Biogeochemistry of beetle-killed forests: Explaining a weak nitrate response

Charles C. Rhoades[a], James H. McCutchan, Jr.[b], Leigh A. Cooper[b,c], David Clow[d], Thomas M. Detmer[b,c], Jennifer S. Briggs[e], John D. Stednick[f], Thomas T. Veblen[g], Rachel M. Ertz[c], Gene E. Likens[h,i,j], and William M. Lewis, Jr.[b,c,1]

[a]US Department of Agriculture Forest Service, Rocky Mountain Research Station, Fort Collins, CO 80523; [c]Department of Ecology and Evolutionary Biology, [g]Department of Geography, and [b]Center for Limnology, Cooperative Institute for Research in Environmental Sciences, University of Colorado, Boulder, CO 80309; [e]Rocky Mountain Geographic Science Center, US Geological Survey, Denver Federal Center, Denver CO 80225; [d]US Geological Survey, Water Resources Division, Denver Federal Center, Denver, CO 80225; [f]Forest and Rangeland Stewardship, Colorado State University, Fort Collins, CO 80523-1472; [h]Cary Institute of Ecosystem Studies, Millbrook, NY 12545; [i]Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT 06269; and [j]Department of Limnology, Evolutionary Biology Centre, Uppsala University, 751 05 Uppsala, Sweden

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A current pine beetle infestation has caused extensive mortality of lodgepole pine (*Pinus contorta*) in forests of Colorado and Wyoming; it is part of an unprecedented multispecies beetle outbreak extending from Mexico to Canada. In United States and European watersheds, where atmospheric deposition of inorganic N is moderate to low (<10 kg·ha·y), disturbance of forests by timber harvest or violent storms causes an increase in stream nitrate concentration that typically is close to 400% of predisturbance concentrations. In contrast, no significant increase in streamwater nitrate concentrations has occurred following extensive tree mortality caused by the mountain pine beetle in Colorado. A model of nitrate release from Colorado watersheds calibrated with field data indicates that stimulation of nitrate uptake by vegetation components unaffected by beetles accounts for significant nitrate retention in beetle-infested watersheds. The combination of low atmospheric N deposition (<10 kg·ha·y), tree mortality spread over multiple years, and high compensatory capacity associated with undisturbed residual vegetation and soils explains the ability of these beetle-infested watersheds to retain nitrate despite catastrophic mortality of the dominant canopy tree species.

nitrogen biogeochemistry | streamwater chemistry | nitrate loss | watershed disturbance

Bark beetles have infested 1.6 million hectares of coniferous forest in Colorado and Wyoming during an outbreak that began in 1996 and accelerated after 2004 (1). Although several species of bark beetle are harmful to North American conifers, the native mountain pine beetle (*Dendroctonus ponderosae*) has caused the most damage since 1996, particularly through its infestation of lodgepole pine (*Pinus contorta*), which often grows in nearly monospecific stands dominated by trees of similar age. The Colorado/Wyoming outbreak is part of a severe general upsurge in infestation affecting dominant conifer species from northern Mexico to British Columbia (2). Beetle infestations have been present historically in western montane forests of North America, but climate change (drought, warming) and stand uniformity appear to have increased vulnerability of forests to extensive bark beetle outbreaks (2, 3).

Timber harvest and other watershed-scale canopy disturbances often affect the amount of runoff, water quality, and ecosystem metabolism of streams and rivers (4–10). One of the strongest responses is increased export of nitrogen, especially in the form of nitrate, which moves readily to streams via subsurface drainage.

Although nitrate released in response to forest disturbances can be taken up by stream autotrophs (11, 12), removal of nitrate in streams typically is greatly exceeded by nitrate release following strong disturbances of the terrestrial ecosystem. Release of nitrate to streams can be caused by reduced vegetative uptake of nitrate that follows damage to or removal of vegetation. In addition, decreased uptake of ammonium caused by tree mortality may facilitate or increase production of nitrate by soil microbes, which contributes to increased nitrate concentrations in streams (4, 5, 9, 10). We show here that extensive tree mortality caused by the mountain pine beetle in Colorado has, contrary to expectation, not been accompanied by any large increase in streamwater concentrations of nitrate; we offer an explanation for the retention of nitrate in beetle-infested forests.

Often, pine beetle infestation in a given watershed is established first at locations that are more xeric than the watershed as a whole because water-stressed trees are less able to defend themselves against the beetles (2). Furthermore, the mountain pine beetle preferentially infests large trees, which have a large phloem volume for growth of larvae as well as thick bark that may protect beetle larvae from potentially lethal winter temperatures (13, 14). Thus, the initial infestation is spatially heterogeneous (14).

During infestations, beetles spread widely from ideal sites to less favorable sites and to smaller trees over a period of multiple years (13, 15), but their dispersal may be affected by winter air temperatures or soil moisture in a given year. Infestation ultimately may cover entire watersheds (e.g., 60% of lodgepole, 90% of large lodgepole) (15, 16).

Methods and Study Sites

Changes of nitrate concentrations in Colorado streams within watersheds dominated by mature lodgepole pine with a range of beetle-induced mortality were documented in three concurrent studies at 65 sites over a range of 150 km in Colorado's Rocky Mountains (*SI Text 1*). The Fraser Experimental Forest (FEF) study included weekly measurements of streamwater nitrate concentration beginning before 2003, prior to the onset of beetle infestation, and extending through 2011, by which time beetle mortality had reached 20–90% of the canopy trees (*SI Text 1*) (16). The Willow Creek Study (WC) consisted of monthly measurements of nitrate concentration from June to September 2009 in 11 watersheds with varied intensity of beetle infestation. A spatially distributed study (SD) documented bimonthly nitrate concentrations at 53 sites in central Colorado during the ice-free season of 2009. A nitrogen assimilation study (NA) for noninfested trees was based on measurements of foliar nitrogen, an index of compensatory N uptake from groundwater (17), for lodgepole pine-dominated sites with varied degrees of pine beetle infestation (*SI Text 1*).

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[1]To whom correspondence should be addressed. E-mail: lewis@spot.colorado.edu.

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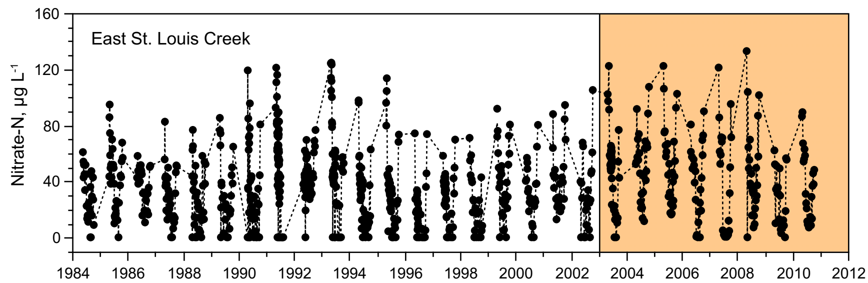

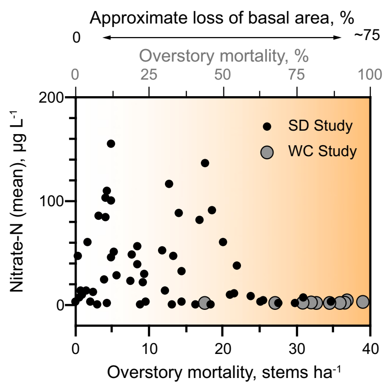

Variable	Estimate (± SE)	Sequential R²
Intercept	0.45 (±0.33)	---
Slope (mean), %	0.08 (±0.013)	0.54
Log_{10} Discharge, m^3 s^{-1}	0.48 (±0.080)	0.70
Northing, km	-0.0032 (±0.0012)	0.74

Fig. 1. (*Upper*) Nitrate concentrations in East St. Louis Creek, Fraser Experimental Forest, Colorado, beginning before extensive beetle kill of trees and extending into years of progressive beetle kill (shaded area). (*Lower*) Relationship between beetle-induced mortality (based on US Forest Service aerial survey of forest overstory tree mortality, which covers only the upper canopy) and discharge weighted streamwater nitrate concentrations in the SD and WC studies; site characteristics but not the extent of overstory mortality caused by bark beetles explain significant variation of stream nitrate concentrations as shown for the SD study (see table in figure).

Results

The FEF study demonstrated no large increase of nitrate concentrations in streams associated with beetle kill (Fig. 1). By 2007, when beetles had killed 50–95% of the canopy (primarily lodgepole pine), the mean increase in concentration of nitrate in streams relative to prior years with no infestation was <30%, which is <2% of the 2–5 kg·ha^{-1}·y^{-1} deposition of nitrate plus ammonium (DIN) entering the watershed through atmospheric N deposition (*SI Text 2*).

The WC study and the SD study (Fig. 1) showed no statistical relationship of nitrate concentration to the extent of tree mortality (Fig. 1), confirming preliminary data at other locations (18). Factors other than beetle-induced mortality explain statistically a high proportion of the variation in nitrate concentrations among the WC and SD watersheds (Fig. 1).

The NA study showed a positive relationship between foliar N and percent tree mortality (r^2 = 0.18, P < 0.001) (*SI Text 2*), which is also related to other variables (r^2 = 0.41 for percent tree mortality, elevation, diameter at breast height, stand density, and slope). The NA analysis showed that tree mortality of 50% led to an average increase in foliar nitrogen of 23% (*SI Text 2*).

Discussion

The most direct comparison for evaluating the effect of beetle-induced tree mortality on stream nitrate concentrations in the Colorado study area is derived from stream nitrate concentrations following patch clear-cut harvesting in the absence of significant bark beetle activity in a lodgepole-dominated watershed at the FEF near the beetle-kill watersheds for which information is presented in this article (19) (*SI Text*). Patch clear-cuts conducted on about 30% of the basin increased stream nitrogen

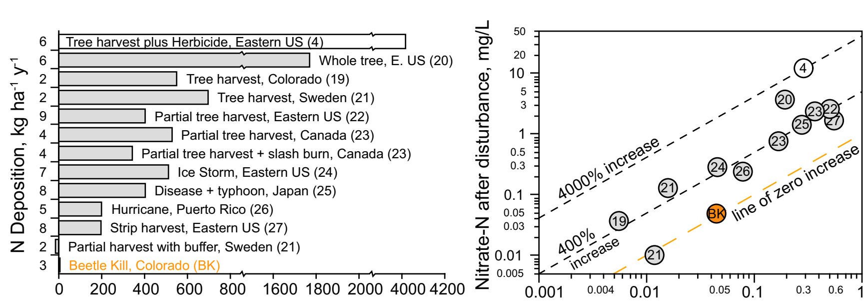

Fig. 2. (*Left*) Percent increase in streamwater nitrate concentrations following canopy disturbance of forests. Atmospheric wet deposition of inorganic N is shown for each location (*SI Text 2*). (*Right*) Relationship of nitrate concentrations before and after disturbance for sites shown on the *Left*. The trend line excludes four outliers (see text, r^2 = 0.96). The bar for beetle-kill effects on nitrate (*Left*) is drawn from three sources, one of which (FEF study) shows a small effect; the other two (WC and SD studies) (*SI Text 2*) show no effect. Numbers in parentheses (*Left*) and circles (*Right*) represent refs. 4 and 19–27. *SI Text 4* explains harvest details for specific sites.

concentrations, in contrast to the beetle-infested watersheds, which showed either a very small increase or no detectable increase in nitrate concentrations for streams.

More broadly, the literature on nitrate concentrations for unpolluted streams in paired watersheds that are undisturbed (no extensive mortality) and disturbed (with extensive mortality or physical disturbance) can be compared with streams in Colorado watersheds showing beetle-induced mortality (Fig. 2 and *SI Text 3*) (4, 19–27). Wet DIN deposition is shown for each of the sites; only watersheds with low-to-moderate DIN deposition(<10 $kg\cdot ha^{-1}\cdot y^{-1}$) were chosen for inclusion in Fig. 2. For this group of watersheds there is no statistical relationship between DIN deposition and the proportional increase in stream nitrate concentrations following disturbance ($r^2 = 0.04$, $P = 0.50$) (i.e., atmospheric deposition does not explain the trend shown in Fig. 2).

There is a strong relationship between stream nitrate concentrations before and after disturbance, but there are four strongly divergent outliers (all four outside the 95th percentile confidence limits) (Fig. 2). The first of these, which is well above the trend line, is for the classic study at the Hubbard Brook Experimental Forest (HBEF) involving catchment clear-cut harvesting of an entire watershed followed by 3 y of herbicide treatment, which removed postharvest demand by plants for inorganic nitrogen (4). This experiment produced the highest postharvest export response on record, probably by an acceleration of nitrification in soil following cessation of plant uptake of ammonium and by absence of residual vegetation that otherwise would have taken up inorganic nitrogen (4, 5). Numerous other studies have confirmed the importance of residual vegetation in sequestering nitrate following removal of vegetation (10). In addition, above the trend line but less extremely so, is a whole tree harvest of an entire watershed at HBEF, which may be divergent because of greater disturbance required for removal of all aboveground tree biomass (20).

The Colorado watersheds with beetle-induced mortality (pooled for Fig. 2), along with a partial tree harvest, including buffer strips in a Swedish forest (21), are outliers below the trend line. Beetle kill is unlike the HBEF harvest/herbicide watershed treatment in that it involves no physical disturbance and leaves much residual vegetation. The partial tree harvest in a Colorado watershed near the beetle-kill study sites (*SI Text 4*) falls near the trend line with 550% increase in nitrate export (19) (Fig. 2). Comparable data for beetle-induced mortality from other forest types are not yet available (*SI Text 3*).

The lack of a large streamwater nitrate response after extensive canopy mortality caused by bark beetles may be explained by some combination of two factors. Heterogeneous mortality (spatial and temporal) would be expected to reduce the amount of nitrate loss at any given time over the progression of infestation. In addition, compensatory responses by residual live vegetation are likely to respond to the increased resources available following overstory mortality. Multiple studies have documented increased foliar N content in the remaining live trees after surrounding trees were killed by bark beetles (NA study) (28). Increased establishment of new seedlings and faster growth of understory trees further demonstrate compensatory responses to the bark beetles (16). An estimate of the relative role of (*i*) temporal and spatial heterogeneity of mortality and (*ii*) compensatory response through accelerated uptake of DIN can be obtained by use of process modeling, the starting point for which is the deviation between the expected release of nitrate from disturbed watersheds based on the regression line shown in Fig. 2 and the observed (negligible) nitrate loss from Colorado watersheds with extensive beetle kill.

A common pattern of watershed nutrient release in response to disturbance of vegetation is captured in a conceptual model proposed by Vitousek and Reiners (29) and elaborated with modifications by others (5); it incorporates a spike in stream nutrient concentrations following a disturbance, a steep subsequent decline in concentrations extending below the original baseline that reflects recovery of vegetation, and slow return to an asymptote equal to the baseline (Fig. 3). Data on nitrate export following disturbance in numerous watersheds shows the model to be conceptually realistic, but the onset of nitrate release and breadth of the concentration peak vary considerably from one disturbance type or forest type to another (10), and the model may lose its realism over multiple decades because of changes in climate, occurrence of other disturbances, or nutrient processing by streams (12). It is possible to calibrate the model with empirical data for disturbances other than beetle mortality, then modify it sequentially to account for observed negligible loss of nitrate from watersheds with extensive beetle kill (Fig. 3). The basis for the model modifications is a hypothetical, spatially

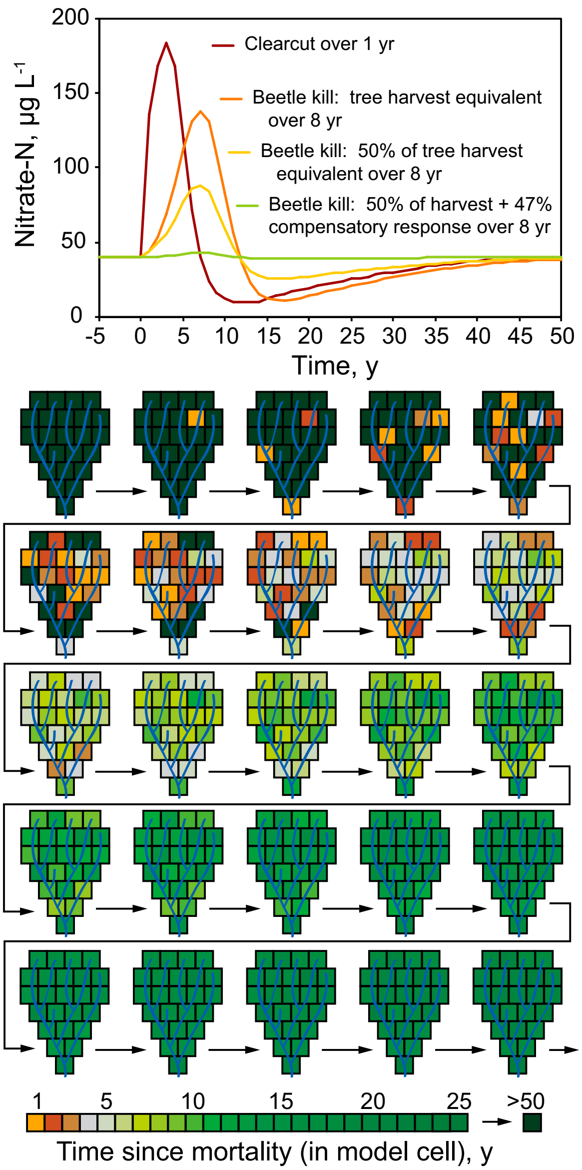

Fig. 3. (*Upper*) Modeled nitrate release for Rocky Mountain forests calibrated for tree harvest, to which three factors that differ between harvest and beetle kill are added sequentially, based on field studies. (*Lower*) A 25-y spatial sequence of canopy mortality for a hypothetical watershed with beetle kill spread over 8 y terminating at 100% cumulative infestation, as used in deriving the modeling results shown above.

segmented watershed consisting of watershed blocks; individual blocks are assumed to experience beetle-induced mortality on an incremental basis over a defined period that can be adjusted to mimic typical progressions of infestation (*SI Text 5*). For simplicity, any given watershed block experiencing beetle kill is assumed to show complete loss of nitrogen uptake by the canopy trees during the year of infestation. Cessation of water uptake by lodgepole pine shortly after beetle infestation (28) and the increase in soil nitrogen availability beneath recently killed pines (18) justify this assumption.

The first step in adapting the general model to beetle-induced mortality of trees is based on the assumption that beetle-kill response for nitrate is the same as the tree harvest response except that it is spread through time over an interval of 8 y (*SI Text 5* gives results of modeling for other durations). The temporal distribution of beetle kill reduces predicted maximum nitrate concentrations (Fig. 3), but the reduction is not nearly sufficient to account for the observed extreme difference between harvested and beetle-infested watersheds.

A second step in adaptation of the model is to assume that beetle-induced mortality, although killing much or most of the original canopy, does not disturb beetle-resistant overstory trees and the understory vegetation that would be lost or damaged during tree harvest. Based on data for Colorado forests, residual vegetation is estimated for modeling purposes at 50% of the original vegetative cover (16) (*SI Text 5* shows the effect of other assumptions about percent residual canopy) and would include some scattered large lodgepole (e.g., 20% of the original stand) as well as numerous small lodgepole, other beetle-resistant tree or plant species, and a mixed species strip of riparian vegetation. Presence of this residual vegetation, with the baseline assumption that its nitrogen demand remains at preinfestation levels, reduces the expected increase in nitrate concentrations considerably, but not to the extent reported by field studies (Fig. 3).

A third and final step in the sequence of modeling modifications is to attribute the residual difference between the modeled and observed nitrate concentrations associated with beetle kill to factors that can be designated collectively as "compensatory response." In this way, the model predicts the quantitative significance of the increased nitrogen uptake by remaining vegetation when canopy is removed and microbial processes (e.g., suppressed nitrification caused by deficiency of labile carbon following loss of fresh litterfall and root exudates) that may work against the mobilization of nitrate in response to beetle kill (30–32).

Modeling indicates that the magnitude of compensatory response as defined here accounts for about half of the suppression of nitrate release from forests with beetle kill; spatial and temporal heterogeneity of beetle kill accounts for the other half. Thus, compensatory response can provide potent water quality protection against adverse effects of elevated concentrations of inorganic N (33) in these western forests, but only if substantial vegetation (e.g., 50%) survives overstory mortality, as it does in the case of beetle kill.

Compensatory response deserves more detailed study given its potentially strong effect on nitrate release following canopy damage. Quantification of the understory component in particular has implications for harvest management. The close relationship between nitrate concentrations before and after tree harvesting or other severe canopy damage that involves collateral damage to understory is useful as an index of compensatory response. Because harvesting of beetle-killed forests stimulates regeneration of new seedlings (34), careful logging has the potential to mitigate increases in streamwater nitrogen concentrations. Ideal management that involves cutting would seek a mode of tree removal that produces nitrate concentrations significantly below the canopy-damage trend line (Fig. 2) by coupling canopy removal with protection of soils and residual vegetation.

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1. USDA Forest Service Forest Health and its Partners. Results of forest health, Aerial detection surveys. Available at www.fs.usda.gov/goto/r2/fh. Updated February 20, 2012. Accessed February 25, 2012.
2. Raffa KF, et al. (2008) Cross-scale drivers of natural disturbances prone to anthropogenic amplification: The dynamics of bark beetle eruptions. *Bioscience* 58(6):501–517.
3. Fettig CJ, et al. (2007) The effectiveness of vegetation management practices for prevention and control of bark beetle infestations in coniferous forests of the western and southern United States. *For Ecol Manage* 238(1–3):24–53.
4. Likens GE, Bormann FH, Johnson NM, Fisher DW, Pierce RS (1970) Effects of forest cutting and herbicide treatment on nutrient budgets in the Hubbard Brook watershed-ecosystem. *Ecol Monogr* 40(1):23–47.
5. Bormann FH, Likens GE (1979) *Pattern and Process in a Forested Ecosystem* (Springer, New York), 253 pp.
6. Sørensen R, et al. (2009) Forest harvest increases runoff most during low flows in two boreal streams. *Ambio* 38(7):357–363.
7. Pugh E, Small E (2011) The impact of pine beetle infestation on snow accumulation and melt in the headwaters of the Colorado River. *Ecohydrology* 5(4):467–477.
8. Love LD (1955) The effect on stream flow of the killing of spruce and pine by the Engelmann spruce beetle. *Trans Am Geophys Union* 36(1):113–118.
9. Vitousek PM, Melillo JM (1979) Nitrate losses from disturbed forests: Patterns and mechanisms. *For Sci* 25(4):605–619.
10. Gundersen P, Schmidt IK, Raulund-Rasmussen K (2006) Leaching of nitrate from temperate forests—Effects of air pollution and forest management. *Environ Rev* 14(1):1–49.
11. Bernhardt ES, Likens GE, Buso DC, Driscoll CT (2003) In-stream uptake dampens effects of major forest disturbance on watershed nitrogen export. *Proc Natl Acad Sci USA* 100(18):10304–10308.
12. Bernhardt ES, et al. (2005) Can't see the forest for the stream? In-stream processing and terrestrial nitrogen exports. *Bioscience* 55(3):219–230.
13. Amman GD (1972) Mountain pine beetle brood production in relation to thickness of lodgepole pine phloem. *J Econ Entomol* 65(1):138–139.
14. Safranyik L (1971) Some characteristics of spatial arrangement of attacks by the mountain pine beetle, *Dendroctonus ponderosae* (Coleoptera: Scolytidae), on lodgepole pine. *Can Entomol* 103:1607–1625.
15. Romme WH, Knight DH, Yavitt JB (1986) Mountain pine beetle outbreaks in the Rocky Mountains: Regulators of primary productivity. *Am Nat* 127(4):484–494.
16. Collins B, Rhoades C, Hubbard R, Battaglia M (2011) Tree regeneration and future stand development after bark beetle infestation and harvesting in Colorado lodgepole pine stands. *For Ecol Manage* 261(11):2168–2175.
17. Aber JD, Nadelhoffer KJ, Steudler P, Melillo JM (1989) Nitrogen saturation in northern forest ecosystems. *Bioscience* 39(6):378–386.
18. Clow DW, Rhoades C, Briggs J, Caldwell M, Lewis WM, Jr. (2011) Responses of soil and water chemistry to mountain pine beetle induced tree mortality in Grand County, Colorado, USA. *Appl Geochem* 26(Suppl):S174–S178.
19. Stottlemyer R (1987) Natural and anthropic factors as determinants of long-term streamwater chemistry. *Management of Subalpine Forests: Building on 50 Years of Research, Proceedings of a Technical Conference, Silver Creek, Colorado*. USDA Forest Service General Technical Report RM-149. pp. 86–94.
20. Scott NA, Likens GE, Eaton JS, Siccama TG (2001) Trace metal loss following whole-tree harvest of a northeastern deciduous forest, U.S.A. *Biogeochemistry* 54(2):197–217.
21. Löfgren S, Ring E, von Brömssen C, Sørensen R, Högbom L (2009) Short-term effects of clear-cutting on the water chemistry of two boreal streams in northern Sweden: A paired catchment study. *Ambio* 38(7):347–356.
22. Burns DA, Murdoch PS (2005) Effects of a clearcut on the net rates of nitrification and N mineralization in a northern hardwood forest, Catskill Mountains, New York, USA. *Biogeochemistry* 72(1):123–146.
23. Feller MC, Kimmins JP (1984) Effects of clearcutting and slash burning on streamwater chemistry and watershed nutrient budgets in southwestern British Columbia. *Water Resour Res* 20(1):29–40.
24. Houlton BZ, et al. (2003) Nitrogen dynamics in ice storm-damaged forest ecosystems: Implications for nitrogen limitation theory. *Ecosystems (N Y)* 6(5):431–443.
25. Tokuchi N, Ohte N, Hobara S, Kim SJ, Masanori K (2004) Changes in biogeochemical cycling following forest defoliation by pine wilt disease in Kirya Experimental Catchment in Japan. *Hydrol Processes* 18(14):2727–2736.

26. Schaefer DA, McDowell WH, Scatena FN, Asbury CE (2000) Effects of hurricane disturbance on stream water concentrations and fluxes in eight tropical forest watersheds of the Luquillo Experimental Forest, Puerto Rico. *J Trop Ecol* 16:189–207.
27. Hornbeck JW, et al. (1987) The northern hardwood forest ecosystem: Ten years of recovery from clearcutting. USDA Forest Service Report NE-RP-596.
28. Hubbard RM, Rhoades CC, Elder K, Negron JF (2013) Changes in transpiration and foliage growth in lodgepole pine trees following mountain pine beetle attack and mechanical girdling. *For Ecol Manage* 29:312–317.
29. Vitousek PM, Reiners WA (1975) Ecosystem succession and nutrient retention: A hypothesis. *Bioscience* 25(6):376–381.
30. Veblen TT, Hadley KS, Reid MS, Rebertus AJ (1989) Blowdown and stand development in a Colorado subalpine forest. *Can J For Res* 19(10):1218–1225.
31. Sibold JS, et al. (2007) Influences of surface fire, mountain pine beetle, and blowdown on lodgepole pine stand development in the northern Colorado Front Range. *Ecol Appl* 17(6):1638–1655.
32. Parsons WFJ, Knight DH, Miller SL (1994) Root gap dynamics in lodgepole pine forest: Nitrogen transformations in gaps of different sizes. *Ecol Appl* 4(2):354–362.
33. Lewis WM, Jr., Wurtsbaugh WA, Paerl HW (2011) Rationale for control of anthropogenic nitrogen and phosphorus to reduce eutrophication of inland waters. *Environ Sci Technol* 45(24):10300–10305.
34. Collins B, Rhoades C, Battaglia M, Hubbard R (2012) The effects of bark beetle outbreaks on forest development, fuel loads and potential fire behavior in salvage logged and untreated lodgepole pine forests. *For Ecol Manage* 284:260–268.

Signs of Recovery for Colorado Forests in the Wake of the Mountain Pine Beetle

October 2010

The mountain pine beetle (MPB) has affected 2.3 million acres of Colorado lodgepole pine forests since 1996 (USFS 2009). In infested stands, live lodgepole basal area typically declines by 70% and often exceeds 90% in mature, even-aged stands (Klutsch et al., 2009; Collins et al., 2010). Lodgepole pine is well known to rapidly regenerate into dense forests after wildfire or harvesting.

Yet, in the initial phase of this outbreak, it remains uncertain how Colorado lodgepole forests will recover from MPB. Recent evidence from beetle-infested lodgepole pine forests in British Columbia found that pine seedlings failed to reestablish for more than a decade (Astrup et al., 2008). In Colorado, land managers and the public share the following general concerns about the recovery of our forests after the beetle outbreak:

- *Will poor seedling establishment be widespread in beetle-infested lodgepole forests in Colorado?*
- *Will the species composition of the forests that establish after MPB differ from the species composition of the forests prior to the outbreak?*
- *How long will it take for beetle-infested forests to recover?*

Additionally, there has been a dramatic increase in harvesting of beetle-infested trees on federal, state and private forests throughout northern Colorado to reduce the potential for wildfire and minimize risks for public safety and infrastructure from falling trees. The ultimate consequences of current management will not be clear for many years, but initial indications about how forest regeneration may differ between harvested and unharvested beetle-infested stands can guide and validate management decisions as the outbreak progresses. On-going operational-scale research can answer the following questions:

- *Does harvesting of beetle-infested stands change the density or composition of stands relative to uncut stands?*
- *Is harvesting necessary to ensure recovery of an adequate density of preferred species?*
- *Does post-harvest seedling colonization differ between beetle-infested and live lodgepole forests?*

With support from the USFS, the Colorado Forest Restoration Institute and the Colorado Water Conservation Board, Rocky Mountain Research Station scientists are collaborating with USFS and CSFS managers to design studies to address these general questions and to characterize the initial trajectory of forest recovery in the wake of the MPB.

Colorado Forest Restoration Institute

Colorado State University

Rocky Mountain Research Station

Forest Conditions

The Sulphur Ranger District was at the center of the MPB outbreak that reached epidemic levels in the late 1990s. The Fraser Experimental Forest first experienced MPB activity in 2003; by 2006, the majority of the area was infested by the beetle. In spite of the substantial management response, USFS managers expect to harvest less than 15% of the total area affected by the MPB outbreak. Century-old lodgepole pine dominates the overstory and subalpine fir, Engelmann spruce and quaking aspen are common in the understory of these study areas. In other locations, lodgepole pine forests lack the same understory species diversity and are likely to respond differently to MPB or other forest disturbance.

Key Findings

Seedling Colonization in Unharvested and Harvested Beetle-infested Stands

Since 2008, lodgepole pine and subalpine fir seedlings and aspen sprouts have become established both beneath the dead overstory and in recently harvested beetle-infested stands (Fig. 1); pine and aspen recruits were three times more abundant in harvested stands. Subalpine fir trees were the most common new trees in uncut stands, whereas aspen and pine trees dominated in harvested areas.

Based on these field measurements (Fig. 1), forest growth simulations suggest that in harvested areas lodgepole pine will be the dominant species. Forest structure (i.e., tree density and stand basal area) should return to pre-outbreak levels within 80 to 120 years regardless of whether stands were cut or uncut. Aspen is projected to become a significant part of the overstory in both cut and uncut areas during the first 50 years after the MPB infestation, but then be overtaken by conifers. In the unharvested stands that will occupy the majority of the area affected by the current MPB outbreak (i.e., >85%), subalpine fir will surpass lodgepole pine as the dominant overstory species.

Post-Harvest Seedling Colonization in Infested and Pre-Outbreak, Live Forests

The density of seedlings colonizing clearcuts did not differ statistically between live and beetle-infested forests (Fig. 2; Collins et al. 2010), and lodgepole pine accounted for more than 90% of post-harvest seedling recruitment during both periods.

In general, post-harvest seedling recruitment was high (4,700 trees ha^{-1}; 1,900 trees ac^{-1}) during both pre-outbreak and outbreak periods, and few plots failed to restock with new seedlings. In lodgepole pine forests of the southern Rockies, a minimum of 370 trees ha^{-1} (i.e., 150 trees ac^{-1}) is required on 70% of plots to certify that treated areas have regenerated successfully (USDA, 1997), and managers consider that development of well-stocked stands will require post-harvest seedling densities about ten-fold higher than this minimum threshold. In our study, post-harvest recruitment surpassed minimum stocking requirements in 100% and 94% of pre-outbreak and outbreak harvest units, respectively, and more than half of all harvest units were considered well-stocked.

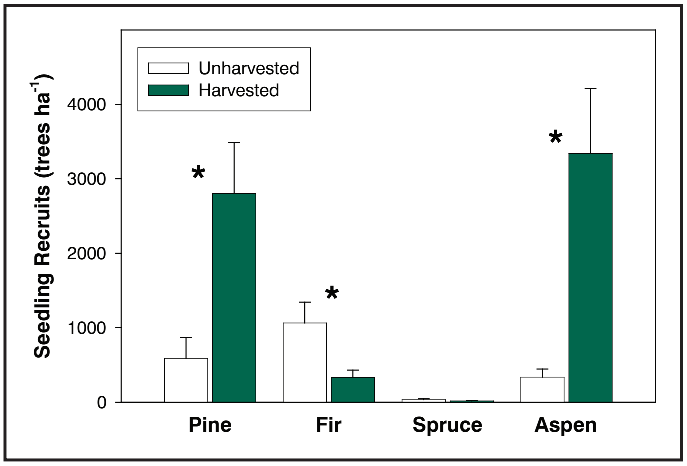

Figure 1. Mean density of seedlings that have established since 2008 in unharvested (n = 39 plots) and harvested areas (n = 75 plots) in 10 paired stands at the USFS Fraser Experimental Forest (Collins 2010). Asterisks indicate a statistically significant difference (α = 0.05) between uncut and cut areas.

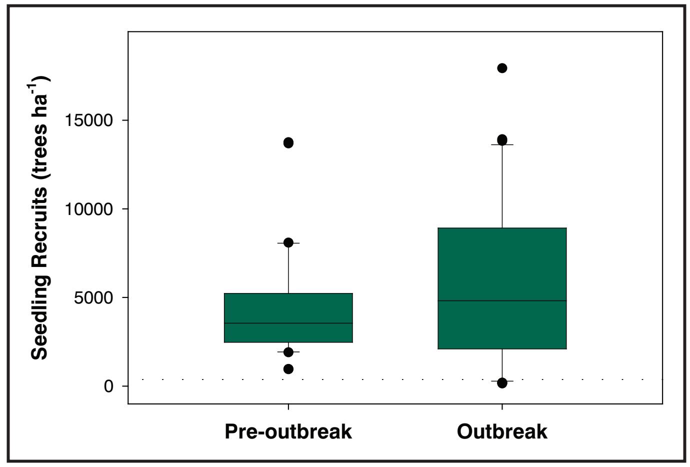

Figure 2. Post-harvest recruitment in pre-outbreak (n=32) and outbreak (n=30) stands 3 years after harvesting (Sulphur Ranger District; Arapaho-Roosevelt National Forests). Boxes show the median, 25th and 75th percentiles, whiskers represent 10th and 90th percentiles, and solid circles represent outliers (observations outside the 10th and 90th percentile). The dashed line shows the minimum of undamaged seedlings required to certify successful stocking on USFS land.

Implications for Colorado Forests

This research conducted on the Fraser Experimental Forest and Sulphur Ranger District demonstrates that some Colorado forests have begun to recover from the beetle outbreak. Our findings are relevant to forests in northern Colorado that had a pine-dominated overstory and fir, spruce and aspen understory prior to arrival of the pine beetle. In contrast, in pine forests with sparse understory trees, stand recovery will likely be delayed following overstory loss to pine beetle. In general, we can conclude the following:

- New conifer seedlings (mainly pine and fir) and aspen sprouts have colonized beneath the beetle-infested overstory.
- The density of new trees is at least as high in areas harvested in response to the beetle outbreak as in live forests harvested in the past.
- Very few harvest areas (i.e., < 6 %) are poorly-stocked.
- Beetle-infested stands appear to be on a trajectory to return to pre-outbreak forest structure in 80 to 120 years.

Our seedling surveys and growth simulations indicate that the species composition of unharvested, beetle-infested forests is likely to differ from the pine-dominated forests common at the time of the outbreak. Much uncertainty exists regarding the projections of future stand conditions; nevertheless, based on our findings we expect that:

- Subalpine fir will likely surpass lodgepole pine as the most common overstory species in the unharvested areas that will occupy much of the area affected by the outbreak.
- Aspen is projected to be a significant part of the overstory in both harvested and unharvested areas during the first 50 years after the outbreak.
- In harvested areas, lodgepole pine will be the dominant overstory species and develop into stands similar to those that were attacked by the pine beetle.

These findings document initial seedling colonization in harvested and unharvested beetle-infested forests, but raise questions about how these forests will develop in the future. For example, dwarf mistletoe affects lodgepole pine growth in these and many Colorado forests; yet it is unknown how MPB and MPB-related harvesting may alter the prevalence of mistletoe or its impact on stand development. Also, our growth simulations predict that fir will become more abundant in the Colorado High County, though mature forests dominated by subalpine fir are currently uncommon to the area. The species is relatively short-lived and is susceptible to a number of insects and diseases, so it is unlikely to form dense, even-age stands, in spite of the high density of fir seedlings and saplings we measured. It is, however, reasonable to expect a shift from the uniform age and size conditions common in lodgepole pine-dominated forests to stands with more fir and greater size, age and overstory species diversity. Future resurvey of our study sites will help to answer these questions.

The implications of greater abundance of subalpine fir on High Country forests and communities remain uncertain. These findings represent the first stage in development of new forests following the beetle outbreak during a period of dramatic change that will have consequences for Colorado ecosystems and economies for many decades to come.

Literature Cited

Astrup, R., Coates, K.D., and Hall, E. 2008. Recruitment limitations in forests: Lessons from an unprecedented mountain pine beetle epidemic. Forest Ecology & Management 256: 1743-1750.

Klutsch, J.G., Negron, J.F., Costello, S.L., Rhoades, C.C., West, D.R., Popp, J., and Caissie, R. 2009. Stand characteristics and downed woody debris accumulations associated with a mountain pine beetle (*Dendroctonus ponderosae* Hopkins) outbreak in Colorado. Forest Ecology & Management 258: 641-649.

USDA Forest Service, 2009. Forest insect and disease aerial survey data, Rocky Mountain region. Available from http://www.fs.fed.us/r2/resources/fhm/aerialsurvey/download/

Project Partners

U.S. Forest Service, Rocky Mountain Research Station: *Chuck Rhoades (crhoades@fs.fed.us), Rob Hubbard, Byron Collins, Mike Battaglia, and Kelly Elder*

U.S. Forest Service, Arapaho Roosevelt NF (Sulphur Ranger District): *Jeff Underhill*

Colorado Forest Restoration Institute: *Tony Cheng*

For an in-depth description of research, see:

Collins, Byron J. 2010 Initial and future stand development following mountain pine beetle in harvested and uncut lodgepole pine forests. M.Sc. Thesis, Dept. of Forest, Rangeland & Watershed Stewardship, Colorado State University, Fort Collins, Colorado.

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. Canadian Journal of Forest Research 40: 2452-2456.

Colorado Forest Restoration Institute

Colorado State University

Colorado Forest Restoration Institute
132 Forestry Building, 1001 West Drive
Colorado State University
Fort Collins, CO 80523-1472
(970) 491-2104 (voice)
(970) 491-6754 (fax)
http://cfri.colostate.edu/