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A Decade of Streamwater Nitrogen and Forest Dynamics after a Mountain Pine Beetle Outbreak at the Fraser Experimental Forest, Colorado

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ABSTRACT

Forests of western North America are currently experiencing extensive tree mortality from a variety of bark beetle species, and insect outbreaks are projected to increase under warmer, drier climates. Unlike the abrupt biogeochemical changes typical after wildfire and timber harvesting, the outcomes of insect outbreaks are poorly understood. The mountain pine bark beetle (*Dendroctonus ponderosae*) began to attack lodgepole pine (*Pinus contorta*) at the Fraser Experimental Forest in 2002 and spread throughout the research area by 2007. We compared streamwater nitrogen (N) from 2003 through 2012 with data from the previous two decades in four watersheds with distinct forest management histories, stand structures, and responses to the beetle outbreak. Watersheds dominated by old-growth had larger trees and lost 85% of overstory pine and 44% of total basal area to bark beetles. In contrast, managed watersheds containing a mixture of second-growth (30–60 year old) and old-growth (250- to 350-year old) had higher density of subcanopy trees, smaller mean tree diameter, and lower bark beetle-

induced mortality (~26% of total basal area). Streamwater nitrate concentrations were significantly higher in old-growth watersheds during the outbreak than pre-outbreak levels during snowmelt and base flow seasons. In mixed-age stands, streamwater nitrate concentrations were unaffected by the outbreak. Beetle outbreak elevated inorganic N export 43 and 74% in two old-growth watersheds though the amounts of N released in streamwater were low (0.04 and 0.15 kg N ha⁻¹) relative to atmospheric inputs (<2% of annual N deposition). Increased height, diameter, and foliar N of measured in residual live trees augmented demand for N, far in excess of the change in N export during the outbreak. Reallocation of soil resources released after pine mortality to overstory and understory vegetation helps explain high nutrient retention in watersheds affected by bark beetle outbreaks.

Key words: watershed biogeochemistry; forest disturbance; nitrate; Rocky Mountains.

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Author Contributions All authors conceived the study performed research and analyzed data. CCR wrote the paper with input from the others.

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INTRODUCTION

Bark beetle outbreaks have created a severe, extensive, and synchronous disturbance in recent decades that has transformed many North Ameri-

can forests. Mountain pine beetle (MPB) outbreaks often kill more than 80% of overstory trees in Colorado lodgepole pine forests (*Pinus contorta* Dougl. ex. Loud. var. *latifolia*); (Collins and others 2011; Diskin and others 2011). Native bark beetles (Scolytidae) are common to conifer forests throughout the region (Veblen and Donnegan 2005; Raffa and others 2008), yet for the first time on record, concurrent outbreaks have spanned from Colorado to British Columbia (Aukema and others 2006; van Mantgem and others 2009). Since 1996, bark beetles have infested 100,000 km² of western North America forests and more than 13,300 km² of Colorado pine forests (US Forest Service 2013). The outbreaks in the Rocky Mountains states were triggered by regional-scale drought conditions around 2002 (Chapman and others 2012; Creeden and others 2014), consistent with expectations that warmer, drier conditions will expand insect activity and forest disturbance (Bentz and others 2010; Choat and others 2012; Allen and others 2015). Projections that changing climate will create more frequent or extensive insect outbreaks (Logan and others 2003; Anderegg and others 2015; Trumbore and others 2015) have potential consequences for ecosystem processes and watershed biogeochemistry.

The effects of beetle attack on individual trees and within forest stands are dramatic. Within months of a successful attack, bark beetles, and more specifically the fungi they introduce to infested trees, halt water and nutrient uptake (Christiansen and others 1987; Hubbard and others 2013). The decline in nutrient demand after tree mortality elevates soil ammonium and nitrate 2–5 times above that found in stands of healthy trees (Morehouse and others 2008; Clow and others 2011; Griffin and others 2011; Xiong and others 2011; Cigan and others 2015). Low understory plant uptake following tree mortality has also been linked to higher nitrate leaching in Bavarian spruce forests (Huber 2005; Kana and others 2013). Higher litter nitrogen (N) inputs and increased production of inorganic soil N (that is, net N mineralization and nitrification) are common in infested stands as outbreaks proceed (Morehouse and others 2008; Griffin and others 2011; Kana and others 2013). The broader-scale consequences of beetle attacks are likely to depend on the relative degree of host tree mortality and the compensating responses of residual live trees, understory vegetation, and soil microbes.

Unlike the abrupt increase in streamwater nitrogen (N) that commonly follows wildfire and timber harvesting, the watershed-scale, biogeo-

chemical outcomes of bark beetle outbreaks are poorly understood. A recent comparison of independent watershed-scale studies, for example, found surprisingly minor changes in stream nitrate during the initial years of the bark beetle outbreak in Colorado lodgepole pine forests (Rhoades and others 2013). Watershed attributes (aspect, slope, area, and forest extent) were better related to stream nitrate than to the density of dead trees in MPB-affected Colorado basins during one post-attack snowmelt season (Clow and others 2011). In those cases, nitrate losses were much less than those typical after logging or other types of forest disturbance (Vitousek and others 1979; Rhoades and others 2011). The large spatial and temporal variability in MPB-induced forest mortality requires analyses that span the outbreak period and consider changes in forest vegetation.

Stimulated growth of nonhost vegetation is likely to mediate stand and watershed-scale responses to MPB outbreaks. Healthy trees in beetle-infested pine stands grew faster (Romme and others 1986) and had 20 to 30% higher foliar N content than trees in unaffected pine stands (Griffin and others 2011); these differences remained evident for decades following infestation. Nutrient uptake by live trees limited nitrate leaching in gaps created to simulate bark beetle outbreaks in southern Wyoming lodgepole pine forests (Parsons and others 1994). Probably in response to changes in soil resources, the foliar N content of residual live trees increased within 2 years of infestation in a Colorado pine stand (Hubbard and others 2013). The minimal stream N responses reported by the Colorado studies (Clow and others 2011; Rhoades and others 2013) are consistent with high plant and soil microbial nutrient demand and low nutrient supply typical of undisturbed lodgepole pine ecosystems in the Southern Rockies (Fahey and others 1985; Knight and others 1985; Stottlemeyer and others 1997). Nevertheless, to elucidate how stand conditions and host tree mortality influence watershed biogeochemistry, there is a need for longer-term comparisons that encompass pre-disturbance conditions and the full extent of the outbreak.

Bark beetles were detected in 2003 in lodgepole pine trees at the Fraser Experimental Forest (FEF) in trees attacked in 2002. Epidemic levels of beetle emergence were measured in various locations at Fraser the following year (Tishmack and others 2004). As expected (Roe and Amman 1970), bark beetles preferentially attacked the larger diameter pine trees at FEF killing 90% of trees at least 30 cm in diameter (Figure 1). Watershed-scale harvesting

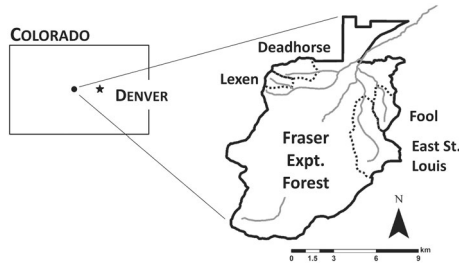


Figure 1. Study watersheds at the US Forest Service, Fraser Experimental Forest, Colorado.

research has created distinct forest conditions at FEF that allow us to examine the linkages between forest structure, tree mortality, and watershed-scale biogeochemical responses to MPB. Here, we analyze streamwater data in four research watersheds for the decade following onset of the outbreak (2003–2012) with a twenty-year record of pre-outbreak conditions. An earlier cross-study synthesis (Rhoades and others 2013) used a portion of the data record for a single FEF watershed. We hypothesize that changes in stream N will reflect differences in lodgepole pine abundance and stem diameter. As such, we predict smaller changes in stream N in watersheds with more younger, smaller trees and lower MPB-induced mortality.

METHODS

Site Description

The Fraser Experimental Forest (FEF) lies west of Denver and the Continental Divide on the western edge of Colorado's Front Range (Figure 1). The forests at FEF are a mix of lodgepole pine, subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*), and part of the temperate steppe mountain ecoregion that extends from New Mexico to southern Canada (Bailey 1998). Lodgepole pine dominates the overstory of lower elevation and south-aspect stands (Huckaby and Moir 1998). Shade-tolerant conifers (fir and spruce) are common to the understory of pine-dominated stands. Mixed-species forests occupy valley bottom and north-facing slopes and extend to treeline (3300–3500 m); fir and spruce dominance increases with elevation and stand age. Low-stature shrubs (*Vaccinium scoparium*, *V. myrtillus*, *V. caespitosum*, and *Shepherdia canadensis*) form a dense understory beneath the coniferous overstory (Popovich and others 1993).

Fraser has long cold winters and short cool summers; mean annual air temperature is 0.6°C with January and July average temperatures of

–10 and 12.2°C, respectively (USFS unpublished 1976–2005 data). As recorded throughout Colorado (Lukas and others 2014), daily minimum temperatures at FEF have increased during the past 30 years (Fraser Experimental Forest, unpublished data). Total annual precipitation averages 750 mm, primarily as snowfall (75%). Annual inorganic N deposition and stream export averaged 2.6 and 0.1 kg N ha⁻¹, respectively, the decade before onset of the outbreak. The heavily glaciated FEF is underlain by metamorphosed rock, most commonly biotite schist and hornblende or calc-silicate gneiss (Shroba and others 2010). Soils are typically skeletal, sandy loam Dystric and Typic Cryochrepts (Alstatt and Miles 1983); subsurface soils contain 20–30% gravel and 30–50% cobble-sized materials.

Historic Watershed Treatments

The four watersheds included in this analysis represent two paired watershed studies designed to quantify the effects of forest management on vegetation and hydrology. Harvesting of the Fool Creek–East Saint Louis Creek study occurred between 1954 and 1956. Approximately half of the forested, gauged portion of the Fool Creek watershed, was cleared in strip cuts; the gauged portion of the East Saint Louis Creek watershed was not logged. Harvesting of the Deadhorse Creek–Lexen Creek study was conducted between 1977 and 1984. Approximately 30% of the forested portion of the Deadhorse Creek watershed was cleared in circular and irregular clear cuts; the Lexen Creek watershed was not harvested. The East Saint Louis and Lexen Creek watersheds represent old-growth forest conditions and the two managed watersheds (Fool and Deadhorse Creek) contain a mixture of old- and second-growth forest.

Sampling and Analysis

Since the early 1980s, stream water samples have been collected at stream gauges and analyzed for nutrients and major anions and cations weekly between April and October and less frequently during winter. Samples for dissolved inorganic nitrogen (NO₃-N and NH₄-N) analysis were collected in opaque plastic bottles. Prior to use, plastic sample bottles were triple washed with deionized water (electrical conductivity <1.0 µS cm⁻¹). Stream water samples were collected after triple-rinsing bottles in sample water. Samples were refrigerated after collection then filtered through 0.45-µm mesh membrane filters (Millipore Durapore PVDF). Dissolved organic carbon (DOC) has been analyzed at FEF since 2008; DOC samples

were collected in precombusted (heated for 1 h at 500°C) amber, glass bottles and then filtered through 0.7- μm mesh glass fiber prefilters (Millipore Corporation, Billerica, MA).

Stream water nitrate ($\text{NO}_3\text{-N}$) and ammonium ($\text{NH}_4\text{-N}$) concentrations were determined by ion chromatography (Waters Co. Milford, MA.) and conductivity detection with a Dionex AS12A Anion-Exchange column, an AG12A guard column, and Waters IC-Pak Cation M/D column; APHA 1998a) using EZChrom Elite Software (Scientific Software Inc., Pleasanton, CA). Detection limits were 4 and 8 $\mu\text{g L}^{-1}$ for $\text{NO}_3\text{-N}$ and $\text{NH}_4\text{-N}$, respectively. Sample concentrations that were below the instrument recording limit were replaced with 0.5 times the minimum machine detection limit (2 and 4 $\mu\text{g L}^{-1}$ for $\text{NO}_3\text{-N}$ and $\text{NH}_4\text{-N}$, respectively). Analysis of DOC was determined by high-temperature combustion catalytic oxidation using a Shimadzu TOC-V_{CPN} total organic carbon analyzer (Shimadzu Corporation Columbia, MD). Detection limits for DOC were 50 $\mu\text{g L}^{-1}$.

The MPB outbreak spread across research areas at FEF by 2006. To capture the bulk of the forest mortality, we inventoried trees status (live, MPB-killed), diameter, and density in the old-growth and mixed-age watersheds in 2007, 4 years after onset of the outbreak. Overstory (>10 cm diameter) and subcanopy trees (<10 cm diameter) were measured in 68 old-growth- and 65 mixed-age, 10 m radius plots. Plots are associated with the long-term snow sampling network distributed across aspect, elevation and landscape position in FEF's primary research watersheds. Pre-outbreak, live pine density and diameter was summed or averaged from beetle-killed and live pine trees. Projected forest leaf area was calculated from allometric equations developed for conifer species at FEF (Kaufmann and others 1982). In 2010, we measured the annual height increment of understory conifers for the previous four years of the outbreak period.

We compared unmanaged, old-growth (East St. Louis, Lixen) and managed, mixed-age watersheds (Fool, Deadhorse) for two decades of pre-outbreak conditions and the decade following onset of the outbreak. In the southern Rockies, streamflow increases in April, peaks in early to mid-June, and returns to near baseflow levels in September (Figure 2). The rising and falling limbs of the hydrograph each span 3-month period and baseflow conditions extend from October through March. Instantaneous N concentrations from weekly grab samples were discharge weighted using daily mean streamflow. Statistical analysis of stream N con-

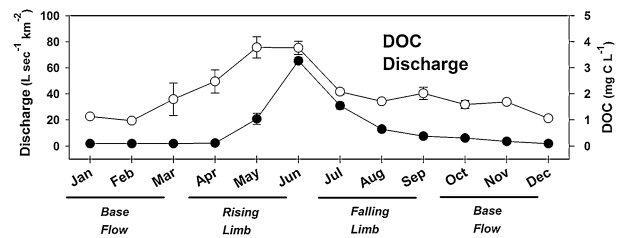


Figure 2. Seasonal carbon and discharge patterns in East St. Louis Creek, Fraser Experimental Forest, Colorado. Mean monthly concentrations and stream discharge with standard error (2008–2012). Analysis of dissolved organic carbon (DOC) began during the outbreak so consequences of bark beetles on this analyte are unknown.

centrations and export were partitioned among rising limb, falling limb, and baseflow periods based on typical snowmelt dominated streamflow patterns (Figure 2). We compared pre- and post-outbreak conditions within seasons using oneway and mixed-model analysis of variance (SPSS V. 22, IBM CO, Chicago, IL) with bark beetle outbreak phase and hydrological season as fixed effects and watershed as a random effect. Levene's statistic was used to test homogeneity of variance resulting from sample size differences between the pre- and post-outbreak record, and data were log-transformed prior to conducting analysis of variance when needed. Statistical significance is reported where $P < 0.05$ except where noted.

RESULTS

Stand Conditions and Responses to Bark Beetle Outbreak

Harvesting created a mixture of regenerating and old-growth stands in Fool Creek and Deadhorse Creek distinct from the two old-growth dominated, untreated watersheds (Table 1). Diameter and basal area of overstory lodgepole pine (>10 cm diameter) were lower in mixed-age watersheds, and subcanopy pine (<10 cm diameter) was more abundant. Lodgepole pine comprised 52% of overstory basal area in old-growth watersheds and only 37% in mixed-age watersheds. Subalpine fir was the most common subcanopy tree, representing 61–65% of live understory basal area and tree density in both watershed types. Fir, pine, and total understory tree density were all significantly higher in the mixed-age watersheds.

Bark beetles killed 90% of trees at least 30 cm in diameter (Figure 3). This resulted in the loss of 85% of overstory lodgepole pine trees in the two old-growth watersheds, equivalent to 44% loss of

Table 1. Stand Structure in Old-Growth and Mixed-Age Watersheds at the Fraser Experimental Forest

	Engelmann spruce	Subalpine fir	Lodgepole pine pre-MPB ^a	All species	MPB mortality	
					% of Pine	% of All
Overstory						
Diameter (cm)						
Old-growth watersheds	23.5	17.4	27.5***	22.6		
Mixed-age watersheds	24.5	17.0	23.4	21.6		
Basal area (m ² ha ⁻¹)						
Old-growth watersheds	13.2	8.5	23.1***	44.7***	84.7***	43.8
Mixed-age watersheds	13.5	9.4	13.2	36.2	60.0	26.4
Stand density (t ha ⁻¹)						
Old-growth watersheds	255.6	307.5	365	928	76.6***	32.5***
Mixed-age watersheds	217.4	371.2	280	869	49.9	16.7
Subcanopy						
Diameter (cm)						
Old-growth watersheds	5.5	5.1	6.1	5.5**		
Mixed-age Watersheds	5.1	4.9	5.3	5.1		
Basal area (m ² ha ⁻¹)						
Old-growth watersheds	0.7	1.5***	0.2**	2.3***	1.9	0.3
Mixed-age watersheds	0.7	2.3	0.8	3.8	0.0	0.0
Stand density (t ha ⁻¹)						
Old-growth watersheds	271.0	635.7***	67.4**	974.1***	6.0***	1.9
Mixed-ge watersheds	288.4	1028.4	330.6	1647.4	0.0	0.0

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Data are means for live overstory (> 10 cm diameter) and subcanopy trees (< 10 cm diameter) sampled in 2007 in 10 m radius plots ($n = 68$ old-growth plots and $n = 65$ mixed-age plots). Pre-mountain pine beetle (MPB)^a, pine was calculated from beetle-killed and residual live trees.

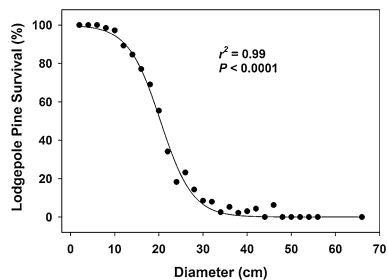


Figure 3. Relation between lodgepole pine survival and tree diameter, summarized by 2 cm diameter classes during mountain pine beetle outbreak at the Fraser Experimental Forest. Trees were sampled in 10 m radius plots in 2007, four years after onset of the outbreak.

overstory basal area. In contrast, in mixed-age watersheds, beetles killed 26% of total overstory basal area and support 1.7-fold higher live under-story tree density (Table 1). For subcanopy pine, fir, and spruce trees, average height growth was greater after bark beetle infestation, and height increment the four years after arrival of the beetles was proportional to beetle-related basal area or leaf area reduction of the surrounding overstory (Figure 4).

Streamwater Responses

In general, seasonal stream nitrate fluctuations and variation among watersheds were more pronounced than differences between the pre- and post-MPB periods (Figure 5). Peak nitrate concentrations were generally higher during the MPB period in East St. Louis compared with the pre-MPB record. The highest peak was measured in December 2011 and seven peak concentrations exceeded pre-MPB maxima ($\sim 125 \mu\text{g N L}^{-1}$) during the outbreak. Stream nitrate has been consistently lower in Fool Creek than East St. Louis since regular sampling began (1982), forty years after the harvesting treatments occurred (Stottlemeyer 1987). Nitrate was generally below the analytical detection limit in Fool Creek, with periodic spikes that exceed $50 \mu\text{g N L}^{-1}$; the MPB outbreak has not altered the magnitude or frequency of high nitrate values. Similarly, any residual effect of harvesting on stream nitrate, such as the general increase from the mid-1980s through mid-1990s in Deadhorse, was no longer evident at the onset of the bark beetle outbreak.

The inorganic nitrogen response to bark beetles varied among watersheds reflecting their forest

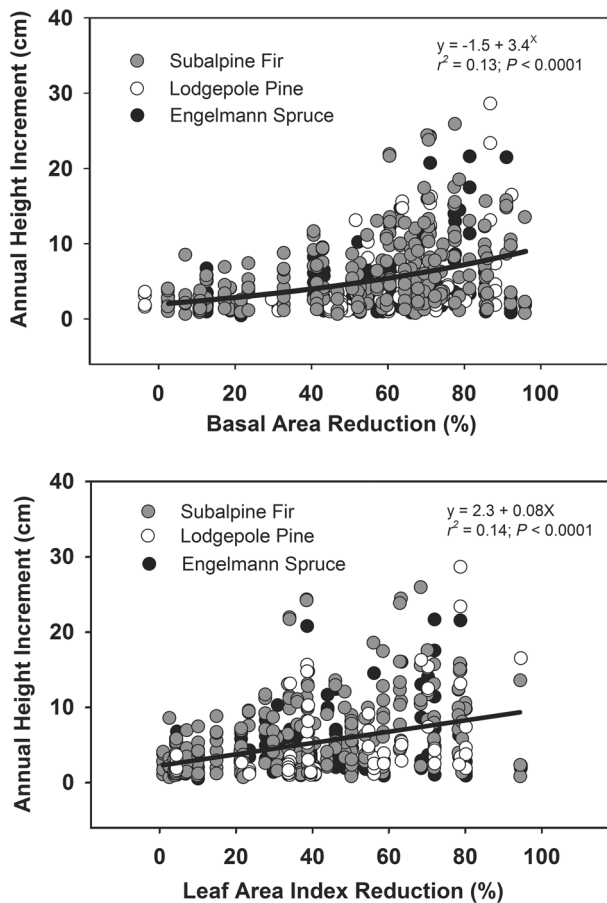


Figure 4. Mean height growth of understory trees (2007–2010) in four Fraser Experimental Forest watersheds and loss of basal area and projected leaf area index due to beetle-related mortality of surrounding overstory trees.

management history and among seasons. For example, discharge-weighted stream nitrate was significantly higher the decade after onset of the beetle outbreak in old-growth, but not mixed-age watersheds (Figure 6). In the two old-growth basins, the response to bark beetles was largest during base flow when stream nitrate increased 1.7-fold on average, and specifically from 53 to 89 $\mu\text{g N L}^{-1}$ and from 14 to 24 $\mu\text{g N L}^{-1}$ in East St. Louis and Lexen, respectively. Nitrate responses in these two basins were also significant during the rising limb of the hydrograph, though increases were relatively small. The effects of MPB were marginal statistically for one old-growth watershed (Lexen; $P = 0.095$) during the falling limb of the hydrograph when nitrate concentrations were lowest. Similar to the pattern observed for nitrate, baseflow ammonium concentrations were generally higher in response to beetle infestation, with little changes in other seasons (data not shown).

Total dissolved inorganic N (DIN = nitrate + ammonium) export was significantly higher from two old-growth watersheds during the MPB outbreak, though the magnitude of the increase was small (Figure 7). Annual DIN export is 0.3 and 0.1 kg N ha^{-1} from East St. Louis and Lexen, respectively, with about 50% of the annual flux occurring during the rising limb of the hydrograph. The two streams released 0.06 and 0.02 kg N ha^{-1} more DIN annually in the decade after arrival of the beetles. During the MPB outbreak, the two old-growth streams exported 1.4- and 1.8-fold more DIN during the rising limb. There were no significant changes during other seasons or in the mixed-age watersheds.

DISCUSSION

Linking Forest and Watershed Responses

The stream water N response of FEF watersheds to extensive overstory tree mortality was surprisingly minor. We detected no increase in inorganic N in mixed-age watersheds and in old-growth watersheds the beetle-related increase in DIN export amounted to only 1.5% of annual N deposition. Decreased tree N uptake and increased litter N inputs the months and years after bark beetle outbreaks have been associated with changes in soil N availability (Morehouse and others 2008; Clow and others 2011; Griffin and others 2011). Substantial increases in N losses have followed bark beetle attacks in some places, notably in areas with high N deposition (Huber 2005; Kana and others 2013). Yet some combination of plant, soil (Edburg and others 2011) and in stream (Bernhardt and others 2003) processes have limited the net biogeochemical effect of forest mortality in Fraser watersheds.

There are multiple lines of evidence indicating that higher nutrient demand resulting from growth of residual and new vegetation may help explain the weak watershed-scale patterns in stream N loss we document at Fraser and others have found elsewhere (Rhoades and others 2013). In spite of high levels of overstory mortality, the density of residual live trees was high (Collins and others 2011; Diskin and others 2011; Baker and Williams 2015). In 2007, 5 years after onset of the outbreak, there were about 1000 live subcanopy trees per hectare in old-growth and 1650 trees per hectare in mixed-age watersheds (Table 1), and another 626 and 724 live trees per hectare in the overstory of the two watershed types. This is equivalent to 2×2 m approximate spacing for live overstory and subcanopy stems in mixed-age watersheds. In

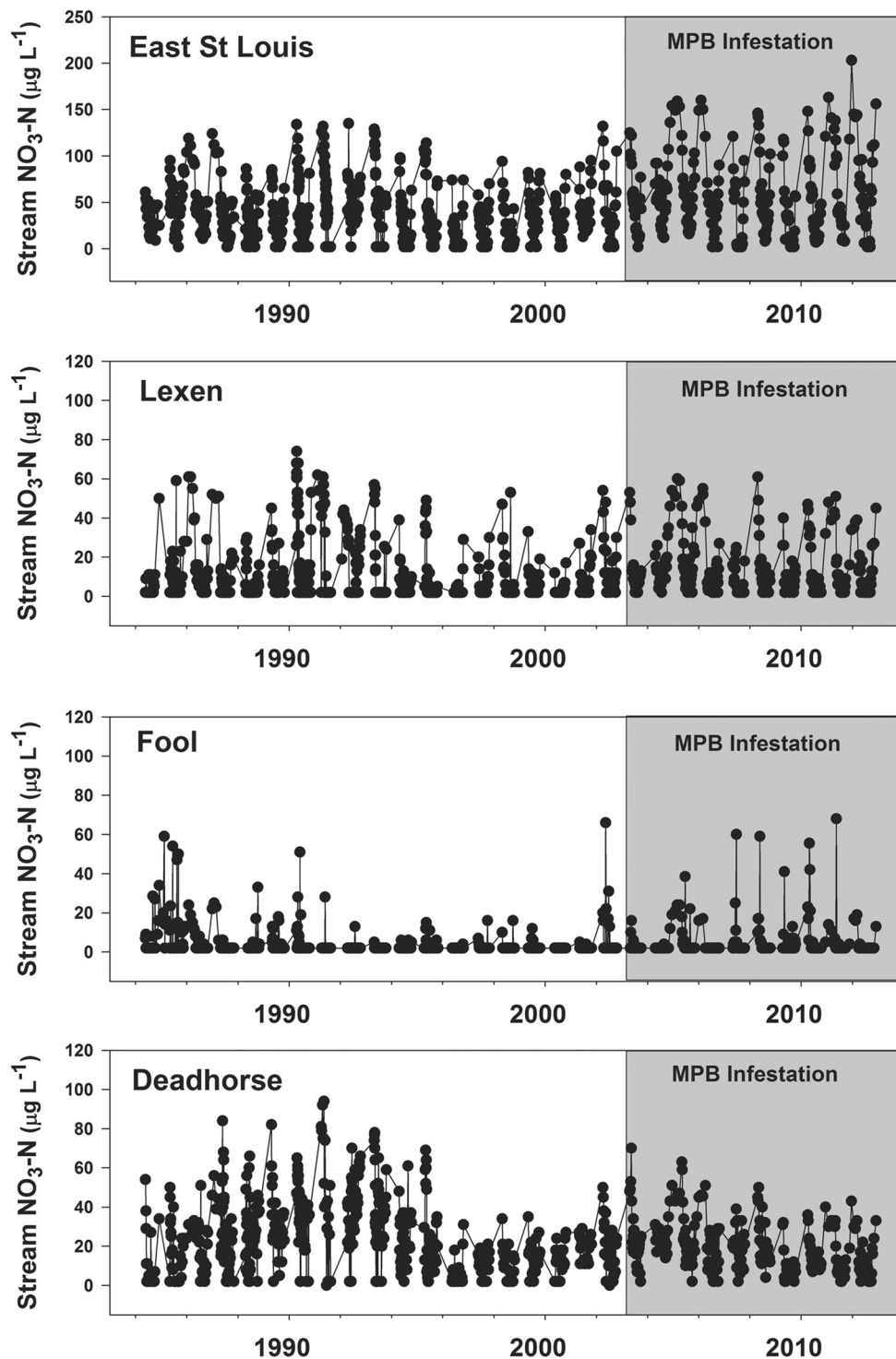


Figure 5. Instantaneous stream nitrate-N concentrations in two old-growth (East St. Louis, Lexen) and two mixed-age (Fool, Deadhorse) watersheds for 20 years before and 10 years after onset of tree mortality from mountain pine beetle (MPB) in 2003.

nearby stands, overstory mortality stimulated establishment of approximately 2000 new pine and fir recruits and aspen sprouts per hectare within 5 years of beetle infestation (Collins and others 2011).

We measured positive growth responses in canopy and subcanopy trees released after overstory

pine mortality in our 10 m radius inventory plots (Figure 4) and elsewhere at FEF. Height growth more than doubled for nearly 50% of understory conifers between 2007 and 2010, with growth increasing proportionally to overstory mortality. Analysis of annual rings from 123 live pine and spruce trees showed that growth responses were

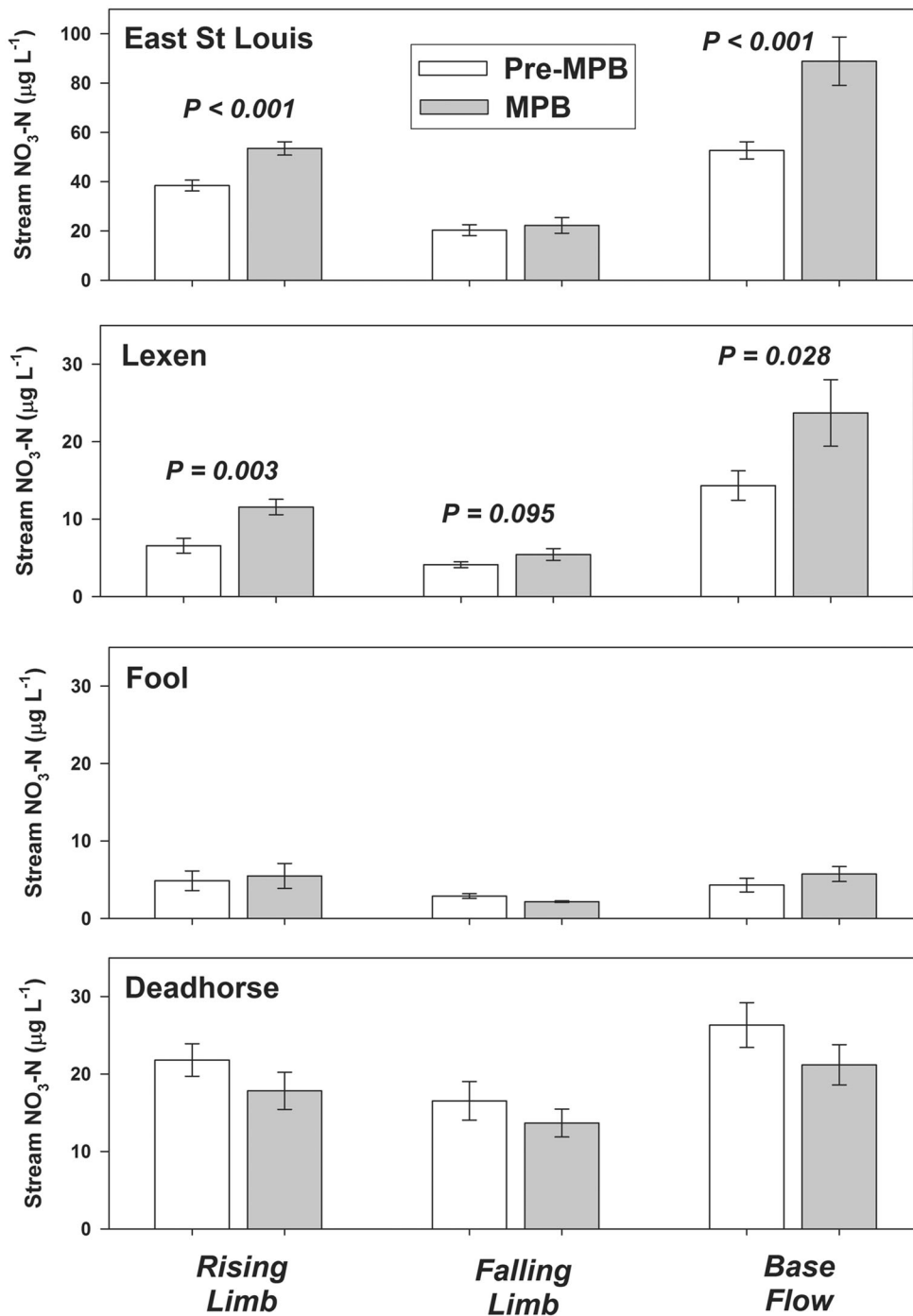


Figure 6. Stream discharge-weighted stream nitrate-N concentrations for two old-growth (East St. Louis, Lexen) and two mixed-age (Fool, Deadhorse) watersheds at the Fraser Experimental Forest. Data are seasonal mean concentrations (and standard error) for 20 years before and 10 years after onset of tree mortality from mountain pine beetle (MPB) in 2003. Rising and falling limb periods span April through June and July through September, respectively, and the base flow period the remaining 6 months.

also widespread for overstory trees. About 25% of the trees cored grew more than 25%, faster since the onset of the outbreak compared to the 30 years prior; 16% are growing faster than at any time in the past 100 years (data not shown). The foliar N concentration of live pine trees surrounded by dead, MPB-attacked trees increased from 1.0 to 1.3% the year after infestation (Hubbard and others 2013; Rhoades and others 2013). If, for

example, all residual live trees added 15% more foliar biomass with 30% higher foliar N content, Fraser forests would store an additional 2 kg ha⁻¹ of foliar N as a consequence of the outbreak. As quantified after both bark beetles (Griffin and others 2011) and wildfire (Metzger and others 2006) in other lodgepole forests, increased foliar N in common sedge (*Carex geyeri*) and woody understory species (for example, *Vaccinium scopar-*

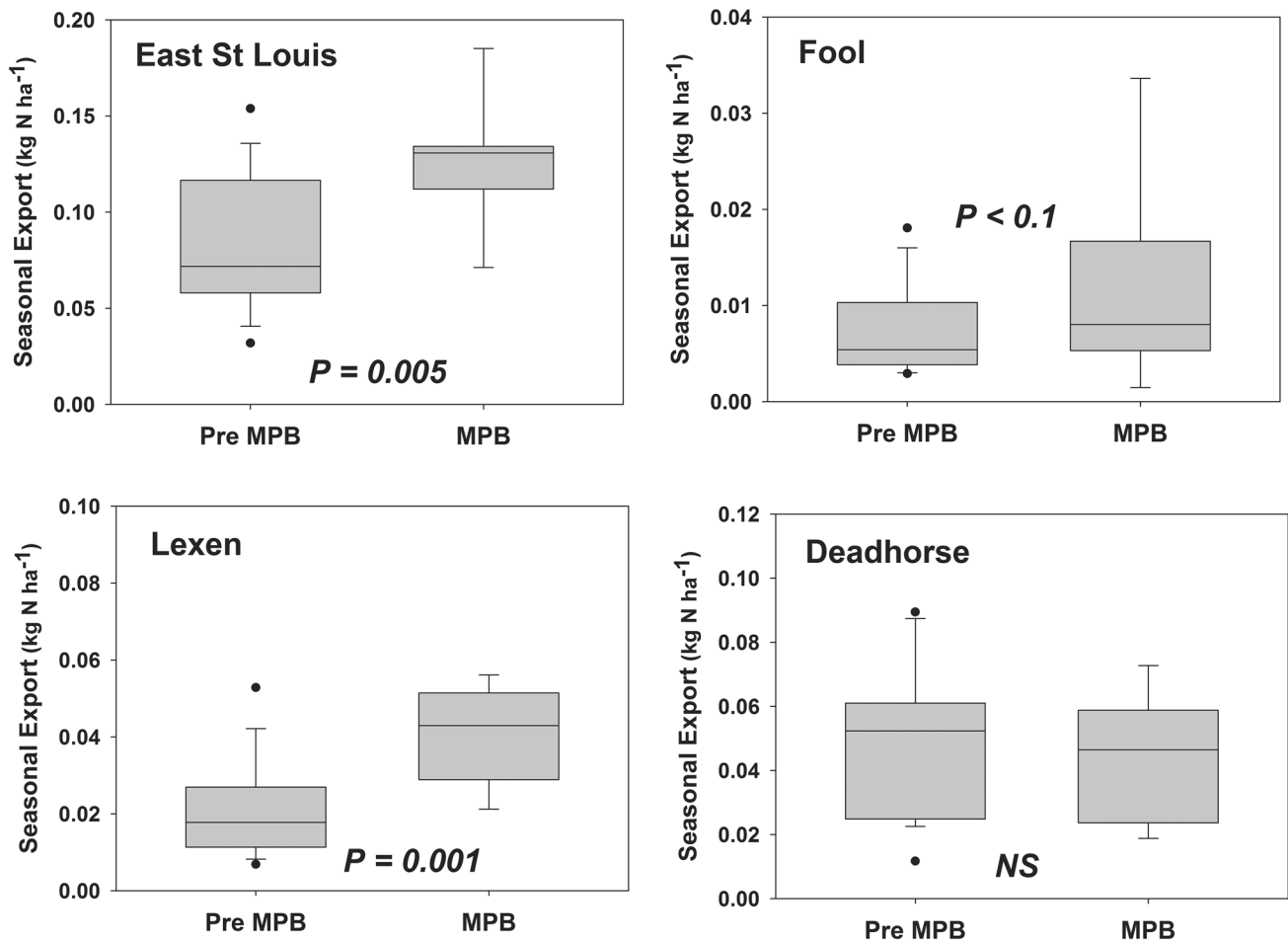


Figure 7. Export of dissolved inorganic N (nitrate-N + ammonium-N) from two old-growth (East St. Louis, Lexen) and two mixed-age (Fool, Deadhorse) watersheds during spring snowmelt, rising limb, from April thru June. Boxes denote the 25th, 50th, 75th percentiles, bars denote the 5th and 95th percentiles, and dots denote outliers; data for 20 years before ($n = 20$) and 10 years after ($n = 10$) onset of tree mortality from mountain pine beetle (MPB) in 2003.

ium) likely augment post-outbreak plant N demand at FEF.

Stand structure, age, and composition differences between old-growth and mixed-age forests likely explain the distinct stream N responses of the watershed types. Mountain pine beetles prefer larger diameter trees (Roe and Amman 1970; Lotan and Perry 1983; Figure 2). At Fraser, forests in East St. Louis and Lexen watersheds had larger trees on average and experienced higher levels of mortality than the mixed-aged watersheds where trees were smaller (Table 1). Total basal area declined 44% and leaf area declined 25% in the old-growth watersheds; changes were nearly twice those of the mixed-age watersheds. Tree diameter, sapwood area, leaf area, and nutrient demand are tightly linked (Raison and Myers 1992), so larger reductions may contribute to the greater responses of the

old-growth watersheds. Conversely, there were 1.7-times more live subcanopy trees in the mixed-age forests, and these would account for a larger potential increase in foliar N content in mixed-age than old-growth stands (2.5 vs 1.5 kg ha⁻¹) due to the outbreak. However, smaller conifers use more soil resources per unit leaf area than larger trees (R. Hubbard, unpublished data), so their impact on nutrient demand and losses from mixed-age stands is likely greater. Similarly, uptake by understory pines was credited with limiting soil nutrient losses from experimental bark beetle gaps created in Wyoming lodgepole pine stands (Parsons and others 1994). Forest N and biomass accumulation peaks at about 50 years in southern Rockies lodgepole pine forests (Fahey and Knight 1986; that is, 50- vs 100-year old trees). This corresponds to the age of regenerating stands at FEF and may

further explain the low pre-outbreak stream N and lack of response of the mixed-age watersheds.

Plant growth and nutrient uptake responses by residual live trees and understory plants have been documented after bark beetle attacks elsewhere (Romme and others 1986; Huber 2005; Berg and others 2006; Griffin and others 2011; Pec and others 2015). Positive growth responses were ubiquitous following overstory lodgepole pine mortality in British Columbia, though the degree of change varied with tree species and age (Brown and others 2010; Amoroso and others 2013; Hawkins and others 2013). By preferentially killing larger trees, bark beetles thinned these stands from above and stimulated growth of younger and understory trees. Understory trees and herbaceous plants grew more in response to the increased light resulting from tree mortality than overstory trees (Hawkins and others 2013; Pec and others 2015). The slow colonization of understory plants was credited for persistent N losses after bark beetle mortality in Bavarian spruce stands (Huber 2005). Enhanced post-outbreak tree growth is known to continue for decades (Romme and others 1986; Veblen and others 1991) and to yield lasting changes in forest species composition and structure (Brown and others 2010; Pelz and Smith 2012; Amoroso and others 2013).

Evidence of forest vegetation responses does not preclude the likelihood that other factors contribute to nutrient retention after bark beetle outbreaks. Microbial uptake represents a large demand on soil N in undisturbed forests (Stark and Hart 1997, 1999) that is known to consume much of the inorganic N supply in lodgepole forests recovering from wildfire (Smithwick and others 2005). Immobilization of inorganic N was high in organic soil layers of beetle-killed ponderosa forests, though no higher than in live forests (Morehouse and others 2008). Our study cannot shed light on post-infestation soil N processes, but it seems likely that the effect of changing substrate and abiotic conditions on soil microbial activities would track differences in overstory mortality. Our study does not address in stream nutrient processes that may have been altered by the beetle outbreak. Increased light, litter, and wood entering streams after a severe ice storm were credited with enhancing nitrate processing and lowering nitrate export from Hubbard Brook Experimental Forest watersheds (Bernhardt and others 2003). Near FEF streams, spruce, and fir are the dominant tree species and MPB-related lodgepole pine mortality, and changes in subcanopy light or organic matter inputs would be relatively small, and these patterns would not

differ between mixed-age and old-growth forests. Prior to recovery of plant cover after stand-replacing wildfires, microbial immobilization is a key source of soil N retention in disturbed lodgepole ecosystems (Kaye and Hart 1998; Turner and others 2007). Conversely, abundant residual live vegetation after bark beetle infestations maintains feedbacks between plant nutrient demand and soil nutrient availability that conserve nutrients in upland and riparian landscapes.

IMPLICATIONS AND CONCLUSIONS

The biogeochemical consequences of bark beetle outbreaks on forest watersheds result from short- and longer-term changes that regulate nutrient retention and release. Water and nutrient demand cease weeks after beetles enter trees and introduce blue stain fungi to the vascular system (Hubbard and others 2013), consequently altering soil moisture and nitrate-N levels (Clow and others 2011). The pulse of N inputs occurs several years after beetle attack when trees shed red needles (Morehouse and others 2008; Griffin and others 2011). The changes in canopy structure from limb breakage and snag windthrow (Mitchell and Preisler 1998) that alter canopy interception, understory growth (Pec and others 2015), and soil nutrient cycling continue for years to decades.

Vegetation growth and recovery from disturbance is generally slow in subalpine forests due to the long, cold winters. Following a historic bark beetle outbreak in Colorado spruce forests, stream runoff volume was elevated over a 25-year period as canopy structure and understory vegetation readjusted to overstory mortality (Bethlahmy 1974). Little is known about the duration of MPB effects on stream N in lodgepole ecosystems, though in other conifer forests canopy mortality generated significant, long-lasting increases in cation and nitrate leaching (Tokuchi and others 2004; Huber 2005). Although the watershed-scale biogeochemical responses we document the decade following the outbreak are small relative to other forest disturbances, seasonal fluctuations, and atmospheric N deposition, the changes in forest composition and structure will influence forest dynamics for decades (Collins and others 2011; Pelz and Smith 2012).

It was previously thought that bark beetle outbreaks would disrupt tightly coupled biogeochemical cycles resulting in nutrient release similar to harvesting and wildfires (Fahey and Knight 1986). Our findings and those of others demonstrate that this is not the case and that responses to bark beetle

outbreaks and logging are distinct (Rhoades and others 2013). The significant mortality of mature pine trees represents a severe forest disturbance (*sensu* White and Pickett 1985) expected to have concomitant ecosystem responses, yet abundant nonhost overstory and small diameter residual trees dampened the ecosystem-scale consequences of the outbreak. Live understory and canopy trees are poised to release rapidly and reduce surplus resources in forests that have experienced severe overstory mortality (Brown and others 2010; Collins and others 2011; Amoroso and others 2013; Hawkins and others 2013). Overstory mortality also stimulates pulses of seed inputs from canopy seed banks (Aoki and others 2011; Teste and others 2011) that establish new tree cohorts. Unlike harvesting, forest dieback does not disrupt the forest floor and contributes litter that can effectively immobilize N (Morehouse and others 2008). The understory beneath beetle-killed pines favors growth of more shade-tolerant tree species, unlike the exposed conditions following harvesting that favor early successional species (Pelz and Smith 2012; Amoroso and others 2013; Pelz and others 2015). These aggregate differences in species composition, tree abundance, and understory conditions beneath beetle-killed pines compared with harvested or burned forests create distinct nutrient demand and retention.

Like patterns reported from a growing number of studies (Turner and others 2007; Turner 2010), these bark beetle-infested ecosystems did not “leak” nutrients. Increased regeneration density and higher growth and nutrient demand by understory and live overstory trees in upland and riparian areas may balance the elevated soil nutrients measured beneath beetle-killed trees (Clow and others 2011) and explain the high nutrient retention of recovering watersheds. The shift of nutrient and water demand from the pine-dominated overstory to residual live overstory and understory plants highlights the value of protecting live growing stock during forest management operations. The limited mortality and stream N response of the mixed-age watersheds support a rationale of managing to maintain diversity in stand age, structure, and species composition. Our findings will likely differ from lodgepole forests in drier regions where understory trees are sparse (Lotan and Critchfield 1990; Strong 2015) and from beetle outbreaks in forests that receive much higher N deposition (Huber 2005; Kana and others 2013), but they may be generally similar to other conifer forests that contain mixed stand structure and tree species composition.

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