

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

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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⁻¹), 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⁻¹), 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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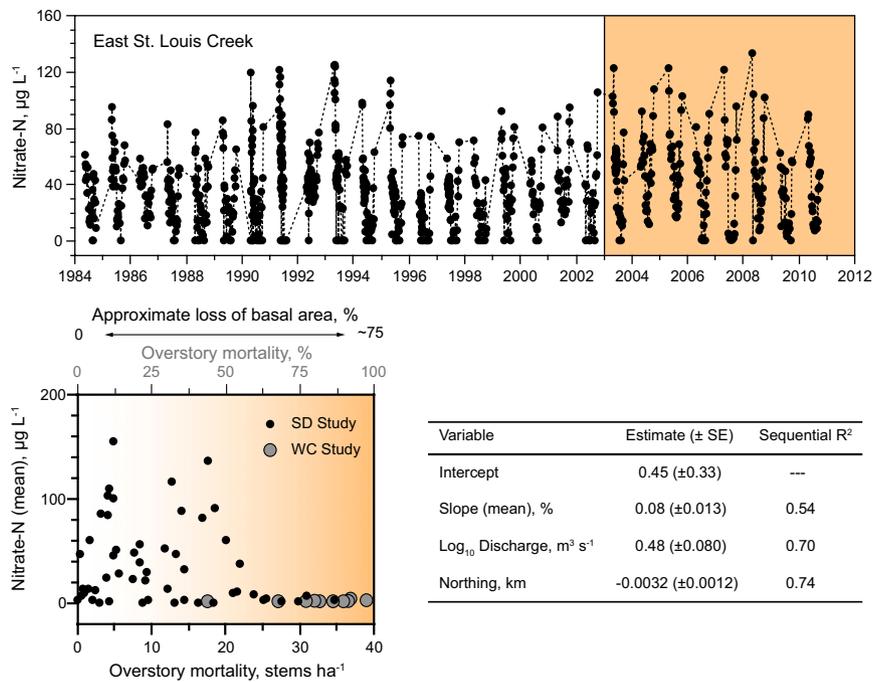


Fig. 1. (Upper) Nitrate concentrations in East St. Louis Creek, Fraser Experimental Forest, Colorado, beginning before extensive beetle kill of trees and extending into years of progressive beetle kill (shaded area). (Lower) Relationship between beetle-induced mortality (based on US Forest Service aerial 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

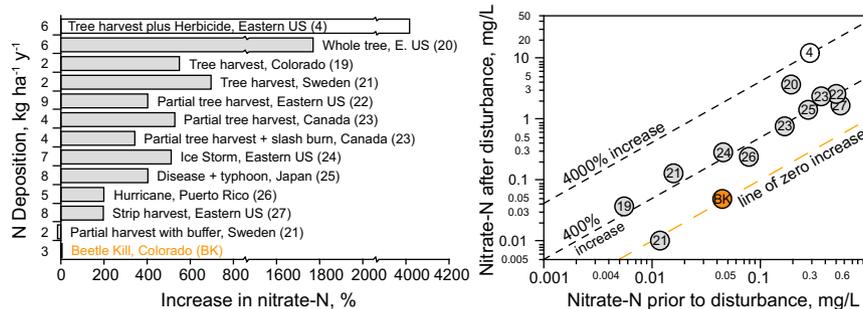


Fig. 2. (Left) Percent increase in streamwater nitrate concentrations following canopy disturbance of forests. Atmospheric wet deposition of inorganic N is shown for each location (SI Text 2). (Right) Relationship of nitrate concentrations before and after disturbance for sites shown on the Left. The 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·ha⁻¹·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

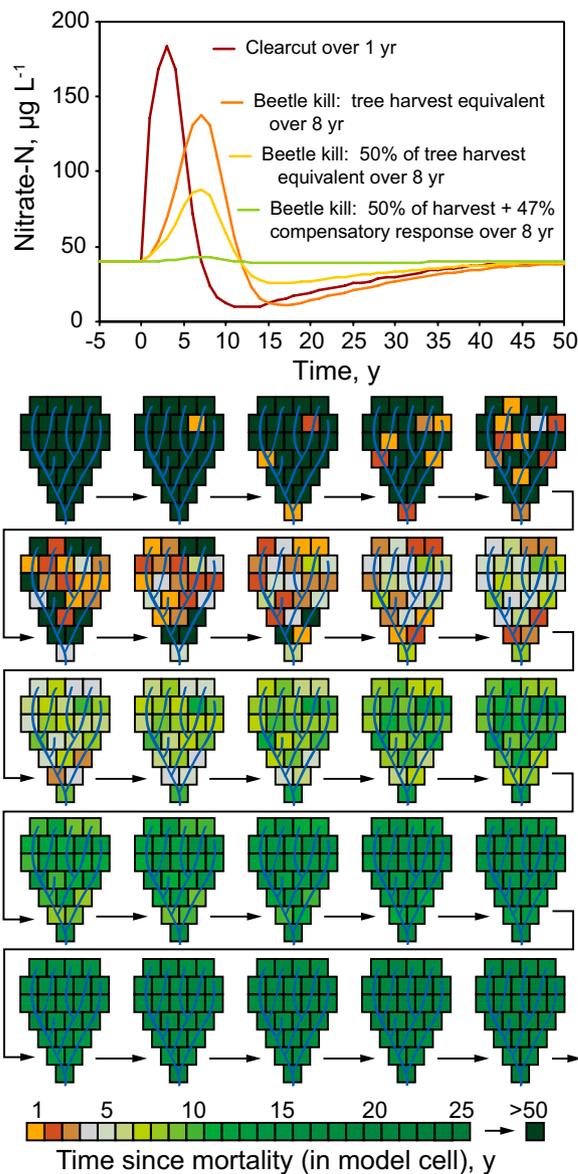


Fig. 3. (Upper) Modeled nitrate release for Rocky Mountain forests calibrated for tree harvest, to which three factors that differ between harvest and beetle kill are added sequentially, based on field studies. (Lower) A 25-y spatial sequence of canopy mortality for a hypothetical watershed with beetle 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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