

Changes to the N cycle following bark beetle outbreaks in two contrasting conifer forest types

Jacob M. Griffin · Monica G. Turner

Received: 28 April 2011 / Accepted: 26 March 2012
© Springer-Verlag 2012

Abstract Outbreaks of *Dendroctonus* beetles are causing extensive mortality in conifer forests throughout North America. However, nitrogen (N) cycling impacts among forest types are not well known. We quantified beetle-induced changes in forest structure, soil temperature, and N cycling in Douglas-fir (*Pseudotsuga menziesii*) forests of Greater Yellowstone (WY, USA), and compared them to published lodgepole pine (*Pinus contorta* var. *latifolia*) data. Five undisturbed stands were compared to five beetle-killed stands (4–5 years post-outbreak). We hypothesized greater N cycling responses in Douglas-fir due to higher overall N stocks. Undisturbed Douglas-fir stands had greater litter N pools, soil N, and net N mineralization than lodgepole pine. Several responses to disturbance were similar between forest types, including a pulse of N-enriched litter, doubling of soil N availability, 30–50 % increase in understory cover, and 20 % increase in foliar N concentration of unattacked trees. However, the response of some ecosystem properties notably varied by host forest type. Soil temperature was unaffected in Douglas-fir, but lowered in lodgepole pine. Fresh foliar %N was uncorrelated with net N mineralization in Douglas-fir, but positively correlated in lodgepole pine. Though soil ammonium and nitrate, net N mineralization, and net nitrification all doubled, they remained low in both forest types ($<6 \mu\text{g N g soil}^{-1} \text{NH}_4^+$ or NO_3^- ; $<25 \mu\text{g N g soil}^{-1} \text{year}^{-1}$ net

N mineralization; $<8 \mu\text{g N g soil}^{-1} \text{year}^{-1}$ net nitrification). Results suggest that beetle disturbance affected litter and soil N cycling similarly in each forest type, despite substantial differences in pre-disturbance biogeochemistry. In contrast, soil temperature and soil N–foliar N linkages differed between host forest types. This result suggests that disturbance type may be a better predictor of litter and soil N responses than forest type due to similar disturbance mechanisms and disturbance legacies across both host-beetle systems.

Keywords *Pseudotsuga menziesii* · *Pinus contorta* var. *latifolia* · Disturbance ecology · Greater Yellowstone Ecosystem · Biogeochemistry · Rocky Mountains

Introduction

Insect outbreaks are a common and widespread disturbance type, 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,

Communicated by Jason Kaye.

J. M. Griffin (✉) · M. G. Turner
Department of Zoology, University of Wisconsin, Birge Hall,
430 Lincoln Drive, Madison, WI 53706, USA
e-mail: jgriffin2@wisc.edu

M. G. Turner
e-mail: turnermg@wisc.edu

ecosystems organized around such foundation species, i.e., species with specific traits that control ecosystem dynamics (sensu 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 % (Negrón 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 2 or 3 years (gray stage) (Negrón 1998; McMillin and Allen 2003). Canopy opening and subsequent inputs of needle litter to the forest floor induced by bark beetles may influence soil temperature (Griffin et al. 2011) by increasing soil insulation (Byers 1984), incident radiation (Hais and Kucera 2008), and air flow through the stand (Boon 2009). These changes in soil temperature and litter cover may in turn have an influence on soil N cycling (Remsburg and Turner 2006).

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). The 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). Bark beetle disturbance has been shown to increase fresh needle litter N concentration in both ponderosa pine (*Pinus ponderosae* Laws.) and lodgepole pine (Morehouse et al. 2008; Griffin et al. 2011), potentially increasing the rate of litter decomposition. Changing concentrations of other elements in foliage such as Mn could also influence future decay rates of litter (Berg et al. 2007). Furthermore, in undisturbed forests, Douglas-fir generally has greater amounts of soil inorganic N and greater rates of net N mineralization relative to lodgepole pine (Thomas and Prescott 2000). Greater baseline soil N stocks are 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 outbreaks may be greater in Douglas-fir forests relative to lodgepole pine, leading to greater accumulation of inorganic N in soils. 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 temperature, and N cycling through litter, soils, and vegetation in Douglas-fir forests? And (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 temperature, litter nitrogen pools, soil N, net N mineralization, net nitrification, and foliar N pools were measured in both undisturbed and gray stage (4–5 years after peak outbreak) beetle-killed forests. Hypothesized bark beetle effects and suggested mechanisms are summarized in Table 1. We expected beetle disturbance to decrease live canopy biomass and initiate a pulse of litter to the forest floor that is enriched in N relative to typical senesced litter. Insulation by litter and shading by the growth of understory vegetation was expected to lower soil temperatures, while soil N cycling rates and amounts of inorganic soil 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 inorganic N, net N mineralization, and net nitrification to be larger in Douglas-fir. However, proportional increases were predicted to be larger in lodgepole pine and therefore potentially have a greater impact on plant available N. Foliar N response to changing soil N availability could also vary among forest type, with the more N-poor lodgepole pine forests showing larger increases in foliar N.

Table 1 Hypothesized impacts of bark beetle disturbance in Douglas-fir (*Pseudotsuga menziesii*) and lodgepole pine (*Pinus contorta*) ecosystems

Ecosystem component	Hypothesized bark beetle effects in Douglas-fir forests	Hypothesized differences in beetle effects in Douglas-fir compared to lodgepole pine forests
Soil temperature	Decreased soil temperature <ul style="list-style-type: none"> • Insulating litter input • Shading by understory growth 	Similar effects; cooler soil temperatures in beetle-killed forests of both species
Understory cover	Increased cover <ul style="list-style-type: none"> • Canopy opening • Increased light, H₂O, nutrients 	Increased understory cover in beetle-killed forests of both types, with more cover overall in Douglas-fir
Litter	Increased litter mass, depth, and %N of fresh needle litter	Greater increases in litter %N and N pool size in Douglas-fir; greater litter N in Douglas-fir overall
Soils	Increased NH ₄ ⁺ , NO ₃ ⁻ , net N mineralization, and net nitrification	Larger increases in pool size and flux rate in Douglas-fir; greater soil N in Douglas-fir overall
Canopy of unattacked trees	Increased %N in canopy foliage. Sharp decline in N pool size	Similar effects; increased %N in canopy foliage and decreased N pool size in beetle-killed stands of both species

Materials and methods

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/Bufalo River Valley Region. July temperatures average 14.9 °C, January temperatures average -11.2 °C, with 595 mm of annual precipitation occurring mostly as snow (WRCC 2010). The most recent outbreak of DFB in this area began in the early 2000s, 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 2006a, b). In 2008, we sampled ten spatially independent (>2 km apart) Douglas-fir stands (five undisturbed, and five which had peak bark beetle attack in 2003–2004 and which were in the gray stage at the time of sampling). DFB-disturbed stands were initially identified using aerial surveys of insect damage (USFS 2006a, b), with subsequent field inspection. Within each stand, an 8-m radius (201-m²) plot was installed with GPS location, elevation, and slope recorded at the plot center.

Undisturbed and beetle-killed Douglas-fir sites were selected from a suite of possible study sites primarily for similarity in stand structure (pre-disturbance), composition, soils, slope, and aspect, and then secondarily for similarity in elevation since accounting for this experimental control variable was limited by the spatial distribution of insect activity. However, small differences in elevation (<150 m) among sites with the same aspect are likely to have much

less influence on soil N transformations and soil temperatures than large differences in aspect would have for sites at the same elevation. Due to the timing of both the Douglas-fir beetle outbreak and our sampling, we did not have the opportunity to establish sites in the earlier red stage (1–2 years after outbreak), where trees are dead but needles remain mostly in the canopy. In other beetle-killed forest types, impacts on N and C cycling have been shown to occur during this earlier red stage (Huber 2005; Morehouse et al. 2008; Tahovska et al. 2010; Griffin et al. 2011), but were not able to be evaluated in this study of Douglas-fir.

Vegetation

All live and dead trees greater than breast height (1.4 m) 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 basal area increment of surviving trees 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, 2.5, and 3.5 m; and three at 4.5 m) and random bearings (in 10° increments) from the plot center, and averaged by plot.

Soil temperature

To evaluate variation in growing-season soil temperature, hourly measurements were made in three of the five plots within each disturbance class from July 4 to August 31, 2008, using three pairs of iButton datalogger probes (Maxim Integrated Products/Dallas Semiconductor, Sunnyvale, CA, USA) per plot. One iButton of each pair was installed at the bottom of the litter layer (Oi), and the second was installed 10 cm below the Oi layer. 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, maxima, and minima 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 (Oi) was recorded at three locations and a 400-cm² sample of the litter layer (Oi) was collected and oven-dried at 60 °C. Plot-level litter depth and mass (Oi) were obtained by averaging values from the ten microplots. Litter (Oi) 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 within the Oi horizon combined); and total litter (all foliar litter components and woody litter components <1.0 cm wide within the Oi). Sorted litter was composited by plot for each category and ground to powder for C:N analysis (Leco CNS-2000 at the University of Wisconsin Soil and Plant Analysis Laboratory; UWSPAL 2010).

Soil chemistry, soil N, N mineralization, and nitrification

One soil core was collected from each 0.25-m² microplot ($n = 10$ per plot) using a 5-cm-diameter \times 15-cm-long PVC corer. Soils were not sub-sampled by horizon, and all soil analyses were performed on composite samples (Oe, A, and upper B horizons combined). Soils were processed on the day of collection, and stored under refrigeration until processing. 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 (0.45 μ m) and frozen for later analysis of NH₄⁺ and NO₃⁻; and 20 g air-dried and bulked by plot for soil texture and chemical analyses. Air-dried soil was analyzed for pH (water extract with Sikora buffer; Sikora 2006), total N (Kjeldahl digestion; Bremner 1965), exchangeable Ca, Mg, and K (NH₄OAc extraction; Thomas 1982), available P (Bray P1 extract; Bray and Kurtz 1945), and organic matter (LOI 360 °C; Schulte and Hopkins 1996) 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.

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 1 year (July 2008–June 2009) in each 0.25-m² microplot. Incubated cores consisted of a 5-cm-diameter \times 15-cm-long PVC tube of soil with an ion-exchange resin bag placed at the bottom. The litter layer (Oi) was brushed aside, and cores were installed through the Oe, A, and upper B soil horizons, with the Oi then replaced over the core. Resin bags in the base of each core were constructed using 20 g of ion exchange resin (IONAC NM-60 mixed bed exchange resin, strong acid/strong base; sulfonated alkyl quaternary ammonium polystyrene; 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 2 M KCl in the same manner as the 2008 initial soil samples described above. All KCl extractions were analyzed for NH₄⁺-N and NO₃⁻-N using colorimetric methods on an Astoria Pacific II segmented 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 $\mu\text{g N g dry core soil}^{-1} \text{ year}^{-1}$. The efficiency of resin extraction was not evaluated. Values were then averaged by plot. Atmospheric N inputs in the region are low ($\sim 1 \text{ kg N ha}^{-1} \text{ year}^{-1}$; <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. 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) (UW-SPAL 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.

Lodgepole pine sampling

Lodgepole pine study area, site characteristics, and all lodgepole pine data used for our comparisons of forest type are reported in Griffin et al. (2011), with the exception of non-N foliar chemistry data which is first reported here for both forest types. Vegetation, litter, and soil sampling methods in mountain pine beetle-disturbed lodgepole pine forests were identical to those described here for Douglas-fir beetle-disturbed forests. No stands of either species had any evidence of fire scarring on trees, or other more recent disturbance including windthrow or older beetle outbreaks. In brief, lodgepole pine sites were located within Yellowstone National Park and Bridger-Teton National Forest of northwestern Wyoming, USA. Undisturbed and gray sites were $2,400 \pm 17$ and $2,476 \pm 48$ m in elevation, respectively (mean \pm 2SE; $n = 5$). Lodgepole pine study sites were approximately 200 m higher in elevation than Douglas-fir sites, in accordance with the stratified distribution of forest types in this region.

Statistical analyses

All statistical analyses were performed in SAS (SAS Institute 2003), and unless otherwise noted all reported variance values are \pm 2SE. All variables were checked for normality and transformed if necessary to satisfy the assumptions of statistical methods. A sample size of $n = 5$ per disturbance class was used for all analyses of Douglas-fir forests except those using soil temperature data, where $n = 3$ as only three of five plots per disturbance class were instrumented. For all analyses comparing forest types, $n = 10$.

ANOVA 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, foliar N concentrations, and foliar N pools. We also used ANCOVA 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, though no significant effects were found. 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 forest type.

Results

Douglas-fir forests

Site characteristics, stand structure, and soil temperature

Undisturbed and beetle-killed Douglas-fir stands occupied similar landscape positions, with no differences in either slope or aspect between disturbance classes (Table 2). 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 (Table 2). Soil horizon depth (Oe + A) was similar between disturbance classes, as were soil organic matter, Ca, Mg, K, P, and pH (Table 2). Douglas-fir basal area comprised 97 % of total stand basal area among all sites and did not differ between undisturbed and beetle-killed sites (Table 2). 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 2). In beetle-killed stands, Douglas-fir mortality averaged 93 % of stem density, with an estimated concurrent decline in live canopy biomass averaging $15,796 \pm 1,704$ kg ha⁻¹ (Table 2). Total cover of understory vegetation was greater in beetle-killed compared to undisturbed stands (103 vs. 79 %, respectively), driven by greater forb (36 vs. 19 %) and grass (49 vs. 18 %) cover (Fig. 1). Growing season soil temperatures were not significantly different between Douglas-fir disturbance classes at either soil depth (Table 2). Mean daily temperature ranges, minimums, and maximums were also consistent between disturbance classes at both depths (Table 2).

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 $1,842 \pm 247$ g m⁻² (Table 2). However, litter quality did differ between disturbance classes. The N concentration in needle litter of all ages increased by 55 % in beetle-killed stands, and total litter layer N concentration increased by 25 % (Table 3). Current-year needle litter N concentrations were 0.70 and 0.79 % in undisturbed and gray stands, respectively, but this difference was not significant (Table 3). Increases in litter %N resulted in significant concurrent declines in litter C:N ratio in all

three litter categories. However, differences in total litter N pool size (product of total litter mass and total litter %N) were not significant (Table 3), as litter mass varied considerably among sites.

Soil N, N mineralization, and nitrification

Soil inorganic N and soil N transformation rates differed between undisturbed and beetle-killed Douglas-fir stands (Table 3). Extractable ammonium in beetle-disturbed stands was twice that of undisturbed stands (0.47 ± 0.07 vs. 0.24 ± 0.08 g N m⁻²; see Table 3 for units in $\mu\text{g N g soil}^{-1}$), extractable nitrate was almost four times greater

Table 2 Site characteristics in undisturbed and bark beetle-killed Douglas-fir forests

Site characteristic	Douglas-fir disturbance class		ANOVA <i>P</i>
	Undisturbed	Beetle-killed	
Topography			
Elevation (m)	2,186 ± 38	2,325 ± 107	0.0400
Aspect (SW index)	0.367 ± 0.691	-0.085 ± 0.566	0.9201
Slope	26 ± 12	22 ± 11	0.6282
Canopy vegetation			
Basal area (m ² ha ⁻¹)			
Total	62.7 ± 9.9	75.3 ± 12.2	0.1468
Douglas-fir	58.7 ± 12.6	75.1 ± 12.1	0.0973
Live Douglas-fir	57.6 ± 13.2	5.2 ± 2.9	0.0001
Dead Douglas-fir	1.1 ± 1.2	69.9 ± 11.2	<0.0001
Live foliar biomass (kg ha ⁻¹)	15,179 ± 4,021	2,551 ± 1,538	0.0004
Soils			
Growing season temperature			
Litter-soil interface (°C)			
Mean	13.5 ± 0.7	12.7 ± 2.0	0.5073
Range	8.2 ± 1.2	9.4 ± 2.8	0.4607
Maximum	18.1 ± 1.0	18.3 ± 3.7	0.9094
Minimum	9.9 ± 0.8	8.9 ± 1.0	0.1953
10 cm soil depth (°C)			
Mean	11.2 ± 1.1	10.5 ± 1.6	0.4899
Range	1.4 ± 0.6	1.5 ± 0.3	0.7494
Maximum	11.9 ± 1.3	11.3 ± 1.7	0.5892
Minimum	10.5 ± 0.8	9.8 ± 1.5	0.4284
Composite soil properties (Oe, A, B combined to 15 cm depth)			
Organic (Oe, A) depth (cm)	4.2 ± 1.5	5.5 ± 2.0	0.3078
Organic matter (%)	8.4 ± 4.8	8.6 ± 2.2	0.9299
pH	6.2 ± 0.3	6.4 ± 0.2	0.2073
Ca ($\mu\text{g g}^{-1}$; exch.)	2,401 ± 808	2,702 ± 253	0.4974
Mg ($\mu\text{g g}^{-1}$; exch.)	187 ± 52	220 ± 14	0.2527
K ($\mu\text{g g}^{-1}$; exch.)	225 ± 79	218 ± 42	0.8696
P ($\mu\text{g g}^{-1}$; exch.)	49 ± 8.4	51 ± 15	0.7950
Litter (Oi)			
Depth (cm)	3.0 ± 0.5	3.5 ± 0.6	0.2968
Mass (g m ⁻²)	1,760 ± 365	1,924 ± 357	0.5385

n = 5 per disturbance class. Significant ($\alpha < 0.05$) ANOVA *P* values are shown in bold

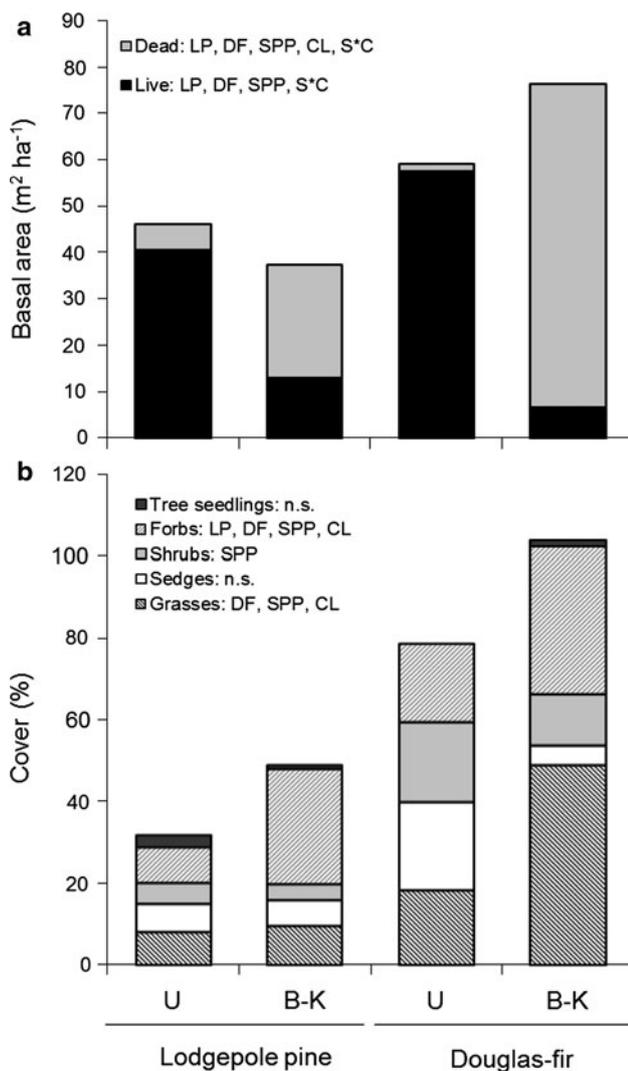


Fig. 1 **a** Tree basal area and **b** understory cover by plant functional group in undisturbed and bark beetle-killed lodgepole pine and Douglas-fir forests. Plotted values are untransformed mean \pm 2SE. *LP* and *DF* denote a significant effect of disturbance class within lodgepole pine (*LP*) or Douglas-fir (*DF*) forests only ($P < 0.05$; $n = 10$; GLM: $y =$ disturbance class). *SPP*, *CL*, and $S \times C$ denote significant ($P < 0.05$; $n = 20$) effects of species (*SPP*), disturbance class (*CL*), and their interaction ($S \times C$) in the global GLM: $y =$ species + disturbance class + species \times disturbance class. Total basal area *SPP*, $S \times C$. Total cover *LP*, *DF*, *SPP*, *CL*. Lodgepole pine data have been previously published in Griffin et al. (2011). *U* undisturbed sites; *B-K* beetle-killed sites

(0.51 ± 0.46 vs. 0.13 ± 0.06 g N m⁻²; see Table 3 for units in $\mu\text{g N g soil}^{-1}$), and total extractable inorganic N ($\text{NH}_4^+ + \text{NO}_3^-$) in beetle-disturbed stands was more than double that in undisturbed stands (0.98 ± 0.40 vs. 0.37 ± 0.12 g N m⁻²; see Table 3 for units in $\mu\text{g N g soil}^{-1}$). Annual net N mineralization rates were highly variable and were not significantly different between disturbance classes. Annual net nitrification rates increased 50 % in beetle-disturbed stands relative to undisturbed (0.69 ± 0.12 vs.

0.45 ± 0.16 g N m⁻² year⁻¹; see Table 3 for units in $\mu\text{g N g soil}^{-1}$ year⁻¹). Neither net N mineralization nor net nitrification rates were significantly correlated with any metric of soil temperature (Pearson $P > 0.05$; $n = 6$; data not shown), nor was net N mineralization correlated with any metric of litter N (Pearson $P > 0.05$; $n = 10$; data not shown). Nitrification fraction (the proportion 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 inorganic N (Table 3).

Foliar N

The DBH range of trees sampled for foliar N was smaller in beetle-killed stands because only smaller trees remained after outbreak. Mean DBH of trees sampled for foliar N was 40.1 ± 10.9 cm (range 16.5–98 cm) in undisturbed stands and 19.5 ± 4.0 cm (range 5.5–33.0 cm) in beetle-killed stands. However, there was no relationship between DBH and foliar N in either class (linear regression; $P > 0.5$; $df = 14$) and only a weak relationship across all stands (linear regression; $P = 0.03$; $R^2 = 0.16$; $df = 29$). 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, with a concurrent decrease in C:N ratio (Table 3). Foliar N pool size mirrored changes in live foliar biomass and declined sharply by 79 % (Table 3). Neither fresh foliar %N nor 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 200 m lower in elevation ($2,255 \pm 71$ vs. $2,438 \pm 35$ m; $P < 0.0001$; Douglas-fir data in Table 2, 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 greater concentrations of organic

Table 3 N concentrations, pool sizes, and transformations in litter, soil, and canopy of undisturbed and bark beetle-killed Douglas-fir forests

N concentration, pool, or flux	Douglas-fir disturbance class		ANOVA <i>P</i>
	Undisturbed	Beetle-killed	
Litter (Oi)			
Total litter N pool (g N m ⁻²)	19.3 ± 3.3	26.4 ± 5.8	0.0666*
Total litter %N	1.10 ± 0.06	1.37 ± 0.13	0.0054
Total litter C:N	44 ± 2	35 ± 3	0.0008
All needles %N	0.89 ± 0.07	1.38 ± 0.10	<0.0001
All needles C:N	57 ± 5	36 ± 2	<0.0001
<1 year old needles %N	0.70 ± 0.06	0.79 ± 0.07	0.0641*
<1 year old needles C:N	72 ± 6	62 ± 5	0.0266
Soil (Oe, A, and B to 15 cm depth)			
Total soil N pool (g N m ⁻²)	192 ± 78	237 ± 42	0.3353
%N	0.23 ± 0.15	0.26 ± 0.07	0.7782
C:N	19.2 ± 2.9	16.7 ± 0.4	0.1109 ^d
Organic N (mg N g ⁻¹)	2.34 ± 1.52	2.58 ± 0.70	0.7836
NH ₄ ⁺ ^a	2.5 ± 0.6	5.0 ± 0.8	0.0010
NO ₃ ^{-a}	1.5 ± 1.0	5.5 ± 5.2	0.0520 ^{c*}
Total inorganic N ^a	4.0 ± 1.7	10.5 ± 4.7	0.0060^c
Net N mineralization ^b	14.3 ± 9.3	24.8 ± 11.2	0.0950 ^c
Net nitrification ^b	4.8 ± 0.6	7.2 ± 1.0	0.0295
Nitrification fraction	0.42 ± 0.18	0.34 ± 0.11	0.4724
Canopy foliage			
Foliar N pool (g N m ⁻²)	11.5 ± 1.7	2.4 ± 1.5	0.0004
All needle %N	0.76 ± 0.04	0.90 ± 0.07	0.0101
All needle C:N	63 ± 3	54 ± 4	0.0046
<1 year needle %N	1.23 ± 0.19	1.34 ± 0.12	0.3853
<1 year needle C:N	40 ± 7	36 ± 3	0.3499

n = 5/disturbance class; values in table are untransformed mean ± 2SE. Significant ($\alpha < 0.05$) ANOVA *P* values are shown in **bold**

* Results for which $0.05 < P < 0.07$

^a $\mu\text{g N g soil}^{-1}$

^b $\mu\text{g N g soil}^{-1} \text{ year}^{-1}$

^c ANOVA performed on $\log(x)$ transformed data

^d ANOVA performed on $1/x$ transformed data

matter, Ca, Mg, K, and P than lodgepole pine ($P < 0.01$; Douglas-fir data in Table 2, 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 ± 8.5 vs. 42.7 ± 7.6 ; $P = 0.0003$; Fig. 1), beetle-killed basal area (Fig. 1), and percent mortality of pre-outbreak living stems >1.4 m (93 ± 3 vs. 52 ± 17 %).

Undisturbed forests

In the absence of bark beetles, forest types differed in understory cover, understory composition, and soil temperature. Total biotic cover was greater in Douglas-fir (79 ± 6 vs. 29 ± 10 %; $P < 0.0001$), driven by greater cover of shrubs, total graminoids (grasses + sedges), and tree seedlings compared to lodgepole pine ($P < 0.02$; Fig. 1). Soil temperatures at the litter–soil interface in undisturbed forests were cooler and had a lower range in Douglas-fir (temperature 13.5 ± 0.7 vs. 15.4 ± 1.0 °C; temperature range 8.2 ± 1.2 vs. 27.4 ± 2.9 °C; $P \leq 0.03$; Douglas-fir data in Table 2, 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 ± 0.6 °C. However, the range of 10-cm depth temperatures was lower in Douglas-fir (1.4 ± 0.6 vs. 2.4 ± 0.2 °C; $P = 0.0236$; Douglas-fir data in Table 2, 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 (Fig. 2), though there was no difference in total litter mass. In soils, extractable NH₄⁺, NO₃⁻, total inorganic N, and total organic N were also greater in Douglas-fir (Fig. 3). Net N mineralization rates did not differ between undisturbed forest types; however net nitrification rates in undisturbed Douglas-fir were twice that of undisturbed lodgepole pine (Fig. 3). Composite foliage in undisturbed forests did not differ in foliar biomass, %N, or N pool size (Fig. 4), however fresh foliar %N was greater in Douglas-fir (Fig. 4). P, K, Ca, and B concentrations in fresh foliage were also greater in Douglas-fir, while Mn and Al concentrations were greater in lodgepole pine (Table 4).

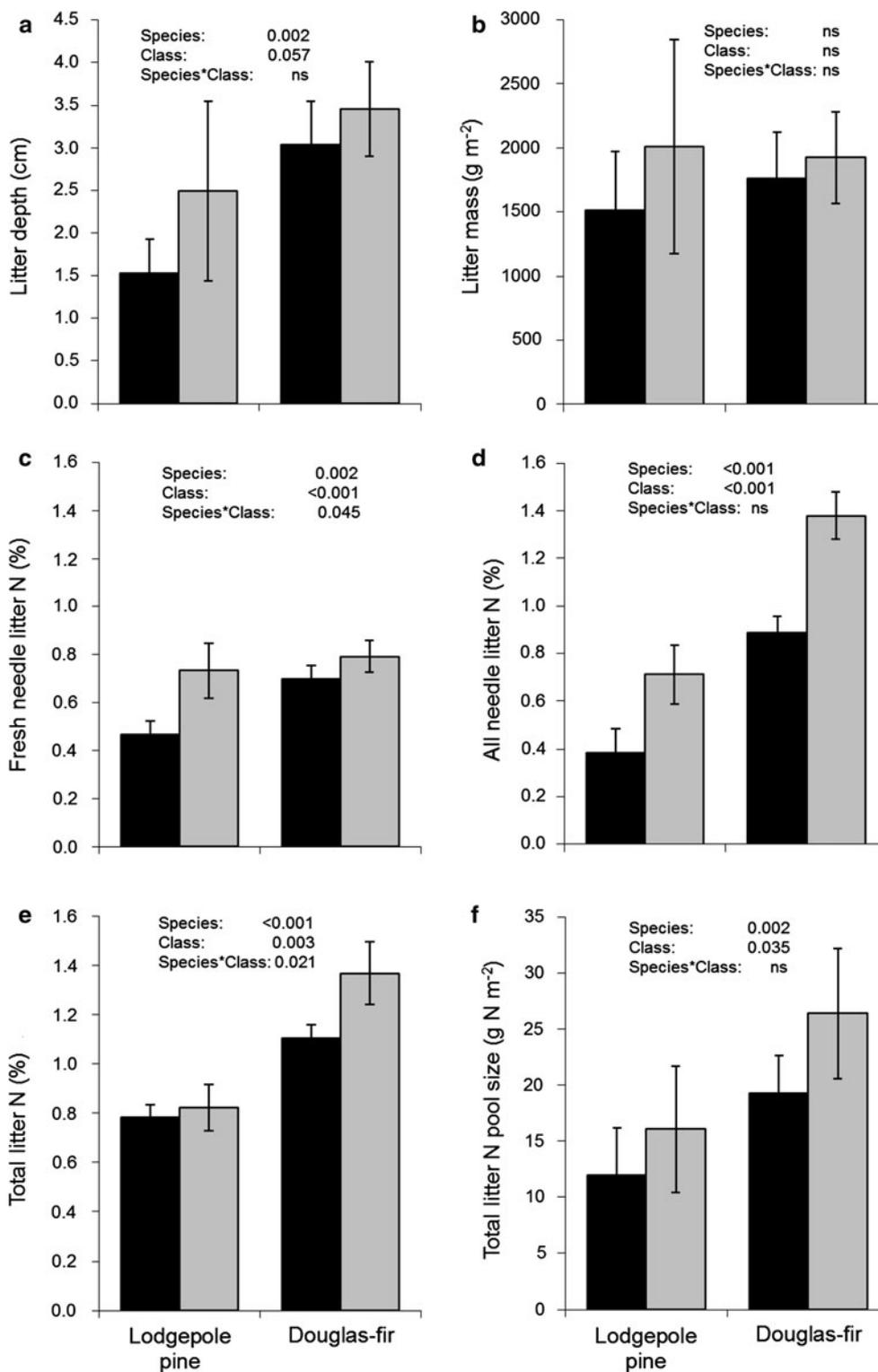


Fig. 2 Litter (Oi) quantity and N metrics in undisturbed and bark beetle-killed lodgepole pine and Douglas-fir forests. Plotted values are untransformed mean \pm 2SE. **a** Litter depth, **b** litter mass, **c** fresh (<1 year) needle litter %N, **d** all needle litter %N, **e** total litter %N, **f** total litter N pool. Values inset within each panel are P values from

the GLM: $y = \text{species} + \text{disturbance class} + \text{species} \times \text{disturbance class}$. Lodgepole pine data have been previously published in Griffin et al. (2011). Black bars undisturbed sites, gray bars beetle-killed sites

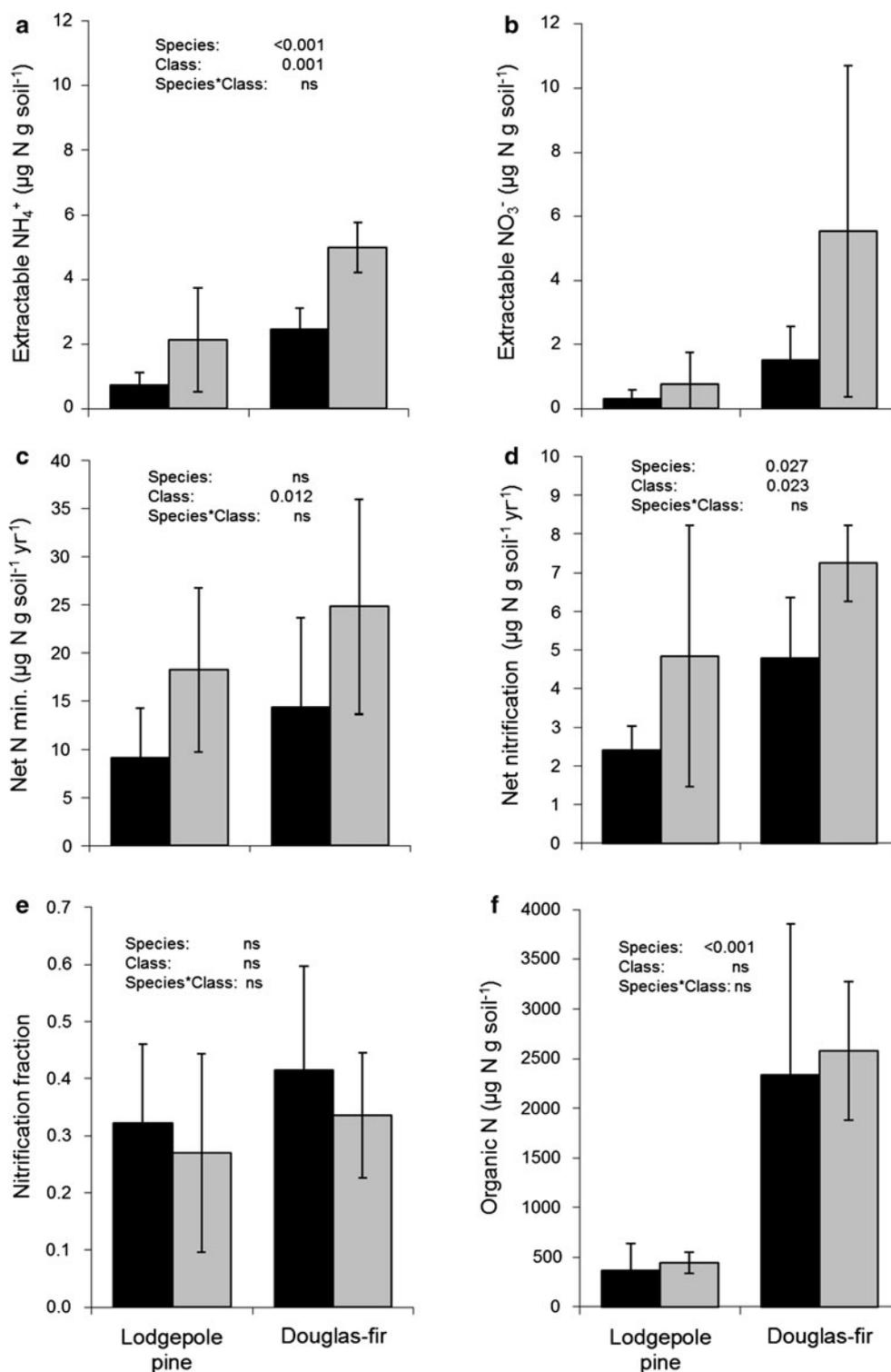


Fig. 3 Soil N metrics in undisturbed and bark beetle-killed lodgepole pine and Douglas-fir forests. Plotted values are untransformed mean \pm 2SE. **a** Extractable NH_4^+ , **b** extractable NO_3^- , **c** net N mineralization, **d** net nitrification, **e** nitrification fraction, **f** organic N. Values inset within each panel are *P* values from the GLM; y =

species + disturbance class + species \times disturbance class. Lodgepole pine data, with the exception of nitrification fraction, have been previously published in Griffin et al. (2011). Black bars undisturbed sites, gray bars beetle-killed sites

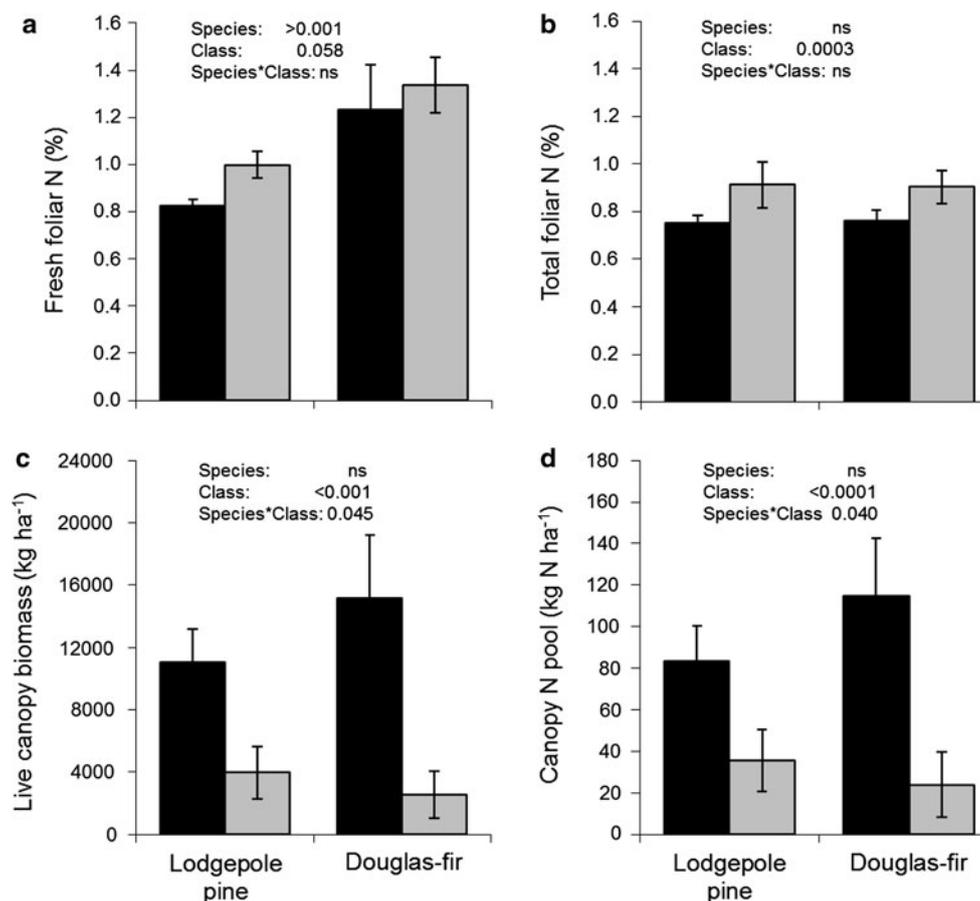


Fig. 4 Canopy foliar N metrics and foliar biomass in undisturbed and bark beetle-killed lodgepole pine and Douglas-fir forests. Plotted values are untransformed mean \pm 2SE. **a** Fresh foliar %N, **b** total foliar %N, **c** live canopy biomass, **d** canopy N pool. Values inset

within each *panel* are *P* values from the GLM: $y = \text{species} + \text{disturbance class} + \text{species} \times \text{disturbance class}$. Lodgepole pine data have been previously published in Griffin et al. (2011). Black bars undisturbed sites, gray bars beetle-killed sites

Ecosystem response to bark beetle disturbance

Despite differing pre-disturbance communities, the response of understory cover to comparable bark beetle disturbances was similar between forest types. Significant disturbance class effects were found for increased grass and forb cover ($P \leq 0.04$; Fig. 1), but there were no significant interactions between species and disturbance class for any cover variable (Fig. 1). However, soil temperature response did vary between forest types. 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 ($P < 0.04$; Douglas-fir data in Table 2; lodgepole pine data reported in Griffin et al. 2011). No significant disturbance class or species \times disturbance class effects were found for 10-cm depth soil temperatures.

Outbreak-induced changes in N cycling also varied between 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 (Fig. 2). 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 (Fig. 2). In soils, significant disturbance class effects were found for increases in extractable NH_4^+ and 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 (Fig. 3). In stands unattacked by bark beetles, all foliar N metrics showed a significant disturbance class effect except for fresh foliar %N (Fig. 4). N concentration of unattacked current year foliage was higher in beetle-killed lodgepole pine stands, and composite foliar N was higher in

Table 4 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

Foliar nutrient	Douglas-fir			Lodgepole pine			Species comparison ANOVA <i>P</i>		
	Undisturbed	Beetle-killed	ANOVA <i>P</i>	Undisturbed	Beetle-killed	ANOVA <i>P</i>	Species	Class	Species × class
N (%)	1.23 ± 0.19	1.34 ± 0.12	0.3853	0.82 ± 0.03 ^f	1.00 ± 0.06 ^f	0.0048	< 0.0001	0.0578*	0.6043
C:N	39.7 ± 7.1	35.8 ± 3.3	0.3499	59.1 ± 3.9 ^f	49.5 ± 2.4 ^f	0.0044	< 0.0001	0.0154	0.2613
N:P	5.5 ± 0.4	5.3 ± 0.4	0.5771	6.1 ± 0.2	6.4 ± 0.5	0.4200	0.0010	0.7615	0.3123
P (%)	0.23 ± 0.03	0.25 ± 0.03	0.2099	0.14 ± 0.00	0.16 ± 0.01	0.0555*	< 0.0001	0.0426	0.9067 ^a
K (%)	1.2 ± 0.1	1.1 ± 0.1	0.4180	0.50 ± 0.04	0.58 ± 0.04	0.5153	< 0.0001	0.3032	0.9785 ^a
Ca (%)	0.40 ± 0.05	0.31 ± 0.04	0.0236	0.14 ± 0.04	0.15 ± 0.04	0.8026	< 0.0001	0.1104	0.0565*
Mg (%)	0.11 ± 0.00	0.10 ± 0.01	0.0344	0.09 ± 0.01	0.10 ± 0.01	0.4742	0.2624	0.9954	0.1255
S (%)	0.09 ± 0.01	0.10 ± 0.01	0.7073	0.07 ± 0.00	0.08 ± 0.01	0.8023	0.0011	0.6660	0.8831
Zn (ppm)	28.5 ± 4.3	27.5 ± 4.0	0.7352	31.9 ± 1.5	31.5 ± 9.4	0.4993 ^c	0.2523	0.6608	0.9437 ^a
B (ppm)	13.6 ± 0.7	13.7 ± 2.8	0.9178	12.0 ± 0.9	11.9 ± 3.1	0.9644	0.1836	0.9822	0.9203
Mn (ppm)	132 ± 45	67 ± 22	0.0331	340 ± 18	200 ± 34	0.0010	< 0.0001	< 0.0001	0.0537*
Fe (ppm)	44.4 ± 28.4	33.7 ± 7.9	0.5810 ^d	32.0 ± 2.4	29.1 ± 3.5	0.2780	0.3743	0.4461	0.6734 ^b
Cu (ppm)	7.3 ± 3.1	7.7 ± 2.5	0.8277	2.3 ± 0.6	3.1 ± 0.8	0.1714	0.0001	0.2954	0.5322 ^a
Al (ppm)	52.0 ± 41.9	18.8 ± 8.4	0.0780 ^a	492 ± 114	329 ± 48	0.0217	< 0.0001	0.0048	0.4533 ^c
Na (ppm)	12.4 ± 4.5	11.2 ± 1.4	0.6255	8.7 ± 3.2	11.3 ± 3.4	0.3455	0.3085	0.6951	0.2966

n = 5 stands per disturbance class; values in table are untransformed mean ± 2SE. Significant ($\alpha < 0.05$) ANOVA *P* values are shown in *bold*. %N and C:N values for lodgepole pine forests have been previously published in Griffin et al. (2011)

* Results for which $0.05 < P < 0.07$

^a ANOVA performed on $\log_{10}(x)$ transformed data

^b ANOVA performed on x^{-2} transformed data

^c ANOVA performed on \sqrt{x} transformed data

^d ANOVA performed on $1/x$ transformed data

^e ANOVA performed on $1/x^2$ transformed data

^f Previously published in Griffin et al. (2011)

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 (Fig. 4). Fresh foliar %N was positively related to net N mineralization in soils of lodgepole pine (Adj. $R^2 = 0.56$; $P = 0.0202$; data not shown) but not in Douglas-fir.

Foliar concentrations of Ca, Mg, and Mn in fresh foliage (needles <1 year) of unattacked Douglas-fir trees were significantly lower in beetle-killed stands than in undisturbed stands, while foliar concentrations of P, K, Mg, S, Zn, B, Fe, Cu, Al, and Na did not differ between Douglas-fir disturbance classes (Table 4). Foliar Mn and Al were also substantially lower in beetle-killed lodgepole pine forests (Table 4). Forest types differed overall in foliar P, K, Ca, and S with higher concentrations in Douglas-fir. Foliar Mn, Cu, and Al also differed by type, with greater concentrations in lodgepole pine (Table 4). 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 4).

Discussion

Comparable bark beetle disturbances 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. Disturbed sites were measured 4–5 years after peak outbreak, thus observed changes are likely the result of several important processes occurring since initial tree death including loss of canopy plant demand, inputs of litter, microbial turnover, and enhanced understory growth. Patterns of increased litter depth, needle litter N concentration, and litter N pool size were consistent in these two 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. This was surprising, given that Douglas-fir has more N-rich soils overall with approximately six-fold greater organic N content, as well as a greater amount of graminoid cover which would produce relatively low C:N and low lignin litter. Increases in net N mineralization may be driven

by reduced plant demand, or by the turnover of microbial N which accumulated in response to disturbance-induced litter inputs. Live foliar N pools declined sharply with beetle-killed basal area in both forest types.

Two important ecosystem properties, soil temperature and soil N–litter N linkages, did vary between these foundation species (Ellison et al. 2005), and may be explained by differences in pre-disturbance ecosystem characteristics. 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 higher overall N stocks in Douglas-fir forests, which may explain why 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 lower 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 periods of time-since-disturbance (30 years) in lodgepole pine (Griffin et al. 2011); however, neither forest type showed this relationship using data from undisturbed and gray stage periods 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 (2–4 years) followed by a longer period (decades) of reduced litterfall until canopy biomass is replaced. Though dead conifer needles may leach some N compounds before dropping (Stadler et al. 2005), bark beetles do not alter fluxes of inorganic N from the canopy 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).

Effects of bark beetle disturbance on the cycling of other elements 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 may 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. Observed declines in foliar Al are more difficult to interpret, as foliar Al has been shown to increase in conifer foliage following other disturbance types (MacDonald et al. 1998). Decreased foliar Al in the live trees of beetle-killed stands may be indicative of increased vigor in these survivors (Hallett and Hornbeck 1997).

A recent conceptualization of disturbance that emphasizes the importance of initial system properties, mechanisms of disturbance, and disturbance legacies (Peters et al. 2011) may provide insight into why the response of Douglas-fir and lodgepole pine forests to bark beetle outbreaks were similar. Although some initial system properties differed (e.g., nitrogen stocks and foliar chemistry) between forest types, stand structure and biomass were similar in these mature stands prior to the outbreaks. Carbon stocks are remarkably similar in Rocky Mountain conifer forests >100 years old, despite differences in elevation, climate, and species composition (Bradford et al. 2008). Regional climate drivers were also likely to be comparable in both forest types, and although there were some differences in soil nutrients these soils are all relatively infertile. Further, the mechanism of disturbance (selective mortality of large trees) was the same in both forest types, as were the legacies of disturbance (i.e., litter inputs, surviving trees, herbaceous vegetation). Collectively, these similarities in initial system state, disturbance mechanisms, and disturbance legacies were associated with qualitatively similar responses to bark beetle disturbance, which suggests the possibility that other bark beetle–host pairings might also respond in analogous ways.

Conclusions

Forest types dominated by different species can have unique biogeochemical responses to a common disturbance type. In this study, litter and soil N cycling was significantly impacted by bark beetle outbreak in Douglas-fir forests, and patterns of change in these properties were similar to those previously observed in lodgepole pine forests. Contrasts

between forest types in pre-disturbance ecosystem structure and N status resulted in differing responses of soil temperature and differing soil N–foliar N relationships following disturbance. Though soil temperature and plant uptake can affect soil N dynamics, Douglas-fir and lodgepole pine forests showed qualitatively similar responses of increased litter N inputs, increased soil N transformations, and increased soil inorganic N concentrations despite substantial differences in pre-disturbance N stocks. Together, these data suggest that litter and soil N stocks may be stronger controls over N mineralization in beetle-disturbed forests than abiotic conditions (temperature) or plant uptake (soil N–foliar N linkage). Changes in foliar chemistry were also similar across forest types including a decline in foliar Mn, which could result in slower litter decomposition rates and thus slower return of N to soils following beetle disturbance. These results suggest that disturbance type may be a better predictor of ecosystem response to disturbance than forest type, due to similar disturbance mechanisms and legacies across multiple beetle–host systems.

Acknowledgments We thank Gary Lovett, Bill Romme, Dan Donato, Jason Kaye and four anonymous reviewers for constructive comments that improved this manuscript. We also thank Emily Stanley, James Thoyre, and the Center for Limnology at the University of Wisconsin for use of the NTL-LTER laboratory. For help in the field and the laboratory, we appreciate the assistance of several University of Wisconsin students: Heather Lumpkin, Erin Mellenthin, Alex Rahmlow, Amanda Rudie, and Ben Ruh. This research was funded by grants from the US Forest Service Western Wildlands Environmental Threat Assessment Center, US Forest Service Joint Fire Science Program, and the University of Wisconsin Graduate School.

References

- Berg B, Steffen KT, McClaugherty C (2007) Litter decomposition rate is dependent on litter Mn concentrations. *Biogeochemistry* 82:29–39
- Binkley D, Bell R, Sollins P (1992) Comparison of methods for estimating soil-nitrogen transformations in adjacent conifer and alder-conifer forests. *Can J For Res* 22:858–863
- Boon S (2009) Snow ablation energy balance in a dead forest stand. *Hydrol Process* 23:2600–2610
- Bradford JB, Birdsey RA, Joyce LA, Ryan MG (2008) Tree age, disturbance history, and carbon stocks and fluxes in subalpine rocky mountain forests. *Glob Change Biol* 14:2882–2897
- Bray RH, Kurtz LT (1945) Determination of total, organic, and available forms of phosphorus in soil. *Soil Sci* 59:39–45
- Bremner JM (1965) Total nitrogen. In: Black CA (ed) *Methods of soil analysis*. Part 2 Agronomy. American Society of Agronomy, Madison, pp 1149–1178
- Brown JK (1978) Weight and density of crowns of rocky mountain conifers. USFS Intermountain Forest and Range Experimental Station General Technical Report INT-16
- Byers JA (1984) Electronic multiprobe thermometer and multiplexer for recording temperatures of microenvironments in the forest litter habitat of bark beetles (Coleoptera, Scolytidae). *Environ Entomol* 13:863–867
- Cullings K, Ishkhanova G, Henson J (2008) Defoliation effects on enzyme activities of the ectomycorrhizal fungus *Suillus granulatus* in a *Pinus contorta* (lodgepole pine) stand in Yellowstone National Park. *Oecologia* 158:77–83
- Despain DG (1990) Yellowstone vegetation. Roberts Rinehart, Boulder
- Ellison AM, Bank MS, Clinton BD, Colburn EA, Elliott K, Ford CR, Foster DR, Kloeppel BD, Knoepp JD, Lovett GM, Mohan J, Orwig DA, Rodenhouse NL, Sobczak WV, Stinson KA, Stone JK, Swan CM, Thompson J, Von Holle B, Webster JR (2005) Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Front Ecol Environ* 3:479–486
- Fahey TJ, Yavitt JB, Pearson JA, Knight DH (1985) The nitrogen-cycle in lodgepole pine forests, southeastern Wyoming. *Biogeochemistry* 1:257–275
- Giardina CP, Ryan MG, Hubbard RM, Binkley D (2001) Tree species and soil textural controls on carbon and nitrogen mineralization rates. *Soil Sci Soc Am J* 65:1272–1279
- Griffin JM, Turner MG, Simard M (2011) Nitrogen cycling following mountain pine beetle disturbance in lodgepole pine forests of Greater Yellowstone. *For Ecol Manag* 261:1077–1089
- Haack RA, Byler JW (1993) Insects and pathogens—regulators of forest ecosystems. *J Forest* 91:32–37
- Hais M, Kucera T (2008) Surface temperature change of spruce forest as a result of bark beetle attack: remote sensing and GIS approach. *Eur J For Res* 127:327–336
- Hallett RA, Hornbeck JW (1997) Foliar and soil nutrient relationships in red oak and white pine forests. *Can J For Res* 27:1233–1244
- Hawkins BJ, Boukcim H, Plassard C (2008) A comparison of ammonium, nitrate and proton net fluxes along seedling roots of Douglas-fir and lodgepole pine grown and measured with different inorganic nitrogen sources. *Plant Cell Environ* 31:278–287
- Huber C (2005) Long lasting nitrate leaching after bark beetle attack in the highlands of the Bavarian forest National Park. *J Environ Qual* 34:1772–1779
- Keane RE (2008) Biophysical controls on surface fuel litterfall and decomposition in the northern Rocky Mountains, USA. *Can J For Res* 38:1431–1445
- Koukol O, Benova B, Vosmanska M, Frantik T, Vosatka M, Kovarova M (2008) Decomposition of spruce litter needles of different quality by *Setulipes androsaceus* and *Thysanophora penicillioides*. *Plant Soil* 311:151–159
- le Mellec A, Habermann M, Michalzik B (2009) Canopy herbivory altering C to N ratios and soil input patterns of different organic matter fractions in a Scots pine forest. *Plant Soil* 325:255–262
- Lovett GM, Weathers KC, Arthur MA, Schultz JC (2004) Nitrogen cycling in a northern hardwood forest: do species matter? *Biogeochemistry* 67:289–308
- Lovett GM, Canham CD, Arthur MA, Weathers KC, Fitzhugh RD (2006) Forest ecosystem responses to exotic pests and pathogens in eastern North America. *Bioscience* 56:395–405
- Mac Donald SE, Schmidt MG, Rothwell RL (1998) Impacts of mechanical site preparation on foliar nutrients of planted white spruce seedlings on mixed-wood boreal forest sites in Alberta. *For Ecol Manag* 110:35–48
- McMillin JD, Allen KK (2003) Effects of Douglas-fir beetle (Coleoptera : Scolytidae) infestations on forest overstory and understory conditions in western Wyoming. *West N Am Nat* 63:498–506
- Morehouse K, Johns T, Kaye J, Kaye A (2008) Carbon and nitrogen cycling immediately following bark beetle outbreaks in southwestern ponderosa pine forests. *For Ecol Manag* 255:2698–2708
- Negron JF (1998) Probability of infestation and extent of mortality associated with the Douglas-fir beetle in the Colorado Front Range. *For Ecol Manag* 107:71–85
- Peters DPC, Lugo AE, Chapin FS, Pickett STA, Duniway M, Rocha AV, Swanson FJ, Laney C, Jones J (2011) Cross-system

- comparisons elucidate disturbance complexities and generalities. *Ecosphere* 2:art81
- Pitman RM, Vanguelova EI, Benham SE (2010) The effects of phytophagous insects on water and soil nutrient concentrations and fluxes through forest stands of the level II monitoring network in the UK. *Sci Total Environ* 409:169–181
- Prescott CE (2005) Do rates of litter decomposition tell us anything we really need to know? *For Ecol Manag* 220:66–74
- Prescott CE, Chappell HN, Vesterdal L (2000) Nitrogen turnover in forest floors of coastal Douglas-fir at sites differing in soil nitrogen capital. *Ecology* 81:1878–1886
- Przybyl K, Karolewski P, Oleksyn J, Labedzki A, Reich PB (2008) Fungal diversity of Norway spruce litter: Effects of site conditions and premature leaf fall caused by bark beetle outbreak. *Microb Ecol* 56:332–340
- Raffa KF, Berryman AA (1987) Interacting Selective pressures in conifer-bark beetle systems—a basis for reciprocal adaptations. *Am Nat* 129:234–262
- Remsburg AJ, Turner MG (2006) Amount, position, and age of coarse wood influence litter decomposition in postfire *Pinus contorta* stands. *Can J For Res* 36:2112–2123
- Safranyik L, Wilson B (eds) (2006) The mountain pine beetle: a synthesis of biology, management, and impacts on lodgepole pine. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria
- SAS Institute (2003) SAS/STAT statistical software, v.9.1, 3rd edn. SAS Institute, Cary
- Schowalter TD (1981) Insect herbivore relationship to the state of the host plant—biotic regulation of ecosystem nutrient cycling through ecological succession. *Oikos* 37:126–130
- Schulte EE, Hopkins BG (1996) Estimation of soil organic matter by weight loss-on-ignition. In: Magdoff FR, Tabatini MA, Hanlon EA (eds) Soil organic matter: analysis and interpretation. Soil Science Society of America, Madison
- Scott NA, Binkley D (1997) Foliage litter quality and annual net N mineralization: comparison across North American forest sites. *Oecologia* 111:151–159
- Shore TL, Safranyik L, Hawkes BC, Taylor SW (2006) Effects of the mountain pine beetle on lodgepole pine stand structure and dynamics. In: Safranyik L, Wilson B (eds) The mountain pine beetle: a synthesis of biology, management, and impacts on lodgepole pine. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, pp 95–114
- Sikora FJ (2006) A buffer that mimics the SMP buffer for determining lime requirement of soil. *Soil Sci Soc Am J* 70:474–486
- Spielvogel S, Prietzel J, Auerswald K, Kogel-Knabner I (2009) Site-specific spatial patterns of soil organic carbon stocks in different landscape units of a high-elevation forest including a site with forest dieback. *Geoderma* 152:218–230
- Stadler B, Muller T, Orwig D, Cobb R (2005) Hemlock woolly adelgid in new England forests: canopy impacts transforming ecosystem processes and landscapes. *Ecosystems* 8:233–247
- Tahovska K, Kopacek J, Santruckova H (2010) Nitrogen availability in Norway spruce forest floor—the effect of forest defoliation induced by bark beetle infestation. *Boreal Environ Res* 15:553–564
- Thomas GW (1982) Exchangeable cations. In: Page AL (ed) Methods of soil analysis. Part 2. Agronomy Monograph ASA and SSSA, Madison
- Thomas KD, Prescott CE (2000) Nitrogen availability in forest floors of three tree species on the same site: the role of litter quality. *Can J For Res* 30:1698–1706
- USDA Forest Service (2006a) Forest insect and disease aerial survey, region 2. <http://www.fs.fed.us/r2/resources/fhm/aerialsurvey/>. Accessed 1 Feb 2008
- USDA Forest Service (2006b) Forest insect and disease aerial survey, regions 1 and 4. <http://www.fs.fed.us/r1-r4/spf/fhp/aerial/index.html>. Accessed 1 Feb 2008
- UWSPAL (2010) Soil and plant analysis. In: Peters J (ed) Wisconsin procedures for soil testing, plant analysis and feed & forage analysis. University of Wisconsin Soil and Plant Analysis Lab, Madison. <http://uwlab.soils.wisc.edu/procedures.htm>
- WRCC (2010) Moran, WY, climate summary. Western regional climate center. <http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?wy6440>. Accessed 11 Apr 2011