

Soil Nitrogen Leaching in Logged Beetle-Killed Forests and Implications for Riparian Fuel Reduction

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Abstract

Recent extensive forest mortality and subsequent salvage logging may threaten the water supply from headwater catchments in western North America. Land managers confronting current insect outbreaks and projected increases in forest disturbance require information about the potential water quality consequences of these changes. This study is a hillslope-scale evaluation of soil N and C leaching in lodgepole pine forests that have experienced 80% overstory tree mortality. I measured extractable inorganic and ion resin exchangeable-N forms, in situ net mineralization and nitrification, and leaching in upland and riparian forests with the following treatment combinations: (i) uncut upland with uncut riparian, (ii) harvested upland with uncut riparian buffer, and (iii) harvested upland with harvested riparian. This design permitted comparison of N cycling and leaching in 30-m-wide riparian buffers and a riparian fuel break designed to remove canopy fuels and reduce wildfire concerns in areas with extensive bark beetle infestation. Harvesting increased $\text{NO}_3\text{-N}$, total dissolved N, and dissolved organic C leachate concentrations in upland landscapes but had little effect on net N transformations. Leachate N and C concentrations were 1.5 times higher in riparian buffers downslope of harvested uplands than those in riparian zones downslope of uncut uplands. Riparian forest harvest increased N leaching relative to uncut buffers, although postharvest concentrations remained well below regional water quality standards. Thus, while this study provides evidence that N leaching from dead buffers is low, it also suggests that riparian fuel reduction may complement wildfire mitigation objectives without compromising watershed protection.

Core Ideas

- Nitrogen leaching was low in riparian buffers even though most trees were dead.
- Harvest of dead riparian forest increased N losses, but concentration remained low.
- Novel riparian management may achieve both wildfire mitigation and watershed protection.

RIPARIAN FOREST BUFFERS are areas along perennial and intermittent streams where timber harvesting, grazing, and other activities are restricted to protect water quality and watershed condition (USDA Forest Service, 2006; Cristan et al., 2018). This best management practice is commonly implemented to reduce sediment, nutrient, and chemical delivery to streams (Cristan et al., 2016), but also to regulate stream discharge, temperature, incident light, and storm flows and to enhance fish habitat and other aquatic and upland values. Watershed management aimed at protecting aquatic resources by restricting management within riparian corridors is based on research in nutrient-enriched agricultural watersheds (Lowrance et al., 1997; Schultz et al., 2004) or from eastern and western North American forests (Naiman and Bilby, 1998; Verry et al., 2000; Witt et al., 2016). As such, managers working in interior Rocky Mountain ecosystems lack specific information about how upland and riparian biogeochemical processes (Triska et al., 1993; Grimm et al., 2003; Jencso et al., 2009) respond to land management and forest disturbance.

Lodgepole pine (*Pinus contorta* Dougl. Ex. Loud. var. *latifolia*) forests are one of the most common ecosystems in western North America. Since the early 2000s, bark beetles have infested 13,800 km² of Colorado forests (CSFS, 2016), and throughout the Rocky Mountains, such outbreaks often kill 40 to >90% of overstory trees (Raffa et al., 2008; Chapman et al., 2012; Berner et al., 2017). The unprecedented severity and extent of this forest mortality has prompted salvage logging (Collins et al., 2010) intended, among other things, to reduce short-term crown fire risk and longer-term risk of damage from severe wildfires burning the heavy fuels that accumulate after tree fall (Mitchell and Preisler, 1998; Page et al., 2013). To comply with current watershed best management practices, bark beetle salvage operations typically retain dead trees within riparian buffers (USDA Forest Service, 2006). However, the biogeochemical and conservation value of riparian buffers occupied by dead trees is uncertain, and under these conditions, riparian buffers may be at odds with wildfire risk reduction objectives. Widespread insect outbreaks and hazardous fuel accumulation has increased interest in riparian fuel reduction options and reconsideration of riparian buffer design (Western Governors Association, 2002; Stone et al., 2010). However, prior to adopting new practices to address these

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Abbreviations: DIN, dissolved inorganic nitrogen; DOC, dissolved organic carbon; DON, dissolved organic nitrogen; DTN, dissolved total nitrogen; IER, ion exchange resin.

priorities, there is need to evaluate nutrient leaching in standard riparian buffers dominated by dead trees, as well as in experimental fuel reduction treatments.

Lodgepole pine ecosystems are one of the most N-limited ecosystems in the world (Fahey et al., 1985), with high retention of nutrient inputs and very low stream N export in undisturbed catchments (Stottlemeyer et al., 1997). Timber harvesting and other disturbances in lodgepole pine ecosystems increase soil N availability and the potential for nutrient leaching to surface waters (Giardina and Rhoades, 2001; Clow et al., 2011; Rhoades et al., 2018). In such forests in the subalpine zone in Colorado, timber harvesting is known to increase shallow subsurface flow and N export for several years (Reuss et al., 1997), and to influence catchment- (Troendle and King, 1985) and hillslope-scale discharge (Starr, 2003) for decades. In spite of increased soil water and NO_3^- -N available for leaching measured after bark beetle outbreaks (Griffin et al., 2011; Pugh and Small, 2012; Brouillard et al., 2017), nutrient export from subalpine forests remains relatively low (Rhoades et al., 2017). This suggests that a compensatory mechanism, such as in-stream uptake (Bernhardt et al., 2003) or increased plant nutrient demand, potentially within the riparian zone, may limit export of surplus nutrients to streams (Parsons et al., 1994; Rhoades et al., 2013; Biederman et al., 2016).

The severity and extent of recent bark beetle outbreaks has prompted questions about how to balance fuel reduction priorities and watershed protection objectives to maintain productive forests, soils, and clean water after extensive tree mortality and subsequent salvage logging. Land managers currently lack information regarding nutrient leaching in riparian buffers affected by severe bark beetle infestation. This study measures nutrient leaching in 30-m-wide riparian buffers consisting of beetle-killed trees downslope of upland clear-cut logging, as well as the N leaching impact of riparian harvesting conducted for wildfire risk mitigation. Both upland and riparian harvesting are expected to increase soil N availability and leaching, but this study will evaluate if leachate concentrations from beetle-killed, harvested riparian forests are likely to threaten stream water quality. Findings from the study will help guide forest and watershed managers concerned with balancing the relative risks and benefits of retaining or removing dead trees from riparian areas.

Materials and Methods

Site Description

This research was conducted on the Arapaho–Roosevelt National Forest in the headwaters of the Williams Fork River, a tributary to the Colorado River located on the western edge of Colorado's Front Range (39°53' N, 106°4' W). The local climate is temperate and continental with long cold winters and short cool summers. Mean annual temperature is 0.6°C with January and July average temperatures of −10 and 12.2°C at 2760-m elevation (USDA Forest Service, unpublished data, 2010). Total annual precipitation averages 60 cm, with 64% comprising snowfall received between October and May. Peak snowpack accumulation occurs at the beginning of April, and peak runoff occurs in early June. The study area is underlain by metamorphosed rock (Kellogg et al., 2008) dominated by biotite schist and gneiss (Shroba et al., 2010). Upland soils are gravelly, sandy-loams classified as Haplocrypts and Dystrocrypts formed on glacial till and colluvium (Soil

Survey Staff, 2010). Soils are 60 to 150 cm deep with 35 to 60% cobble-sized materials (Alstatt and Miles, 1983).

Forests of the study area are dominated by lodgepole pine, with subalpine fir [*Abies lasiocarpa* (Hook.) Nutt.], Engelmann spruce [*Picea engelmannii* Parry ex. Engelm.], and quaking aspen [*Populus tremuloides* Michx.]. Low-stature shrubs, primarily grouse whortleberry [*Vaccinium scoparium* Leiberg ex. Coville] with occasional russet buffaloberry [*Shepherdia canadensis* (L.) Nutt.] occur beneath overstory conifers (Huckaby and Moir, 1998). Even-aged (~110-yr-old) lodgepole pine forests of the Williams Fork drainage were among the first to experience severe mortality in the late 1990s, at the outset of Colorado's recent pine beetle outbreak (Chapman et al., 2012). Many of these forests regenerated after historical lumbering and became susceptible to bark beetle attack due to their advanced age, relatively large diameter, and dense stocking (Mata et al., 2003). Air temperature, and importantly minimum daily temperatures that regulate bark beetle population growth and survival, have increased steadily in the Colorado Rockies during recent decades (Lukas et al., 2014). Bark beetles reached epidemic levels around 2000, and their activity peaked around 2006 in this part of Colorado (Tishmack et al., 2004; Chapman et al., 2012), often killing 70 to 90% of the overstory lodgepole basal area (Collins et al., 2011; Rhoades et al., 2018).

Study areas were part of a forest health project administered by the US Forest Service, in response to extensive bark beetle-caused tree mortality. Salvage logging was confined to beetle-infested, lodgepole pine-dominated stands; lodgepole pine comprised 87% of the preharvest overstory basal area (range = 58–100%) for stands in both upland and riparian hillslope locations in the project area (Collins et al., 2010). Average overstory basal area was 34.6 m² ha^{−1}, quadratic mean diameter was 18 cm, and average tree height was 27 m.

Treatments, Sampling, and Analysis

To assess the effects of harvesting and riparian buffer zone retention on N and C leaching in beetle-killed forests, I compared (i) uncut upland with uncut riparian zones, (ii) harvested uplands with uncut riparian buffers, and (iii) harvested uplands with harvested riparian zones. The three treatments were replicated on five independent study blocks distributed across a 5-km² project area. All five blocks had similar forest composition and aspect and had 10 to 30% slope. Uncut hillslopes were adjacent to harvest units and were retained because of road access, skid distance, or other factors unrelated to stand composition and thus had similar tree species composition, degree of beetle-kill, and hillslope conditions.

Salvage logging operations clear cut the beetle-killed pine overstory to reduce canopy fuels, stimulate tree regeneration, and capture the value of the dead timber. Harvesting occurred over ≥1 m of snow and frozen soils with tracked, feller bunchers during winter 2005–2006. Regional watershed protection guidelines require retaining a 30-m-wide riparian buffer of untreated forest along both sides of perennial streams (USDA Forest Service, 2006). To facilitate this study, harvest of all dead pine trees was permitted within 500-m-long sections of riparian forest downslope of upland clear-cut units. Mechanized equipment did not enter riparian buffers during harvesting; tree boles were carefully retracted by feller buncher booms or felled manually and winched from outside.

Each of the five study blocks contained upland and riparian sample transects located along the slope contour. To characterize leachate within riparian buffers and the consequence of harvesting on riparian soil N cycling and leaching, sample transects were installed 10 to 15 m from the streambank at the center of designated buffer zone. Upland transects were located on uniform planar slopes, 200 m away from the stream. The riparian zones were generally flat, streamside terraces adjacent to planar hillslopes. Riparian sampling did not aim to characterize conditions at the stream edge but to evaluate current riparian retention and proposed removal of the standard 30-m-wide riparian buffer. Streamwater was collected from first-order perennial streams adjacent to each study block. The catchments contain extensive, recent, and historical harvesting, so stream sampling was not intended to isolate individual hillslope inputs. Rather, streamwater nutrient, C, and chemistry are presented as supplemental material to identify potential sensitivity to salvage logging.

Soil Solution Leachate

To collect soil solution leachate concentrations at the base of the rooting zone, five porous cup, falling-head tension lysimeters (Soil Moisture Corporation) were inserted to a depth of 30 cm at 10-m intervals along each transect. Leachate was sampled four times annually from late May through early July during 2007, 2008, and 2009. Tension was applied to lysimeters 24 h prior to sample collection; samples were refrigerated and analyzed within 1 wk of collection. Supplemental streamwater grab samples were collected and analyzed in conjunction with each set of lysimeter samples.

Dominant cations and anions and dissolved C and N species were analyzed to characterize the nutrient and chemical composition of soil solution leachate and streamwater. Samples were collected after triple rinsing bottles in sample water. Samples for anion and cation analyses were collected in opaque plastic bottles; those used for dissolved organic C (DOC) and total N (DTN) analyses were collected in amber glass bottles. Prior to use, plastic sample bottles were triple washed with deionized water (electrical conductivity $< 1.0 \mu\text{S cm}^{-1}$), and glass bottles were heated for 1 h at 500°C in a muffle furnace. Ion chemistry samples were filtered through $0.45\text{-}\mu\text{m}$ mesh membrane filters, and DOC and DTN samples were filtered through $0.7\text{-}\mu\text{m}$ mesh glass fiber pre-filters (Millipore Corporation).

Anion and cation concentrations were determined by ion chromatography (Waters Company) and conductivity detection with a Dionex AS12A anion-exchange column, an AG12A guard column, and Waters IC-Pak cation M/D column (APHA, 1998) using EZChrom Elite software (Agilent Technologies, 2006). Conductivity suppression was used to detect anion concentrations (Dionex ASRS Ultra-II 4 mm). Detection limits were 0.01 mg L^{-1} for NO_3^- and NH_4^+ . Dissolved organic C and DTN were determined by high-temperature combustion catalytic oxidation using a Shimadzu TOC-V_{C_{PN}} total organic C analyzer with a TNM-1 total N detection unit (Shimadzu Corporation). Dissolved organic N (DON) was calculated by subtracting dissolved inorganic N ($\text{DIN} = \text{NO}_3^- + \text{NH}_4^-$) from DTN. The detection limits for both DOC and DTN were 0.05 mg L^{-1} .

Soil Nitrogen Cycling

Plant-available soil N was assessed using ion exchange resin (IER) bags (Binkley and Matson, 1983). Resin bags were buried

10 cm deep in mineral soil at 10-m intervals along each transect (five resin bags per transect). Bags were constructed of permeable nylon fabric and filled with a mixture of cation and anion exchange resins (Ionac C 249 and ASB1P, Sybron Chemicals) to retain NO_3^- -N and NH_4^- -N as these inorganic N forms percolate through the soil. Resin bags were installed in September and removed in May to sample winter–spring snowmelt during 2007, 2008, and 2009. After collection, bags were stored at 5°C until the resins were extracted with 100 mL of 2 M KCl and analyzed for NO_3^- -N and NH_4^- -N by colorimetric spectrophotometry (Bundy and Meisinger, 1994; Lachat Company, Loveland, CO).

The production of inorganic forms of soil N (NO_3^- -N and NH_4^- -N) was examined using net mineralization and nitrification incubations of O horizon (organic soil) and A horizon (0- to 15-cm-deep mineral soil) layers. Five samples of each soil layer were collected along each upland and riparian transect, and samples were placed in plastic coolers immediately after sampling and stored at 4°C . Ten-gram subsamples were extracted with 50 mL of 2 M KCl within 72 h of sampling, and extracts were analyzed as above. A second subsample was oven dried at 105°C for 24 h to determine soil moisture content. A third 10-g set of subsamples was incubated for 21 d at 24°C at 60% of field capacity (Binkley and Hart, 1989). Field capacity was approximated as the gravimetric water content of a subsample wetted to saturation then allowed to drain for 12 h. The incubated subsamples were extracted and analyzed as described above. Net mineralization was calculated as the change in NO_3^- -N plus NH_4^- -N, and net nitrification as the change in NO_3^- -N between initial and incubated extracts.

Vegetation and Ground Cover

Tree regeneration was sampled in August 2007, the second growing season after harvesting. We tallied new seedling recruits ($< 25 \text{ cm}$), advance regeneration ($25\text{--}100 \text{ cm}$) and sapling ($100\text{--}200 \text{ cm}$) size classes by species in three 40-m^2 circular plots within upland and riparian zones in each study block. Understory plant (graminoid, forb, and shrub) and cover of litter, bare soil, coarse wood (100- and 1000-h woody fuels classes > 2.5 in diameter) were sampled in 12 1-m^2 quadrats in each hillslope zone and study block. Herbaceous biomass (annual graminoid and forb growth) was clipped from sample quadrats, dried for 48 h at 60°C , and weighed.

Statistical Analysis

We evaluated the effect of upland harvesting and riparian buffer retention and removal on soil leachate, soil nutrients, and tree and understory plant cover. Data from individual lysimeters, IERs, soil mineralization assays, and plant cover quadrats were aggregated within upland and riparian transects. The two upland treatments (uncut and cut) and three riparian treatments (uncut, buffer, and cut) were compared using ANOVA as fixed effects with hillslope blocks as random effects in SPSS version 22 (IBM Corporation, 2013). A repeated-measures term was added for analysis of leachate and IER plant-available soil N. Where fixed effects were significant pairwise, Tukey-adjusted comparisons were used to identify differences among the treatments. Levene's statistic was used to test assumptions of homogeneity of variance; IER, extractable soil N, and net mineralization data violated this assumption and were log-transformed prior to analyses. Throughout the manuscript, statistical significance is reported only when $\alpha \leq 0.05$, unless otherwise stated.

Results

Soil Solution Leachate

Over the 3-yr study period, leachate $\text{NO}_3\text{-N}$, DIN, DON, and DTN concentrations were 2.4 to 2.9 times greater in cut compared with uncut uplands (Fig. 1, $p \leq 0.006$ for all). Leachate $\text{NH}_4\text{-N}$ averaged 0.06 mg N L^{-1} and did not differ between the upland treatments. Nitrate comprised >80% of leachate DIN in both cut and uncut uplands. Leachate DOC was 1.5 times more on cut uplands on average throughout the study ($p < 0.001$). Overall, DON represented a slightly smaller portion of the DTN leached from the cut uplands (43 vs. 48%, $p < 0.001$), whereas DIN presented the inverse pattern ($p < 0.001$), and the ratio of DOC to DTN was lower compared with uncut uplands (32 vs. 49%, $p < 0.001$). Nitrate and DTN both declined throughout the study in the cuts ($p = 0.005$), although both N forms remained significantly higher than uncut uplands in the final year of the study.

Within the riparian zone, average leachate N and C concentrations also differed between cut and uncut treatments (Fig. 2). Dissolved total N and DOC were both 60% higher in 30-m-wide buffers beneath cut uplands compared with uncut riparian zones

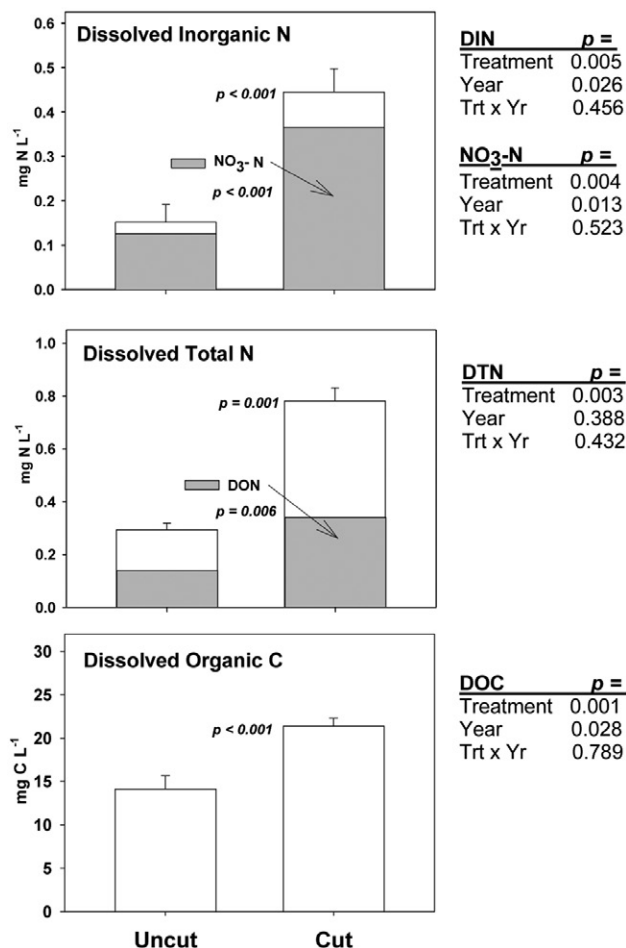


Fig. 1. Upland leachate N and C in uncut and salvage-logged beetle-killed lodgepole pine forests. Bars show mean dissolved inorganic N (DIN), dissolved total N (DTN), and dissolved organic C (DOC) and SE for five hillslope blocks sampled four times annually from 2007 to 2009 ($n = 60$). Dissolved inorganic N is the sum of $\text{NO}_3\text{-N}$ + $\text{NH}_4\text{-N}$, and DTN is the sum of DIN and dissolved organic N. Significance of treatment effects for partial bar (gray) or total bar (gray + white or solid white bar) is shown in the lower or upper portion of panels.

below uncut uplands ($p = 0.01$ and $p < 0.001$, respectively). Neither $\text{NO}_3\text{-N}$ nor DIN differed significantly between the uncut and buffer treatments, although mean values were marginally higher in the buffers ($p = 0.09$). Leachate $\text{NH}_4\text{-N}$ averaged 0.04 mg N L^{-1} and was unaffected by the riparian treatments. In contrast, $\text{NO}_3\text{-N}$ was 4.7 times greater in the cut compared with the uncut riparian zone beneath uncut hillslopes ($p < 0.001$), and double that measured in buffers ($p = 0.005$). Similarly, leachate DTN was twice as high in cut compared with uncut riparian zones ($p < 0.001$), and 30% higher than in the buffers ($p = 0.05$). The proportion of DTN comprised by DIN was significantly higher in the cut riparian zone compared with either the uncut riparian or the buffer zones ($p = 0.005$). On average, DIN and DON comprised 33 and 80% of DTN in the uncut hillslope treatment, respectively, compared with 63 and 45% in the cut riparian zone. Leachate $\text{NO}_3\text{-N}$ and DTN concentrations remained elevated in the cut riparian zone, although concentrations of both N forms declined significantly for uncut hillslopes and buffers over the course of the study ($p = 0.05$).

Soil Nitrogen Availability

Harvesting increased plant-available N measured with IER (IER-N) in both hillslope locations (Fig. 3). Cut uplands had 1.4 times more IER $\text{NH}_4\text{-N}$ ($p = 0.016$) and twice as much IER $\text{NO}_3\text{-N}$ ($p = 0.009$) as uncut uplands on average during 3 yr of sampling. Conversely, IER $\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$ were

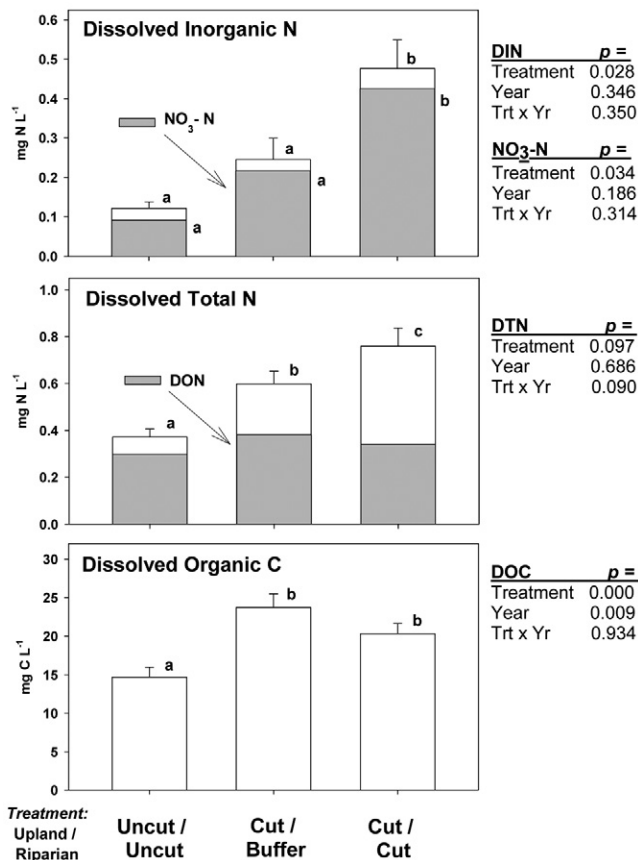


Fig. 2. Riparian zone leachate N and C in beetle-killed lodgepole pine forests. Bars show mean dissolved inorganic N (DIN), dissolved total N (DTN), and dissolved organic C (DOC) and SE for five hillslope blocks sampled four times annually from 2007 to 2009 ($n = 60$). Dissolved inorganic N is the sum of $\text{NO}_3\text{-N}$ + $\text{NH}_4\text{-N}$, and DTN is the sum of DIN and dissolved organic N. Different letters indicate that treatment means differ according to Tukey's pairwise adjusted comparisons at $\alpha \leq 0.05$.

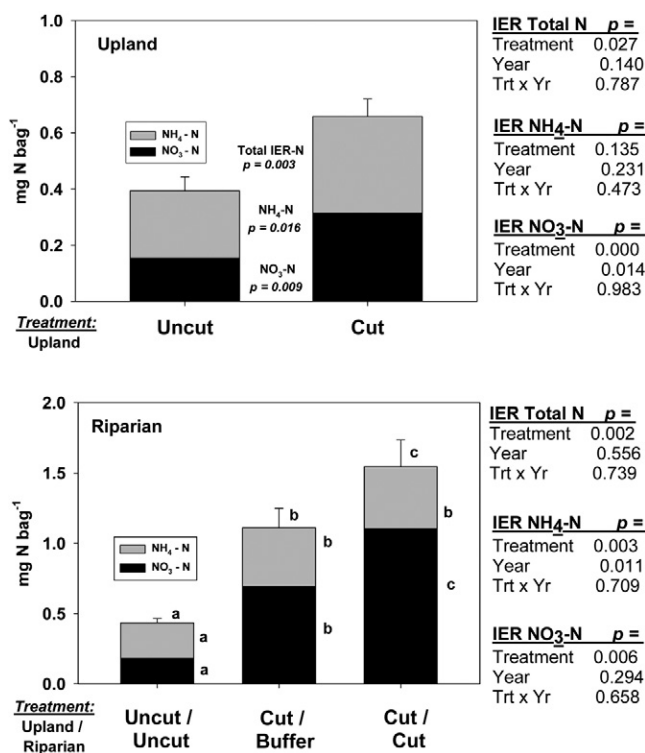


Fig. 3. Ion exchange resin soil N (IER-N) collected at 10-cm depth in upland and riparian zones of beetle-killed lodgepole pine forests. Bars show mean $\text{NO}_3\text{-N}$, $\text{NH}_4\text{-N}$, and total IER-N (with SE) for five hillslope blocks sampled during winter-snowmelt seasons from 2007 to 2009 ($n = 15$). Significant harvest effects were indicated by significance values for the uplands and by letters for Tukey's pairwise adjusted comparisons for the riparian zone at $\alpha \leq 0.05$.

1.7 and 3.8 times higher, on average, in the buffers than in uncut riparian zones below uncut hillslopes ($p < 0.001$ and $p = 0.005$, respectively). Riparian harvesting increased IER $\text{NO}_3\text{-N}$ and total IER-N further. For example, these N forms were 1.6 and 1.4 times greater in cut riparian zones compared with uncut buffers ($p = 0.028$ and $p = 0.024$, respectively) and were 6.1 and 3.6 times greater than in uncut riparian zones below uncut hillslopes ($p < 0.001$ and $p < 0.001$, respectively).

Plant-available soil N, assayed by extractable inorganic N pools and net transformations, displayed similar patterns in the upland and riparian zones (Table 1). Ammonium was the predominant

form of extractable inorganic N (>94%), and there was 2 to 10 times more $\text{NH}_4\text{-N}$ in O than in A horizons for both hillslope zones. Nitrification was consistently negative, indicating net $\text{NO}_3\text{-N}$ immobilization within the O horizon, compared with consistent release in the A horizon. Conversely, positive mineralization rates increased inorganic N availability in the O horizon, whereas immobilization reduced it in the A horizon.

Harvesting decreased soil water content in the O and A horizons of both upland and riparian areas (Table 1). It doubled extractable $\text{NH}_4\text{-N}$ in upland O-horizon soils, and there was a similar (though nonstatistically) significant pattern in the riparian zone. Conversely, harvesting decreased extractable soil $\text{NH}_4\text{-N}$ by 30 to 50% in the A horizon compared with uncut uplands and riparian zones. There was no statistically significant effect of harvesting on extractable $\text{NO}_3\text{-N}$ or net nitrification. Net mineralization was unaltered by cutting in the O horizon, but N immobilization (negative net mineralization) was significantly reduced in the A horizon in both hillslope zones.

Vegetation

Lodgepole pine was the most abundant understory tree species overall and in the advance regeneration and sapling size classes of the upland zone (Supplemental Table S1). Subalpine fir was the most abundant species in all size classes in the riparian zone. Aspen occurred on both zones of uncut hillslopes in one or more size classes, although it was the least abundant species.

Harvesting increased pine recruit density 3.5-fold in the upland zone compared with uncut conditions ($p < 0.06$) but reduced the density of other size classes of pine and other species (Supplemental Table S1). Harvesting reduced total fir and spruce density by 98 and 92% respectively, compared with uncut hillslopes ($p < 0.001$ and $p = 0.008$, respectively). Within the uncut riparian buffer, harvesting in the adjacent uplands increased total aspen density 20-fold compared with uncut riparian zones ($p = 0.007$) with the largest increase in the sapling size class. Harvesting shifted aspen from the least abundant to the most abundant species within the riparian zone. In contrast, pine was the dominant species in upland harvests for all size classes.

Understory plant cover averaged 71 and 90% in upland and riparian zones of uncut hillslopes (Supplemental Table S2). Harvesting reduced total understory cover in the uplands by

Table 1. Soil water, extractable N, and net N transformations for cut and uncut upland and riparian zones in bark beetle-infested lodgepole pine forests. Data are July 2007 means and SEs (in parentheses) from five hillslope blocks. Analysis of variance was performed on log-transformed data.

Trait	Upland				Riparian					
	O Horizon		A Horizon		O Horizon			A Horizon		
	Uncut	Cut	Uncut	Cut	Uncut	Buffer	Cut	Uncut	Buffer	Cut
Gravimetric soil water (g g^{-1})	0.19 (0.03)	0.11† (0.01)	0.12 (0.01)	0.08† (0.01)	0.35a‡ (0.08)	0.19b (0.02)	0.22ab (0.02)	0.15a (0.02)	0.07b (0.01)	0.08b (0.01)
Extractable $\text{NO}_3\text{-N}$ ($\mu\text{g N g}^{-1}$)	1.55 (0.8)	4.60 (1.5)	0.01 (0.01)	0.10 (0.05)	2.03 (0.8)	4.09 (3.0)	0.36 (0.2)	0.03 (0.03)	0.17 (0.1)	0.20 (0.2)
Extractable $\text{NH}_4\text{-N}$ ($\mu\text{g N g}^{-1}$)	37.46 (7.0)	71.78† (8.9)	17.81 (3.0)	12.44 (1.4)	42.68 (10.1)	85.21 (24.0)	62.54 (6.3)	21.74a (3.6)	8.28b (1.2)	14.56ab (4.0)
Net nitrification ($\mu\text{g N g}^{-1} \text{ 21 d}^{-1}$)	-1.31 (0.8)	-2.33 (1.8)	0.14 (0.10)	0.23 (0.12)	-1.78 (0.6)	-2.39 (2.0)	-0.30 (0.2)	0.16 (0.1)	0.14 (0.2)	0.02 (0.1)
Net mineralization ($\mu\text{g N g}^{-1} \text{ 21 d}^{-1}$)	24.53 (8.1)	22.40 (8.8)	-13.49 (3.3)	-6.53* (1.7)	31.31 (21.1)	7.57 (27.5)	10.64 (14.1)	-13.55a (3.8)	0.44b (3.2)	-6.24ab (3.4)

* Significant at the 0.05 probability level.

† Significant at the 0.005 probability level.

‡ Different lowercase letters indicate that values differ within the riparian zone according to Tukey's adjusted comparison.

about half ($p = 0.008$) but had no net effect in the riparian zone due to offsetting increases and decreases for the three plant growth forms. Shrub cover, primarily low-growing grouse whortleberry, was the predominant understory growth form on all positions of uncut hillslopes (Supplemental Table S2). Harvesting reduced shrub cover by 78 and 50% in the upland and riparian zones ($p < 0.001$ and $p < 0.001$, respectively), whereas it increased forb cover roughly threefold in both zones ($p < 0.1$ and $p = 0.002$, respectively). Harvesting decreased upland litter cover by 27% and increased coarse wood by 64% ($p = 0.047$ and $p < 0.1$, respectively) but had no significant effect on bare soil or any components of surface cover in the riparian zone (Supplemental Table S2).

Discussion

Nitrogen Retention in Mountain Pine Beetle-Infested Forests

In spite of extensive tree mortality and salvage logging, N remained low in streams draining the hillslope study areas (Supplemental Fig. S1). Average N concentrations were similar to reference conditions, typical of “least-disturbed” cold rivers and streams in the Western Forest Region of the United States (0.01 and 0.12 mg N L⁻¹ for NO₃-N and total N; USEPA, 2000). This is notable, since the study was conducted within actively managed watersheds including forests with extensive mortality, recently salvage-logged stands, and younger forests regenerating after earlier timber harvests. Storm events were not intentionally sampled, yet there was no evidence of nutrient-related water quality impairment during the 3-yr study.

Decreased tree nutrient demand and increased litter inputs have been linked to higher soil N availability after beetle-related tree mortality (Clow et al., 2011; Griffin et al., 2011; Brouillard et al., 2017). Increased soil N leaching has been documented in beetle-killed forests (Biederman et al., 2016), especially where atmospheric N deposition is high (Huber, 2005; Kaňa et al., 2013). In the current study, leachate NO₃-N averaged 0.13 and 0.09 mg N L⁻¹ and DTN averaged 0.3 and 0.4 mg N L⁻¹ in uncut, beetle-infested upland and riparian forests; maximum concentrations were 0.5 and 1.0 mg N L⁻¹ for the two N forms. In forests at the nearby Fraser Experimental Forest that lost 20% of stand basal area to bark beetles, NO₃-N averaged 0.01 and did not exceed 0.13 mg N L⁻¹ in hillslope-scale, subsurface flow (1- to 4-m depth) during 5 yr after the onset of the outbreak (B. Starr, USFS, personal communication, 2011). Stream NO₃-N increased only slightly in catchments at Fraser Experimental Forest where beetles killed 85% of lodgepole pine trees, although concentrations never exceeded 0.2 mg L⁻¹ (Rhoades et al., 2017). The beetle-related increase in inorganic N export amounted to only 1.5% of annual N deposition in local forests. These studies indicate that some combination of plant, soil (Edburg et al., 2011), and in-stream (Bernhardt et al., 2003) processes limit the net biogeochemical effect of forest mortality in beetle-affected watersheds.

Nutrient demand by residual and newly established vegetation is likely to contribute to the weak leachate and stream N response found here, like that reported elsewhere (Parsons et al., 1994; Rhoades et al., 2013). Trees surviving within beetle-infested pine stands grew faster (Romme et al., 1986) and nutrient uptake by residual, live trees limited NO₃-N leaching in simulated beetle outbreaks in Wyoming pine forests (Parsons et al., 1994). In this

study, there were 3000 to 4500 trees ha⁻¹ (0–200 cm tall) on uncut hillslopes (Supplemental Table S1) and dense understory plant cover (Supplemental Table S2), similar to conditions seen in nearby beetle-infested forests (Fornwalt et al., 2018; Rhoades et al., 2018). Greater light and soil resource availability beneath dead overstory trees stimulate understory plants (Hawkins et al., 2013; Pec et al., 2015) and regenerating trees (Pelz et al., 2018), and this compensatory growth and nutrient demand appears sufficient to limit N losses.

Nitrogen Attenuation in Beetle-Infested Riparian Forests

Leachate N concentrations were relatively low in beetle-killed riparian forests. Upland logging increased leachate NO₃-N and DTN about threefold compared with uncut upland forests (Fig. 1), although the effect on leaching in downslope buffers was less (Fig. 2). Comparison of leaching in the protected buffer and the increased leaching in the logged riparian zone provides an estimate of the amount of N attenuated by the dead riparian forest. Riparian logging increased N leaching relative to uncut buffers, providing an estimate of N attenuation within dead riparian forests. For example, the concentration of NO₃-N leached in the uncut buffers was 62% of that measured after riparian harvesting. This estimate is comparable with riparian N attenuation reported elsewhere. For example, across a variety of vegetation types and buffer widths, riparian zones attenuated 68% of groundwater N on average (Mayer et al., 2007). Nitrogen removal efficiency varied widely among individual studies (–75 to 100%; Mayer et al., 2007), across hydrogeomorphic conditions (60–90%; Vidon and Hill, 2004) and physiographic regions (35–95%; Weller et al., 2011). Herbaceous plant cover and understory tree species differed between upland and riparian forests (Supplemental Tables S1 and S2), but there was no evidence that riparian soils were a greater source of inorganic N supply than upland soils (Table 1), as has been documented elsewhere (Blackburn et al., 2017).

Lack of nutrient uptake by dead riparian trees influenced these findings, and N attenuation within live forests under similar conditions may be greater. Riparian N attenuation is often limited where N inputs from upland areas are low (Sabater et al., 2003; Mayer et al., 2007), as observed here. This study reports early-summer N leached from the base of the rooting zone, but not that occurring earlier or at greater depth that may have been more concentrated. At the nearby Fraser Experimental Forest, NO₃-N concentrations were highest at the onset of subsurface discharge (Reuss et al., 1997) before seasonal site access allowed leachate sampling for the current study. Leachate sampled during this study is representative of the bulk of the subsurface flow and peak discharge season, however, when hydrologic connectivity between upland and downslope landscapes was greatest (Stottlemeyer and Troendle, 1999). The year-long resin exchangeable soil N measurements captured similar harvest and attenuation patterns and further support the soil lysimeter findings.

Effects of Harvesting Dead Riparian Forests

Riparian harvesting substantially increased soil leachate N and C concentrations and IER soil NO₃-N availability compared with buffered and uncut hillslope riparian zones. Increased N leaching after harvesting is associated with reduced nutrient uptake when live trees are removed, but since most of the riparian trees were dead in these sites (>80%), this was not the case.

Neither did increased nitrification or mineralization supply more inorganic N (Table 1) available for leaching, as often occurs after harvesting (Giardina and Rhoades, 2001; Prescott et al., 2003). The rapid increase in herbaceous plants and aspen sprouts after the riparian harvest suggests that nutrient demand by recovering vegetation (Fortier et al., 2015) may limit postharvest biogeochemical responses. As reported in this study, aspen commonly responds rapidly to harvest of beetle-infested conifer stands, and the species is projected to increase in abundance locally for several decades (Collins et al., 2010; Rhoades et al., 2018).

Soil N leaching remained elevated throughout 3 yr of postharvest sampling compared with uncut, dead forests, although the longevity of the treatment effects remains unknown. Nitrate leaching increased over four postharvest years in nearby live forests and remained above baseline for more than a decade (Reuss et al., 1997; Starr, 2003). The leachate N concentrations in the dead forests of this study were a fraction of those measured in the green forests (~25%), suggesting that a pulse of increased soil N availability and leaching may have occurred the first years after tree mortality (Clow et al., 2011), prior to timber harvesting. High-elevation forests require nearly a century to regrow preharvest forest structure in this region (Collins et al., 2010), although recovery of plant nutrient demand may occur sooner (Vitousek et al., 1979). For example, stream N concentrations and flux in nearby watersheds harvested 30 to 60 yr previously were equal to or lower than those in untreated watersheds (Stottlemeyer and Troendle, 1987; Rhoades et al., 2017), potentially due to high N uptake by dense, regenerating forests. Owing to the fast growth of aspen sprouts in the riparian study areas, it seems likely that postharvest plant nutrient demand will recover relatively rapidly.

Removal of dead riparian trees in this experimental study appears to have accommodated fuel reduction objectives without compromising source water protection. Although soil N leaching increased in harvested buffers, N in adjacent streams remained well below regional water quality thresholds (Supplemental Fig S1). Other studies have measured greater leachate N in deeper groundwater and early spring snowmelt events in the region (Starr, 2003; Biederman et al., 2016), and these fluxes would not have been captured by this study. Nonetheless, reducing the risk of significant wildfire-related damage to streams, riparian zones, and catchments may justify minor or short-term changes in stream nutrients. Water quality protection from riparian buffers varies with local topography, hydrological, and edaphic conditions (Vidon and Hill, 2004; Ocampo et al., 2006). As such, site-specific buffer design has potential to both protect fragile sections of riparian corridors and groundwater discharge zones (Kuglerová et al., 2014) and help delineate zones where harvesting may be appropriate. Developing and testing guidelines for careful harvesting within riparian zones (Clinton, 2011; Knoepp and Clinton, 2009; Witt et al., 2016) may lead to more flexible, but equally protective, management prescriptions compared with uniform, fixed-width buffers (Richardson et al., 2012).

Fuel reduction harvests after severe bark beetle outbreaks represent a case that supports flexible riparian buffer design. During the past decade, wildfires have burned >140,000 ha of beetle-affected Colorado and Wyoming forests (Eidenshink et al., 2007), and concern about forest recovery after combined insect and wildfire disturbances (Jenkins et al., 2012; Rhoades et

al., 2018) is used to justify active forest management. There are numerous ecosystem and biodiversity consequences of salvage logging, however (Lindenmayer et al., 2004; Müller et al., 2018), and their potential negative outcomes may be underestimated by experimental research (Leverkus et al., 2018). The unknown responses to the unprecedented level of forest mortality from recent insect outbreaks caution against drastic changes to existing watershed best management practice. This study documents that new forests are regenerating rapidly after logging on both upland and riparian hillslope positions (Supplemental Table S1), and that tree densities are in excess of the mandated stocking level (370 trees ha⁻¹). Further research and longer-term monitoring should accompany efforts to expand riparian fuel reduction harvesting in beetle-killed forests.

Conclusions

This study found low soil N leachate concentrations in riparian buffers composed of dead lodgepole pine. Leachate N was lower in uncut buffers than upland harvest areas, indicating that these buffers likely attenuate NO₃-N and DTN originating in upslope clear cuts. Removal of the dead trees increased resin exchangeable NO₃-N and soil N and C leaching significantly, highlighting the value of retaining dead riparian buffers.

Riparian harvesting and fuel reduction has become widespread in the western United States during recent decades (Stone et al., 2010). Bark beetles have killed pine on 10 million ha including riparian and upland forests in the region since the mid-1990s (Raffa et al., 2008; USDA Forest Service, 2013). This has prompted a widespread increase in salvage logging that has continued for more than a decade. This 3-yr study found that N leaching in harvested riparian areas was unlikely to cause serious nutrient enrichment in this high-elevation ecosystem. However, greater N leaching concentrations have been documented in beetle-infested forests elsewhere (Huber, 2005; Biederman et al., 2016). Adequate watershed protection under changing forest conditions requires understanding of the biogeochemical and other ecosystem consequences of riparian harvesting across a wide range of forest and catchment conditions.

Supplemental Material

Supplemental Fig. S1 shows streamwater and leachate solute concentrations in beetle-killed lodgepole pine forests. Stream NO₃-N and DTN averaged 0.02 and 0.16 mg N L⁻¹ during the study and never exceeded 0.07 and 0.24 mg N L⁻¹, respectively. Tree regeneration (Supplemental Table S1) and understory plant and surface cover and herbaceous plant biomass (Supplemental Table S2) in bark beetle-infested lodgepole pine forests.

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References

- Agilent Technologies. 2006. Agilent EZChrom Elite user's guide. Sci. Softw., Pleasanton, CA.
- Alstatt, D., and R.L. Miles. 1983. Soil survey of Grand County area, Colorado. U. S. Gov. Print. Office, Washington, DC.
- APHA. 1998. Single-column Method 4110C. In: L.S. Clesceri, et al., editors, Standard methods for the examination of water and waste water. 20th ed. Am. Public Health Assoc., Washington, DC. p. 4-6-4-8.
- Berner, L.T., B.E. Law, A.J.H. Meddens, and J.A. Hicke. 2017. Tree mortality from fires, bark beetles, and timber harvest during a hot and dry decade in the western United States (2003–2012). *Environ. Res. Lett.* 12:065005. doi:10.1088/1748-9326/aa6f94
- Bernhardt, E.S., G.E. Likens, D.C. Buso, and C.T. Driscoll. 2003. In-stream uptake dampens effects of major forest disturbance on watershed nitrogen export. *Proc. Natl. Acad. Sci. USA* 100:10304–10308. doi:10.1073/pnas.1233676100
- Biederman, J.A., T. Meixner, A.A. Harpold, D.E. Reed, E.D. Gutmann, J.A. Gaun, and P.D. Brooks. 2016. Riparian zones attenuate nitrogen loss following bark beetle-induced lodgepole pine mortality. *J. Geophys. Res. Biogeosci.* 121:933–948. doi:10.1002/2015JG003284
- Binkley, D., and P. Matson. 1983. Ion exchange resin bag method for assessing forest soil nitrogen availability. *Soil Sci. Soc. Am. J.* 47:1050–1052. doi:10.2136/sssaj1983.03615995004700050045x
- Binkley, D., and S.C. Hart. 1989. The components of nitrogen availability assessments in forest soils. *Adv. Soil Sci.* 10:57–112.
- Blackburn, M., J.L.J. Ledesma, T. Näsholm, H. Laudon, and R.A. Sponseller. 2017. Evaluating hillslope and riparian contributions to dissolved nitrogen (N) export from a boreal forest catchment. *J. Geophys. Res. Biogeosci.* 122:324–339. doi:10.1002/2016JG003535
- Brouillard, B.M., K.M. Mikkelsen, C.M. Bokman, E.M. Berryman, and J.O. Sharp. 2017. Extent of localized tree mortality influences soil biogeochemical response in a beetle-infested coniferous forest. *Soil Biol. Biochem.* 114:309–318. doi:10.1016/j.soilbio.2017.06.016
- Bundy, L.G., and J.J. Meisinger. 1994. Nitrogen availability indices. In: R.W. Weaver, et al., editors, Methods of soil analysis. Part 2. Agron. Mongr. 5. ASA and SSSA, Madison, WI. p. 951–984.
- Chapman, T.B., T.T. Veblen, and T. Schoennagel. 2012. Spatiotemporal patterns of mountain pine beetle activity in the southern Rocky Mountains. *Ecology* 93:2175–2185. doi:10.1890/11-1055.1
- Clinton, B.D. 2011. Stream water responses to timber harvest: Riparian buffer width effectiveness. *For. Ecol. Manage.* 261:979–988. doi:10.1016/j.foreco.2010.12.012
- Clow, D.W., C. Rhoades, J. Briggs, M. Caldwell, and W.M. Lewis. 2011. Responses of soil and water chemistry to mountain pine beetle induced tree mortality in Grand County, Colorado, USA. *Appl. Geochem.* 26:S174–S178. doi:10.1016/j.apgeochem.2011.03.096
- Collins, B.J., C.C. Rhoades, R.M. Hubbard, and M.A. Battaglia. 2011. Tree regeneration and future stand development after bark beetle infestation and harvesting in Colorado lodgepole pine stands. *For. Ecol. Manage.* 261:2168–2175. doi:10.1016/j.foreco.2011.03.016
- Collins, B.J., C.C. Rhoades, J. Underhill, and R.M. Hubbard. 2010. Post-harvest seedling recruitment following mountain pine beetle infestation of Colorado lodgepole pine stands: A comparison using historic survey records. *Can. J. For. Res.* 40:2452–2456. doi:10.1139/X10-172
- Colorado State Forest Service (CSFS). 2016. 2015 Report on the health of Colorado's forests: 15 years of change. Colorado State Univ., Fort Collins.
- Cristan, R., W.M. Aust, M.C. Bolding, S.M. Barrett, and J.F. Munsell. 2018. National status of state developed and implemented forestry best management practices for protecting water quality in the United States. *For. Ecol. Manage.* 418:73–84. doi:10.1016/j.foreco.2017.07.002
- Cristan, R., W.M. Aust, M.C. Bolding, S.M. Barrett, J.F. Munsell, and E. Schilling. 2016. Effectiveness of forestry best management practices in the United States: Literature review. *For. Ecol. Manage.* 360:133–151. doi:10.1016/j.foreco.2015.10.025
- Edburg, S.L., J.A. Hicke, D.M. Lawrence, and P.E. Thornton. 2011. Simulating coupled carbon and nitrogen dynamics following mountain pine beetle outbreaks in the western United States. *J. Geophys. Res. Biogeosci.* 116:G04033. doi:10.1029/2011JG001786
- Eidenshink, J., B. Schwind, Z.L. Zhu, B. Quayle, and S. Howard. 2007. A project for monitoring trends in burn severity. *Fire Ecol.* 3:3–21. doi:10.4996/fireecology.0301003
- Fahey, T.J., J.B. Yavitt, J.A. Pearson, and D.H. Knight. 1985. The nitrogen cycle in lodgepole pine forests, southeastern Wyoming. *Biogeochemistry* 1:257–275.
- Fornwalt, P., C. Stevens-Rumann, and B. Collins. 2018. Overstory structure and surface cover dynamics in the decade following the Hayman Fire, Colorado. *Forests* 9:152. doi:10.3390/f9030152
- Fortier, J., B. Truax, D. Gagnon, and F. Lambert. 2015. Biomass carbon, nitrogen and phosphorus stocks in hybrid poplar buffers, herbaceous buffers and natural woodlots in the riparian zone on agricultural land. *J. Environ. Manage.* 154:333–345. doi:10.1016/j.jenvman.2015.02.039
- Giardina, C.P., and C.C. Rhoades. 2001. Clear cutting and burning affect nitrogen supply, phosphorus fractions and seedling growth in soils from a Wyoming lodgepole pine forest. *For. Ecol. Manage.* 140:19–28. doi:10.1016/S0378-1127(00)00272-3
- Griffin, J.M., M.G. Turner, and M. Simard. 2011. Nitrogen cycling following mountain pine beetle disturbance in lodgepole pine forests of Greater Yellowstone. *For. Ecol. Manage.* 261:1077–1089. doi:10.1016/j.foreco.2010.12.031
- Grimm, N.B., S.E. Gergel, W.H. McDowell, E.W. Boyer, C.L. Dent, P.M. Groffman, et al. 2003. Merging aquatic and terrestrial perspectives of nutrient biogeochemistry. *Oecologia* 137:485–501. doi:10.1007/s00442-003-1382-5
- Hawkins, C.D.B., A. Dhar, and N.A. Balliet. 2013. Radial growth of residual overstory trees and understory saplings after mountain pine beetle attack in central British Columbia. *For. Ecol. Manage.* 310:348–356. doi:10.1016/j.foreco.2013.08.035
- Huber, C. 2005. Long lasting nitrate leaching after bark beetle attack in the highlands of the Bavarian Forest National Park. *J. Environ. Qual.* 34:1772–1779. doi:10.2134/jeq2004.0210
- Huckaby, L.S., and W.H. Moir. 1998. Forest communities at Fraser Experimental Forest, Colorado. *Southwest. Nat.* 43:204–218.
- IBM Corporation. 2013. SPSS Statistics for Windows. Version 22.0. IBM Corp., Armonk, NY.
- Jencso, K.G., B.L. McGlynn, M.N. Gooseff, S.M. Wondzell, K.E. Bencala, and L.A. Marshall. 2009. Hydrologic connectivity between landscapes and streams: Transferring reach- and plot-scale understanding to the catchment scale. *Water Resour. Res.* 45:W04428. doi:10.1029/2008WR007225
- Jenkins, M.J., W.G. Page, E.G. Hebertson, and M.E. Alexander. 2012. Fuels and fire behavior dynamics in bark beetle-attacked forests in western North America and implications for fire management. *For. Ecol. Manage.* 275:23–34. doi:10.1016/j.foreco.2012.02.036
- Kaňa, J., K. Tahovská, and J. Kopáček. 2013. Response of soil chemistry to forest dieback after bark beetle infestation. *Biogeochemistry* 113:369–383. doi:10.1007/s10533-012-9765-5
- Kellogg, K.S., R.R. Shroba, B. Bryant, and W.R. Premo. 2008. Geologic map of the Denver west 30' × 60' quadrangle, north-central Colorado. USGS Sci. Invest. Map 3000. USGS, Reston, VA. Scale: 1:100,000.
- Knoepf, J.D., and B.D. Clinton. 2009. Riparian zones in southern Appalachian headwater catchments: Carbon and nitrogen responses to forest cutting. *For. Ecol. Manage.* 258:2282–2293. doi:10.1016/j.foreco.2009.04.006
- Kuglerová, L., A. Ågren, R. Jansson, and H. Laudon. 2014. Towards optimizing riparian buffer zones: Ecological and biogeochemical implications for forest management. *For. Ecol. Manage.* 334:74–84. doi:10.1016/j.foreco.2014.08.033
- Leverkus, A.B., J.M.R. Benayas, J. Castro, D. Boucher, S. Brewer, B.M. Collins, et al. 2018. Salvage logging effects on regulating and supporting ecosystem services: A systematic map. *Can. J. For. Res.* 48:983–1000. doi:10.1139/cjfr-2018-0114
- Lindenmayer, D.B., D.R. Foster, J.F. Franklin, M.L. Hunter, R.F. Noss, F.A. Schmiegelow, and D. Perry. 2004. Salvage harvesting policies after natural disturbance. *Science* 303:1303. doi:10.1126/science.1093438
- Lowrance, R., L.S. Altier, J.D. Newbold, R.R. Schnabel, P.M. Groffman, J.M. Denver, et al. 1997. Water quality functions of riparian forest buffers in Chesapeake Bay watersheds. *Environ. Manage.* 21:687–712. doi:10.1007/s002679900060
- Lukas, J., J. Barsugli, N. Doesken, I. Rangwala, and K. Wolter. 2014. Climate change in Colorado: A synthesis to support water resources management and adaptation. 2nd ed. Colorado Water Conserv. Board, Western Water Assess., Univ. of Colorado, Boulder.
- Mata, S.A., J.M. Schmid, and W.K. Olsen. 2003. Growth of lodgepole pine stands and its relation to mountain pine beetle susceptibility. Res. Paper RMRS-RP-42. USDA, For. Serv., Rocky Mountain Res. Stn., Fort Collins, CO. doi:10.2737/RMRS-RP-42
- Mayer, P.M., S.K. Reynolds, M.D. McCutchen, and T.J. Canfield. 2007. Meta-analysis of nitrogen removal in riparian buffers. *J. Environ. Qual.* 36:1172–1180. doi:10.2134/jeq2006.0462
- Mitchell, R.G., and H.K. Preisler. 1998. Fall rate of lodgepole pine killed by the mountain pine beetle in central Oregon. *West. J. Appl. For.* 13:23–26.
- Müller, J., R.F. Noss, S. Thorn, C. Bässler, A.B. Leverkus, and D. Lindenmayer. 2018. Increasing disturbance demands new policies to conserve intact forest. *Conserv. Lett.* e12449. doi:10.1111/cons.12449 (in press).

- Naiman, R.J., and R.E. Bilby. 1998. River ecology and management in the Pacific Coastal ecoregion. In: R.J. Naiman and R.E. Bilby, editors, *River ecology and management: Lessons from the Pacific Coastal ecoregion*. Springer, New York. p. 1–10. doi:10.1007/978-1-4612-1652-0_1
- Ocampo, C.J., C.E. Oldham, and M. Sivapalan. 2006. Nitrate attenuation in agricultural catchments: Shifting balances between transport and reaction. *Water Resour. Res.* 42:W01408. doi:10.1029/2004WR003773
- Page, W.G., M.E. Alexander, and M.J. Jenkins. 2013. Wildfire's resistance to control in mountain pine beetle-attacked lodgepole pine forests. *For. Chron.* 89:783–794. doi:10.5558/ffc2013-141
- Parsons, W.F.J., D.H. Knight, and S.L. Miller. 1994. Root gap dynamics in lodgepole pine forest: Nitrogen transformations in gaps of different sizes. *Ecol. Appl.* 4:354–362. doi:10.2307/1941939
- Pec, G., J. Karst, A. Sywenky, P. Cigan, N. Erbilgin, S. Simard, and J. Cahill Jr. 2015. Rapid increases in forest understory diversity and productivity following a mountain pine beetle (*Dendroctonus ponderosae*) outbreak in pine forests. *PLoS ONE* 10:e0124691. doi:10.1371/journal.pone.0124691
- Pelz, K.A., C.C. Rhoades, R.M. Hubbard, and F.W. Smith. 2018. Severity of overstory mortality influences conifer recruitment and growth in mountain pine beetle-affected forests. *Forests* 9:536. doi:10.3390/f9090536
- Prescott, C.E., G.D. Hope, and L.L. Blevins. 2003. Effect of gap size on litter decomposition and spruce nitrate concentration in a high-elevation spruce-fir forest. *Can. J. For. Res.* 33:2210–2220. doi:10.1139/x03-152
- Pugh, E., and E. Small. 2012. The impact of pine beetle infestation on snow accumulation and melt in the headwaters of the Colorado River. *Ecology* 93:467–477. doi:10.1002/eco.239
- Raffa, K.F., B.H. Aukema, B.J. Bentz, A.L. Carroll, J.A. Hicke, M.G. Turner, and W.H. Romme. 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: The dynamics of bark beetle eruptions. *BioScience* 58:501–517. doi:10.1641/B580607
- Reuss, J.O., R. Stottlemeyer, and C.A. Troendle. 1997. Effect of clear cutting on nutrient fluxes in a subalpine forest at Fraser, Colorado. *Hydrol. Earth Syst. Sci.* 1:333–344. doi:10.5194/hess-1-333-1997
- Rhoades, C.C., R.M. Hubbard, and K. Elder. 2017. A decade of streamwater nitrogen and forest dynamics after a mountain pine beetle outbreak at the Fraser Experimental Forest, Colorado. *Ecosystems* 20:380–392. doi:10.1007/s10021-016-0027-6
- Rhoades, C.C., J.H. McCutchen, Jr., L.A. Cooper, D.W. Clow, T.M. Detmer, J.S. Briggs, et al. 2013. Biogeochemistry of beetle kill: Explaining a weak nitrate response. *Proc. Natl. Acad. Sci. USA* 110:1756–1760. doi:10.1073/pnas.1221029110
- Rhoades, C.C., K.A. Pelz, P.J. Fornwalt, B.H. Wolk, and A.S. Cheng. 2018. Overlapping bark beetle outbreaks, salvage logging and wildfire restructure a lodgepole pine ecosystem. *Forests* 9:101. doi:10.3390/f9030101
- Richardson, J.S., R.J. Naiman, and P.A. Bisson. 2012. How did fixed-width buffers become standard practice for protecting freshwaters and their riparian areas from forest harvest practices? *Freshw. Sci.* 31:232–238. doi:10.1899/11-031.1
- Romme, W.H., D.H. Knight, and J.B. Yavitt. 1986. Mountain pine beetle outbreaks in the Rocky Mountains: Regulators of primary productivity. *Am. Nat.* 127:484–494. doi:10.1086/284497
- Sabater, S., A. Butturini, J.C. Clement, T. Burt, D. Dowrick, M. Hefting, et al. 2003. Nitrogen removal by riparian buffers along a European climatic gradient: Patterns and factors of variation. *Ecosystems* 6:0020–0030. doi:10.1007/s10021-002-0183-8
- Schultz, R.C., T.M. Isenhardt, W.W. Simpkins, and J.P. Colletti. 2004. Riparian forest buffers in agroecosystems- structure, function and management- Lessons learned from the Bear Creek watershed project in central Iowa. In: P.K.R. Nair, et al., editors, *New vistas in agroforestry*. Kluwer Acad. Publ., Dordrecht, the Netherlands. doi:10.1007/978-94-017-2424-1_3
- Shroba, R.R., B. Bryant, K.S. Kellogg, P.K. Theobald, and T.R. Brandt. 2010. Geologic map of the Fraser 7.5-minute quadrangle, Grand County, Colorado. USGS Sci. Invest. Map 3130. USGS, Reston, VA. Scale: 1:24,000.
- Soil Survey Staff. 2010. Keys to soil taxonomy. 11th ed. USDA Nat. Resour. Conserv. Serv., Washington, DC.
- Starr, B.J. 2003. Long-term effects of clearcutting on N availability and soil solution chemistry in the Fraser Experimental Forest, Colorado. MS thesis, Colorado State Univ., Fort Collins.
- Stone, K.R., D.S. Pilliod, K.A. Dwire, C.C. Rhoades, S.P. Wollrab, and M.K. Young. 2010. Fuel reduction management practices in riparian areas of the western USA. *Environ. Manage.* 46:91–100. doi:10.1007/s00267-010-9501-7
- Stottlemeyer, R., and C.A. Troendle. 1987. Trends in streamwater chemistry and input-output balances, Fraser Experimental Forest, Colorado. USDA For. Serv., Rocky Mountain For. Range Exp. Stn., Fort Collins, CO.
- Stottlemeyer, R., and C.A. Troendle. 1999. Effect of subalpine canopy removal on snowpack, soil solution, and nutrient export, Fraser Experimental Forest, CO. *Hydrol. Processes* 13:2287–2299.
- Stottlemeyer, R., C.A. Troendle, and D. Markowitz. 1997. Change in snowpack, soil water, and streamwater chemistry with elevation during 1990, Fraser Experimental Forest, Colorado. *J. Hydrol.* 195:114–136. doi:10.1016/S0022-1694(96)03241-6
- Tishmack, J., S.A. Mata, J.M. Schmid, and L. Porth. 2004. Mountain pine beetle emergence from lodgepole pine at different elevations near Fraser, CO. Res. Paper RMRS-RN-27. USDA For. Serv., Rocky Mountain Res. Stn., Fort Collins, CO.
- Triska, F.J., J.H. Duff, and R.J. Avanzino. 1993. The role of water exchange between a stream channel and its hyporheic zone in nitrogen cycling at the terrestrial-aquatic interface. *Hydrobiologia* 251:167–184. doi:10.1007/BF00007177
- Troendle, C.A., and R.M. King. 1985. The Fool Creek watershed: Thirty years later. *Water Resour. Res.* 21:1915–1922. doi:10.1029/WR021i012p01915
- USDA Forest Service. 2006. Watershed conservation practices handbook. FSH 2509.25. Rocky Mountain region R2. USDA For. Serv., Denver, CO.
- USDA Forest Service. 2013. Forest insect and disease aerial survey data, Rocky Mountain region. USDA For. Serv. State Private For., For. Health Prot., Lakewood, CO.
- USEPA. 2000. Nutrient criteria technical guidance manual. Rivers and streams. EPA-822-B-00-002. Office Water, USEPA, Washington, DC.
- Verry, E.S., J.W. Hornbeck, and C.A. Dolloff. 2000. Riparian management in forests of the continental eastern United States. Lewis Publ., Boca Raton, FL.
- Vidon, P.G.F., and A.R. Hill. 2004. Landscape controls on nitrate removal in stream riparian zones. *Water Resour. Res.* 40:1–14. doi:10.1029/2003WR002473
- Vitousek, P.M., J.R. Gosz, C.C. Grier, J.M. Melillo, W.A. Reinert, and R.L. Todd. 1979. Nitrate losses from disturbed ecosystems. *Science* 204:469–474. doi:10.1126/science.204.4392.469
- Weller, D.E., M.E. Baker, and T.E. Jordan. 2011. Effects of riparian buffers on nitrate concentrations in watershed discharges: New models and management implications. *Ecol. Appl.* 21:1679–1695. doi:10.1890/10-0789.1
- Western Governors Association. 2002. A collaborative approach for reducing wildland fire risks to communities and the environment: 10-year comprehensive strategy implementation plan. Western Gov. Assoc., Denver, CO.
- Witt, E.L., C.D. Barton, J.W. Stringer, R.K. Kolka, and M.A. Cherry. 2016. Influence of variable streamside management zone configurations on water quality after forest harvest. *J. For.* 114:41–51.