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REGULAR ARTICLE

Influence of bark beetle outbreaks on nutrient cycling in native pine stands in western Canada

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Abstract
Aims Using a natural gradient of recent (0–4 years) mountain pine beetle (*Dendroctonus ponderosae*)-caused mortality in lodgepole pine (*Pinus contorta*) stands in west central Alberta, Canada, we tested the effects of different levels of tree mortality, and time since bark beetle infestation, on initial abiotic environmental changes, and nutrient inputs and cycling.
Methods We quantified the impacts of *D. ponderosae* outbreak on input rates of pine needle litter and nutrients, live root mass (both course and fine), supply rates of plant-available nutrients, and concentrations of total mineral soil phenols.
Results Pine needle litter, nutrient concentrations, and needle nutrient inputs are all increased as a function of either tree mortality or time since bark beetle infestation. Supply rates of many mineral nutrients increased in soils across gradients of mortality or time. Shallow fine root mass declined by half in response to beetle disturbance; concentrations of soil phenols also shrank by over half, potentially due to increased root losses. Soil phenolics were negatively associated with the supply rate of soil nitrate.
Conclusion We concluded that the effects of tree mortality on stand biogeochemistry in pine stands with no recorded history of mountain pine beetle is similar to earlier studies conducted in the beetle's historical range.

Keywords Biogeochemistry · Litter chemistry · Soil phenolics · Mountain pine beetle · Insect outbreak

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Introduction

Bark beetles (Coleoptera: Curculionidae, Scolytinae) display episodic and severe population eruptions on decadal to millennial time scales driven by host-tree condition and abundance, and more recently climate warming (Bentz et al. 2010). The mountain pine beetle (*Dendroctonus ponderosae* Hopkins), is an aggressive, coniferophagous species that is currently undergoing continent-scale range expansion throughout conifer forests of western North America (Cudmore et al. 2010). Outbreak populations now span unprecedented gradients of latitude, elevation, and forest composition, and have killed conifers, mainly lodgepole pine (*Pinus contorta* Doug ex. Loud. Engelm) on over millions of hectares (Safranyik et al. 2010). They have also expanded eastwards into the jack pine (*Pinus banksiana* Lamb.) forests, thus posing a transcontinental threat to most boreal forest ecosystems in Canada (see references in Erbilgin et al. 2014).

Bark beetle-driven tree mortality can cause a cascade of interlinked effects on key abiotic conditions and biotic processes tied to biogeochemical cycling in forest stands (Romme et al. 1986; Morehouse et al. 2008; Clow et al. 2011; Griffin et al. 2011; Keville et al. 2013). For example, after tree mortality, deposition of litter from canopies contributes to changes in soil and surface temperatures (Hais and Kucera 2008; Griffin et al. 2011; Griffin and Turner 2012), may increase soil moisture levels (Cullings et al. 2003), and potentially increase leaching and decomposition of needle litter (Yavitt and Fahey 1986; Prescott 2005). Specifically, needle loss increases canopy openness, potentially altering moisture inputs (Pugh and Small 2012) and forest-floor temperature (Prescott 2005; Hais and Kucera 2008; Griffin and Turner 2012), while accumulation of surface litter may potentially influence soil temperature and moisture —key factors in decomposition—and promote leaching inputs of organic compounds into soils, such as macronutrient and secondary chemicals (Yavitt and Fahey 1986; Prescott 2005). Similarly, elevated litter-nutrient concentrations linked to beetle-driven mortality may compound nutrient inputs to soils (Morehouse et al. 2008; Griffin et al. 2011). However, decomposition and N mineralization are also influenced by the abundance and function of tree roots (Meier and Bowman 2008; Meier et al. 2008; Xiong et al. 2011), but the role of living roots in nutrient cycling and their sensitivity to a bark beetle-driven mortality remain poorly understood.

Increases in root mortality and cessation of root functions, such as water and mineral nutrient uptake as well as exudation and rhizodeposition of dissolved organic carbon compounds (e.g., phenolics and tannins), may have profound impacts on soil nutrient cycling (Meier and Bowman 2008; Xiong et al. 2011). Root mortality at the stand level may impair nutrient and water uptake, increasing these pools of soil nutrients. Soil inputs of polyphenolics, a broad class of carbon-rich plant secondary metabolites, are well-known to influence nutrient cycling by enhancing or inhibiting the availability of some essential nutrients, particularly N. Entering soils as exudates and leachates from living (e.g., fine roots) and senesced (e.g., pine litter) plant tissues, phenolics may influence key aspects of N cycling such as rates of mineralization and nitrification; specifically, the loss of phenolics may promote N mineralization (Yavitt and Fahey 1986; Northup et al. 1995; Hattenschwiler and Vitousek 2000; Meier and Bowman 2008).

These aspects of nutrient cycling may, in turn, drive post-disturbance vegetative dynamics and can affect successional trajectories (Suding et al. 2004; Meier and Bowman 2008). Thus, a likely but untested consequence of *D. ponderosae* disturbance could be decreases in both living roots and phenolics with impacts on the biogeochemical cycling of N and other mineral nutrients. Investigating the association of this latter mechanism on soil nutrient cycling may expand the current understanding of key mechanisms driving nutrient supply which are linked to vegetative dynamics and succession after *D. ponderosae* outbreaks.

The goals of this research were to determine the role of bark beetle-induced tree mortality and time since beetle infestation on initial changes in abiotic conditions and organic inputs, particularly pine needlefall as a result of tree mortality, tied to biogeochemical cycling during the growing season (May-September). Specifically, we quantified: (1) input rates of pine needle litter and nutrients; (2) decomposition rates of needle litter; (3) soil nutrient supply rates; (4) mass of shallow-living fine roots; and (5) concentrations of total mineral soil phenolics. Our study stands apart from previous works by, first, tracking abiotic conditions and processes tied to nutrient cycling through time in a region with no recorded history of *D. ponderosae* outbreaks; second, quantifying tree mortality-associated shifts in shallow roots and soil phenolics; third, integrating novel evidence from the latter two belowground phenomena into existing framework concerning key mechanisms of nutrient cycling in *D. ponderosae*-killed pine stands.

Materials and methods

Study area and characterization of overstory structure

In 2006 and 2009, long-distance in-flights of *D. ponderosae* from British Columbia (Canada) initiated a regional outbreak that spread into stands of mature lodgepole pine forests at record-breaking mortality in west central Alberta (AESRD 2013). The current study was conducted in these pine-dominated stands of fire origin (circa. 1900) within the Lower Foothills natural sub-region (118° 59′W; 54°39′N; 1027 m) located roughly 60 km southwest of the city of Grande Prairie (see Treu et al. 2014 for site selection and description including location and stand composition). The regional climate is humid-continental with long cold winters and

short cool summers during which most precipitation occurs in June (76.1 mm), with a mean annual precipitation of 445.1 mm. Mean annual temperature is 2.2 °C, with mean daily minimum values of −19 °C in January and mean daily maximum values of 22.6 °C in July (Environ Can 2013).

The topography of the study area consists of gently undulating to rolling till-covered hills and plateaus at elevations between 950 and 1100 m above sea level. Soils are Orthic Gray Luvisols derived from weakly to moderately calcareous, medium- to fine-textured glacial tills that are well to imperfectly drained, and support the most diverse forest tree species communities in Alberta (NRC 2006). Species mixtures comprising the secondary species structure within many lodgepole pine-dominated sites within the region include black spruce (*Picea mariana* Mill.), white spruce (*Picea glauca* (Moench) Voss.), balsam fir (*Abies balsamea* (L.) Mill.), trembling aspen (*Populus tremuloides* Michx.), paper birch (*Betula papyrifera* Marshall), and green alder (*Alnus viridis* (Chaix) DC). The understory vegetation includes mixtures of devil's club (*Oplopanax horridus* (Sm.) Miq.), fire weed (*Chamerion angustifolium* (L.)) Holub, wild sarsaparilla (*Aralia nudicaulis* L.), and Canadian mayflower (*Maianthemum canadense* Desf).

We located 11 lodgepole pine stands showing various levels of *D. ponderosa*-caused tree mortality within a 50 km region bordering provincial Permanent Sampling Plots with overstories dominated (≥80 %) by even-aged (120±0.4 SE years old) lodgepole pine trees. Each stand was then characterized based on the three prominent stages of crown color and time since beetle attacks (Safranyik et al. 2010): (1) *green-attack* –dead trees with full crowns of fading needles, occurring 0–1 year post attack; 2) *red-attack* –dead trees with the majority of orange-colored needles remaining, occurring 1–3 years post attack; 3) *gray-attack* –dead trees with no needles remaining; occurring 3 or more years post attack.

In May 2011, we installed one 30×30 m plot in each stand, within which four subplots (6×6 m) were positioned at each corner to sample forest structure and *D. ponderosae* infestation. We measured the total height and diameter at breast height (DBH; cm) of all live and dead standing trees (woody stems≥12 cm at DBH) and saplings (woody stems<12 cm at DBH and total height≥ 1.4 m). All trees were recorded for species, condition (live or dead), stage of crown color (green, red, and gray), estimated number of years dead (as described by Klutsch et al. 2009), and proximate cause of death (e.g., *D. ponderosae*; disease; unknown). Mean overstory age was determined by accessing provincial records for each of the adjacent Permanent Sampling Plots.

Beetle attacks were confirmed by the presence of adult emergence holes, pitch tubes, boring dust (only for the current year of attacks), and subcortical life stages (Safranyik et al. 2010). To estimate year of attack on all beetle-killed trees, we cross-checked records for stages of crown color and degradation classes (1–≥ 6 years dead) with physical signs of beetle attack. From these estimates, we determined the number of years elapsed between initial infestations of beetles and the start of our field sampling (hereafter, time since beetle; TSB). In June and September 2012, and in June 2013, we re-visited all previously sampled trees to document levels of current-year beetle-caused tree mortality and update crown color stages and degradation classes. From these data, we calculated density and basal area by stem type, species, and of beetle kill. Percent tree mortality was calculated as the proportion of pre-beetle (i.e., prior to outbreak, ca. 2006) live tree basal area that was killed by *D. ponderosae*, multiplied by 100.

We quantified canopy openness and leaf area index using hemispherical photography and Gap Light Analyser image analysis software (Canham 1988; Frazer et al. 1999). A camera equipped with an 180° field-of-view lens was mounted on a tripod and positioned at five standard locations in each plot (center of plot and four subplots; 0.5 m above forest floor) to capture clear-sky images of canopies pre-dawn. Images were scanned, post-processed, and analysed using Gap Light Analyser. We selected the blue plane setting for image-color contrast to improve image contrast between canopies and sky. Means per plot were calculated for canopy openness and effective leaf area index (integrated over the zenith angles 0 to 60°) (Stenberg et al. 1994).

Aboveground inputs: pine needle deposition and decomposition rates, and nutrient concentrations

In each plot, we established a systematic grid (4×7 m) originating 1 m from the base of the southwest-most tree to locate ten points for sampling soil surface and subsurface temperature, rates of needle deposition and decomposition, living root mass, soil nutrient supply rates and moisture, and soil phenolics. To determine rates of needlefall, litter traps (22×50 cm) were positioned at each point. Litter was collected monthly from June to September in 2011 and 2012, and from June to August

in 2013. Non-pine needle litter (e.g., twigs, non-pine foliage) was omitted from the analyses. Within 2 days of collection, needle samples were shipped to the University, oven-dried at 60 °C for 48 h, and weighed. We analyzed macro- and micronutrient chemistry by compositing then grinding July-collected samples by plot as Page et al. (2012) showed that the respective concentrations of needle phosphorus, potassium, and magnesium from beetle-infested lodgepole pine trees were comparable among samples collected in July, August, and September. Total N was analyzed by the Dumas Combustion Method using a Costech 4010 Elemental Analyzer System (Costech Analytical Tech. Inc., Valencia, CA, USA). Total P was analyzed by colorimetry following an acid digest using SmartChem Discrete Wet Chemistry Analyzer, Model 200 (Westco Scientific, Limited, Brookfield, CT, USA). Metal cations (Ca, K, Mg and Ca) were analyzed using atomic absorption spectrophotometry at the University of Alberta, Natural Resources Analytical Lab (Baker and Suhr 1982).

To quantify needle decomposition, we collected fresh-fallen litter from the ten litter traps at each plot in May 2012. We separated litter samples by their respective plots, dried them at 60 °C for 48 h, and removed all non-pine needle litter from the samples. Decomposition bags (20×20 cm) were constructed with 1 mm polypropylene mesh and filled with 4±0.01 g of needles. We transported each decomposition bag from lab to field inside an individual plastic bag. Careful handling of bags during transport prevented visible loss of needle debris from the decomposition bags. On June 9, 2012, ten decomposition bags were secured to the forest floor in each plot at a distance of 1 m from each of ten litter traps. Sixteen months later, each decomposition bag was carefully detached from the forest floor and placed into a paper 'traveler' bag. Residual needles were carefully removed from the decomposition and traveler bags, dried at 40 °C for 7 days and then weighed. Percent mass loss was calculated by dividing the difference between the final and initial mass by the initial mass and multiplying by 100. Data were pooled by plot.

Soil characteristics and nutrient pools: nutrient supply rates, moisture, and temperature

From June to August, 2011–2013, we sampled supply rates of soil macro- and micronutrients ((aluminum (Al^{3+}), nitrate (NO_3^--N), ammonium (NH_4^+-N), calcium (Ca^{2+}), iron (Fe^{3+}), potassium (K^+), magnesium (Mg^{2+}), manganese (Mn^{2+}), phosphorus ($H_2PO_4^-$—P), sulphur (SO_4—-S), and zinc (Zn^{2+})). We used Plant Root Simulator (PRS™) probes (plastic stakes with an encapsulated ion-exchange resin membrane; Western Ag Innovations, Inc., Saskatoon, SK, Canada) to capture a cumulative (i.e., residence term) measure of bioavailable concentrations of mineral ions in soils. Probes were inserted into the mineral soil A-horizon at a distance of 20–50 cm from each of the ten litter traps. The sampling density per point was four pairs of probes, each consisting of one cation and anion probe; the four probe pairs were composited prior to elution, generating one observation per point. Probes where extracted in August of each year, shipped to the laboratory for deionized water rinsing, and then re-shipped to the laboratories of Western Ag Innovations for eluation and analysis of ion concentrations. Units are expressed as the weight of nutrient adsorbed per surface area of ion-exchange membrane over time (μg nutrient/10 cm^2 ion-exchange membrane surface area/time of burial).

Soil volumetric moisture content was measured over 2 days in August (2011, 2012 and 2013) at a distance of 25 cm from each pair of PRS-probes using a portable ML2 Theta Probe Soil Moisture Sensor (Dynamax Inc., Houston, TX, USA). In July (2011 and 2013), soil pH and particle size distribution (2012 only) was determined by collecting and pooling 25 dispersed soil sub-samples per plot. Samples were promptly air-dried, and shipped to the University of Alberta, Natural Resources Analytical Lab for analysis (Bouyoucos 1962; McLean 1982).

Soil surface temperature and relative humidity was measured in seven locations at a distance of 0.5 m from each of seven litter traps per plot. Sensors (HOBO U23 Pro v2 Temperature/Relative, Onset Computer Corp., Bourne, MA, USA) were housed in PVC pipe (5 cm diameter × 12 cm long) staked to the forest floor. Readings were logged at 30 min intervals from June through August 2012 and 2013. Soil temperature was measured in 10 locations at a distance of 3 m from each litter trap per plot. Sensors (HOBO Pendant Temperature Data Logger 8K-UA-001-08) were inserted vertically to a depth of 10 cm from the mineral soil surface. Readings were logged at 30 min intervals from June through August 2013.

Belowground losses: living root mass and soil phenol concentrations

In August 2012, we sampled total living root mass using a relative measure to determine if patterns of root mass

are associated with tree mortality. At one random location within 2 m of each of the 110 litter traps, we removed the organic layer and extracted a soil core (20 cm depth × 5 cm width) and measured roots' length (±5 mm). Root samples were kept frozen until processed, which involved washing roots over a 2 mm sieve and collecting approximately 95 % of visible roots for analysis. Living roots were distinguished from dead roots based on integrity and color of vascular tissue. Fine (<2 mm dia) and coarse (≥2 mm dia) roots were separated, dried at 60 °C for 48 h, and weighed. We standardized estimates of root mass by dividing the mass of each root sample by the volume of its soil core (i.e., g m^{-3}) and by the total basal area of trees greater than 1.5 m in height at each plot. Pre-beetle living basal area of trees was used in this calculation.

In July 2012 and 2013, we measured total mineral soil phenolics using a quantitative assay for phenolic acids and compounds (Tel and Covert 1992). Soil samples were collected 1 m from each of seven litter traps per plot. Four soil cores (6 cm depth × 2 cm width) were extracted from the top of the A-horizon to a depth of 6 cm, composited by point location, placed on ice, and shipped to the laboratory for 48 h of air-drying. We added the Folin-Ciocalteau phenol reagent (Sigma-Aldrich, Oakville, ON, Canada) to soil water extracts and performed spectroscopy (Enesys 10S UV-vis Spectrophotometer, Thermo, Fisher Scientific, Madison, WI, USA) to determine absorbance (750 nm). Amounts of phenolics were expressed as μg per g of soil.

Statistical analyses

Data for most response variables were collected during three consecutive growing seasons (May-August, 2011–2013). We averaged the observations for each response variable by plot and sampling year, testing annual plot-level means for analyses, which were used to determine significance results at $\alpha<0.05$ for all tests. To test the role of beetle disturbance—(1) percent tree mortality, and (2) time since beetle infestation (TSB) —on response variables, we used both linear mixed effects (LME) and generalized linear (GL) statistical models in R (R development core team 2013; Pinheiro et al. 2004). We used LME models to control for annual resampling of plots (i.e., temporal pseudoreplication) while testing significant main effects and interactions among independent and response variables with multi-year datasets; GL models were used for response variables with single-year datasets (i.e., leaf area index, canopy openness, root mass, needle decomposition, and soil temperature). Fixed factors in the LME models were TSB, year, percent tree mortality, and interactions between and among each; the random factor was plot (N= 33; 11 plots × 3 years). Percent tree mortality was a numeric factor used to determine the effect of beetle-caused tree mortality on response variables. Time since beetle was also a numeric factor used to quantify time sensitivity of response variables to disturbance 1–4 years after initial infestation, and to account for potential variation arising from a 0–2 years discrepancy in initial infestations among plot. Year was a categorical factor used to isolate variation in our response variables attributable to environmental stochasticity among sampling years (e.g., mean summer precipitation).

Exploratory analysis using Pearson product-moment (i.e., correlation) tests revealed significant collinearity between percent tree mortality and TSB ($P<0.001$; r= 0.68) in the dataset for 2012. To disentangle the unique from shared contribution of each of these two explanatory variables on the response variables measured in 2012 only, we used sequential regressions (Graham 2003). We used a simple linear regression to regress TSB (2012) against percent tree mortality (2012), and computed the residual error values (i.e., TSB residuals) which then replaced the raw TSB values in the subsequent GL models for leaf area index, canopy openness, and root mass; this factor substitution was unnecessary for soil temperature (collected in 2013). In the GL models for root mass, we included as a covariate pre-beetle live tree basal area (see Belowground losses: living root mass and soil phenol concentrations) to adjust for variation in root mass attributable to differences in tree density across plots. Explanatory variables for all GL models were percent tree mortality and either TSB or TSB residuals, except for needle decomposition, which included as fixed factors the respective means of percent tree mortality and TSB between 2012 and 2013 to capture average conditions over the incubation period (N=11; 11 plots × 1 year).

To ensure there was an absence of collinearity between above- and belowground plot characteristics (i.e., topography, forest structure, soil texture) and beetle disturbance in our LME and GL models, we performed an additional series of Pearson product-moment tests; these revealed an absence of significant (and thus confounding) collinearity. In all models, we tested for the presence of normality, homoscedasticity, and spatial autocorrelation

on residuals (using Shapiro-Wilk tests, Bartlett's test, and correlograms, respectively); where the assumptions of our parametric tests were violated, we log transformed data and retested to ensure these assumptions were satisfied. No spatial autocorrelation was detected.

Results

Forest structure and *D. ponderosa* infestation

Across the 11 plots, pre-beetle live basal area ranged from 36 to 708 m^2 ha^{-1} (mean± SE=52±3.0), of which *P. contorta* comprised between 60 and 100 % (94± 3.5 %; Table 4). The percent tree mortality ranged from 0 to 84 % (Table 4) and was not related to pre-beetle live tree basal area or any pre-beetle topographic (elevation, slope, aspect) or edaphic plot characteristics (forest structure, soils texture) (Table 5). From 2011 to 2013, 'time since beetle' (TSB) ranged from 0 to 4 years (Table 4), and showed no relationship to any pre-beetle topographic or edaphic plot characteristics (Table 5). Average age of overstory trees was similar (121± 0.4 years) across study plots (Table 4). Leaf area index decreased with increasing percent tree mortality and TSB residuals (from 1.82 to 1.42), while canopy openness increased with percent tree mortality and TSB residuals (from 20 to 28 % canopy openness) (Table 1).

Pine needle deposition and decomposition rates, and nutrient concentrations

In the absence of beetle disturbance, rates of pine needle litter over the growing season (May-September; 84 days) varied from 15 to 155 g m^{-2}. Needle litter decreased with TSB and the effect of tree mortality depended on year (Table 2; Fig. 2). In 2011, there was a positive relationship between needle litter and extent of tree mortality; however in both 2012 and 2013, the relationship significantly weakened. After 2011 (2–4 years following the beetle outbreak), litterfall rates were on average 49 g m^{-2}. Nitrogen and P concentrations of needles fallen from the canopy increased across the gradients of tree mortality and TSB, and varied by year (Tables 2 and 6). Needle N and P concentrations were highest in 2013 (N: 0.85 %±0.03; P: 0.11 %± 0.002). Needle K concentrations were negatively related to tree mortality in 2011, but positively related for both 2012 and 2013 (Tables 2 and 6). In contrast, concentrations of needle Ca were positively related to tree mortality in 2011, but negatively related for both 2012 and 2013 (Tables 2 and 6). Needle Mg concentrations displayed a three-way interaction among percent tree mortality, TSB, and year (Tables 2 and 6).

Over the growing season, rates of needle N and P input (mg per m^2 84 $days^{-1}$) increased with percent tree mortality, and with TSB, but only in 2011 (Table 2; Fig. 3). In 2011, N and P inputs peaked at approximately 120 and 13 mg m^{-2}, respectively. In 2012 and 2013, nutrient inputs ranged between 7.5–65 mg m^{-2} and 1.7–8.2 mg m^{-2} for N and P, respectively. Rates of needle Ca input increased in relation to tree mortality in the first year, decreased in the following 2 years, and decreased in relation to TSB overall (Table 7). Rates of input for needle K, Ca, and Mg decreased with increasing TSB and varied by year (Tables 2 and 7). Rate of needle decomposition showed no relationship to the explanatory factors of beetle disturbance (Table 1). Over the 16 month burial time, mean litter mass loss was 68 %± 1.2.

Soil characteristics and nutrient pools: soil nutrient supply rates, moisture, and temperature

The supply rates of soil NH_4^+ displayed an interaction between tree mortality and TSB, in which supply rates increased over both the percent tree mortality and time gradient but did not depend on year (Table 3; Fig. 4). Supply rates of soil NO_3^- increased in response to increasing levels of tree mortality and varied between years (Table 3; Fig. 4). Supply rates of phosphate increased with tree mortality but no pronounced trends were evident for TSB and year. Soil K^+ supply rates varied by years (Tables 3 and 8). Supply rates of soil Fe^{3+}, and Zn^{2+} increased with increasing tree mortality and TSB, and varied between years (Tables 3 and 8). Supply rates of Mg^{2+} displayed a three-way interaction among percent tree mortality, TSB, and year; slopes were negative in relation to percent tree mortality and TSB, but positive across years (Tables 3 and 8). Supply rate of S increased with TSB during the first and second sampling year, but declined over this gradient in the third (Tables 3 and 8). Supply rates of soil Mn^{2+} were influenced by TSB, but no trend was evident (Tables 3 and 8). Soil supply rates of Al^{3+} increased with tree mortality, while supply rates of both Al^{3+} and SO_4^- increased with TSB in 2011 and 2013, but decreased in relation to TSB in 2013 (Tables 3 and 8).

Table 1 Results from generalized linear models on direction, effect size, precision, and significance of main effects between and interactions among mountain pine beetle (*Dendroctonus ponderosae*; MPB) disturbance (i.e., tree mortality (% Tree mortality) and time since beetle infestation (TSB)) and living root biomass (fine and coarse), soil surface temperature, canopy openness, leaf area index (LAI) and litter decomposition

Fixed factor	% Tree mortality 2012	TSB residuals 2012	% Tree mortality 2012 X TSB residuals 2012	Pre MPB live basal area	
Fine root mass	−1.57e-6±6.38e-7	−1.07e-4±3.62e-5	1.86e-6±1.18e-6	7.31e-6±1.21e-6	
Coarse root mass	2.03e-6±1.76e-6	−2.02e-4±9.98e-5	6.31e-6±3.26e-6	9.92e-6±3.33e-6	
Soil temperature	−0.002±0.01	0.18±0.19	0.002±0.004	–	
Canopy openness	0.06±0.03	3.33±1.62	−0.02±0.06	–	–
LAI	−0.005±0.002	−0.14±0.12	−0.001±0.004	–	–
Decomposition	−0.20±0.13	−2.94±1.74	0.07±0.04	–	–

Responses were measured in 2012 or 2013 (soil temperature) only. Co-linearity between percent tree mortality (2012) and time since beetle (2012) necessitated the replacement in the models of that factor with its residuals that result from being regressed against percent tree mortality (2012). Coefficients bolded are significant at $P<0.05$

Across all years, soil moisture increased with percent tree mortality (Table 3; Fig. 5). Soil pH increased with tree mortality and varied among years; with time pH tended to increase across plots (Table 3; Fig. 5). Soil temperature showed only a marginally significant increase with TSB (Table 1); temperature at the soil surface varied by 1 °C across plots (mean=13.1 °C). Relative humidity at the soil surface increased with percent tree mortality and TSB (Table 3); in 2012 relative humidity ranged from 75 % in undisturbed stands to 88 % in stands with high levels of tree mortality. The same trend was evident in 2013, however, values were approximately higher by 3 %.

Belowground losses: root mass and soil phenolic concentrations

The dry mass of fine versus coarse living shallow roots responded differently to beetle disturbance: though both root fractions were positively related to the covariate,

Table 2 Results from linear mixed effects models to determine significance of main effects between and interactions among *Dendroctonus ponderosae* disturbance (i.e., tree mortality and time since beetle) and responses in pine needle litter nutrients, biomass, and nutrient inputs

	Intercept[a]	%BK	TSB	Yr	%BK*TSB	%BK*Yr	TSB*Yr	%BK*TSB*Yr
ndf,ddf [b]	1,11	1,11	1,11	2,11	1,11	2,11	2,11	2,11
Needlefall	197.2****	1.1	72.3****	23.2****	5.2*	8.3**	0.4	0.4
Foliar N	1348.7****	44.6****	5.3*	57.0****	0.6	1.0	0.2	2.2
Foliar P	1204.6****	41.2****	13.8**	13.2**	0.6	0.6	2.0	1.0
Foliar K	336.1****	6.1*	0.9	0.7	0.3	7.3**	0.7	1.5
Foliar Mg	1724.9****	4.9*	10.3**	47.6****	0.0	1.3	0.3	4.2*
Foliar Ca	1172.9****	3.2	4.1	6.8**	0.2	11.2**	0.6	2.4
N input	3717.7****	5.1*	14.9**	16.9***	0.8	0.0	0.4	0.4
P input	3110.9****	6.7*	10.9**	8.1**	4.6	0.9	0.3	0.1
K input	70.3****	0.0	20.7***	8.4**	1.2	0.1	0.9	0.8
Mg input	142.9****	0.1	13.9**	5.8**	2.1	2.9	0.4	1.1
Ca input	268.5****	0.1	17.9***	11.8***	3.8	7.0*	0.7	1.9

[a] F values followed by *P* values were reported. Means are significant at $\alpha<0.05$. * $P<0.05$, ** $P<0.01$, *** $P<0.001$, **** $P<0.0001$

[b] ndf,ddf represent numerator and dominator degrees of freedoms respectively

Needles were dead and collected from soil surface. Fixed factors included sampling year (2011–2013), percent tree mortality (%BK), year (Yr), and time since beetle (TSB) residuals. Co-linearity between percent tree mortality and time since beetle necessitated the replacement in the models of that factor with its residuals that result from being regressed against percent tree mortality

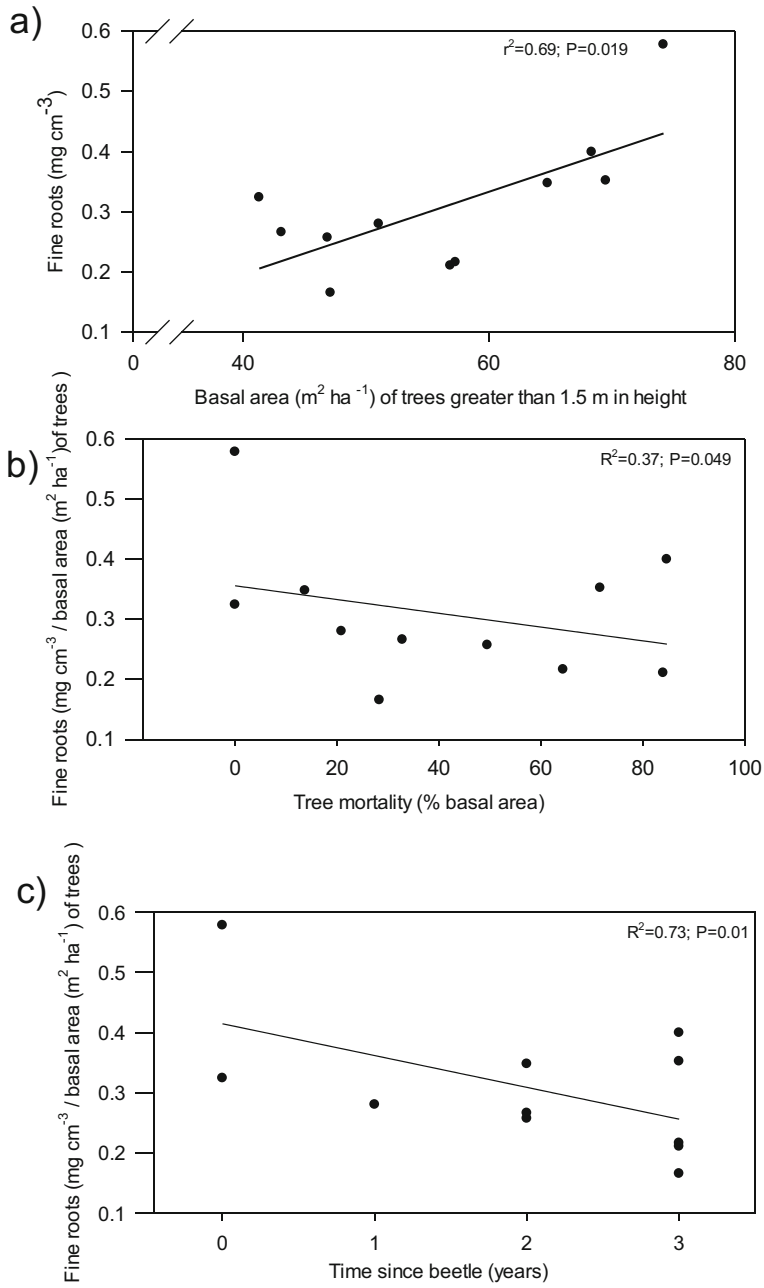

Fig. 1 Relationships between fine root mass and **a**) basal area (m^{-2} ha^{-1}) of trees greater than 1.5 m in height, **b**) tree mortality caused by *Dendroctonus ponderosae*,and **c**) time since beetle outbreak in lodgepole pine (*Pinus contorta* var. *latifolia* Engelm) forests in western Alberta (Canada). Roots were extracted in the top 20 cm of mineral soil using soil cores (5 cm diameter) at ten locations at each of the 11 sites and pooled by site . In **b**) and **c**), root mass was standardized by core volume (cm^{-3}) and total basal area of trees (m^2 ha^{-1}) at each site. Points are raw data values

pre-beetle live basal area (Table 1; Fig. 1a). Fine root mass declined by approximately half with increasing tree mortality and TSB residuals (Fig. 1b and c), while coarse root mass showed no relationship to tree mortality (Table 1). Concentrations of soil phenolics generally declined with increasing percent tree mortality (P= 0.033); the strength of this relationship varied by year (P=0.029) (Fig. 6). Specifically, the relationship became weaker over time. Across 2012 and 2013, soil phenolics were negatively associated with the supply rate of soil NO_3^- (Fig. 7).

Discussion

Our study tested the presence of three key pathways of nutrient cycling on soil nutrient supply following *D. ponderosae* outbreak in naive lodgepole pine forests

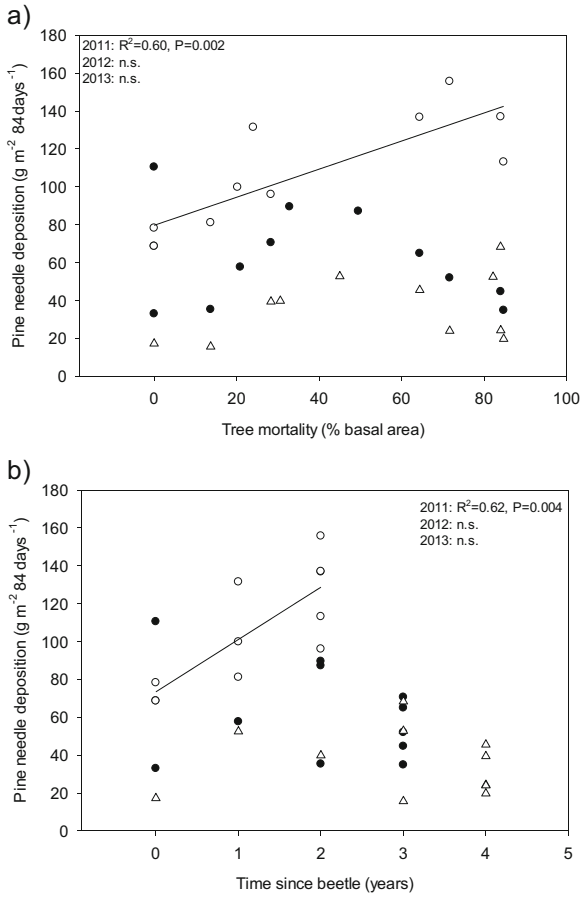

Fig. 2 Relationship between pine needle deposition and **a**) tree mortality caused by *Dendroctonus ponderosae* and **b**) time since beetle outbreak in lodgepole pine (*Pinus contorta* var. *latifolia* Engelm) forests in western Alberta (Canada) for 2011 (*open circles*), 2012 (*closed circles*) and 2013 (*triangles*). Litter traps were positioned at ten locations within each of the 11 sites and values were pooled by site over a growing season (May-September). Points are raw data values

in western Canada: aboveground canopy inputs (pine needlefall), loss of living fine root mass, and associated processes linked to mineralization and uptake. Below, we discuss the relative importance of, and possible linkages among, such pathways of nutrient cycling in lodgepole pine forests within the expanded range of *D. ponderosae*.

Beetle-caused tree mortality and increased needle nutrient input

Tree mortality as a consequence of the *D. ponderosae* outbreak increased rates of needlefall, and concentrations of macronutrients (N, P, K, Mg) were higher in needles in beetle-killed stands than healthy stands thus compounding nutrient inputs from canopy to forest floor. Tree mortality accelerated rates of needlefall, but rates declined over time as needle were depleted from tree crowns. Recent evidence also shows elevated concentrations of N (Morehouse et al. 2008; Griffin et al. 2011, 2013) and P (Page et al. 2012) in needles from *D. ponderosae*-killed trees; this is attributed to a lack of nutrient resorption prior to needle abscission. Though needles falling from beetle-killed trees had more N- and P than needles falling from healthy pines, this did not translate into differences in decomposition rates over gradients of tree mortality or time. These results are in agreement with earlier studies, which found that bark beetles do not immediately (4–5 years after peak outbreak) alter fluxes of inorganic N from the canopy to soils in lodgepole pine forests in western North America (Griffin et al. 2011).

We suspect several mechanisms may account for these results. Most breakdown occurs in mineral soil horizons rather than soil surfaces (Prescott et al. 2004), which in our sites typically included a thick (3–8 cm) organic layer. Substantial input of C associated with a pulse of needle deposition may, despite higher background concentrations of N, P, K, and Mg, initiate a period of temporary deficit in the supply of some nutrients, particularly N, driven by rapid immobilization into microbial biomass (i.e., N depression) (Fahey 1983), and/or translocation of N from mineral to organic horizons of soil (Yavitt and Fahey 1986). For example, fresh lodgepole pine litter on the forest floor accumulated N for about 8 years until net N mineralization occurred, at which point 60 % of original mass was lost (Yavitt and Fahey 1986). Although concentrations of N and P in litter leachates were initially high in the same study, concentrations declined rapidly and were dominated by organic rather than mineral forms of these elements; little change in the P content of litter occurred overall (Yavitt and Fahey 1986). The cumulative effects of macronutrient inputs on mineral nutrient supply in soil may not peak until at least 5 years after beetle disturbance (Huber 2005) as organic matter decomposes and nutrients gradually mobilize into mineral horizons (Remsburg and Turner 2006; Griffin et al. 2011; Griffin and Turner 2012). This is consistent with our findings of increased availability of most macro- and micronutrients over 0–4 year period after initial beetle infestation, during which some mineralization of litter and leachate as well as minor shifts in absolute (rather than relative) decomposition rates probably each lead to a limited

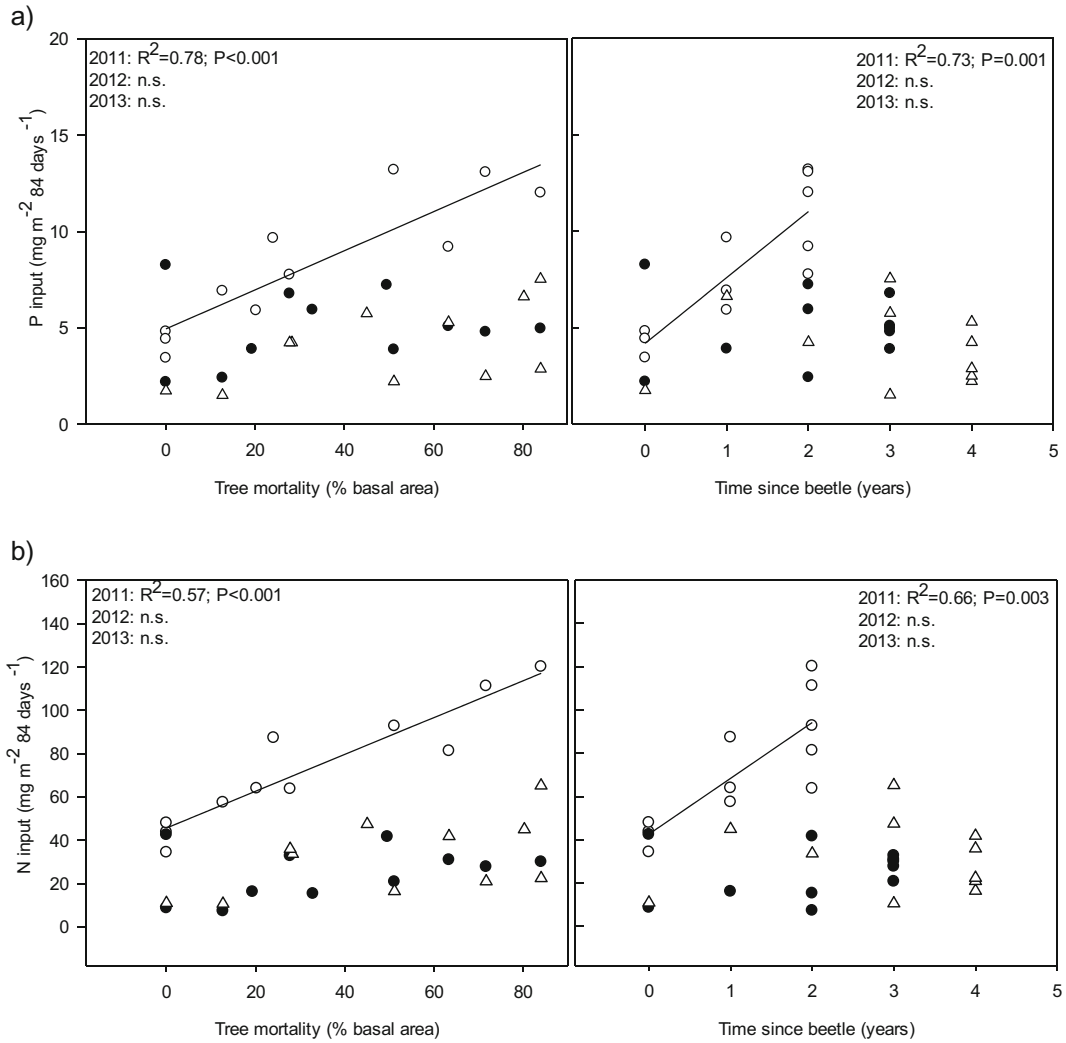

Fig. 3 Relationships between growing season (May-September) canopy **a**) phosphorus and **b**) nitrogen inputs and tree mortality caused by *Dendroctonus ponderosae* and time since beetle outbreak in lodgepole pine (*Pinus contorta* var. *latifolia* Engelm) forests in western Alberta (Canada) for 2011 (*open circles*), 2012 (*closed circles*) and 2013 (*triangles*). Points are raw data values

amount of mineral nutrient input over time. Overall, however, these results indicate that, within that same time frame, supply of mineral N in soils may be driven by belowground processes related to the loss of living roots resulting in reduced plant demand (Griffin and Turner 2012). In addition to the possible mechanisms discussed above, it appears that pre-disturbance ecosystem characteristics, such as amounts of N reserved in the soil (Griffin and Turner 2012), litter quality (lignin:N ratio (Scott and Binkley 1997; Prescott 2005) and moisture (Remsburg and Turner 2006)), as well as resident plant communities (Hobbie 1992) may also affect litter decomposition and therefore fluxes of inorganic N from the canopy to soils.

Decrease in root mass and soil phenolics and increase in soil nitrification

Reduction in the abundance and possibly in production of living root mass may have influenced soil nutrient supply rates via decreases in uptake and exudate production (Griffin et al. 2011; Simard et al. 2011). In association with beetle-driven tree mortality, the loss of root processes, particularly water and mineral nutrient uptake (Hubbard et al. 2013), may be one of the most important factors influencing the belowground environment (Xiong et al. 2011). Shallow fine roots declined in abundance as a function of time since beetle infestation,

Table 3 Results from linear mixed effects models to determine significance of main effects between and interactions among beetle disturbance (i.e., tree mortality and time since beetle) and responses in soil moisture, pH, supply of nutrients, and soil surface relative humidity

Responses	Intercept[a]	%BK	TSB	Year	%BK * TSB	%BK * Yr	TSB * Yr	%BK*TSB*Yr
ndf,ddf [2]	1,11	1,11	1,11	2,11	1,11	2,11	2,11	2,11
Soil moisture	218.1****	9.1**	0.4	2.3	0.5	3.1	0.1	1.1
Soil pH	193.3****	8.5**	0.1	131.3****	0.1	0.5	0.3	0.4
Al	135.1****	58.9****	83.9****	53.6****	0.0	0.8	6.0**	0.3
Ca	492.3****	0.3	4.1	1.3	0.0	1.2	0.2	2.0
Fe	23.5***	5.5*	15.5**	14.9***	4.6	0.6	1.4	2.1
K	38.6****	0.2	0.4	9.2**	2.3	0.4	0.5	1.3
Mg	108.9****	0.1	1.2	14.5***	0.3	2.5	0.4	4.6*
Mn	32.6****	0.3	5.3*	1.6	0.1	1.1	0.2	0.2
NH_4^+-N	49.3****	1.7	4.4	0.6	13.3**	0.3	0.4	3.0
NO_3^-N	175.9****	10.5**	4.2	10.2**	17.8***	1.2	0.8	0.4
P	83.5****	25.5***	47.0****	37.4****	0.1	2.2	1.0	0.7
S	40.3****	3.1	28.1***	2.6	0.0	2.7	9.9**	1.7
Zn	50.1****	36.6****	7.3*	6.4*	1.1	1.0	0.4	0.7
Relative Humudity	546.8****	253.9****	1561.8****	348.4****	0.1	4.7	4.9	8.6*

[a] F values followed by *P* values were reported. Means are significant at $\alpha<0.05$. * $P<0.05$, ** $P<0.01$, *** $P<0.001$, **** $P<0.0001$

[b] ndf,ddf represent numerator and dominator degrees of freedoms respectively

Fixed factors included sampling year (2011–2013), percent tree mortality (%BK), and time since beetle (TSB) residuals. Co-linearity between percent tree mortality and time since beetle necessitated the replacement in the models of that factor with its residuals that result from being regressed against percent tree mortality

which is consistent with slow decomposition of fine roots reported in an earlier review (Silver and Miya 2001). As the proportion of beetle-killed trees in a stand accumulates over time, a cumulative decline in water and nutrient demand and uptake likely promoted increased availability of soil resources, etching a time signal in our results (Griffin et al. 2011; Griffin and Turner 2012; Hubbard et al. 2013).

While a lag effect of tree mortality is consistent with supply trends for most minerals reported in the literature (Mikkelson et al. 2013), soil moisture and NO_3^- were not sensitive to time, but were sensitive to tree mortality. For example, studies conducted in other conifer systems in western North America have reported low NO_3^- production and export after a large portion of trees are killed (by insect or fire) or are removed (harvesting) (Parsons et al. 1994; Prescott et al. 2003; Thiel and Perakis 2009). This may reflect immediate and sustained demand for water and NO_3^- by surviving vegetation at rates in excess of those for input, mineralization, and mobilization that would otherwise promote accumulations over time (Griffin et al. 2011). In the case of NO_3^- supply, however, this result may suggest that other ecologically significant mechanisms are contributing to soil NO_3^- supply after extensive tree death, such as chemical interactions between N and soil phenolics.

Living roots are a major source of organic acid inputs to the rhizosphere, including phenolics which can potentially influence N cycling in forest soils via allelopathic interference (Hattenschwiler and Vitousek 2000; Meier et al. 2008). Phenolics may inhibit the mineralization of organic matter and the activity of nitrifying bacteria (e.g., *Nitrosomas* spp.), in effect slowing rates at which NH_4^+ is converted to NO_3^- (i.e., nitrification) (Northup et al. 1995). Loss of soil phenolics, likely linked to reductions in live tree root mass and hence in the current study, phenolics production, may accelerate rates of N mineralization and nitrification (Hattenschwiler

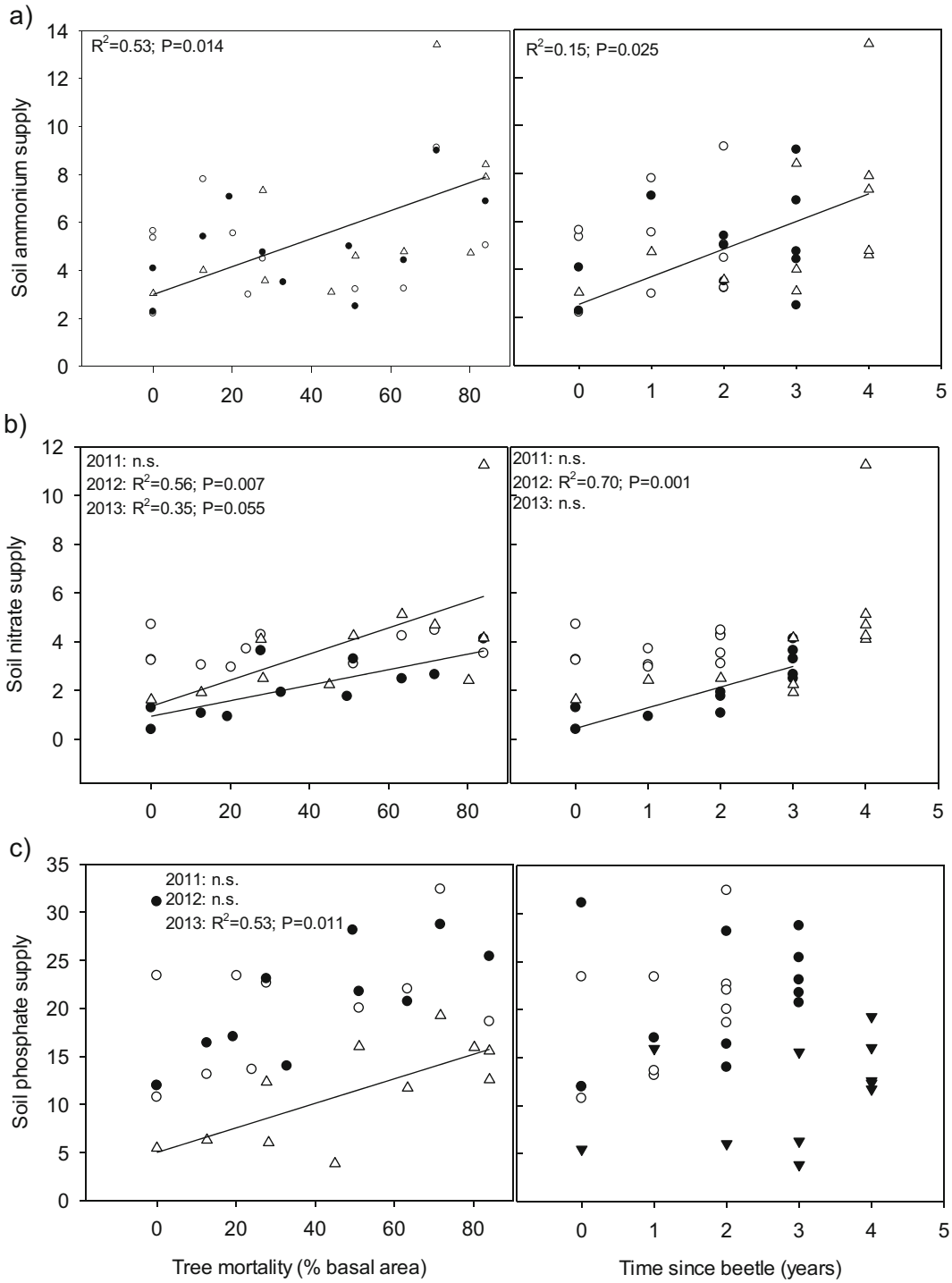

Fig. 4 Relationships between supply of soil **a**) ammonium, **b**) nitrate, and **c**) phosphate and tree mortality caused by *Dendroctonus ponderosae* and time since beetle outbreak in lodgepole pine (*Pinus contorta* var. *latifolia* Engelm) forests in western Alberta (Canada) for 2011 (*open circles*), 2012 (*closed circles*) and 2013 (*triangles*). Supply rates are measured in the top 10 cm of mineral soil at ten locations at each of the 11 sites and pooled. Supply rates were measured as the weight of nutrient adsorbed per surface area of ion-exchange membrane over time (μg nutrient/10 cm^2 ion-exchange membrane surface area/time of burial)

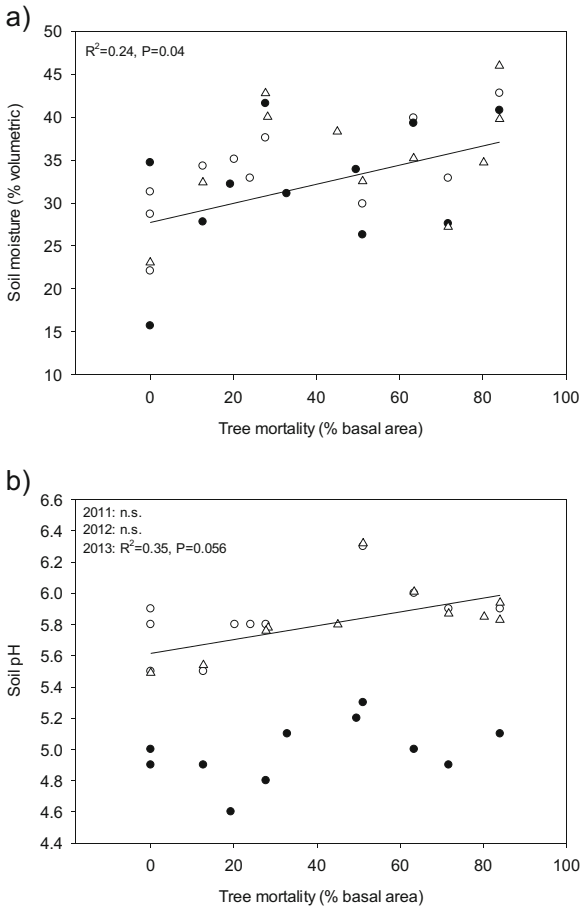

Fig. 5 Relationships between soil **a**) moisture, and **b**) pH and tree mortality caused by a *Dendroctonus ponderosae* outbreak in lodgepole pine (*Pinus contorta* var. *latifolia* Engelm) forests in western Alberta (Canada) for 2011 (*open circles*), 2012 (*closed circles*) and 2013 (*triangles*). Both moisture and pH were measured in the top 10 cm of mineral soil at ten locations at each of the 11 sites and pooled

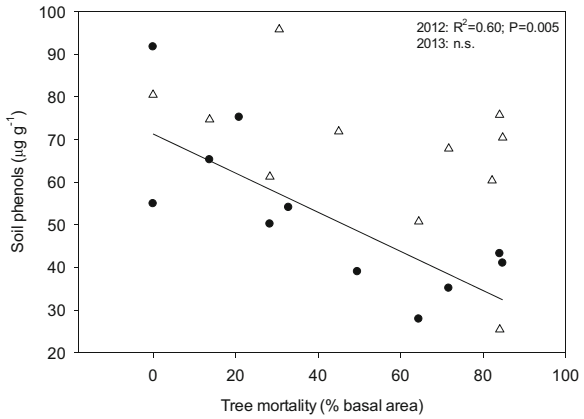

Fig. 6 Relationship between soil phenolics and tree mortality caused by *Dendroctonus ponderosae* outbreak in lodgepole pine (*Pinus contorta* var. *latifolia* Engelm) forests in western Alberta (Canada) in 2012 (*circles*) and 2013 (*triangles*). Phenolics were extracted from mineral soils to a depth of 6 cm collected 1 m from each of seven litter traps and values were pooled by site (n=11). Points are raw data values expressed as µg phenolics per g of soil

and Vitousek 2000; Meier et al. 2008). Elevated supply of NH_4^+ and NO_3^- may be partially explained by accelerated rates of mineralization and nitrification both of litter leachates and pre-existing organic matter within soils following reduced phenolics-mediated allelopathic constraint on cycling processes.

While no previous evidence links bark beetle outbreaks to shifts in soil phenolics, the known effects of phenolic reductions are consistent with the soil responses reported in earlier investigations of *D. ponderosae* outbreaks, including increased rates of net mineralization (Griffin et al. 2011), net nitrification (Morehouse et al. 2008; Griffin et al. 2011), and pools of both NH_4^+ (Morehouse et al. 2008; Clow et al. 2011; Griffin et al. 2011; Xiong et al. 2011) and NO_3^- (Clow et al. 2011; Keville et al. 2013). In these studies, beetle disturbance was postulated to impact soil N dynamics by altering needle input and subsequent N mineralization (Morehouse et al. 2008; Griffin et al. 2011), soil temperature and moisture (Collins et al. 2011; Clow et al. 2011; Griffin et al. 2013), vegetative uptake and long-term retention (Collins et al. 2011; Griffin

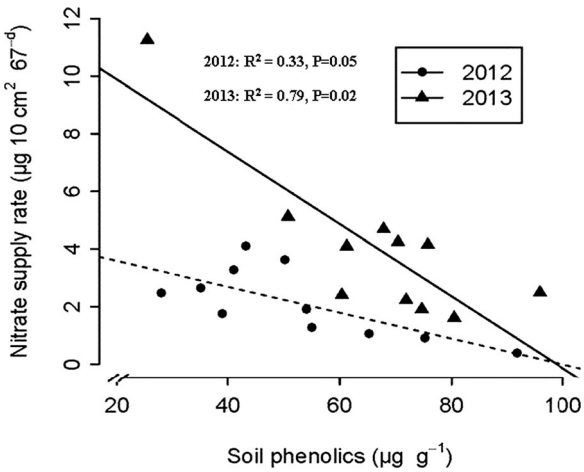

Fig. 7 Relationship between soil nitrate supply rate and soil phenolics in 2011 (*circles*) and 2012 (*triangles*). Points are raw data values

et al. 2011), and hydrological export (Clow et al. 2011). Based on these results, we hypothesize that, in addition to changes in needle nutrient input, altered biogeochemical interactions involving the loss of living roots, associated shifts in root-based phenolics, and subsequent interactions between phenolics and N cycling processes, may also affect NH_4^+ and NO_3^- concentrations in the soil.

Although our study links *D. ponderosae* outbreak to decreased concentrations of soil phenolics through reduced abundance of shallow fine roots, greater needle deposition may have partially countered this effect. Polyphenolics leach rapidly from lodgepole pine litter, comprising about 80 % of litter leachate (Yavitt and Fahey 1986). However, leaching gains appear insufficient to offset root-based losses in phenolics input, as soil phenolic concentrations decreased along the tree mortality gradient in 2011 despite elevated rates of needle deposition. Phenolic-rich litter leachates may have accounted for a smaller overall fraction of the soil phenolics content relative to that produced by roots, formed insoluble phenolics-protein complexes, were removed either by surface runoff or water percolation to lower soil horizons, or combinations therein (Hattenschwiler and Vitousek 2000).

Conclusions

Our study adds to a growing body of evidence demonstrating that die-backs caused by *D. ponderosae* lead to changes in forest stand biogeochemistry (Edburg et al. 2012; Mikkelson et al. 2013), which has implications for long-term outcomes concerning nutrient cycling and vegetation dynamics. Nutrient loss, particularly NO_3^- through surface runoff and subsoil percolation, may rise due to increased soil moisture and temperature and N input; however, recent evidence suggests losses are minimal. For example, findings from post-beetle regeneration studies (Collins et al. 2011) as well as observational (Clow et al. 2011) and model simulation (Rhoades et al. 2013) studies on watershed discharge of NO_3^- show a compensatory response, whereby tree mortality spurs increased growth and N uptake in surviving vegetation, buffering nutrient loss. Moreover, Griffin et al. (2011) reported significant correlations between net N mineralization rates and N concentrations in current-year lodgepole pine foliage, suggesting N release through mineralization is matched closely by N uptake after outbreak. In addition, elevated foliar N concentrations persisted 30 years after outbreak in the same study, demonstrating a mechanism for long-term N storage. As the abundance increases for limiting soil resources such as N, extant saplings and advance regeneration will increase in growth (Collins et al. 2011) and factor more prominently into nutrient cycling during the stem exclusion stage of stand development.

Following *D. ponderosae* disturbance, soil nutrient cycling is influenced by effects associated with premature needle drop and root loss. Our findings show that rapid decline of key root functions in the rhizosphere, including the production and release of phenolics, and likely water and mineral uptake, may partially be responsible for the changes in N cycling in beetle-killed lodgepole pine stands. Although our study was limited to 1–4 years post-outbreak, we suspect that the effects of needle deposition on soil nutrient cycling will likely increase over time via increased decomposition and mineralization rates (Yavitt and Fahey 1986; Huber 2005; Edburg et al. 2012; Mikkelson et al. 2013). Increased soil nutrients will likely improve growth rates of residual and regenerating tree species, thus accelerating return to a pre-disturbance standing-live carbon volume (Collins et al. 2011). However, some pre- and post-disturbance forest management activities, such as tree regeneration surveys and seedling planting, may be needed to address understocked forest conditions and other recently identified barriers to seedling establishment in forests of western Canada (Astrup et al. 2008).

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Appendix

Table 4

Table 4 Characteristics of forest structure and mountain pine beetle (*Dendroctonus ponderosae;* MPB) disturbance in lodgepole pine (*Pinus contorta* var. *latifolia* Engelm) forests in western Alberta (Canada) by site (means; N=11)

Site ID	Overstory tree age (yrs)	Pre MPB live tree basal area (m^2 ha^{-1})	Pre MPB live tree basal area (PICO; %)	Pre MPB live tree density (trees ha^{-1})	Tree mortality 2011 (m^2 ha^{-1})	Tree mortality 2012 (m^2 ha^{-1})	Tree mortality 2013 (m^2 ha^{-1})	Time since beetle (Yr; TSB; 2011–'13)
1	121	70.8	92	2154.5	0	0	0	0, 0, 0
2	120	47.4	92.3	903.5	0	9.1	13.4	0, 1, 2
3	123	36.4	97.6	625.5	0	0	29.2	0, 0, 1
4	121	61.7	94	2154.5	7.8	7.8	7.81	1, 2, 3
5	121	41.8	100	903.5	10.1	13.7	18.8	1, 2, 3
6	119	43.9	100	834	8.9	21.7	36.9	1, 2, 3
7	120	44.9	97.9	764.5	12.5	12.5	12.5	2, 3, 4
8	123	50.6	60.3	625.5	25.8	25.8	25.8	2, 3, 4
9	120	54.8	98.4	834	34.7	34.7	34.7	2, 3, 4
10	123	60.1	100	973	43.1	43.1	43.1	2, 3, 4
11	121	54.5	100	834	45.9	45.9	45.9	2, 3, 4

Trees were recorded as stems≥12 cm diameter at breast height (1.3 m). Lodgepole pine is coded as "PICO."

Table 5 Results from Pearson product-moment correlations to determine the significance and direction of relationships between lodgepole pine (*Pinus contorta* var. *latifolia* Engelm) forest structure and soil parameters, and the percentage of basal area killed by, and time since initial infestation of, mountain pine beetle (*Dendroctonus ponderosae*; MPB) (0–84 % and 0–4 years, respectively)

Response variables	Model statistics		Explanatory variables	
	r	P	Variable	Df (ndf, ddf)
Topography				
Elevation (m)	−0.51	0.11	% Tree mortality	1,9
Elevation (m)	−0.41	0.21	TSB	1,9
Slope (%)	0.39	0.23	% Tree mortality	1,9
Slope (%)	0.48	0.14	TSB	1,9
Aspect (0–360°)	0.16	0.64	% Tree mortality	1,9
Aspect (0–360°)	0.17	0.64	TSB	1,9
Forest structure				
Pre-MPB live basal area	0.23	0.51	% Tree mortality	1,9
Pre-MPB live basal area	0.2	0.56	TSB	1,9
Soils texture				
% sand	0.42	0.2	% Tree mortality	1,9
% sand	0.41	0.22	TSB	1,9
% silt	−0.41	0.22	% Tree mortality	1,9
% silt	−0.5	0.13	TSB	1,9
% clay	−0.19	0.58	% Tree mortality	1,9
% clay	−0.03	0.93	TSB	1,9

Table 5
Table 6
Table 7
Table 8

Table 6 Nutrient concentrations (% dry mass) of lodgepole pine (*Pinus contorta* var. *latifolia* Engelm) needles collected in July at 11 sites in western Canada

Site ID	Year	P	N	K	Mg	Ca
1	2011	0.062	0.559	0.209	0.055	0.260
2	2011	0.065	0.698	0.122	0.061	0.292
3	2011	0.050	0.501	0.303	0.082	0.174
4	2011	0.085	0.708	0.144	0.087	0.327
5	2011	0.074	0.664	0.124	0.089	0.343
6	2011	0.059	0.640	0.248	0.089	0.274
7	2011	0.081	0.663	0.273	0.071	0.285
8	2011	0.117	0.819	0.222	0.083	0.309
9	2011	0.067	0.594	0.195	0.050	0.221
10	2011	0.084	0.714	0.226	0.087	0.298
11	2011	0.088	0.877	0.075	0.091	0.347
1	2012	0.067	0.262	0.117	0.129	0.456
2	2012	0.068	0.280	0.144	0.115	0.310
3	2012	0.075	0.384	0.160	0.132	0.398
4	2012	0.068	0.208	0.143	0.104	0.393
5	2012	0.066	0.171	0.196	0.122	0.307
6	2012	0.083	0.477	0.244	0.116	0.297
7	2012	0.096	0.464	0.266	0.131	0.316
8	2012	0.112	0.597	0.303	0.122	0.307
9	2012	0.078	0.476	0.211	0.113	0.260
10	2012	0.092	0.533	0.265	0.126	0.255
11	2012	0.111	0.671	0.327	0.152	0.276
1	2013	0.101	0.638	0.124	0.119	0.428
2	2013	0.107	0.845	0.211	0.122	0.335
3	2013	0.126	0.858	0.270	0.112	0.248
4	2013	0.097	0.677	0.124	0.094	0.356
5	2013	0.109	0.898	0.221	0.107	0.344
6	2013	0.110	0.955	0.290	0.118	0.318
7	2013	0.108	0.912	0.240	0.116	0.339
8	2013	0.113	0.832	0.194	0.106	0.430
9	2013	0.116	0.918	0.226	0.107	0.313
10	2013	0.104	0.872	0.174	0.093	0.286
11	2013	0.119	0.925	0.241	0.108	0.287

Refer to Appendix Table 4 for values of extent tree mortality caused by mountain pine beetle (*Dendroctonus ponderosae*) and time since outbreak of each site

Table 7 Nutrient inputs (mg m^{-2} over 84 days) derived from deposition of lodgepole pine (*Pinus contorta* var. *latifolia* Engelm) needles at 11 sites in western Canada

Site ID	Year	*P*	*N*	*K*	Mg	Ca
1	2011	48.20	437.37	163.37	43.27	203.11
2	2011	44.30	479.44	83.61	42.21	200.51
3	2011	34.45	343.85	207.95	56.49	119.75
4	2011	69.12	574.40	116.85	70.44	265.13
5	2011	96.64	873.04	163.02	116.42	450.42
6	2011	59.12	639.14	247.64	88.64	273.43
7	2011	77.61	636.84	262.04	67.80	273.77
8	2011	132.06	926.82	250.95	94.16	349.76
9	2011	92.04	812.39	266.30	68.23	302.42
10	2011	130.79	1111.75	352.52	135.62	463.23
11	2011	120.19	1201.85	103.12	124.35	475.00
1	2012	21.95	86.60	38.76	42.55	150.33
2	2012	39.05	161.69	83.32	66.51	179.07
3	2012	82.64	424.60	176.93	145.61	439.70
4	2012	24.14	73.26	50.52	36.83	138.79
5	2012	59.44	152.89	175.25	108.94	274.43
6	2012	72.28	415.88	212.98	100.78	258.96
7	2012	67.82	327.26	187.43	92.75	222.78
8	2012	38.82	207.76	105.36	42.49	106.93
9	2012	50.91	309.32	137.00	73.24	168.94
10	2012	47.98	277.13	137.64	65.46	132.37
11	2012	49.72	299.91	146.06	68.09	123.59
1	2013	17.48	110.05	21.31	20.57	73.80
2	2013	42.42	336.52	83.93	48.50	133.31
3	2013	66.28	450.11	141.53	58.91	130.31
4	2013	15.19	106.10	19.47	14.71	55.86
5	2013	57.56	474.16	116.82	56.25	181.52
6	2013	75.41	652.04	198.32	80.86	216.88
7	2013	42.46	359.76	94.78	45.61	133.81
8	2013	22.26	164.16	38.34	21.01	84.78
9	2013	52.99	418.22	102.81	48.88	142.77
10	2013	24.93	209.24	41.75	22.37	68.67
11	2013	28.85	224.51	58.55	26.10	69.56

Refer to Appendix Table 4 for values of extent tree mortality caused by mountain pine beetle (*Dendroctonus ponderosae*) and time since outbreak of each site

Table 8 Mineral soil A-horizon nutrient supply rates of 11 lodgepole pine (*Pinus contorta* var. *latifolia* Engelm) sites in western Canada

Site ID	Year	NO3 N	NH4 N	Ca	Mg	K	P04	Fe	Mn	Zn	S	Al
1	2011	3.26	2.20	1625.1	344.0	53.66	10.75	4.18	5.60	1.23	49.45	16.17
2	2011	3.23	5.36	1584.9	268.0	99.27	11.97	13.20	37.40	4.42	35.80	30.81
3	2011	4.71	5.64	1827.8	268.0	38.99	23.41	17.76	99.00	3.89	97.32	40.69
4	2011	3.04	7.80	1311.8	268.3	155.13	13.13	35.49	109.50	3.60	63.77	46.32
5	2011	3.70	2.99	1673.4	255.2	28.90	13.64	30.08	27.95	2.98	61.43	32.71
6	2011	2.95	5.54	1630.0	227.7	75.19	23.40	12.57	48.50	4.32	75.96	37.26
7	2011	4.28	4.48	1681.7	250.7	71.51	22.64	11.49	66.50	5.39	94.94	57.76
8	2011	3.09	3.22	1795.7	226.4	114.66	20.03	6.22	27.70	2.62	53.30	19.89
9	2011	4.23	3.24	1884.2	214.4	25.36	22.02	15.05	30.80	2.90	138.43	34.20
10	2011	4.47	9.12	1404.6	254.5	150.19	32.41	3.77	93.00	4.07	20.52	29.52
11	2011	3.51	5.04	1559.1	241.1	133.57	18.62	43.35	86.40	3.22	83.25	41.93
1	2012	0.39	2.28	1623.6	356.2	102.12	11.95	9.99	16.10	1.23	49.45	16.17
2	2012	0.92	7.07	1466.5	267.2	156.60	17.05	5.69	22.40	4.42	35.80	30.81
3	2012	1.28	4.08	1782.5	302.9	110.04	31.11	8.87	75.30	3.89	97.32	40.69
4	2012	1.06	5.41	1228.2	263.7	193.17	16.40	8.62	37.70	3.60	63.77	46.32
5	2012	1.91	3.51	2026.2	336.1	65.85	14.00	11.86	59.80	2.98	61.43	32.71
6	2012	1.75	5.00	1907.5	298.9	124.72	28.14	14.73	66.40	4.32	75.96	37.26
7	2012	3.63	4.75	1852.2	266.1	76.18	23.09	10.80	61.00	5.39	94.94	57.76
8	2012	3.28	2.50	1821.0	239.7	118.94	21.76	4.94	23.40	2.62	53.30	19.89
9	2012	2.47	4.42	2012.9	250.2	58.81	20.71	12.29	49.10	2.90	138.43	34.20
10	2012	2.65	8.99	1479.5	278.4	202.90	28.73	6.02	80.80	4.07	20.52	29.52
11	2012	4.11	6.88	1737.3	278.8	172.97	25.42	16.96	77.90	3.22	83.25	41.93
1	2013	1.62	3.04	1495.8	379.7	78.60	5.45	25.49	7.99	2.38	71.13	53.64
2	2013	2.49	3.58	1840.3	280.8	44.25	6.03	118.23	28.33	5.50	45.62	51.19
3	2013	2.41	4.73	1618.8	273.5	86.40	15.94	48.09	67.48	5.34	111.26	66.07
4	2013	1.91	4.00	1403.2	265.1	62.41	6.29	137.13	57.08	4.21	50.46	75.54
5	2013	2.24	3.10	1908.7	304.4	39.96	3.83	86.04	27.05	3.14	71.02	56.01
6	2013	4.15	8.41	1885.3	270.1	70.60	15.57	104.29	38.57	6.94	80.25	60.00
7	2013	4.10	7.34	1864.2	268.0	52.95	12.34	102.17	44.55	6.35	43.24	60.06
8	2013	4.25	4.60	1587.3	206.6	168.28	16.03	8.73	10.00	2.57	26.07	39.59
9	2013	5.12	4.78	2079.5	260.5	36.59	11.72	51.80	33.06	3.98	97.92	60.47
10	2013	4.69	13.40	1410.3	265.5	161.91	19.27	11.79	42.95	3.96	20.29	48.41
11	2013	11.25	7.90	1600.0	230.3	132.40	12.58	57.33	64.46	3.75	55.42	63.19

Units are expressed as the weight of nutrient adsorbed per surface area of ion-exchange membrane over time (μg nutrient/10 cm^2 ion-exchange membrane surface area/time of burial (67 days)). Site means are derived from ten locations. Refer to Appendix Table 4 for values of extent tree mortality caused by mountain pine beetle (*Dendroctonus ponderosae*) and time since outbreak of each site

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