**

Douglas-fir study sites were located in the Greater Yellowstone Ecosystem of northwestern Wyoming, USA, within Grand Teton National Park and Bridger-Teton National Forest in the Moran Junction/Buffalo River Valley Region. July temperatures average 14.9 ºC, January temperatures average -11.2 ºC, with 595 mm of annual precipitation occurring mostly as snow (WRCC 2010c). The most recent outbreak of DFB in this area began in the early 2000’s, though the region has experienced widespread outbreak of multiple bark beetle species in recent years including the mountain pine beetle in lodgepole pine and whitebark pine (*Pinus albicaulis* Engelmann), and the spruce beetle (*Dendroctonus rufipennis* Kirby) in Engelmann spruce (*Picea engelmannii* Parry) (USFS 2006). In 2008 we sampled ten spatially independent (>2 km apart) Douglas-fir stands (five undisturbed, five attacked by bark beetles in 2003 and 2004). DFB-disturbed stands were identified using aerial surveys of insect damage (USFS 2006), and field inspection assured selection of stands with comparable structure, basal area, soils, and disturbance intensity. Within each stand, an 8m radius (201 m³) plot was installed with GPS location, elevation, and slope recorded at the plot center.
Vegetation

All live and dead trees greater than breast height (1.4m) were identified to species and measured for diameter at breast height (DBH). Beetle-killed trees were identified by the presence of exit holes on the bark exterior and distinctive *Dendroctonus* galleries underneath the bark. For the beetle-disturbed sites, pre-outbreak basal area was calculated by summing the basal area of live and beetle-killed trees. Mortality rates in disturbed plots were as high as 100% of canopy trees, and survivors were mostly smaller sub-canopy trees contributing little basal area. Thus, the post-disturbance growth (~4yrs worth) of survivors was not considered in calculating the pre-disturbance basal area of beetle-killed stands. Canopy biomass was determined for each tree using allometrics developed for Rocky Mountain conifers (Brown 1978) and summed by plot. Ground cover was visually estimated to the nearest 10% by plant functional groups (forbs, sedges, grasses, shrubs, and tree seedlings) in ten 0.25-m² circular microplots; total cover was allowed to exceed 100% to account for multiple strata of ground vegetation. The microplots were located within the inner 5-m plot radius using a stratified random design of fixed distances (one at 0.5-m; two at 1.5-m, 2.5-m and 3.5-m; and three at 4.5-m) and random bearings (in 10º increments) from the plot center, and averaged by plot.

Microclimate

To evaluate variation in growing-season soil microclimate, soil temperature was measured hourly in three of the five plots within each disturbance class (N = 6 instrumented plots) from July 4 through August 31, 2008, using three pairs of iButton datalogger probes (Maxim Integrated Products Inc., Dallas Semiconductor, Sunnyvale, CA) per plot. One iButton of each pair was installed at the litter-organic soil interface, and the second was installed 10 cm below this interface. For each soil depth, temperature probe data were summarized as follows.
First, plot-level hourly temperatures were determined by averaging data from the three probes per plot. Plot-level daily mean temperatures, ranges, maximums, and minimums were then calculated from the hourly data, and averaged to determine disturbance class-level daily means. Plot-level growing season values were obtained by averaging daily values across the sampling period, and disturbance class-level growing season means were then calculated from these plot-level data.

**Litter quantity and quality**

In each 0.25-m² microplot, litter depth was recorded at three locations and a 400-cm² sample of the litter layer was collected and oven-dried at 60 ºC. Plot-level litter depth and mass were obtained by averaging values from the 10 microplots. Litter from each microplot was sorted into three categories: fresh current-year needle litter, identified by bright red color and lack of mottling on surface (Morehouse et al. 2008); all-needle litter (all ages of needles combined); and total litter (all foliar litter components and woody litter components < 1.0 cm wide). Sorted litter was composited by plot for each category, 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).

**Soil chemistry, N pools, and N fluxes**

One soil core was collected from each 0.25-m² microplot (n = 10 per plot) using a 5-cm diameter x 15-cm long PVC corer. Soils were sieved (2 mm), weighed, and divided into three subsamples: 30 g oven-dried at 60 ºC for gravimetric percent moisture; 20 g extracted in 75 ml of 2M KCl for 2 hours, with the extract then filtered and frozen for later analysis of NH₄⁺ and NO₃⁻ pools; and 20 g air-dried and bulked by plot for soil texture and chemical analyses. 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
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).

Net N mineralization and net nitrification were measured using ion-exchange resin cores (Binkley et al. 1992), with one core incubated *in situ* for approximately one year (July 2008 - June 2009) in each 0.25-m² microplot. Incubated cores consisted of a 5-cm diameter x 15-cm long PVC tube of soil with an ion-exchange resin bag placed at the bottom. 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. Upon retrieval in summer 2009, core soils were sieved (2 mm) and core soils and resin bags were extracted separately in 2M KCl in the same manner as the 2008 initial soil samples described above. All KCl extractions were analyzed for [NH₄⁺] and [NO₃⁻] using colorimetric methods on an Astoria Pacific II continuous flow autoanalyzer. For each microplot, mineralization and net nitrification rates were calculated as:

\[
\text{rate} = \frac{(\text{final soil N} + \text{resin bag N}) - \text{initial soil N}}{\text{incubation time}}
\]

and expressed in units of µg N g soil⁻¹ year⁻¹. Values were then averaged by plot. Atmospheric N inputs in the region are low (~ 1 kg N ha⁻¹ year⁻¹; [www.epa.gov/castnet/charts/YEL408totn.png](http://www.epa.gov/castnet/charts/YEL408totn.png)) and were not factored into the soil N calculations.

**Foliar Chemistry**

In each plot, pole pruners were used to collect canopy foliage from three live trees unattacked by bark beetles. Two fully sunlit branches (0.5-m long) were clipped from each tree and separated into two subsamples: current-year foliage (from one branch per tree), and all-years foliage (from the second branch per tree). Foliar samples were oven-dried at 60°C and ground to powder for chemical analyses at the University of Wisconsin Soil and Plant Analysis Lab. C and N analysis for both current-year fresh foliage and all-year composite foliage was performed on a
Leco CNS-2000 analyzer. In current year fresh foliage, P, K, Ca, Mg, S, Zn, B, Mn, Fe, Cu, Al, and Na were determined by ICP-OES (Thermo Jarrell Ash IRIS Advantage Inductively Coupled Plasma Optical Emission Spectrometry) and ICPMS (VG Plasma Quad PQ2 Turbo Plus Inductively Coupled Plasma Mass Spectrometry) (UWSPAL 2010). Tree-level canopy data ($N=3$ per sample type per plot) were averaged to obtain plot-level data. To compute canopy N pool sizes, the mean foliar N concentration for each plot was multiplied by biomass values derived from the allometrics cited above.

**Statistical analyses**

All statistical analyses were performed in SAS (SAS Institute Inc. 2003), and unless otherwise noted all reported variance values are two standard errors. All variables were checked for normality and transformed if necessary to satisfy the assumptions of statistical methods. $N=10$ (5 per disturbance class) for all analyses of Douglas-fir forests except those using microclimate data, where $N=6$ as only three of five plots per disturbance class were instrumented. For all analyses comparing forest types, $N=20$.

General linear models were used to test for differences between both undisturbed and beetle-killed Douglas-fir forests, as well as undisturbed Douglas-fir and undisturbed lodgepole pine, in basal areas, site characteristics (slope, elevation, aspect, and soil chemistry), understory cover, soil temperatures, litter quantity and quality, soil N pools, foliar N concentrations, and foliar N pools. We also used general linear models to account for potential covariate effects of soil pH, bulk density, and C:N ratio in addition to disturbance class when testing for differences in net mineralization and net nitrification rates in Douglas-fir sites. Relationships between soil N availability and fresh foliar N concentrations were explored using Pearson correlation and linear regression. Linear regression was also used to test whether abiotic changes in soil temperature or
biotic changes in litter N were more closely related to changes in soil N cycling. To test whether litter N, soil N, and foliar chemistry of lodgepole pine and Douglas-fir forests responded differently to bark beetle disturbance, we used general linear models of the form: $y = \text{species} + \text{disturbance class} + \text{species} \times \text{disturbance class}$. A significant ($P \leq 0.05$) interaction term in these analyses indicates differing response to beetle disturbance by type.

RESULTS

**Douglas-fir forests**

**Site characteristics, stand structure, and soil microclimate.** Undisturbed and beetle-killed Douglas-fir stands occupied similar landscape positions, with no difference in either slope or aspect between disturbance classes (Table 1). However, due to the spatial distribution of the Douglas-fir beetle outbreak, beetle-killed sites were on average 140 m higher in elevation than undisturbed (2186 vs. 2325 m; $P = 0.0400$; Table 1). Soil texture (%sand, silt, clay), bulk density, and organic soil horizon depth were similar between disturbance classes, as were soil Ca, Mg, K, P, and pH (Table 1). Douglas-fir basal area comprised 97% (67 of 69 m$^2$ ha$^{-1}$) of total stand basal area among all sites and did not differ between undisturbed and beetle-killed sites (Table 1). Live Douglas-fir basal area averaged 98% of the total Douglas-fir basal area in the undisturbed class and 7% in beetle-killed stands (Table 1). In beetle-killed stands, Douglas-fir mortality averaged 93% of stem density, with an estimated concurrent decline in live canopy biomass averaging 15,796 ± 1704 kg ha$^{-1}$ (Table 1). Total biotic understory cover increased significantly from 79 to 103%, driven by significant increases in forb (19 vs. 36 %) and grass (18 vs 49 %) cover ($P \leq 0.05$; Figure 2). Growing season soil temperatures were not significantly different between Douglas-fir disturbance classes at either soil depth, averaging 13.1 ± 1.0 °C at
the litter-soil interface and 10.9 ± 0.9°C at 10 cm depth below the litter layer (Table 1). Variability in soil temperature was also consistent between disturbance classes at both depths, with no differences in daily temperature means, ranges, minimums, or maximums (Table 1).

**Litter quantity and quality.** Litter quantity did not differ between undisturbed and beetle-killed Douglas-fir stands; litter depth averaged 3.2 ± 0.4 cm, and total litter mass averaged 1842 ± 247 g m⁻² (Table 1). However, litter quality did differ between disturbance classes. The N concentration in needle litter of all ages increased by 55% in beetle killed stands (from 0.89 to 1.38 %N), and total litter layer N concentration increased by 25% (from 1.10 to 1.37 %N; Table 2). Current year needle litter N concentration showed a marginally significant 13% increase (from 0.70 to 0.79, \( P = 0.0641 \); Table 2). Increases in litter %N resulted in significant concurrent declines in litter C:N ratio in all three litter categories. However, total litter N pool size (product of total litter mass and total litter %N) showed only a marginally significant increase (\( P = 0.0666 \)) from 19.3 to 26.4 g N m⁻² (Table 2), as litter mass varied considerably among sites.

**Soil N pools and fluxes.** Soil inorganic N pools and soil N transformation rates differed between undisturbed and beetle-killed Douglas-fir stands (Table 2). Extractable ammonium in beetle-disturbed stands was twice that of undisturbed stands (5.0 ± 0.8 vs. 2.5 ± 0.6 µg N g soil⁻¹), extractable nitrate was almost four times greater (5.5 ± 5.2 vs. 1.5 ± 1.0 µg N g soil⁻¹), and total extractable inorganic N (\( \text{NH}_4^+ + \text{NO}_3^- \)) in beetle-disturbed stands was more than double that in undisturbed (10.5 ± 4.7 vs. 4.0 ± 1.7µg N g soil⁻¹). Annual net N mineralization rates were highly variable and were not significantly different between disturbance classes, though a marginally significant increase (\( P = 0.0611 \)) was found when using soil bulk density as a covariate, with higher rates observed in beetle-killed stands. Annual net nitrification rates increased 50% in beetle-disturbed stands relative to undisturbed (7.2 ± 1.0 and 4.8 ± 0.6 µg N g
Neither net N mineralization nor net nitrification rates were significantly correlated with any metric of soil temperature (Pearson $P < 0.05$; $N=6$), nor was net N mineralization correlated with any metric of litter N (Pearson $P < 0.05$; $N = 10$). Nitrification fraction (the ratio of net nitrification to net mineralization) averaged 0.38 ± 0.10 and did not differ among disturbance classes, nor did soil C:N, soil %N, or soil N pool size (Table 2).

**Foliar N.** Beetle disturbance impacted both foliar N concentration and foliar N pool size. N concentration in the fresh foliage (current year) of unattacked Douglas-fir trees averaged 1.28 ± 0.11% and did not differ between disturbance classes. However, N concentration in all foliage of unattacked Douglas-fir was 18% greater in beetle-disturbed stands than in undisturbed (0.90 ± 0.07 vs. 0.76 ± 0.04 %N), with a concurrent decrease in C:N ratio (Table 2). Foliar N pool size mirrored changes in live foliar biomass and declined sharply by 79% from 11.5 ± 1.7 to 2.4 ± 1.5 g N m$^{-2}$ (Table 2). Neither fresh foliar %N or C:N were significantly correlated with any metric of inorganic soil N, including NH$_4^+$, NO$_3^-$, total inorganic soil N, net mineralization, net nitrification, or soil C:N (Pearson correlation; data not shown). However, foliar %N of all needles was positively related to both soil NO$_3^-$ (linear regression $P = 0.0553$, $F = 5.03$, Adj. $R^2 = 0.31$) and total inorganic soil N (linear regression $P = 0.0132$, $F = 10.06$, Adj. $R^2 = 0.50$), and the C:N ratio of all needles was negatively related to total inorganic soil N (linear regression $P = 0.0253$, $F = 7.53$, Adj. $R^2 = 0.42$).

**Forest type comparison**

Landscape position (slope and aspect) did not differ among Douglas-fir and lodgepole pine sites ($P > 0.08$) though Douglas-fir sites were approximately 200m lower in elevation (2255 ± 71m vs. 2438 ± 35m; $P < 0.0001$; Douglas-fir data in Table 1, lodgepole pine data reported in Griffin et al. (2011)), consistent with the species’ distribution in the region (Despain 1990).
Douglas-fir soils were higher in pH and contained less sand and more silt than lodgepole pine soils, as well as greater concentrations of organic matter, Ca, Mg, K, and P \( (P < 0.01; \text{Douglas-fir data in Table 1, lodgepole pine data reported in Griffin et al. (2011)}) \). Compared to lodgepole pine, Douglas-fir sites contained higher total basal area (all sites: \( 69.0 \pm 8.5 \text{ vs. } 42.7 \pm 7.6; \ P = 0.0003; \text{Figure 2} \)), beetle-killed basal area (beetle-killed sites: \( 69.6 \pm 11.2 \text{ vs. } 13.7 \pm 5.8; \ P < 0.0001; \text{Figure 2} \)), and percent mortality of pre-outbreak living stems <1.4m DBH (\( 93 \pm 3\% \text{ vs. } 52 \pm 17\% \)).

**Undisturbed forests.** In the absence of bark beetles, forest types differed in understory cover composition and soil temperature. Total biotic cover was greater in Douglas-fir \( (79 \pm 6\% \text{ vs. } 29 \pm 10\%; \ P < 0.0001) \), driven by greater cover of shrubs, total graminoids (grasses + sedges), and tree seedlings compared to lodgepole pine \( (P < 0.02; \text{Figure 2}) \). Soil temperatures at the litter-soil interface in undisturbed forests were cooler and had a lower range in Douglas-fir (temperature: \( 13.5 \pm 0.7 \degree C \text{ vs. } 15.4 \pm 1.0 \degree C; \text{temperature range: } 8.2 \pm 1.2 \degree C \text{ vs. } 27.4 \pm 2.9 \degree C; \ P \leq 0.03; \text{Douglas-fir data in Table 1, lodgepole pine data reported in Griffin et al. (2011)})\). Temperatures at 10-cm soil depth in undisturbed forests were not significantly different among forest types, and averaged \( 10.9 \pm 0.6 \degree C \). However, the range of 10-cm depth temperature was lower in Douglas-fir \( (1.4 \pm 0.6 \degree C \text{ vs. } 2.4 \pm 0.2 \degree C; \ P = 0.0236; \text{Douglas-fir data in Table 1, lodgepole pine data reported in Griffin et al. (2011)}) \).

Undisturbed Douglas-fir and lodgepole pine forests also differed in several metrics of litter, soil, and foliar N. Litter depth and all measurements of litter N content and pool size were greater in Douglas-fir \( (P \leq 0.03) \), though there was no difference in total litter mass. In soils, extractable \( \text{NH}_4^+ \), \( \text{NO}_3^- \), total inorganic N, and total organic N were also greater in Douglas-fir \( (P \leq 0.005; \text{Figure 4}) \). Net N mineralization rates were not statistically different, however net
nitrification rates in undisturbed Douglas-fir were twice that of undisturbed lodgepole pine (4.8 vs 2.4 μg N g⁻¹ day⁻¹; Figure 4; \( P = 0.0242 \)). Composite foliage in undisturbed forests did not differ in foliar biomass, N content, or N pool size (Figure 5), however fresh foliar %N was greater in Douglas-fir \( ( P = 0.0185; \text{Figure 5}) \). P, K, Ca, and B in fresh foliage were also greater in Douglas-fir, while Mn and Al were greater in lodgepole pine \( ( P \leq 0.03; \text{Table 3}) \).

**Ecosystem response to bark beetle disturbance.** Despite differing pre-disturbance communities, the response of understory cover to bark beetle disturbance was similar between forest types. Significant disturbance class effects were found for increased grass and forb cover \( ( P \leq 0.04; \text{Figure 2}) \), but there were no significant interactions between species and disturbance class for any biotic cover variable (Figure 2). However, soil temperature response did vary among forest type. Significant disturbance class effects were found for decreases in the mean, range, minimum, and maximum temperature at the litter-soil interface, though significant interactions between species and disturbance class for the range and maximum show that decreases in these variables were limited to lodgepole pine \( ( P < 0.04; \text{Douglas-fir data in Table 1; lodgepole pine data reported in Griffin et al. (2011)}) \). No significant disturbance class or species*disturbance class effects were found for 10-cm depth soil temperatures.

Outbreak-induced changes in N cycling also varied among forest types. Significant effects of disturbance class were found for all metrics of litter quality and quantity except total litter mass, which did not differ by either species or disturbance class (Figure 3). Nitrogen concentration in both fresh and total litter also showed a significant interaction between species and disturbance class, indicating that fresh litter %N increased only in lodgepole pine and total litter %N increased only in Douglas-fir (Figure 3). In soils, significant disturbance class effects were found for extractable \( \text{NH}_4^+ \) and \( \text{NO}_3^- \), net N mineralization, and net nitrification. No
significant effects were found for nitrification fraction, and there were no significant interactions between species and disturbance class for any soil N metric (Figure 4). In trees unattacked by bark beetles, all foliar N metrics showed a significant disturbance class effect except for fresh foliar %N, which was marginally significant (Figure 5). N concentration of unattacked current year foliage was higher in beetle-killed lodgepole pine, and composite foliar N was higher in beetle-killed stands of both species. Live canopy biomass and canopy N pool size were lower in beetle-killed stands of both types, but also showed a significant interaction between species and disturbance class indicating that declines in these variables were greater in Douglas-fir compared to lodgepole pine (Figure 5). Fresh foliar %N was positively related with net N mineralization in soils of lodgepole pine (Adj. $R^2 = 0.56; P = 0.0202$) but not in Douglas-fir.

**Foliar micronutrients**

Bark beetle disturbance significantly lowered foliar concentrations of Ca, Mg, and Mn in fresh foliage (needles < 1yr) of unattacked Douglas-fir trees, while foliar concentrations of P, K, Mg, S, Zn, B, Fe, Cu, Al and Na did not differ between Douglas-fir disturbance classes (Table 3). Foliar Mn also declined substantially in beetle-killed lodgepole pine forests, where decreases in Al were also significant (Table 3). Forest types differed overall in foliar P, K, Ca, and S with higher concentrations in Douglas-fir. Mn, Cu, and Al also differed by type, with greater concentrations in lodgepole pine (Table 3). Across both forest types there was a significant disturbance class effect for P, Mn and Al, with P increasing and Mn and Al decreasing in beetle-killed stands relative to undisturbed (Table 3).
DISCUSSION

Bark beetle disturbance initiated similar changes in N cycling through litter and soil in both Douglas-fir and lodgepole pine forests, despite substantial differences in pre-disturbance forest structure and ecosystem N dynamics. Patterns of increased litter depth, needle litter N concentration, and litter N pool size were consistent across forest types, though concurrent increases in total litter %N were limited to Douglas-fir. In soils, patterns of increased extractable inorganic N and N transformation rates following bark beetle disturbance were proportionally similar among forest types, though Douglas-fir had more N-rich soils overall. Live foliar N pools declined sharply with beetle-killed basal area in both forest types. Differences between these foundation species (Ellison et al. 2005) in pre-disturbance ecosystem characteristics may explain variable responses for some metrics following beetle outbreak. Total inorganic N in soils was four-fold higher in Douglas-fir, and foliar N in undisturbed Douglas-fir averaged 1.23% compared to 0.82% in lodgepole pine. These data suggest a higher overall N capital in Douglas-fir forests and less potential N limitation. Thus, the response of foliar %N in unattacked trees to increased soil N in beetle-killed stands was limited to lodgepole pine forests.

Forest types also differed in the response of abiotic soil conditions. Soil temperature was cooler in beetle-killed lodgepole pine forests, presumably due to insulating effects of litter input and increases in soil moisture. This effect was not seen in Douglas-fir, where the shading effect of abundant understory cover may be the dominant control on soil temperature. Soil temperature has been negatively correlated with net N mineralization across longer time scales of TSB in lodgepole pine (Griffin et al. 2011), however neither forest type showed this relationship using data from undisturbed and gray-stage TSB classes only. Furthermore, no litter N metrics were correlated with net N mineralization in either forest type at this time-scale. Though unmeasured
in this study, soil moisture and soil C dynamics are also potential controls on soil N processes and would be expected to change following bark beetle disturbance (Morehouse et al. 2008, Spielvogel et al. 2009).

Observed changes in litter and soil N cycling of both forest types were consistent with mechanisms of disturbance specific to the bark beetle insect guild. Rapid tree death appears to inhibit the resorption of N from foliage prior to needlefall (Morehouse et al. 2008, Griffin et al. 2011), and deposits a large pulse of needle litter in a relatively short time. Though dead conifer needles may leach some N compounds before dropping (Stadler et al. 2005), bark beetles do not alter fluxes of inorganic N to soils in the same way as the frass of conifer defoliators (le Mellec et al. 2009, Pitman et al. 2010). Beetle-induced inputs of N to the soil surface are largely in the form of organic N in litter, which can be a N sink during a period of net N immobilization in the early stages of decomposition (Fahey et al. 1985, Remsburg and Turner 2006). Thus, disturbance-induced fluxes of N from canopy to soil pools may be spread over longer time periods following bark beetle outbreak compared to defoliators. Minimal inputs of inorganic N to the soil profile could explain why the magnitude of observed increases in net N mineralization following bark beetle disturbance in lodgepole pine was smaller than those following defoliator disturbance in another *Pinus* forest (Tokuchi et al. 2004).

Effects of bark beetle disturbance on micronutrient cycling could also be important for post-beetle N cycling. Beetle-induced tree death reduces the delivery of photosynthate C to ectomycorrhizal fungi. In lodgepole pine stands of the Yellowstone region, a similar loss of C delivery to ectomycorrhizal communities following 50% defoliation has been shown to double the level of manganese peroxidase activity in soils (Cullings et al. 2008), an extracellular fungal enzyme used to metabolize lignin-based C sources. Greater demand for Mn to support increases
in this enzymatic pathway could reduce soil Mn availability to plants and may explain the considerable declines in foliar Mn levels of unattacked, surviving trees in beetle-disturbed stands of both forest types. In turn, litter produced from this foliage will also be lower in Mn content, which is known to slow decomposition rates (Berg et al. 2007) and thus subsequent return of N to soils from the litter layer. Furthermore, increased Mn peroxidase activity is likely to continue for considerable time periods. Canopy foliage (an index of photosynthate C delivery to soil fungi) in 30 yr post MBP lodgepole pine forest remains approximately half the biomass of undisturbed forests (Griffin et al. 2011), and surviving trees may reduce C allocation to fungi under conditions of elevated soil N (Hogberg et al. 2010). Concurrently, input of lignin and woody C to soils increases with root turnover, more decomposing needle litter, and eventually fine and coarse wood which has been shown to sequester large amounts of Mn during decomposition (Daniel et al. 1997). Sustained declines in photosynthate C supply and increases in lignin and woody C inputs could thus result in long-term declines of plant-available Mn.

Disturbance can lead to nutrient loss from forest ecosystems (Bormann and Likens 1979, Chapin et al. 2004), however our data suggest three mechanisms of ecosystem N retention following bark beetle outbreak. (1) Net N mineralization, net nitrification, and pool sizes of the highly leachable NO$_3^-$ ion remained low relative to other disturbance types in conifer ecosystems (Turner et al. 2007, Tan et al. 2008), and nitrification fraction was unaffected. (2) Although the foliar N pool declined in both forest types, increased foliar N of surviving trees partially compensated for N lost in litterfall. (3) Declines in foliar Mn could affect future litter quality, decreasing decomposition rate and slowing the return of inorganic N to the soil. Together, these suggest that the potential for N loss as NO$_3^-$ following bark beetle disturbance is low.
CONCLUSIONS

Forest types dominated by different foundation species (Ellison et al. 2005) can have unique responses to a common disturbance type. N cycling was significantly impacted by bark beetle outbreak in both Douglas-fir and lodgepole pine forests, which showed qualitatively similar responses of increased litter N inputs and soil N processes. However, differences between forest types in pre-disturbance ecosystem structure and N status resulted in variable responses of soil temperature and foliar %N of unattacked trees. Though the magnitude of beetle effects was relatively minor compared to other disturbance types, ecosystem impacts were specific to disturbance by the bark beetle insect guild. Several mechanisms of ecosystem N retention suggest that N losses following this native disturbance may be low.

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REFERENCES


USFS. 2006. Forest Insect and Disease Survey, regions 1, 2, & 4.


Table 1. Site characteristics in undisturbed and bark beetle-killed Douglas-fir forests. $N = 5$ / disturbance class. Significant ($\alpha < 0.05$) ANOVA $P$ values are shown in bold.

<table>
<thead>
<tr>
<th>Site characteristic</th>
<th>Douglas-fir disturbance class</th>
<th>ANOVA $P$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Undisturbed</td>
<td>Beetle-killed</td>
</tr>
<tr>
<td><strong>Topography</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Elevation (m)</td>
<td>2186 ± 38</td>
<td>2325 ± 107</td>
</tr>
<tr>
<td>Aspect (SW index)</td>
<td>0.367 ± 0.691</td>
<td>-0.085 ± 0.566</td>
</tr>
<tr>
<td>Slope</td>
<td>26 ± 12</td>
<td>22 ± 11</td>
</tr>
<tr>
<td><strong>Canopy vegetation</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Basal area (m$^2$ ha$^{-1}$)</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>62.7 ± 9.9</td>
<td>75.3 ± 12.2</td>
</tr>
<tr>
<td>Douglas-fir</td>
<td>58.7 ± 12.6</td>
<td>75.1 ± 12.1</td>
</tr>
<tr>
<td>Live Douglas-fir</td>
<td>57.6 ± 13.2</td>
<td>5.2 ± 2.9</td>
</tr>
<tr>
<td>Dead Douglas-fir</td>
<td>1.1 ± 1.2</td>
<td>69.9 ± 11.2</td>
</tr>
<tr>
<td>Live foliar biomass (kg ha$^{-1}$)</td>
<td>15,179 ± 4021</td>
<td>2551 ± 1538</td>
</tr>
<tr>
<td><strong>Soils</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Growing season temperature</strong></td>
<td></td>
<td></td>
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<tr>
<td>Litter-soil interface ($^\circ$C)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>mean</td>
<td>13.5 ± 0.7</td>
<td>12.7 ± 2.0</td>
</tr>
<tr>
<td>range</td>
<td>8.2 ± 1.2</td>
<td>9.4 ± 2.8</td>
</tr>
<tr>
<td>maximum</td>
<td>18.1 ± 1.0</td>
<td>18.3 ± 3.7</td>
</tr>
<tr>
<td>minimum</td>
<td>9.9 ± 0.8</td>
<td>8.9 ± 1.0</td>
</tr>
<tr>
<td><strong>10 cm soil depth ($^\circ$C)</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>mean</td>
<td>11.2 ± 1.1</td>
<td>10.5 ± 1.6</td>
</tr>
<tr>
<td>range</td>
<td>1.4 ± 0.6</td>
<td>1.5 ± 0.3</td>
</tr>
<tr>
<td>maximum</td>
<td>11.9 ± 1.3</td>
<td>11.3 ± 1.7</td>
</tr>
<tr>
<td>minimum</td>
<td>10.5 ± 0.8</td>
<td>9.8 ± 1.5</td>
</tr>
<tr>
<td><strong>Texture &amp; Structure</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sand (%)</td>
<td>56 ± 3</td>
<td>49 ± 3</td>
</tr>
<tr>
<td>Silt (%)</td>
<td>33 ± 6</td>
<td>36 ± 5</td>
</tr>
<tr>
<td>Clay (%)</td>
<td>12 ± 2</td>
<td>15 ± 2</td>
</tr>
<tr>
<td>Bulk density (g cm$^{-3}$)</td>
<td>0.66 ± 0.22</td>
<td>0.63 ± 0.10</td>
</tr>
<tr>
<td>Organic soil depth (cm)</td>
<td>4.2 ± 1.5</td>
<td>5.5 ± 2.0</td>
</tr>
<tr>
<td>Organic matter (%)</td>
<td>8.4 ± 4.8</td>
<td>8.6 ± 2.2</td>
</tr>
<tr>
<td><strong>Cations</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>pH</td>
<td>6.2 ± 0.3</td>
<td>6.4 ± 0.2</td>
</tr>
<tr>
<td>Ca (µg g$^{-1}$; exch.)</td>
<td>2401 ± 808</td>
<td>2702 ± 253</td>
</tr>
<tr>
<td>Mg (µg g$^{-1}$; exch.)</td>
<td>187 ± 52</td>
<td>220 ± 14</td>
</tr>
<tr>
<td>K (µg g$^{-1}$; exch.)</td>
<td>225 ± 79</td>
<td>218 ± 42</td>
</tr>
<tr>
<td>P (µg g$^{-1}$; exch.)</td>
<td>49 ± 8.4</td>
<td>51 ± 15</td>
</tr>
<tr>
<td><strong>Litter</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Depth (cm)</td>
<td>3.0 ± 0.5</td>
<td>3.5 ± 0.6</td>
</tr>
<tr>
<td>Mass (g m$^{-2}$)</td>
<td>1760 ± 365</td>
<td>1924 ± 357</td>
</tr>
</tbody>
</table>
Table 2. N concentrations, pools, and fluxes in undisturbed and bark beetle-killed Douglas-fir forests. \( N = 5 / \) disturbance class; values in table are untransformed mean ± 2SE. Significant (\( \alpha < 0.05 \)) ANOVA \( P \) values are shown in bold; asterisk (*) denotes marginally significant (0.05 < \( \alpha \) < 0.07) ANOVA \( P \).

<table>
<thead>
<tr>
<th>N concentration, pool, or flux</th>
<th>Douglas-fir disturbance class</th>
<th>ANOVA ( P )</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Undisturbed</td>
<td>Beetle-killed</td>
</tr>
<tr>
<td><strong>Litter</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total litter N pool (g N m(^{-2}))</td>
<td>19.3 ± 3.3</td>
<td>26.4 ± 5.8</td>
</tr>
<tr>
<td>Total litter %N</td>
<td>1.10 ± 0.06</td>
<td>1.37 ± 0.13</td>
</tr>
<tr>
<td>Total litter C:N</td>
<td>44 ± 2</td>
<td>35 ± 3</td>
</tr>
<tr>
<td>All needles %N</td>
<td>0.89 ± 0.07</td>
<td>1.38 ± 0.10</td>
</tr>
<tr>
<td>All needles C:N</td>
<td>57 ± 5</td>
<td>36 ± 2</td>
</tr>
<tr>
<td>&lt; 1 yr old needles %N</td>
<td>0.70 ± 0.06</td>
<td>0.79 ± 0.07</td>
</tr>
<tr>
<td>&lt; 1 yr old needles C:N</td>
<td>72 ± 6</td>
<td>62 ± 5</td>
</tr>
<tr>
<td><strong>Soil</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total soil N pool (g N m(^{-2}))</td>
<td>192 ± 78</td>
<td>237 ± 42</td>
</tr>
<tr>
<td>%N</td>
<td>0.23 ± 0.15</td>
<td>0.26 ± 0.07</td>
</tr>
<tr>
<td>C:N</td>
<td>19.2 ± 2.9</td>
<td>16.7 ± 0.4</td>
</tr>
<tr>
<td>Organic N (mg N g(^{-1}))</td>
<td>2.34 ± 1.52</td>
<td>2.58 ± 0.70</td>
</tr>
<tr>
<td>( \text{NH}_4^+ )</td>
<td>2.5 ± 0.6</td>
<td>5.0 ± 0.8</td>
</tr>
<tr>
<td>( \text{NO}_3^- )</td>
<td>1.5 ± 1.0</td>
<td>5.5 ± 5.2</td>
</tr>
<tr>
<td>Total inorganic N (^1)</td>
<td>4.0 ± 1.7</td>
<td>10.5 ± 4.7</td>
</tr>
<tr>
<td>Net N mineralization (^2)</td>
<td>14.3 ± 9.3</td>
<td>24.8 ± 11.2</td>
</tr>
<tr>
<td>Net nitrification (^2)</td>
<td>4.8 ± 0.6</td>
<td>7.2 ± 1.0</td>
</tr>
<tr>
<td>Nitrification fraction</td>
<td>0.42 ± 0.18</td>
<td>0.34 ± 0.11</td>
</tr>
<tr>
<td><strong>Canopy foliage</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Foliar N pool (g N m(^{-2}))</td>
<td>11.5 ± 1.7</td>
<td>2.4 ± 1.5</td>
</tr>
<tr>
<td>All needle %N</td>
<td>0.76 ± 0.04</td>
<td>0.90 ± 0.07</td>
</tr>
<tr>
<td>All needle C:N</td>
<td>63 ± 3</td>
<td>54 ± 4</td>
</tr>
<tr>
<td>&lt;1yr needle %N</td>
<td>1.23 ± 0.19</td>
<td>1.34 ± 0.12</td>
</tr>
<tr>
<td>&lt;1yr needle C:N</td>
<td>40 ± 7</td>
<td>36 ± 3</td>
</tr>
</tbody>
</table>

\(^1\) \( \mu g \text{ N g soil}^{-1} \)
\(^2\) \( \mu g \text{ N g soil}^{-1} \text{ yr}^{-1} \)
\(^3\) ANOVA performed on log(x) transformed data
\(^4\) ANOVA performed on 1/x transformed data
Table 3. Foliar chemistry of new needles from unattacked trees in undisturbed and beetle-killed stands of Douglas-fir and lodgepole pine in the Greater Yellowstone Ecosystem. $N = 5$ stands per disturbance class; values in table are untransformed mean ± 2SE.

Significant ($\alpha < 0.05$ ) ANOVA $P$ values are shown in bold; asterisk (*) denotes marginally significant (0.05 < $\alpha$ < 0.06) ANOVA $P$.

<table>
<thead>
<tr>
<th>Foliar Nutrient</th>
<th>Douglas-fir</th>
<th>Lodgepole pine</th>
<th>Species Comparison ANOVA $P$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Undisturbed</td>
<td>Beetle-killed</td>
<td>ANOVA $P$</td>
</tr>
<tr>
<td>N (%)</td>
<td>1.23 ± 0.19</td>
<td>1.34 ± 0.12</td>
<td>0.3853</td>
</tr>
<tr>
<td>C:N</td>
<td>39.7 ± 7.1</td>
<td>35.8 ± 3.3</td>
<td>0.3499</td>
</tr>
<tr>
<td>N:P</td>
<td>5.5 ± 0.4</td>
<td>5.3 ± 0.4</td>
<td>0.5771</td>
</tr>
<tr>
<td>P (%)</td>
<td>0.23 ± 0.03</td>
<td>0.25 ± 0.03</td>
<td>0.2099</td>
</tr>
<tr>
<td>K (%)</td>
<td>1.2 ± 0.1</td>
<td>1.1 ± 0.1</td>
<td>0.4180</td>
</tr>
<tr>
<td>Ca (%)</td>
<td>0.40 ± 0.05</td>
<td>0.31 ± 0.04</td>
<td><strong>0.0236</strong></td>
</tr>
<tr>
<td>Mg (%)</td>
<td>0.11 ± 0.00</td>
<td>0.10 ± 0.01</td>
<td><strong>0.0344</strong></td>
</tr>
<tr>
<td>S (%)</td>
<td>0.09 ± 0.01</td>
<td>0.10 ± 0.01</td>
<td>0.7073</td>
</tr>
<tr>
<td>Zn (ppm)</td>
<td>28.5 ± 4.3</td>
<td>27.5 ± 4.0</td>
<td>0.7352</td>
</tr>
<tr>
<td>B (ppm)</td>
<td>13.6 ± 0.7</td>
<td>13.7 ± 2.8</td>
<td>0.9178</td>
</tr>
<tr>
<td>Mn (ppm)</td>
<td>132 ± 45</td>
<td>67 ± 22</td>
<td><strong>0.0331</strong></td>
</tr>
<tr>
<td>Fe (ppm)</td>
<td>44.4 ± 28.4</td>
<td>33.7 ± 7.9</td>
<td>0.5810 4</td>
</tr>
<tr>
<td>Cu (ppm)</td>
<td>7.3 ± 3.1</td>
<td>7.7 ± 2.5</td>
<td>0.8277</td>
</tr>
<tr>
<td>Al (ppm)</td>
<td>52.0 ± 41.9</td>
<td>18.8 ± 8.4</td>
<td>0.0780 1</td>
</tr>
<tr>
<td>Na (ppm)</td>
<td>12.4 ± 4.5</td>
<td>11.2 ± 1.4</td>
<td>0.6255</td>
</tr>
</tbody>
</table>

1 ANOVA performed on log$_{10}(x)$ transformed data
2 ANOVA performed on $x^{-2}$ transformed data
3 ANOVA performed on $\sqrt{x}$ transformed data
4 ANOVA performed on $1/x$ transformed data
5 ANOVA performed on $1/x^2$ transformed data
FIGURE LEGENDS

Figure 1. Hypothesized impacts of bark beetle disturbance in Douglas-fir and lodgepole pine ecosystems. Bark beetle-induced tree mortality is predicted to increase litter N inputs and moderate soil temperature. Both of these changes may accelerate fluxes of inorganic soil N and increase pools of plant-available N. Unattacked trees within beetle-killed stands may respond to these increases by allocating more N to foliage. Forest types are expected to differ in pre-disturbance N pool sizes and flux rates, which may result in variable ecosystem responses.

Figure 2. Tree basal area (A) and understory cover by plant functional group (B) in undisturbed and bark beetle-killed lodgepole pine and Douglas-fir forests. Plotted values are untransformed mean ± 2SE. LP and DF denote a significant effect of disturbance class within lodgepole pine (LP) or Douglas-fir (DF) forests only ($P < 0.05; N = 10$; GLM: $y = \text{disturbance class}$). SPP, CL, and S*C denote significant ($P < 0.05; N = 20$) effects of species (SPP), disturbance class (CL), and their interaction (S*C) in the global GLM: $y = \text{species} + \text{disturbance class} + \text{species*disturbance class}$. Total basal area: SPP, S*C. Total cover: LP, DF, SPP, CL.

Figure 3. Litter quantity and litter N metrics in undisturbed and bark beetle-killed lodgepole pine and Douglas-fir forests. Plotted values are untransformed mean ± 2SE. (A) litter depth, (B) litter mass, (C) fresh (<1 yr) needle litter %N, (D) all needle litter %N, (E) total litter %N, (F) total litter N pool. Values inset within each panel are $P$ values from the GLM: $y = \text{species} + \text{disturbance class} + \text{species*disturbance class}$. 
Figure 4. Soil N metrics in undisturbed and bark beetle-killed lodgepole pine and Douglas-fir forests. Plotted values are untransformed mean ± 2SE. (A) extractable NH$_4^+$, (B) extractable NO$_3^-$, (C) net N mineralization, (D) net nitrification, (E) nitrification fraction, (F) organic N. Values inset within each panel are $P$ values from the GLM: $y = \text{species} + \text{disturbance class} + \text{species} \times \text{disturbance class}$.

Figure 5. Canopy foliar N metrics and foliar biomass in undisturbed and bark beetle-killed lodgepole pine and Douglas-fir forests. Plotted values are untransformed mean ± 2SE. (A) fresh foliar %N, (B) total foliar %N, (C) live canopy biomass, (D) canopy N pool. Values inset within each panel are $P$ values from the GLM: $y = \text{species} + \text{disturbance class} + \text{species} \times \text{disturbance class}$.
### FIGURES

#### Figure 1

<table>
<thead>
<tr>
<th>Ecosystem component</th>
<th>Hypothesized bark beetle effects in Douglas-fir forests</th>
<th>Hypothesized differences in beetle effects in Douglas-fir compared to lodgepole pine forests</th>
</tr>
</thead>
<tbody>
<tr>
<td>Soil temperature</td>
<td>Decreased soil temperature</td>
<td>Similar effects; cooler soil temperatures in beetle-killed forests of both species</td>
</tr>
<tr>
<td></td>
<td>-insulating litter input</td>
<td></td>
</tr>
<tr>
<td></td>
<td>-shading by understory growth</td>
<td></td>
</tr>
<tr>
<td>Understory cover</td>
<td>Increased cover</td>
<td>Increased understory cover in beetle-killed forests of both types, with more cover overall in Douglas-fir.</td>
</tr>
<tr>
<td></td>
<td>-canopy opening</td>
<td></td>
</tr>
<tr>
<td></td>
<td>-increased light, H₂O, nutrients</td>
<td></td>
</tr>
<tr>
<td>Litter</td>
<td>Increased litter mass, depth, and %N of fresh needle litter</td>
<td>Greater increases in litter %N and N pool size in Douglas-fir; greater litter N in Douglas-fir overall</td>
</tr>
<tr>
<td>Soils</td>
<td>Increased NH₄⁺, NO₃⁻, net N mineralization, &amp; net nitrification</td>
<td>Larger increases in pool size and flux rate in Douglas-fir; greater soil N in Douglas-fir overall</td>
</tr>
<tr>
<td>Canopy of unattacked trees</td>
<td>Increased %N in canopy foliage. Sharp decline in N pool size.</td>
<td>Similar effects; increased %N in canopy foliage and decreased N pool size in beetle-killed stands of both species.</td>
</tr>
</tbody>
</table>
Figure 2

A) Basal area (m² ha⁻¹)

- Dead: LP, DF, SPP, CL, S*C
- Live: LP, DF, SPP, S*C

B) % Cover

- Tree seedlings: n.s.
- Forbs: LP, DF, SPP, CL
- Shrubs: SPP
- Sedges: n.s.
- Grasses: DF, SPP, CL

Legend:
- Undisturbed Lodgepole pine
- Beetle-killed Lodgepole pine
- Undisturbed Douglas-fir
- Beetle-killed Douglas-fir
Figure 3

A) Litter depth (cm)
- Species: 0.002
- Class: 0.057
- Species*Class: ns

B) Litter mass (g m⁻²)
- Species: ns
- Class: ns
- Species*Class: ns

C) Fresh needle litter %N
- Species: 0.002
- Class: <0.001
- Species*Class: 0.045

D) All needle litter %N
- Species: <0.001
- Class: <0.001
- Species*Class: ns

E) PICO PSME Total litter %N
- Species: <0.001
- Class: 0.003
- Species*Class: 0.021

F) Total litter N pool size (g N m⁻²)
- Species: 0.002
- Class: 0.035
- Species*Class: ns
Figure 4

A) Extractable NH$_4^+$ (µg N g soil$^{-1}$)

- Species: $<0.001$
- Class: 0.001
- Species*Class: ns

B) Extractable NO$_3^-$ (µg N g soil$^{-1}$)

- Species: $<0.001$
- Class: 0.053
- Species*Class: ns

C) Net N mineralization (µg N g soil$^{-1}$ yr$^{-1}$)

- Species: ns
- Class: 0.012
- Species*Class: ns

D) Net nitrification (µg N g soil$^{-1}$ yr$^{-1}$)

- Species: 0.027
- Class: 0.023
- Species*Class: ns

E) Nitrification fraction

- Species: ns
- Class: ns
- Species*Class: ns

F) Organic N (µg N g soil$^{-1}$)

- Species: $<0.001$
- Class: ns
- Species*Class: ns
Figure 5

A) Fresh foliar %N
Species: >0.001
Class: 0.058
Species*Class: ns

B) Total foliar %N
Species: ns
Class: 0.0003
Species*Class: ns

C) Live canopy biomass (kg ha⁻¹)
Species: ns
Class: <0.001
Species*Class: 0.045

D) Canopy N pool (kg N ha⁻¹)
Species: <0.0001
Class: 0.040
Species*Class: 0.040
CHAPTER 3

Does salvage logging alter ecosystem response to bark beetle disturbance in lodgepole pine forests?

ABSTRACT

Unprecedented outbreaks of native bark beetles in conifer forests of western North America have elicited multiple management strategies including salvage logging. Salvage has the potential to impact a wider range of forest ecosystem components than beetle outbreak alone, which may lead to different ecosystem responses in salvaged forests compared to beetle-killed only. In this study we use a paired and replicated before-after-control-impact (BACI) design to test the first-year effects of salvage on sapling density, understory cover, soil microclimate, and litter and soil N cycling of lodgepole pine (Pinus contorta Dougl.) forests attacked by the mountain pine beetle (Dendroctonus ponderosae Hopkins). Salvage harvest removed most basal area and decreased the density of all tree saplings (height <1.4 m) by 50%, although lodgepole pine sapling density was unchanged and appeared adequate for stand replacement. Understory biotic cover declined with salvage harvest, graminoid and shrub cover was unchanged, and cover of downed coarse wood increased. Mid-summer soil temperature increased by ~1 °C at both the litter-soil interface and 10 cm depth in salvaged plots, and the N concentration of needle litter increased by 30%. Soil and resin bag N were largely unaffected by salvage except for extractable soil NO₃⁻ which tripled in concentration but remained low at 1.5 µg N g soil⁻¹. Collectively, the initial effects of post-beetle salvage were modest. Beetle-induced declines in plant N uptake and increases in litter input appeared to be the main drivers of change in litter and soil N cycling over time, with little additional influence of salvage during the first year following harvest.
INTRODUCTION

Concurrent outbreaks of several native bark beetle species throughout western North America in the past decade have led to concern regarding ecosystem function, timber production, tourism, and forest fire (Flint 2006, Flint and Haynes 2006, McFarlane and Witson 2008). In response, management strategies have utilized both preemptive and post-outbreak approaches to mediate the impact of this disturbance. Preemptive strategies include disrupting or mimicking beetle pheromone communication (Bentz et al. 2005, Progar 2005, Gillette et al. 2006, Jeans-Williams and Borden 2006), and using silvicultural methods to reduce stand susceptibility (Safranyik et al. 1999, Fettig et al. 2007). Both methods have had moderate successes over limited temporal and spatial scales, yet landscape-scale suppression of beetle outbreak is unlikely (Raffa et al. 2008). Post-outbreak remediation techniques include fuel reduction treatments and salvage harvests. Because beetle and salvage logging disturbances affect different ecosystem components, interactions of these disturbance types may result in unique consequences for ecosystem structure and function (Paine et al. 1998) compared to bark beetles alone.

Canopy biomass is a strong control on the rates and retention efficiency of forest N cycling (Prescott 2002). Standing dead wood contains a significant amount of N (Fahey et al. 1985, Edmonds and Eglitis 1989, Herrmann and Prescott 2008) that is exported from the ecosystem by salvage. However, rates of N input from coarse wood are small and contribute little to annual rates of soil N turnover (Laiho and Prescott 2004). Fine woody debris and needle litter (needles, twigs, reproductive structures, and bark) have higher N content and faster turnover than coarse wood, and thus contribute more to overall N cycling in conifer forests (Laiho and Prescott 1999). Beetle-induced tree mortality initiates a pulse of N-enriched needle litter as the canopy decays (Morehouse et al. 2008, Klutsch et al. 2009, Griffin et al. 2011).
Salvage inputs of litter and fine woody debris are variable depending on method and site treatment (Smethurst and Nambiar 1990, Goodman and Hungate 2006), and in beetle-killed stands would likely depend on the extent of canopy deterioration that occurred due to beetles prior to salvage. Litter and slash material may serve as a temporary N sink if it remains on the forest floor undisturbed rather than burned, however slash burning can cause a pulse of soil inorganic N lasting up to three years (Lopushinsky et al. 1992). Slash effects on soil N also vary with time since disturbance and forest type. Following an outbreak of spruce beetle 

(Dendroctonus rufipennis Kirby) in Alaska, Goodman and Hungate (2006) found no effect of salvage on soil inorganic N four years after harvest. In contrast, a variety of slash treatments following non-salvage harvest of Monterey pine (Pinus radiata D. Don.) forests all yielded elevated N mineralization in the first two years after harvest (Smethurst and Nambiar 1990).

Logging activity can have a strong influence on both abiotic and biotic properties of forest soils. Machinery can cause soil compaction and increased bulk density (Blouin et al. 2005) that reduces porosity and water holding capacity, and increases soil strength (Blouin et al. 2008). Soil temperature may also be elevated by logging, though the magnitude is dependent upon site-treatment methods (Smethurst and Nambiar 1990). In contrast, beetle-induced litterfall can decrease soil temperatures in the first few years after attack (Griffin et al. 2011). In turn, these abiotic changes contribute to shifts in microbial community structure (Chatterjee et al. 2008) and mycorrhizal associations (Kranabetter et al. 2006). The net result of these changes on soil N dynamics is unclear. Some studies report short-lived increases in mineralization rates following compaction (Kranabetter et al. 2006); others report reductions in soil inorganic N pool sizes (Blouin et al. 2005, Choi et al. 2005, Kamaluddin et al. 2005). Variability among results may be
due to differing degrees of compaction, variation in slash treatments, or variation among forest
types in nutrient content of ecosystem pools.

Beetle and salvage disturbances also differ in their potential impact on tree saplings (here
defined as stems <1.4 m high), which provide a source of advance regeneration that could
ultimately lead to canopy replacement. In lodgepole pine (*Pinus contorta* Dougl.) forests,
successful mountain pine beetle (*Dendroctonus ponderosae* Hopkins) attack is limited to canopy
and large sub-canopy trees (Safranyik and Carroll 2006). Thus, post-beetle sapling densities are
largely unchanged and are usually sufficient for stand replacement with species compositions
consistent with local substrate and site conditions (Shore et al. 2006, Astrup et al. 2008, Nigh et
al. 2008, Rocca and Romme 2009, Vyse et al. 2009). However, salvage logging can have direct
and indirect, positive and negative effects on sapling density (Jonasova and Prach 2004). Direct
effects include physical damage or mortality of existing seedlings and saplings (Donato et al.
2006). Indirect mechanisms involve the effects of soil compaction and nutrient levels on tree
seedling growth and survival (Blouin et al. 2005, Bulmer and Simpson 2005, Kamaluddin et al.
2005, Blouin et al. 2008) and alteration of microsite conditions such as bare mineral soil or nurse
logs necessary for successful seedling establishment (Jonasova and Prach 2004). A flush of
understory growth and community composition change are common responses to both beetle
(McCambridge et al. 1982, Stone and Wolfe 1996, McMillin and Allen 2000) and salvage
(Hanson and Stuart 2005, del Rio 2006) disturbances, and are likely driven by increased light,
water, nutrient, and substrate availability.

In turn, litter inputs and vegetative cover can affect soil N cycling by shading and cooling
soils, providing N sinks in biomass, or altering rates of N fixation. Studies of other forest
management techniques suggest that soil disturbance is a key driver of vegetation differences
among beetle-killed stands with and without salvage. In cut-and-leave treatments, beetle-killed trees are felled by hand and left on-site, requiring no heavy machinery or log skidding that disturbs soil. Following an outbreak of the southern pine beetle (*Dendroctonus frontalis* Zimmerman) in loblolly pine (*Pinus taeda* (L.)), Coleman et al. (2008) showed few differences in understory tree or ground vegetation responses between beetle-killed stands with and without this treatment type.

In this study, we use field sampling and laboratory analyses to compare stand structure, ground cover, soil temperature, litter quantity and quality, and soil N metrics in beetle-killed vs. beetle-killed + salvage logged stands of lodgepole pine. We hypothesized that salvage would reduce sapling density, and increase the cover of bare soil, coarse wood, and understory vegetation. We also hypothesized litter mass, depth, and N pool size would increase as more material was added to the forest floor following salvage. Expectations for soil temperature were less clear, as canopy opening would tend to increase soil temperatures while additional inputs of litter mass may serve to insulate soils and cool soil temperature. With the addition of soil disturbance from logging in beetle-killed forests, we expected soil inorganic N pools and the accumulation of N on buried resin bags to also increase relative to beetle disturbance alone.

**METHODS**

*Study region and experimental design*

All study sites were located within a 4 km² area of the Green River Lakes region on the Bridger-Teton National Forest in northeastern Wyoming, USA (Figure 1). Forests are dominated by lodgepole pine, with minor components of subalpine fir (*Abies lasiocarpa* Hook.), Engelmann spruce (*Picea engelmannii* Parry), and whitebark pine (*Pinus albicaulis* Engelmann) (Despain
Mean temperature is 14.2 °C July and -10.2 °C in January, and the region averages 297 mm precipitation per year, mostly as snow (WRCC 2010a). Soils are relatively nutrient poor and derived from andesitic substrates. Mountain pine beetle activity in the area peaked in 2005, though affected forests were of a mix of unattacked trees and beetle-killed trees in the red and gray stages of canopy decline (Griffin et al. 2011) at the time of initial sampling in 2007.

We used a paired and replicated before-after-control-impact (BACI) experimental design (Underwood 1994) to test for an effect of salvage-logging on stand structure, ground cover, soil microclimate, and N cycling parameters in litter and soils of beetle-killed lodgepole pine. Pre-salvage structure, litter, and soil N pool data were collected in 2007 from 16 circular plots of 8 m radius. Eight plots were located in beetle-killed stands designated to be salvage-logged, and eight were located in paired similar beetle-killed stands <400m away not designated for salvage. Salvage logging in the beetle + salvage plots occurred in summer 2009. Harvest included both beetle-killed and unattacked trees, though >90% of the basal removed was beetle-killed. Cutting was performed by feller-buncher, with de-limbing done at landing sites and slash returned to and scattered in the plots. Post-salvage structure, litter, and soil N pool data were collected from all 16 plots in summer 2010, while soil temperatures and resin bag N accumulation were measured continuously from summer 2008 through summer 2010.

**Vegetation**

All live and dead trees greater than breast height (1.4m) were identified to species and measured for diameter at breast height (DBH). Beetle-killed trees were identified by the presence of exit holes and pitch tubes on the bark exterior, boring dust at the base of trees, and distinctive J-shaped *Dendroctonus* galleries underneath the bark. Trees <1.4m were tallied by species and measured to the nearest 10-cm height class in the northeast quadrant of each 8-m radius plot.
(50m²), as well as in two 50-m² rectangular plots 15 m to the east and west. Ground cover of litter, coarse wood, bare soil, and three plant functional groups (forbs, sedges, and graminoids (grasses + sedges)) was visually estimated to the nearest 10% in ten 0.25-m² circular microplots; total cover was allowed to exceed 100% to account for multiple strata of ground vegetation. Microplots were located within the central 5-m radius area of the plot using a stratified random design of fixed distances (one at 0.5 m; two at 1.5 m, 2.5 m and 3.5 m; and three at 4.5 m) and random bearings (in 10° increments) from the plot center.

**Microclimate**

Soil temperature was measured hourly in four of the eight 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. Beetle + salvage plots were not instrumented during the salvage period in summer 2009. One of each iButton pair was installed at the litter-organic soil interface, and the second was installed at 10 cm soil depth. For each depth, temperature probe data were summarized as follows. First, plot-level hourly temperatures were determined by averaging hourly data from the three probes per plot. Plot-level daily mean temperatures were then calculated from the hourly data, and averaged to determine treatment-level daily means.

**Litter quantity and quality**

In each 0.25-m² microplot, litter depth was recorded at three locations and a 400-cm² sample of the litter layer was collected and oven-dried at 60 °C. Plot-level litter depth and mass were obtained by averaging values from the 10 microplots. Litter from each microplot was sorted into three categories: fresh current-year needle litter, identified by bright red color and lack of mottling on surface (Morehouse et al. 2008); all-needle litter (all ages of needles combined); and
total litter (all foliar litter components and woody litter components < 1.0 cm wide). Sorted litter was composited by plot for each category, 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).

**Soil chemistry, soil N pools, and resin bag N**

One soil core was collected from each 0.25-m² microplot (N = 10 per plot) using a 5-cm diameter x 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 2M KCl for 2 hours, with the extract then filtered and frozen for later analysis of NH₄⁺ and NO₃⁻ 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 [NH₄⁺] and [NO₃⁻] using colorimetric methods on an Astoria Pacific II continuous flow autoanalyzer.

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 / plot). Sampling occurred in four summer periods (June-August in 2007 and 2008, June-October in 2009, and June-September in 2010) and three winter periods (August-June in 2007-8 and 2008-9, and October-June in 2009-10). Beetle + salvage plots were not measured during the salvage period in summer
2009. Upon retrieval, resins were removed from the nylon and extracted in 2M KCl and analyzed in the same manner as the soil samples described above.

**Statistical analyses**

To test for similarity in pre-salvage site conditions between the beetle only and beetle + salvage stands, 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 <1.4m stems, and ground cover), and litter (quantity and quality) metrics measured in 2007. Potential effects of post-beetle 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 beetle only vs. beetle + salvage plots. 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 first calculated the plot-level difference in mean daily temperatures between like calendar days before and after salvage, then performed paired t-tests for a salvage effect on these differences ($N = 62$ for summer; $N = 59$ for winter). Resin bag data within each sampling period were calculated as the rate of N accumulation ($\mu$g N g resin$^{-1}$ day$^{-1}$) and the mass of N collected ($\mu$g N g resin$^{-1}$). Potential effects of post-beetle salvage logging on resin bag N were tested using paired t-tests of the change over time in beetle only vs. beetle + salvage 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.

**RESULTS**

*Pre-salvage site conditions.*
Beetle only and beetle + salvage plots were similar ($P > 0.05$) in all topographic, vegetation, litter, cover, and soil metrics except for organic soil depth, which was deeper by 0.5 cm in beetle-only sites (Table 1). Mean elevation of all plots was 2518 ± 13 m, with a mean slope of 14.3 ± 4°. Lodgepole pine averaged 97% of the total basal area (live + dead) of all stands, and beetle mortality averaged 60% of lodgepole basal area (Table 1). The density of all saplings was highly variable among all plots prior to salvage but was not significantly different between beetle only and beetle + salvage plots (Table 1). Density of lodgepole pine saplings also did not differ between beetle and beetle + salvage plots (Table 1), and was 61% and 62% of the total density in each, respectively.

**Vegetation and ground cover**

As expected, salvage logging reduced total lodgepole pine basal area by 90%, which included small amounts of both live and non-beetle killed dead basal area in addition to beetle-killed trees (Figure 2a). Live unattacked basal area declined similarly in both beetle only and beetle + salvage sites, and beetle-killed basal area increased in beetle-only plots (Figure 2a). In the understory, salvage reduced total biotic cover, largely in response to a decline in forb cover, and there was no effect on graminoid or shrub cover (Figure 2b). Ground cover of bare soil increased after salvage from 0.1 to 8.4%, and coarse wood cover increased from 2.3 to 11.6 % (Figure 2b).

Salvage logging had a discernable effect on sapling density despite high variability in density change (both positive and negative) between 2007 and 2010 in both beetle only and beetle + salvage plots ($P = 0.045$). Total sapling density in beetle + salvage plots declined on average 1892 ± 1648 stems ha$^{-1}$ down to a mean of 1675 ± 1001 stems ha$^{-1}$. However, though the densities of both 0-30cm and 30-140cm size classes declined in beetle + salvage sites, when
compared to changes in beetle only plots an effect of salvage was limited to the 30-140cm size class (Figure 2a). For lodgepole pine saplings, there was no effect of salvage on either the total density or the density of either the 0-30 or 30-140 cm size classes (Figure 3b).

**Soil microclimate**

Salvage logging had a warming effect on both mid-summer and mid-winter soil temperatures at both the litter-soil interface and 10 cm depth. Salvage increased mid-summer litter-soil interface temperature by $0.8 \pm 0.2 \, ^\circ C$, and 10 cm depth temperature by $1.1 \pm 0.1 \, ^\circ C$ ($P < 0.001$ for both; Figure 3a). Mid-winter temperatures were $0.2 \pm 0.05$ and $0.3 \pm 0.04 \, ^\circ C$ warmer at the litter-soil interface and 10 cm depth, respectively ($P < 0.001$ for both; Figure 3b). Mean daily temperatures at the litter-soil interface peaked at 17 °C in each of the three sampled summers, and reached minimums of -3 and -9 °C in the two sampled winters. At 10 cm depth, temperatures peaked at 12-14 °C in summers, and reached lows of 3 and 6 °C in winters.

**Litter quantity and quality**

Salvage had little effect on litter amounts or N content, though several litter variables changed over time across all plots. Litter mass increased by 37% (1600 to 2200 g m⁻²) between 2007 and 2010 but was unaffected by salvage (Figure 5a). Litter depth averaged 2.7 ± 0.2 cm and did not change over time or with salvage (Figure 5b). Fresh (<1yr) needle litter %N was 0.73 ± 0.03 % across all sites and did not change with either time or salvage (Figure 5d). Though the %N of all needle litter was unchanged in beetle-only sites, it increased following salvage (Figure 5e) from $0.72 \pm 0.08$ to $0.94 \pm 0.07\%$ but was insufficient to cause a significant salvage effect in total litter %N (Figure 5f). Total litter %N did, however, increase across all plots from $0.81 \pm 0.06$ to $0.98 \pm 0.06\%$ between 2007 and 2010 (Figure 5f). Increased litter mass and increased
total litter %N both contributed to a 50% increase over time in the litter N pool across all plots from 1473 ± 148 to 2177 ± 295 g N m⁻², with no additional effect of salvage (Figure 5c).

**Soil and resin bag N**

Pools of extractable soil inorganic N changed through time and with salvage. Soil NH₄⁺ tripled across all plots from 5.7 ± 0.9 to 17.3 ± 0.9 µg N g soil⁻¹, with no additional effect of salvage (Figure 6a). In contrast, soil NO₃⁻ was unchanged in beetle-only plots through time but almost tripled in beetle + salvage plots from 0.6 ± 0.2 to 1.6 ± 0.5 µg N g soil⁻¹ from 2007 to 2010 (Figure 6b). However, this difference in soil NO₃⁻ was insufficient to cause an effect of salvage on total extractable inorganic N, which was dominated by NH₄⁺ and increased from 6.2 ± 1.0 to 18.9 ± 3.0 µg N g soil⁻¹ across all plots between 2007 and 2010.

Resin bag NH₄⁺ accumulation rate increased throughout the study in all plots (Figure 7a). In the pre-salvage period, NH₄⁺ accumulation rate increased in all plots from < 0.10 to ~0.20 µg N g resin⁻¹ day⁻¹ between summer 2007 and summer 2008. NH₄⁺ accumulation rate continued to increase through the post-salvage period in all plots, reaching ~0.35 µg N g resin⁻¹ day⁻¹ in the summer of 2010. Patterns of NH₄⁺ mass collected paralleled those of accumulation rate (Figure 7b). There was no effect of salvage on the changes in seasonal or annual NH₄⁺ accumulation rates, or seasonal mass collected between the year before and the year after the salvage period ($P > 0.05$). Annual mass of NH₄⁺ collected was also unaffected by salvage (Figure 8). Within the consistently increasing trend, resin bag NH₄⁺ accumulation oscillated between higher rates in summer and lower rates in winter (Figure 7a). Resin bag NO₃⁻ accumulation rate was consistent throughout the study and almost always under 0.10 µg N g resin⁻¹ day⁻¹ during both summer and winter (Figure 7b), with parallel patterns in total mass collected (Figure 7d). There was no effect
of salvage on seasonal or annual NO$_3^-$ accumulation rates or seasonal mass of NO$_3^-$ collected ($P > 0.05$). Annual mass of NO$_3^-$ collected was also unaffected by salvage (Figure 8).

**DISCUSSION**

In this study we tested the effects of post-disturbance salvage logging on the structure, microclimate, and N cycling of bark beetle-killed lodgepole pine forests. Bark beetle disturbance alone redistributes material among the canopy and forest floor, and influences both the microclimate and N cycling of the litter-soil profile compared to undisturbed forests (Griffin et al. 2011). We hypothesized that salvage logging of beetle-killed forests would cause further canopy disturbance and litter inputs, as well as new disturbance to saplings, understory vegetation, and the forest floor which together may in turn alter patterns of N cycling in the litter-soil profile compared to beetle-kill alone. Salvage had the greatest impact on forest structure, though there were substantive effects on ground cover, soil microclimate and litter and soil N cycling as well. In addition to declines in total basal area, density of 30 to 140-cm high saplings, and % cover of forbs and all plants, salvage caused an increase in mid-summer and mid-winter soil temperatures, %N content in needle litter, extractable soil NO$_3^-$, and the percent cover of coarse wood.

**Tree sapling density and regeneration potential**

Salvage-induced declines in the total sapling density observed here are consistent with those found in other salvaged forests (Jonasova and Prach 2004, Keyser et al. 2009). However, salvage did not affect the smallest size classes (0 to 30-cm high) of all saplings, or any size class of lodgepole pine sapling. This may be due to the undisturbed forest floor in post-beetle forests which may protect smaller stems from trampling or erosion compared to post-fire forests, and is
a common result following salvage (Vyse et al. 2009). The average density of stems <1.4 m high in salvaged plots of this study remained above 1600 stems ha\(^{-1}\), which is considered sufficient for stand replacement (Vyse et al. 2009), and also remained dominated by lodgepole pine (>50% of total density). Effects of salvage on sapling density are variable among forest types, pre-salvage disturbance types, and salvage method. In a study of post-southern pine beetle (Dendroctonus frontalis Zimmermann) salvage logging in loblolly pine (Pinus taeda L.), Coleman et al. (2008) concluded that cut and leave treatments did not change the successional trajectory of beetle-killed forests. Similarly, Peterson and Leach (2008) found no effect of post-windthrow salvage on sapling densities in loblolly pine, though there was an effect on species composition. In contrast, post-beetle (Ips typographus L.) clear-cut salvage logging in a Norway spruce (Picea abies (L.) Karst.) forest reduced the density of spruce saplings and promoted early successional understory species (Jonasova and Prach 2004, 2008).

**Microclimate and ground cover**

The salvage effect of 1 °C increase in temperature below the litter and at 10-cm depth observed here following beetle salvage is consistent in magnitude with remotely-sensed surface temperatures in beetle-killed spruce and clear-cut forests of the Czech Republic, which showed a difference of 2 °C between beetle-killed and clear-cut forest. (Hais and Kucera 2008). However, initial beetle disturbance has been shown to lower soil temperature compared to undisturbed forests due to increased litter input (Byers 1984, Griffin et al. 2011). Litter mass did not increase with salvage in this study and thus likely did not provide any additional cooling effect on soils. The removal of tree boles and the decreases in biotic ground cover and in the density of stems <1.4 m high may have reduced soil shading, and could explain how salvage increased soil
temperatures. Warmer temperatures may be associated with drier soils, which would have a suppressing effect on soil N turnover.

Increased cover of coarse wood after salvage logging is likely to create more variability in forest floor microsite conditions, influencing the rates of litter decomposition and subsequent return of inorganic N to soils at fine spatial scales (Remsburg and Turner 2006). However, similar changes are likely to occur in beetle-kill only forests as dead trees begin to fall, and over time total coarse wood loading in beetle-kill only forests will likely be much higher than in salvaged forests (Lewis 2009). Decreases in total biotic cover observed 1 year following salvage are not likely to remain (Kurulok and Macdonald 2007), as a flush of understory growth spurred by increased water, light, and nutrients is often observed following both beetle mortality (Stone and Wolfe 1996) and post-beetle salvage harvest (Jonasova and Prach 2008). Though highly variable and not significant in paired analyses, percent cover of bare soil showed an increasing trend in salvaged sites and possibly contributed to significant decreases in biotic cover. However, over time these areas are likely to be colonized by understory vegetation. With more mineral soil substrate exposed as seedbed, colonization by pioneer species may alter understory community composition in salvaged sites relative to beetle-kill alone. In a Colorado spruce-fir forest salvage logged after windthrow, understory communities shifted to dominance by graminoids (del Rio 2006). Thus, despite initial differences in biotic cover after 1 year, prediction of long term impacts of salvage on understory composition is difficult.

**Litter and Soils**

Several metrics of litter and soil N cycling changed similarly over time in all plots, consistent with expectations of canopy deterioration beetle-killed forests (Griffin et al. 2011). Total litter mass, %N, and litter N pool size were unaffected by salvage logging, but all increased
over the three years between sampling. These results suggest that either (1) most foliage had fallen from beetle-killed trees in all plots prior to salvage, or (2) that the amount of salvage-induced litterfall in beetle + salvage plots was equivalent to litterfall in beetle-kill only plots over the same time period. In either scenario, salvage does not appear to increase the amount of litter mass or N input which would already occur following beetle outbreak. Salvage did increase the %N of all needle litter, although this was insufficient to influence the total litter N pool size. This may be due to salvage-induced inputs of green needle litter from trees that survived the outbreak and had elevated foliar N content (Griffin et al. 2011).

Similarly, patterns of change in soil and resin bag N of salvaged forests were mostly consistent with those observed in beetle-killed only forests. Nitrogen availability is largely determined by the balance between plant uptake and inputs of organic N to the forest floor. Equivalent live basal areas between beetle only and beetle + salvage plots over time suggest that canopy plant demand for N was not affected by salvage. Inputs of litter N suggest N supply was also similar, which together may explain why few differences in soil N were observed. Extractable soil NO$_3^-$ pool was the only soil N metric that differed over time between beetle-only and beetle + salvage plots, and though still low, approximately tripled in beetle + salvage plots compared to beetle-kill alone. Increased soil NO$_3^-$ could be due to reduced cover of forbs, which preferentially take up NO$_3^-$ over NH$_4^+$ (Miller and Bowman 2002, Falkengren-Grerup et al. 2004).

An increase in NO$_3^-$ over time was not detected with buried resin bags in either beetle only or beetle + salvage plots, while resin bag NH$_4^+$ increased equally in both. With the exception of increased (but still low) soil NO$_3^-$, salvage does not appear to substantially alter soil N dynamics relative to the changes that would already occur in beetle-killed forests. Other
studies of tree mortality impacts on soil NO₃⁻ in Rocky Mountain conifers are consistent with these results, and show that NO₃⁻ production and export remains low even after substantial tree removal or death (Knight et al. 1991, Parsons et al. 1994, Prescott et al. 2003, Thiel and Perakis 2009). Beetle and salvage induced inputs of litter have high C:N ratios and may serve as N sinks in the early stages of decomposition (Fahey et al. 1985, Remsburg and Turner 2006) and limit the accumulation of N in soils.

CONCLUSIONS

Post-beetle salvage logging had detectable influences on ground cover, soil microclimate, and N cycling through the litter-soil profile during the initial year following tree harvest. However, the effects of salvage harvest were of less magnitude than we expected. Although sapling density declined by 50%, the density of lodgepole pine saplings did not change and appeared adequate for stand replacement. Salvage increased soil temperatures by ~ 1 °C at both the litter-soil interface and at 10cm depth, and increased the %N in all-needle litter but not in the total litter N pool. With no effect on plant N demand (as inferred from basal area) or on litter N inputs, salvage also did not have a substantial effect on soil N other than small increases in extractable soil NO₃⁻. Rather, N cycling in the litter and soils of both beetle only and beetle + salvage sites changed over time in a manner consistent with that expected following bark beetle outbreak with few modifications by salvage harvest. These data suggest that the harvest of beetle-killed trees for wood products can have small initial consequences for many ecosystem response variables. However, loss of snags and the future inputs of coarse wood to the forest floor are likely to be pronounced over longer time frames.
ACKNOWLEDGEMENTS

We thank Emily Stanley, James Thoyre, and the Center for Limnology at UW for access to laboratory equipment. For help in the field and the laboratory, we appreciate the assistance of many University of Wisconsin students: Heather Lumpkin, Erin Mellenthin, Alex Rahmlow, Amanda Rudie, Ben Ruh, Corey Olsen, Ryan Peasley, Greg Skupien, Lucille Marescot, Jaclyn Entringer, Emily Ruebl, Ashton Mieritz, Shane Armstrong, and Nick Labonte.

REFERENCES


### TABLES

Table 1. Pre-salvage characteristics for beetle-killed only and beetle-killed plus salvage-logged sites. $N = 8$ sites per treatment. Boldface indicates significant paired t test at $\alpha = 0.05$.

<table>
<thead>
<tr>
<th>Site characteristic</th>
<th>Disturbance type</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Beetle only</td>
<td>Beetle + Salvage</td>
</tr>
<tr>
<td><strong>Topography</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Elevation (m)</td>
<td>2510 ± 22</td>
<td>2526 ± 12</td>
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<tr>
<td>Aspect (SW index) a</td>
<td>-0.7 ± 0.4</td>
<td>-0.1 ± 0.6</td>
</tr>
<tr>
<td>Slope (°)</td>
<td>14 ± 6</td>
<td>15 ± 5</td>
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<tr>
<td><strong>Soils</strong></td>
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</tr>
<tr>
<td><strong>Texture &amp; Structure</strong></td>
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<td></td>
</tr>
<tr>
<td>Sand (%)</td>
<td>61 ± 5</td>
<td>57 ± 5</td>
</tr>
<tr>
<td>Silt (%)</td>
<td>26 ± 4</td>
<td>29 ± 3</td>
</tr>
<tr>
<td>Clay (%)</td>
<td>13 ± 2</td>
<td>14 ± 2</td>
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<tr>
<td>Bulk density (g cm$^{-3}$)</td>
<td>0.69 ± 0.06</td>
<td>0.72 ± 0.07</td>
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<tr>
<td>Organic soil depth (cm)</td>
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<td>2.7 ± 0.2</td>
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<tr>
<td>Organic matter (%)</td>
<td>4.3 ± 0.8</td>
<td>4.7 ± 1.0</td>
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<tr>
<td><strong>Cations</strong></td>
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<tr>
<td>pH</td>
<td>5.4 ± 0.1</td>
<td>5.3 ± 0.2</td>
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<tr>
<td>Ca (µg g$^{-1}$; exch.)</td>
<td>1132 ± 293</td>
<td>1251 ± 361</td>
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<tr>
<td>Mg (µg g$^{-1}$; exch.)</td>
<td>131 ± 24</td>
<td>141 ± 34</td>
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<td>K (µg g$^{-1}$; exch.)</td>
<td>187 ± 37</td>
<td>185 ± 25</td>
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<td>P (µg g$^{-1}$; exch.)</td>
<td>25 ± 8</td>
<td>28 ± 5</td>
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<td><strong>Nitrogen</strong></td>
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<tr>
<td>NH$_4$ (µg N g$^{-1}$)</td>
<td>5.3 ± 1.4</td>
<td>6.0 ± 1.1</td>
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<tr>
<td>NO$_3$ (µg N g$^{-1}$)</td>
<td>0.5 ± 0.3</td>
<td>0.6 ± 0.3</td>
</tr>
<tr>
<td>Organic N (mg N g$^{-1}$)</td>
<td>0.86 ± 0.25</td>
<td>0.94 ± 0.28</td>
</tr>
<tr>
<td><strong>Litter</strong></td>
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</tr>
<tr>
<td>Mass (g m$^{-2}$)</td>
<td>1614 ± 236</td>
<td>1668 ± 160</td>
</tr>
<tr>
<td>Depth (cm)</td>
<td>2.7 ± 0.4</td>
<td>2.3 ± 0.4</td>
</tr>
<tr>
<td>N pool size (g N m$^{-2}$)</td>
<td>12.6 ± 2.2</td>
<td>13.9 ± 1.8</td>
</tr>
<tr>
<td>&lt;1 yr old needle %N</td>
<td>0.73 ± 0.07</td>
<td>0.69 ± 0.05</td>
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<tr>
<td>All needles %N</td>
<td>0.74 ± 0.07</td>
<td>0.72 ± 0.08</td>
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<tr>
<td>Total litter %N</td>
<td>0.78 ± 0.06</td>
<td>0.84 ± 0.10</td>
</tr>
<tr>
<td><strong>P. contorta basal area (m$^2$ ha$^{-1}$)</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Live unattacked</td>
<td>8.3 ± 2.8</td>
<td>5.6 ± 2.8</td>
</tr>
<tr>
<td>Live attacked</td>
<td>2.1 ± 2.2</td>
<td>0.6 ± 1.2</td>
</tr>
<tr>
<td>Dead unattacked</td>
<td>5.0 ± 3.1</td>
<td>8.0 ± 4.3</td>
</tr>
<tr>
<td>Dead attacked</td>
<td>22.4 ± 4.1</td>
<td>21.9 ± 5.0</td>
</tr>
<tr>
<td><strong>Sapling density (stems ha$^{-1}$)</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>All species</td>
<td>7133 ± 3380</td>
<td>3567 ± 1855</td>
</tr>
<tr>
<td>P. contorta</td>
<td>4383 ± 2854</td>
<td>2225 ± 1326</td>
</tr>
<tr>
<td><strong>Ground cover (%)</strong></td>
<td></td>
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<tr>
<td>Bare soil</td>
<td>0.4 ± 0.5</td>
<td>0.1 ± 0.1</td>
</tr>
<tr>
<td>Litter</td>
<td>42 ± 9</td>
<td>41 ± 10</td>
</tr>
<tr>
<td>Coarse wood</td>
<td>2.6 ± 3.2</td>
<td>2.3 ± 1.7</td>
</tr>
<tr>
<td>Total biotic</td>
<td>62 ± 11</td>
<td>60 ± 13</td>
</tr>
<tr>
<td>Graminoid</td>
<td>16 ± 6</td>
<td>7 ± 4</td>
</tr>
<tr>
<td>Shrub</td>
<td>7 ± 6</td>
<td>3 ± 3</td>
</tr>
<tr>
<td>Forb</td>
<td>37 ± 11</td>
<td>49 ± 9</td>
</tr>
</tbody>
</table>

a calculated as: $\cos$ (aspect-225)

b paired t test performed on log$_{10}$ transformed data
FIGURE LEGENDS

Figure 1. Study area, Green River Lakes Region of the Bridger-Teton National Forest.
Eight plot pairs were established in summer 2007, with one member inside a polygon designated for salvage harvest and the other outside. All forests in the field of view are dominated by lodgepole pine, and mountain pine beetle activity was extensive throughout the area at the time of initial sampling (2007). Salvage harvests occurred in the summer of 2009, and post-salvage data were collected in summer 2010.

Figure 2. Stand structure and ground cover change in beetle only and beetle + salvage plots following logging. N = 8 pairs of plots. Error bars = 2 standard error. (A) Live and dead basal area change (2010 – 2007) in attacked and unattacked lodgepole pine; (B) Ground cover change in abiotic (bare soil, litter, and coarse wood) and biotic (total and by plant functional group) classes. An asterisk indicates a significant difference at α = 0.05.

Figure 3. Change in sapling density in beetle only and beetle + salvage plots following logging. N = 8 pairs of plots. Error bars = 2 standard error. (A) all saplings; (B) lodgepole pine saplings. An asterisk indicates a significant difference at α = 0.05.

Figure 4. Average daily soil temperature in beetle only and beetle + salvage plots. Beetle + salvage sites were not instrumented during the salvage period in summer 2009. Variable width of each plotted time series = daily 95% confidence interval. Beetle-only data (black) is overlaid on beetle + salvage data (gray). (A) temperature at the litter-organic soil interface; (B) temperature at 10-cm soil depth. Salvage logging increased both mid-summer (July-August) temperature at
both soil depths by approximately 1 °C, and mid-winter (January-February) temperatures by 0.2 °C ($P < 0.001$; time periods used in analyses are shown in boxes).

**Figure 5. Change in litter quantity and quality in beetle only and beetle + salvage plots following logging.** $N = 8$ pairs of plots. Error bars = 2 standard error. (A) litter mass; (B) litter depth; (C) %N in <1yr old needle litter; (D) %N in all-needle litter; (E) %N in total litter; (F) total litter N pool size. An asterisk indicates a significant difference at $\alpha = 0.05$.

**Figure 6. Change in soil inorganic N pool sizes in beetle only and beetle + salvage plots following logging.** $N = 8$ pairs of plots. Error bars = 2 standard error. (A) extractable NH$_4^+$; (B) extractable NO$_3^-$; (C) total extractable inorganic N (TIN). An asterisk indicates a significant difference at $\alpha = 0.05$.

**Figure 7. Resin bag N in beetle only and beetle + salvage plots.** $N = 8$. Error bars = 2 standard error. Beetle + salvage sites were not measured during the salvage period in summer of 2009. (A) Resin bag NH$_4^+$ accumulation rate; (B) Resin bag NO$_3^-$ accumulation rate; (C) Mass of resin bag NH$_4^+$; (D) Mass of resin bag NO$_3^-$.

**Figure 8. Change in annual mass of resin bag N in beetle only and beetle + salvage plots following logging.** $N = 8$ pairs of plots. Error bars = 2 standard error. (A) NH$_4^+$; (B) NO$_3^-$; (C) total inorganic N (TIN).
FIGURES

Figure 1
Figure 2

A) Change in basal area (m² ha⁻¹)
- Beetles only
- Beetles + Salvage

B) Change in percent cover (%)
- Bare soil
- Litter
- Coarse wood
- Total biotic
- Graminoid
- Shrub
- Forb

Legend:
- * indicates significant difference
Figure 3

A) Change in total density (saplings ha⁻¹)

- Beetles only
- Beetles + Salvage

B) Change in lodgepole pine density (saplings ha⁻¹)

- All stems
- 0-30 cm
- 30-140 cm
- <140 cm
Figure 4

A) Litter-soil interface temp (°C)

B) 10 cm depth temp (°C)

Pre-salvage
Salvage period
Post-salvage

Beetle + Salvage
Beetle only
Figure 5

A) Change in litter mass (g m$^{-2}$)

B) Change in litter depth (cm)

C) Change in litter N pool (g N m$^{-2}$)

D) Change in <1 yr old needle litter %N

E) Change in all needle litter %N

F) Change in total litter %N
Figure 6

A) Change in soil NH$_4^+$ (µg N g soil$^{-1}$)

B) Change in soil NO$_3^-$ (µg N g soil$^{-1}$)

C) Change in TIN (µg N g soil$^{-1}$)

* Indicates a significant difference.
Figure 7

A) Rate of NH$_4^+$ accumulation

B) Rate of NO$_3^-$ accumulation

C) Mass of NH$_4^+$ accumulated

D) Mass of NO$_3^-$ accumulated
Figure 8

Change in annual mass of resin bag N (ug N g resin⁻¹)

- NH₄⁺  - NO₃⁻  - TIN

■ Beetle only  □ Beetle + Salvage
Disturbances can change and shape ecosystems by creating or reducing spatial heterogeneity, redistributing biomass among ecosystem pools, altering resource availability and abiotic conditions, or initiating community composition change (Bormann and Likens 1979, Pickett and White 1985, Turner and Dale 1998). In Greater Yellowstone and across western North America, bark beetles have thus shaped conifer forests as a native component of the disturbance regime throughout the Holocene (Brunelle et al. 2008). However, recent outbreaks have reached an unprecedented spatial extent and severity (Raffa et al. 2008), the frequency and severity of outbreaks are expected to increase in a warming climate (Logan et al. 2010), and there is growing concern over the impact of beetle outbreak on ecosystem services (Flint 2006) and interactions with other disturbance types (Simard et al. 2011). In this dissertation I have sought to fill large knowledge gaps regarding the impact of beetle disturbance on N cycling, the role of forest type in determining ecosystem response, and the effect of forest management on post-beetle ecosystem function. Following are the main conclusions from this body of work:

1. **Post-beetle patterns of N cycling change in the litter, soil, and vegetation of conifer forests were consistent with the guild-specific impacts of bark beetles on canopy vegetation.** Two to four years after disturbance, both biotic and abiotic controls were important factors in the increase of N content in litter and soils, with concurrent increases in the foliar N of undisturbed vegetation. By thirty years after outbreak, soil N availability returned to undisturbed levels though the canopy N pool remained depleted. Overall impact on soil N cycling was less severe than seen in post-fire forests.
Contrasting conifer forest types have qualitatively similarly responses to beetle disturbance in the litter-soil profile, though the response of undisturbed vegetation varies. Despite substantial differences in the pre-disturbance N dynamics of lodgepole pine and Douglas-fir forests, both showed 25-50% increases in needle litter N content and soil N pools and fluxes. However, only in lodgepole pine did increased soil N availability lead to increased foliar N of unattacked canopy trees.

Beetle-killed forests exhibit several mechanisms of N retention following disturbance, partially mitigating the potential for N loss via soil NO₃⁻ leaching. Minimal increases in nitrification rate and soil NO₃⁻ pools, increased N concentration in undisturbed canopy biomass, and declines in foliar Mn suggest multiple pathways for N retention in beetle-killed forests.

Salvage logging in beetle-killed forests has few additional impacts on N cycling in the first year after harvest. Salvage harvest did not increase litter inputs or soil N cycling any more than would have occurred in un-salvaged beetle-killed forests. However, substantial differences in coarse wood inputs and understory vegetation composition are likely to develop over longer time scales.

Salvage reduced the total density of saplings in beetle-killed forests, though residual densities should be sufficient for stand replacement. Salvage may promote the dominance of lodgepole pine in post-beetle forests, as lodgepole pine saplings were less susceptible to density decline following salvage than other species.
REFERENCES


