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

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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 (WY, 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.

1. Introduction

1.1. 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).

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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.

1.2. 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 *P. 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.

2. Materials and methods

2.1. 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, 2010). 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 1970s and 1980s.

2.2. 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 (Fig. 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

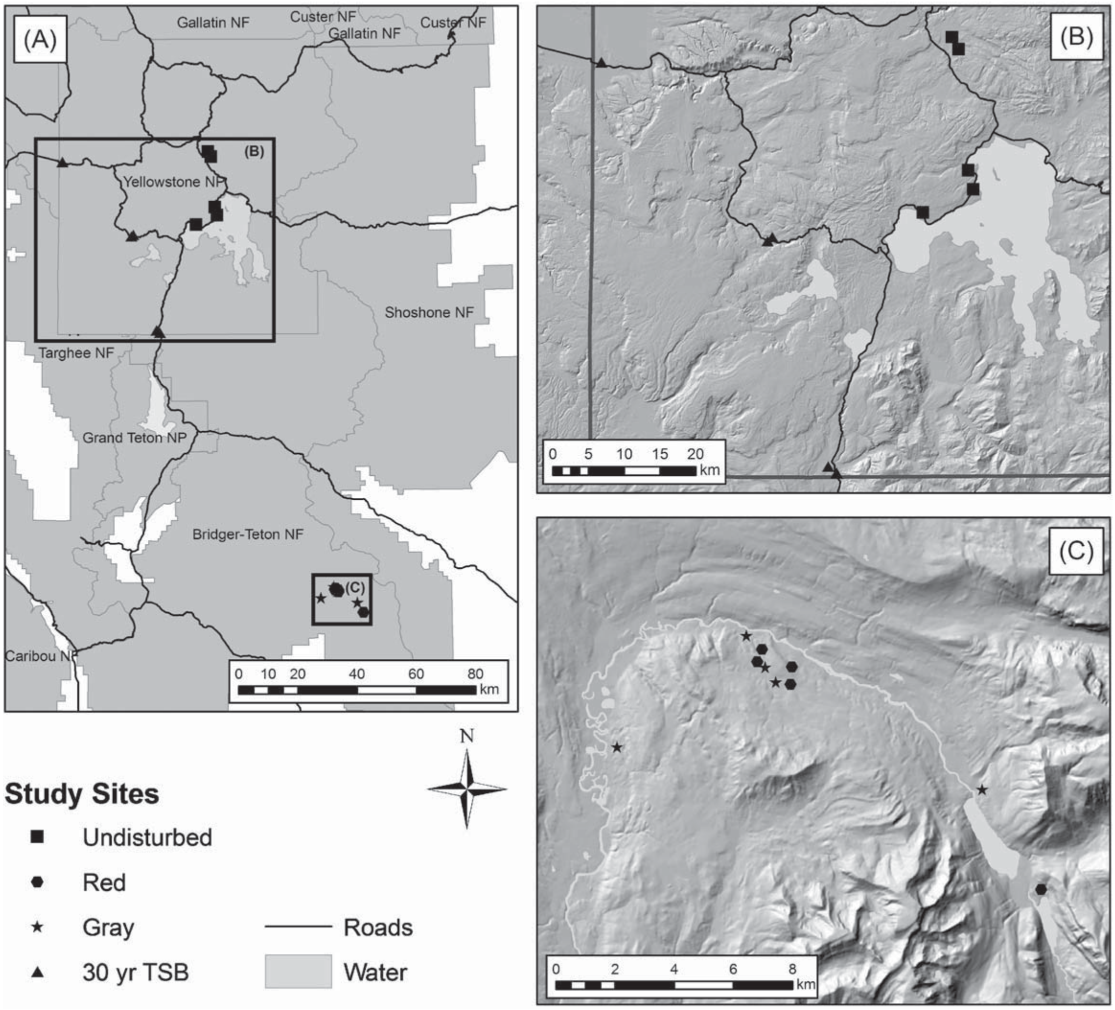

Fig. 1. Location of chronosequence sites in the Greater Yellowstone region. (A) All sites; (B) undisturbed and 30 year TSB (time-since-beetle) sites in Yellowstone National Park and (C) Red and Gray sites in the Green River Lakes region of Bridger-Teton National Forest.

(201 m^2) was established at each site in summer 2007, and slope and aspect were recorded at the plot center.

2.3. 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.

2.4. 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 (50 m^2). 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-m^2 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 *C. geyerii* was calculated from allometrics previously reported for Yellowstone National Park (Turner et al., 2004).

2.5. Litter quantity and quality

In each 0.25-m^2 microplot, litter depth was recorded at three locations and a 400-cm^2 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).

2.6. Soil chemistry, N pools, and N fluxes

One soil core was collected from each 0.25-m^2 microplot using a 5-cm diameter × 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 2 M KCl for 2 h, with the extract then filtered and frozen for later analysis of NH_4^+ and NO_3^- 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-m^2 microplot. Incubated cores consisted of a 5-cm diameter × 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 2 M KCl in the same manner as the 2007 initial soil samples described above. All KCl extractions were analyzed for $[NH_4^+]$ and $[NO_3^-]$ using colorimetric methods on an Astoria Pacific II continuous flow autoanalyzer. For each microplot, mineralization and nitrification rates were calculated as:

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

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/YEL408_totn.png) and were not factored into the soil N calculations.

2.7. 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 (*C. 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 *C. geyerii* N pool sizes, the mean foliar N concentration for each plot was multiplied by biomass values derived from the allometrics cited above.

2.8. 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.

3. Results

3.1. 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 ± 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; $33.7 \pm 3.2\ m^2\ ha^{-1}$) (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

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

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

[a] ANOVA *P* value; n.s. = non significant.
[b] Post-fire stand age at time of mountain pine beetle disturbance.
[c] Data for 30 year TSB sites are from Simard (2011).
[d] Values are an index of southwest-ness ranging from −1 to 1, calculated as: cosine(aspect°-225).

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 (Fig. 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 (Fig. 2). Forb cover averaged 25% in the red class, approximately 2.5× greater than in undisturbed forest (Fig. 2). Grass, sedge and shrub cover did not vary with TSB class ($P > 0.05$).

3.2. 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.

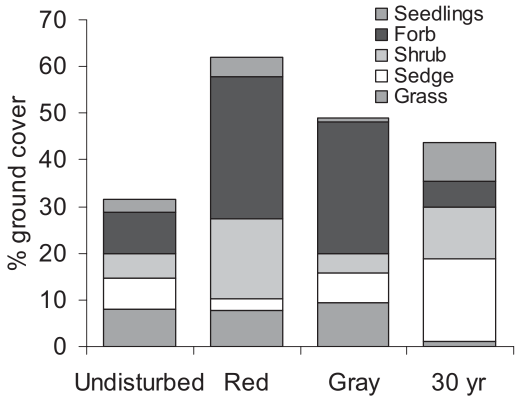

Fig. 2. Understory cover by plant functional group across a chronosequence of mountain pine beetle disturbance in lodgepole pine forest.

3.3. 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 (Fig. 3a). However, total litter mass averaged 1577 ± 149 g m^{-2} and did not vary with TSB class (Fig. 3b). The N concentration in fresh current-year-needle litter (Fig. 3c) and all-needle litter (Fig. 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 (Fig. 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 (Fig. 3f).

Table 2
Air and soil temperatures across a chronosequence of mountain pine beetle disturbance. Letters next to values denote significant differences among classes (Tukey's test, $\alpha = 0.05$). $N = 3$ per class. Error ranges = 2 SE.

Variable	TSB class				
	Undisturbed	Red	Gray	30 years	P^a
Air temperature (°C)					
Mean daily temperature	15.3 ± 0.4 b	15.1 ± 0.3 b	15.0 ± 0.5 b	16.3 ± 0.5 a	0.006
Mean daily range	19.4 ± 1.4 b	21.8 ± 0.8 ab	20.5 ± 1.6 b	25.1 ± 2.8a	0.012
Litter–soil temperature (°C)					
Mean daily temperature	15.4 ± 1.0 b	13.3 ± 0.8 bc	13.0 ± 0.6 c	19.2 ± 1.4 a	<0.001
Mean daily range	27.4 ± 3.5 b	21.8 ± 3.6 b	19.3 ± 1.0 b	38.0 ± 7.0 a	0.001
Mean daily difference from air	0.1 ± 0.8 b	−1.8 ± 1.0 b	−2.0 ± 0.2 b	2.8 ± 1.4 a	<0.001
10 cm soil depth temperature (°C)					
Mean daily temperature	10.5 ± 0.3 b	9.4 ± 0.1 b	9.7 ± 0.4 b	13.8 ± 1.3 a	<0.001
Mean daily range	2.4 ± 0.2 a	2.9 ± 0.8 a	2.8 ± 0.6 a	4.6 ± 1.8 a	n.s.
Mean daily difference from air	−4.8 ± 0.1 b	−5.6 ± 0.3 b	−5.3 ± 0.8 b	−2.5 ± 0.9 a	<0.001
Togography of instrumented sites					
Elevation (m)	2401 ± 4 ab	2471 ± 40 a	2494 ± 68 a	2198 ± 227 b	0.0301
Slope (°)	10.8 ± 10.6 a	6.2 ± 3.4 a	13.7 ± 5.5 a	2.5 ± 3.2 a	n.s.
Aspect[b]	0.26 ± 1.25 a	0.42 ± 0.70 a	0.55 ± 1.34a	−0.09 ± 0.67 a	n.s.

[a] ANOVA P value; n.s. = non significant.

[b] Values are an index of southwest-ness ranging from −1 to 1, calculated as: cosine (aspect°-225).

3.4. Soil N pools and fluxes

Among soil N pools, only soil ammonium pool size varied with TSB class (Fig. 4a). Extractable NH_4^+ was six times greater in the red stands (4.75 μg N g soil^{-1}) compared to the undisturbed stands (0.74 μg N g soil^{-1}) and intermediate in the gray and 30-year TSB stands. Extractable NO_3^- was low (averaging 0.63 ± 0.20 μg N g soil^{-1}) and did not vary with TSB class (Fig. 4b). Total extractable inorganic N averaged 3.11 ± 0.63 μg 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).

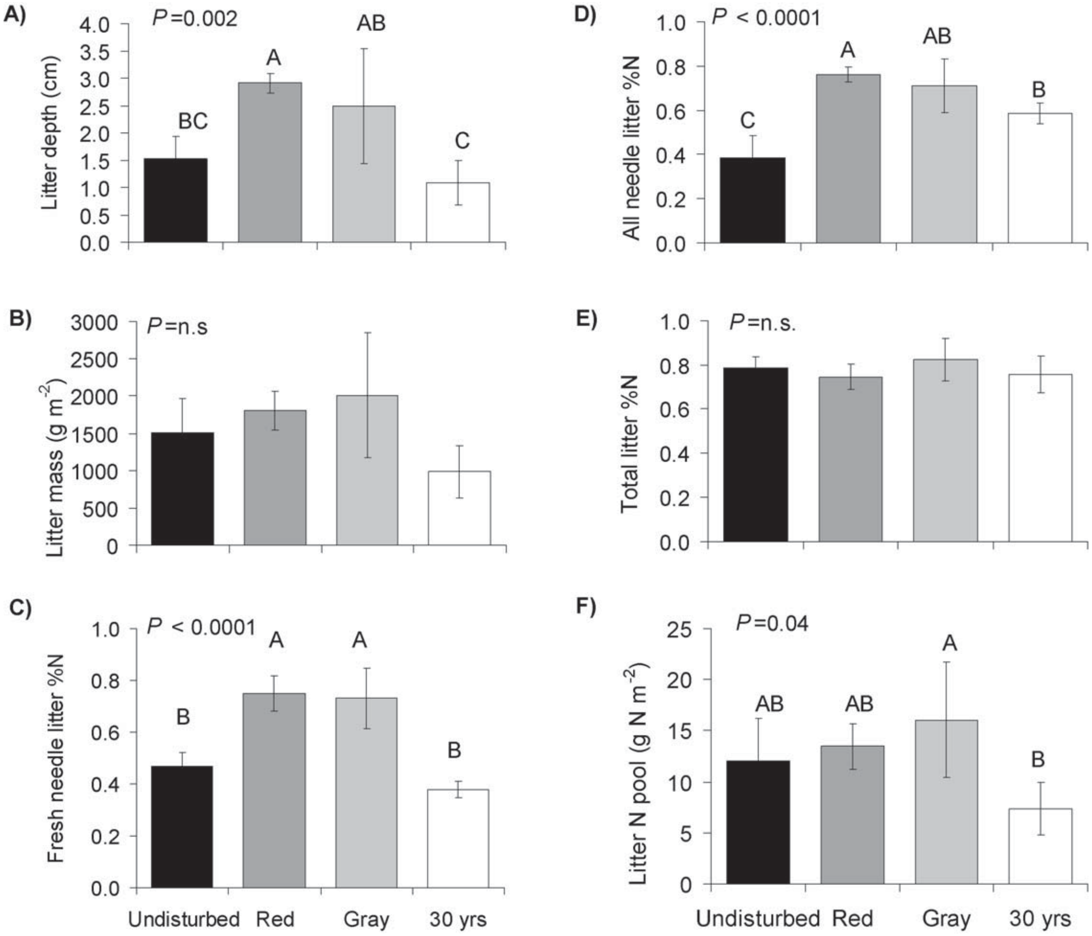

Fig. 3. Litter variables across a chronosequence of mountain pine beetle disturbance in lodgepole pine. (A) litter depth, (B) litter mass, (C) fresh needle litter %N, (D) all-needle litter %N, (E) total litter %N and (F) litter N pool. P values are from ANOVA, and class differences were determined using 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.

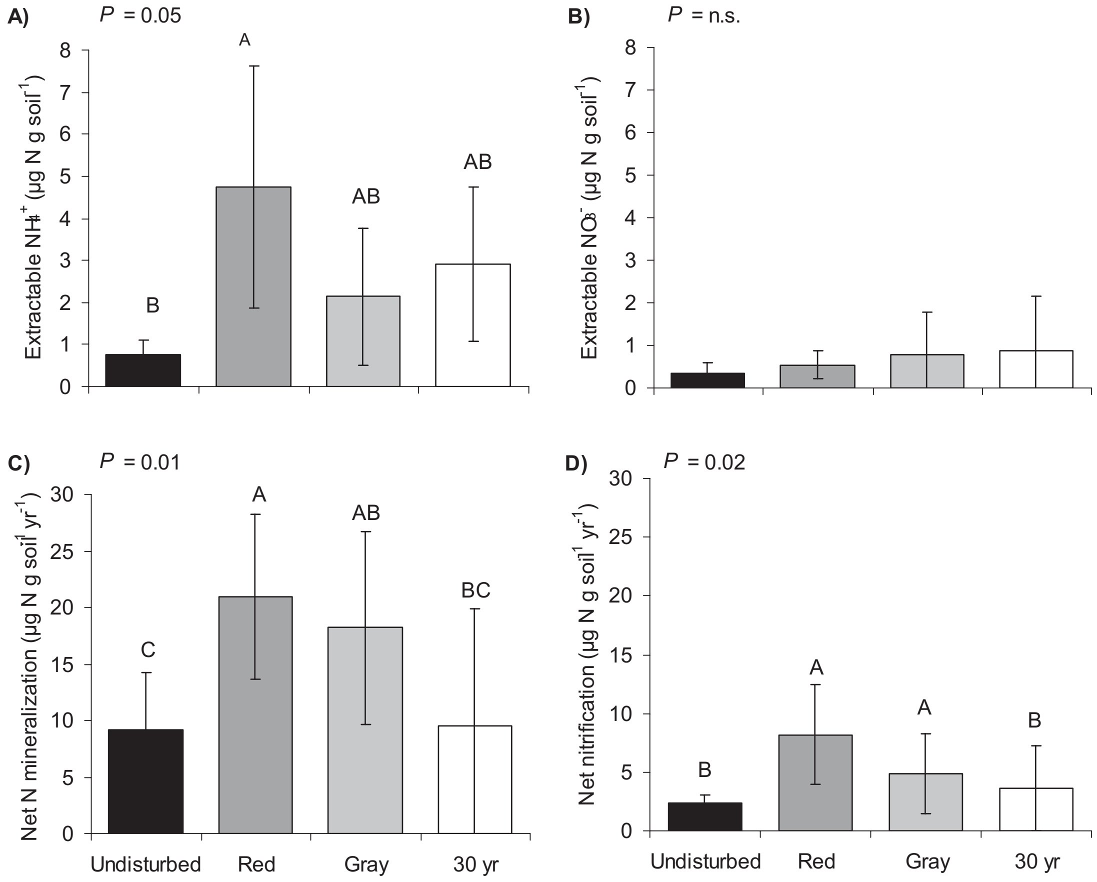

Fig. 4. Soil N pools and fluxes across a chronosequence of mountain pine beetle disturbance in lodgepole pine. For extractable NH_4^+ pool size (panel A), and extractable NO_3^- pool size (panel B), significance levels are from ANOVA and Tukey's HSD test ($\alpha = 0.05$). For net mineralization rate (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 model, and values within the same panel with the same letter are not significantly different. Error bars = 2 standard errors.

Annual net N mineralization rate was approximately double (21 ± 7 µg N g soil^{-1} year^{-1}) in the red and gray stages relative to the undisturbed and 30-year TSB classes (Fig. 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 µg N g soil^{-1} year^{-1}) and about three times greater than in the undisturbed and 30-year TSB stages (Fig. 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 µg N g soil^{-1}) nor the ratio of nitrate to total inorganic N (average 0.29 ± 0.07) differed among classes ($P = 0.1314$ and $P = 0.1710$, respectively; data not shown).

Net nitrogen mineralization rates were more strongly correlated with soil temperature (Fig. 5b; $R^2 = 0.39$) than with litter quality variables (Fig. 5c–f; $R^2 < 0.19$). Increased litter depth in the red and

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.

Response variable	Model fit (R^2, *F*, *P*)	Parameter	Estimate	*F*	*P*
Net N mineralization	0.70, 5.04, 0.007	TSB class	–	5.30	0.01
		Undisturbed	–	–	–
		Red	18.2	–	0.02
		Gray	16.2	–	0.03
		30 years	−8.6	–	0.09
		Bulk density	−32.02	7.68	0.02
		pH	−22.17	4.37	0.06
		C:N	−0.19	5.66	0.03
		Intercept	153.9	–	0.02
Net nitrification	0.52, 4.06, 0.02	TSB class	–	4.58	0.02
		Undisturbed	–	–	–
		Red	1.3	–	0.01
		Gray	1.2	–	0.04
		30 years	−0.31	–	0.53
		Bulk density	−3.56	8.52	0.01
		Intercept	4.01	–	0.0005

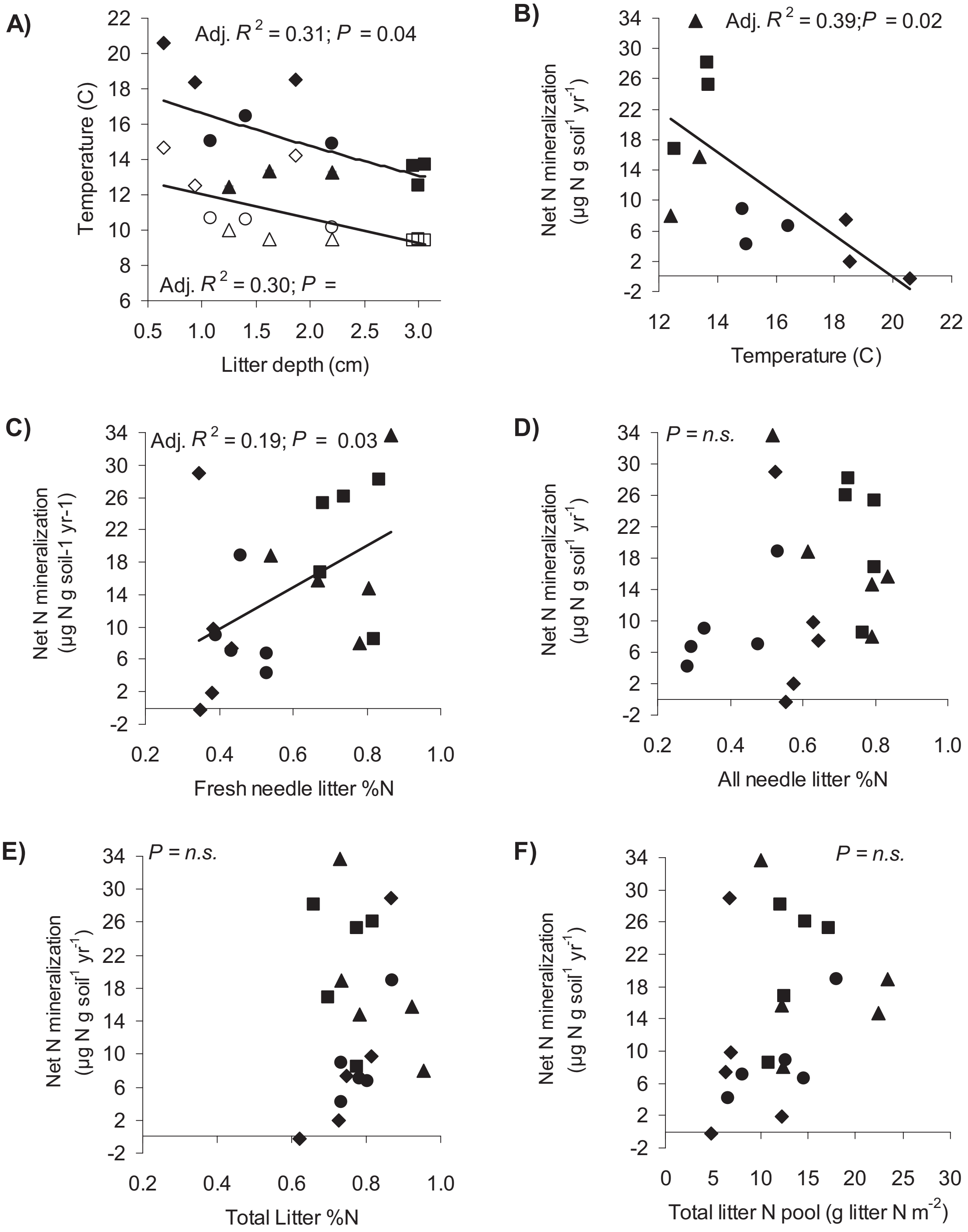

Fig. 5. Relationships between litter depth and N content, soil temperatures, and net N mineralization rates across a chronosequence of mountain pine beetle disturbance in lodgepole pine. ● = undisturbed, ■ = red stage, ▲ = gray stage, ♦ = 30 year after outbreak. (A) Soil temperature vs. litter depth. 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.

gray classes corresponded to decreased soil temperatures, and shallow litter layers in the 30-year TSB class were associated higher soil temperatures (Fig. 5a). Net N mineralization rates declined with increasing soil temperature across the TSB chronosequence (Fig. 5b). Net N mineralization was weakly related to the nitrogen concentration in fresh needlefall (Fig. 5c), but showed no relationship to the nitrogen concentration in all-needle litter or total litter, or to the total litter N pool size (Fig. 5d–f).

3.5. 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 $687 \pm 49\,\mathrm{g\,m^{-2}}$ (data not shown), which also represents the total mass of needle litterfall induced by the outbreak. The N concen-

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. Letters denote significant differences among classes (Tukey's HSD test, $\alpha = 0.05$). Error ranges = 2 SE.

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

[a] ANOVA *P* value; n.s. = non significant.

tration 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 $\mathrm{g\,N\,m^{-2}}$ 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 (Fig. 6a). Biomass of the understory sedge *C. 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 *C. geyerii* was also positively related to annual net N mineralization across all TSB classes (Fig. 6b).

4. 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.

4.1. 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.

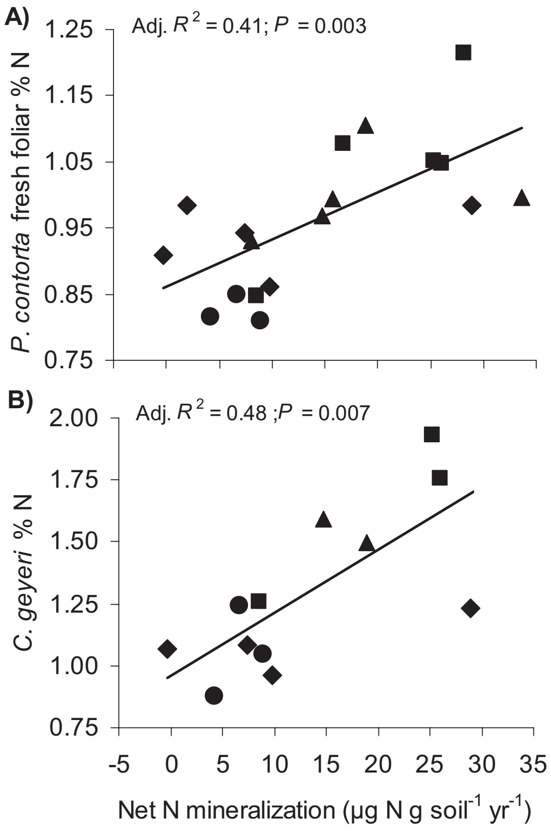

Fig. 6. Foliar %N of unattacked lodgepole pine (A) and %N of the sedge *Carex geyerii* (B) vs. soil N mineralization rate in a chronosequence of mountain pine beetle disturbance in lodgepole pine. ● = undisturbed, ■ = red stage, ▲ = gray stage, ◆ = 30 year after outbreak. Summary statistics are from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

4.2. 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 $687 \pm 49\,\mathrm{g\,m^{-2}}$ (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 $\mathrm{g\,m^{-2}}$, and why increases in litter mass following beetle outbreak (498 $\mathrm{g\,m^{-2}}$) are small relative to the amount of litter already present on the forest floor prior to outbreak ($1512 \pm 457\,\mathrm{g\,m^{-2}}$).

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.

4.3. 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 ($<2\,\mu\mathrm{g\ N\,g\ soil^{-1}\ year^{-1}}$) in undisturbed lodgepole pine (Turner et al., 2007), and despite a significant increase in the red stage, net nitrification was never above $8.2\,\mu\mathrm{g\ N\,g\ soil^{-1}\ year^{-1}}$ 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 $\mathrm{ha^{-1}}$, 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 to 33), and thinning residues were removed.

4.4. 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 NH_4^+ and 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 (McCambridge et al., 1982). Reduced competition and increased light, moisture and nutrients are likely stimulants of this growth. As forbs prefer NO_3^- uptake over NH_4^+ in deciduous woodland (Falkengren-Grerup 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 *C. geyerii* %N also suggests that herbaceous species benefit from increased N availability during bark beetle outbreak. Foliar %N of *C. geyerii* 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).

4.5. 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 NO_3^- 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, NH_4^+ and NO_3^- pools were four times greater than in the red stage of a bark beetle outbreak (20 vs. 5 μg NH_4^+-N g soil^{-1}, 2 vs. 0.5 μg NO_3^--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 3–5-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 et al., 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 Mitchell, 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.

4.6. 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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Disclosure statement

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