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Resilient trees as mechanisms of nitrogen retention following bark beetle attack
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Abstract

Watershed disturbances (a land area sharing a single drainage point for all surface and groundwater flow paths) are often accompanied by a significant increase in the export of nitrogen from the terrestrial to the aquatic ecosystem, mainly in the form of nitrate (NO$_3^-$). Unlike other watershed disturbances, infestation by the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) is not associated with elevated nitrate concentrations in the stream channel (Leigh Cooper, Personal Communication). The lodgepole pine ecosystem of Colorado is nitrogen-limited (Fahey et al. 1985. Biogeochemistry 1: 257-275). Across a landscape, outbreaks of the mountain pine beetle leave a patchy distribution of surviving trees. Surviving trees are nonviable hosts to the beetle. Trees of a smaller diameter at breast height are not host to the beetle, as they do not provide a sufficient food source to developing larvae in the inner bark (Cole and Amman 1969 USDA Forest Service Research Paper: INT-95). Younger, smaller lodgepole pine and spruce that survive an outbreak are, therefore, resilient to mountain pine beetle infestation. Resilient trees are potential nitrogen sinks for any release of inorganic soil nitrogen as a result of neighboring tree death.

Foliar nitrogen concentrations were used as a proxy for plant nitrogen uptake of surviving trees. Of variables estimated, neighboring tree mortality was a strong predictor of foliar nitrogen concentrations of surviving trees (p<0.001, $R^2 = 0.17$). The data suggest increased nitrogen uptake by resilient trees in response to neighboring tree death. Across a watershed, resilient trees that are no longer competing for nitrogen with neighboring trees represent a nitrogen sink for available inorganic soil nitrogen, mitigating significant nitrate loss from the terrestrial to the aquatic ecosystem.
Belowground measurements of soil nitrogen availability and the partitioning of nitrogen between the microbial and plant community could further explain the relative importance of resilient trees in nitrogen retention of watersheds affected by the mountain pine beetle.
Introduction

Recent outbreaks of the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) have spread across the North American Rockies. Beetle populations have reached epidemic levels over much of the region. In Colorado, the epidemic began in 1996, and has since intensified. Approximately 4 million acres of coniferous forest have been affected by the beetle (USDA Forest Service 2011). Species of pine host to the beetle include limber (*Pinus flexilis*), lodgepole (*Pinus contorta* var. Latifolia) and ponderosa pine (*Pinus ponderosa*). Elevations dominated by lodgepole pine experience the highest rates of mortality (Raffa et al. 2008). Although pine beetle outbreaks are historical across montane forests of the West, the current epidemic has exceeded previous elevational limits and entered regions with no previous record of outbreak within the past century (Raffa et al. 2008). The expanded range of the current mountain pine beetle epidemic is likely driven by a combination of recent drought and warm winters (Raffa et al. 2008). Given the unprecedented range of tree mortality across Colorado and elsewhere in the Rocky Mountains, the mountain pine beetle presents a large disturbance to forest biogeochemical cycling (the cycling of nutrients through living and non-living components of an ecosystem) (Morehouse et al. 2008).

The effects of forest disturbance on nitrate export from terrestrial ecosystems

Watershed disturbances, such as clear-cutting (removal of all trees within a tract of land) or insect defoliation have been linked to increases in the export of nitrate (NO$_3^-$) to aquatic ecosystems (Likens et al. 1970, Dahlgren and Driscoll 1994, Matson and Vitousek 1981, Swank et al. 1981). Nitrate is highly water-soluble and moves rapidly through the soil profile, enters groundwater, and quickly moves into streams. As an
essential element in nucleic acids and proteins, nitrogen can limit the capacity for biomass accumulation in an ecosystem (Vitousek and Howarth 1991). In aquatic ecosystems, terrestrially derived nitrogen in the form of nitrate is a significant portion of total nitrogen available for growth, and as such its availability often does limit the growth of algae (photosynthetic organisms of aquatic ecosystems) (Kalff 2001). Increases in nitrate export from a watershed can increase stream production, and can lead to the eutrophication of aquatic ecosystems (biomass accumulation in response to high nutrient concentrations).

An increase in the export of nitrate to the stream following a forest disturbance is associated with both reduced nitrogen uptake of plants and increased nitrification (oxidation of ammonia to nitrate) by soil microbes (Vitousek et al. 1997). Like other disturbances, mountain pine beetle infestation is associated with increased nitrification (Morehouse et al. 2008). However, this shift in the partitioning of mineralized (NH₄⁺) nitrogen in response to beetle infestation does not lead to elevated nitrate concentrations in the stream (Leigh Cooper, personal communication). The absence of increased nitrate concentrations in the stream seems inconsistent with well-established literature on the effects of disturbance on the export of nitrate. However, mountain pine beetle disturbances exhibit several differences from other disturbances (Likens et al. 1970, Dahlgren and Driscoll 1994, Matson and Vitousek 1981, Swank et al. 1981). Spatial patterns in tree mortality associated with mountain pine beetle biology and the nitrogen-limited conditions of lodgepole pine ecosystems are, together, likely explanatory of the weak nitrate response in streams to mountain pine beetle.
Most studies of the effects of forest disturbance on nitrogen cycling have been located in the eastern U.S., which receives considerably more atmospheric nitrogen deposition (the deposition of fixed nitrogen species to terrestrial environments) than Colorado. On average, the Front Range of Colorado receives 0.17-0.08 g m\(^{-2}\) yr\(^{-2}\) of nitrogen (Fahey et al. 1985), while the eastern U.S. receives an input of 0.96 g m\(^{-2}\) yr\(^{-2}\) of nitrogen (Whithall and Paerl 2001). Significant deposition of atmospheric nitrogen causes nitrogen saturation of ecosystems, which can be defined as environmental conditions under which inorganic, bioavailable forms of nitrogen (ammonia and nitrate) exceed total plant and microbial demand (Aber et al. 1989). Under these conditions, primary production of the terrestrial environment is no longer limited by nitrogen availability, and the system becomes “leaky” with respect to nitrogen (Aber et al. 1989). Increases in nitrification rates and in the export of nitrate follow, as the element is abundant within the terrestrial ecosystem. While nitrogen saturation is apparent within northeastern temperate ecosystems (Aber et al. 1998), the phenomenon is less likely to occur in the nitrogen-limited montane forests of Colorado.

Lodgepole pine ecosystems of the Colorado Rockies are severely nitrogen limited, with soil C/N (carbon/nitrogen) ratios of up to 70:1 (Fahey et al. 1985). Nitrogen availability is one of several limitations on net primary production (NPP) in the lodgepole pine ecosystem (Fahey et al. 1985). Therefore, under pre-disturbance conditions, nitrogen availability does not exceed total plant and microbial demand, and the terrestrial system is retentive of nitrogen (Fahey et al. 1985). Potentially, lodgepole pine is so nitrogen-limited that the system remains nitrogen-limited following infestation. If post-
disturbance tree mortality does not exceed the total demand for nitrogen of surviving trees, across the landscape, these trees might present nitrogen sinks for any increases in available mineralized nitrogen.

Presenting a role for resilient trees in nitrogen retention

Resilient trees are trees that are either not host to the beetle, or survive infestation. Subcanopy lodgepole pine are nonviable hosts to the mountain pine beetle, due to an insufficiently sized phloem (sugar transport tissue) to support developing beetle larvae (Cole and Amman 1969). A lodgepole pine with a small diameter at breast height (DBH) is considerably less likely to be infested than a larger dominant lodgepole pine. Lodgepole pine with a DBH of 10 cm or less have been shown to have an infestation rate of approximately 1%, while trees with a DBH greater than 41 cm have been shown to experience infestation rates of 87% (Cole and Amman 1969). As the beetle preferentially kills dominant lodgepole pine, younger, previously suppressed understory trees are released from competition for light and resources with these older, established trees.

The release of understory trees after the removal of dominant trees is well documented in experiments of overstory tree removal (Seidel 1980, McCaughey et al. 1991). Mountain beetle infestations are analogous to the selective logging of dominant trees. Likely, areas of beetle kill experience a similar release of understory trees from competition with mature trees. Growth rates of surviving trees do increase following beetle outbreaks in the Rocky Mountains (Romme et al. 1986). However, whether nitrogen uptake by understory growth compensates for any increase in available inorganic soil nitrogen is not known.
If the availability of soil nitrogen exceeds the demand for and uptake of nitrogen in surviving trees, nitrate will leach out of the rooting zone and into groundwater. The riparian zone might serve as nitrate sink for any nitrate that does leach into groundwater. The riparian zone is the transitional zone between terrestrial and aquatic ecosystems and has distinct flora from the surrounding terrestrial environment (Ranalli and Macalady 2010). In lodgepole pine forests, species composition and potentially, tree vigor of the riparian zone differ from more xeric (areas characterized by low moisture) habitats. Spruce dominates the riparian zones of lodgepole pine forests (Colorado Division of Forestry 2001). Similarly, lodgepole pines experiencing less water stress are potentially more resilient to beetle infestations. Drought and increased water stress are precursors of beetle outbreaks (Christiansen et al. 1987). Therefore, lodgepole pines in less xeric habitats and nearer to a stream are more resilient to an attack. If tree mortality is lower in the riparian zone, trees of the riparian zone could act as a buffer, intercepting nitrate rich groundwater before it enters the stream.

The severe nitrogen limitation of lodgepole pine ecosystems coupled with spatial patterns in tree mortality offer a role for resilient trees in nitrogen retention following mountain pine beetle infestation. Subcanopy release and the existence of a riparian buffer present two possible mechanisms for nitrogen retention in watersheds affected by mountain pine beetle.

*Study Questions*

The present study compared nitrogen uptake between conifers in areas affected by mountain pine beetle with pre-disturbance conditions of nitrogen uptake. Foliar nitrogen concentrations served as a proxy for nitrogen uptake by conifers. According to Aber et
al. (1989), increased plant uptake of nitrogen is evident in foliar N concentrations. Fertilization experiments of lodgepole pine confirm foliar nitrogen concentrations do increase with nitrogen fertilization (Kishchuk et al. 2002). I hypothesized that the nitrogen uptake of resilient trees (both riparian and subcanopy trees) would increase following a beetle outbreak. I predicted that foliar N concentrations would increase with increasing tree mortality, that tree mortality would be lower in the riparian zone when compared to regions uphill of surface flow paths, and that foliar N concentrations would be higher in trees in the riparian zones than in regions uphill.

**Methods**

**Study sites**

Forests dominated by lodgepole pine occur between 8,000 and 9,500 ft (Moir WH 1969). Twelve sites between 8,000 ft and 10,000 ft were chosen on slopes dominated by lodgepole forest, located primarily within Rocky Mountain National Park and surrounding Forest Service land. Sites were chosen on both the eastern and western side of the continental divide to account for the potentially confounding influence of nitrogen deposition on the eastern slope from atmospheric pollution along the Front Range (Lewis, Grant, Saunders 1984). Four control sites and eight treatment sites experiencing various severities of infestation were selected. Two controls and four treatments were selected on the each side of the continental divide.

**Data Collection**

At each site a 25 m² plot was selected adjacent to a stream. Foliar samples of all coniferous trees over 0.5 m tall were collected from lower branches.
first plot, another 25 m² plot was similarly sampled. The third plot was located 5 m upslope of the second. A fourth plot was located 15 m behind the third plot, and a fifth plot was located 25 m uphill of the fourth (figure 1). Measurements of diameter at breast height of each tree, elevation, slope, percent ground cover, aspect, and counts of live and dead trees, as well as tree type (lodgepole, spruce, or fir) were taken from each plot. Sampling extended a total of 70 m from the stream.

**Figure 1.** Sampling scheme at sites. A total of five 25 m² plots were set up moving uphill of a stream.
Data analysis

201 leaf samples were collected, and leaf nitrogen content was analyzed on a Carlo Erba elemental analyzer (Fisons, Parkton MD). Preparation of samples for the elemental analyzer entailed freeze drying of samples, grinding dried samples, and packing samples into 3x5 mm combustible tin capsules. Foliar N was measured as % N per gram dry mass.

Mortality of trees in plots was estimated as the ratio of dead lodgepole to the total tree count (live and dead) for each plot. Live tree density of plots was measured as the number of live trees divided by the total area (25 m²) of each plot. Trees shorter than 1 m were assigned a DBH of 1 cm.

Results

Patterns of tree mortality

The dominant tree type changed with increasing distance from a stream (Figure 2). Tree type frequency was measured as the total counts of tree types across all plots at 0, 5, 15, 35, and 70 m. At 0 m and 5 m from the stream, spruce was the dominant tree type, while plots located at 15, 35, and 70 m were dominated by lodgepole pine. ANOVA of mean tree mortality for all tree types at plots 0, 5, 15, 35, and 70 m revealed a significant difference in average tree mortality of plots (p < 0.05, Figure 3a). A posteriori Tukey HSD test indicated that tree mortality for all tree types of plots at 0 m and 70 m was significantly different (p < 0.05). Mean tree mortality of plot 70 m from a stream was 0.65, and mean tree mortality at plots 0 m from a stream was 0.112. Among only lodgepole pines, there was no significant difference in lodgepole pine mortality of
plots at 0, 5, 15, 35, and 70 m from a stream (p=0.11, Figure 3b). Diameter at breast height of surviving trees was weakly correlated to tree mortality for all tree types in plots, but not significantly so (p=0.13, $R^2 = 0.0187$, Figure 4). In plots affected by over 60% tree mortality, DBH of all surviving trees did not exceed 15 cm.

**Figure 2.** Distribution of tree types at plots 0, 5, 15, 35, and 70 m from the stream. Frequency is the total count of all tree types in plots at 0, 5, 15, 35, and 70 m.

**Figure 3.** Average tree mortality of (a) all tree types at plots 0, 5, 15, 35, and 70 m from a stream. (b) Lodgepole pine at plots 0, 5, 15, 35 and 70 m from a stream.
Diameter at breast height of surviving trees as a function of tree mortality for all tree types in plots. The black line is the least squares regression: $y = -5.612x + 11.257$.

**Figure 4.**

Foliar nitrogen concentrations as predicted by local mortality

There was no significant difference in foliar nitrogen concentrations between control sites on the eastern and western side of the continental divide ($T=6.54, p=0.155$). Mean foliar nitrogen concentrations of sites located on the eastern and western sides of the divide were 0.98 and 1.06, respectively.

A stepwise linear regression of foliar nitrogen concentrations of surviving trees as predicted by the variables, tree mortality, elevation, slope, tree density, diameter at breast height, distance from a stream, and percent cover of plots indicated that elevation was the best predictor of foliar nitrogen concentrations in surviving trees ($R^2=0.19, p<0.001$). Tree mortality of all tree types, slope, tree density and diameter at breast height also contributed significantly to predicting foliar nitrogen concentrations (Table 1). Distances from stream and percent cover were the only variables estimated that did not contribute
significantly to the model. Tree mortality in plots was the second best predictor of foliar nitrogen concentrations of surviving trees following elevation (F=14.689, p < 0.001, \( R^2=0.18 \)). Tree mortality within plots predicted approximately 18% of variability in foliar nitrogen of surviving trees.

**Table 1.** Explanation of variance for foliar nitrogen concentration of surviving trees. Sequential \( R^2 \) is the cumulative explanation of variance predicted with the addition of each variable to the regression.

<table>
<thead>
<tr>
<th>Variable</th>
<th>p</th>
<th>Sequential R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Elevation</td>
<td>0.0000</td>
<td>0.19</td>
</tr>
<tr>
<td>Mortality</td>
<td>0.0000</td>
<td>0.37</td>
</tr>
<tr>
<td>DBH</td>
<td>0.0069</td>
<td>0.39</td>
</tr>
<tr>
<td>Tree Density</td>
<td>0.0050</td>
<td>0.40</td>
</tr>
<tr>
<td>Slope</td>
<td>0.0104</td>
<td>0.41</td>
</tr>
</tbody>
</table>

Linear regression analysis of foliar nitrogen concentrations as predicted by local mortality indicated that the two variables were positively correlated (\( R^2=0.179 \), Figure 5). The slope of the line is significantly larger than 0 (p < 0.001). The data indicate a positive relationship between foliar nitrogen concentrations and mortality. Specifically, 50% mortality in a plot is accompanied by a 22% increase in the foliar nitrogen concentration of surviving trees.
Discussion

Spatial patterns in tree mortality suggest that, although tree mortality of plots is significantly lower at 0 m than at 70 m from the stream, the apparent difference is due mostly to the species composition of the plots and not an improved resilience of lodgepole pine at the stream margin. While the nearness of a lodgepole to a stream was did not affect mean lodgepole mortality significantly, total tree mortality for all tree species was lower next to a stream because spruce are the dominant tree type in the riparian zone. As spruce is a nonviable host to the mountain pine beetle, tree mortality for all tree types is significantly lower in the riparian zone than regions uphill.

Despite reduced tree mortality in the riparian zone, resilient trees, as defined by local mortality, and not an individual tree’s distance from a stream are predictive of foliar nitrogen concentrations of surviving trees. A weak relationship between distance from stream and foliar nitrogen concentrations suggests that, although mortality does increase
with distance from stream, trees at the stream margin are less important to nitrogen retention following infestation. Conversely, resilient trees in areas of high local mortality are likely to respond to nitrogen-enriched soil conditions with increased nitrogen uptake, preventing the loss of nitrate into groundwater.

Other variables correlated with foliar nitrogen concentrations contributed to the large variability in foliar nitrogen concentrations observed within plots. Physical factors affecting foliar nitrogen concentrations are slope and elevation. DBH is also significantly correlated to foliar nitrogen concentrations. The correlation of DBH to foliar nitrogen concentrations is suggestive of relationship between tree age and foliar nitrogen concentrations. Other research has shown that tree age does not influence the foliar nitrogen concentrations of same-aged leaves (Schoettle 1993). Therefore, variation in leaf age contributed little to variability in foliar nitrogen concentrations. Likely, the correlation between foliar nitrogen and DBH is a result of the negative correlation between DBH and mortality. As DBH is correlated with both mortality and foliar nitrogen, foliar nitrogen and DBH are correlated as well. But, as tree age, and therefore DBH, of _P. contorta_ does not determine foliar nitrogen concentration; DBH can be excluded as predictive of foliar nitrogen concentrations.

*The role of resilient trees in nitrogen retention*

The spatial heterogeneity in tree mortality in areas affected by mountain pine beetle is evidenced by the lack of plots sampled experiencing tree mortality of over 70%. Although mountain pine beetle infestation, when viewed across an entire watershed, is responsible for significant tree mortality, quite a few small trees and spruce escape mortality.
Foliar nitrogen concentrations of resilient trees indicate that the trees are responsive to tree mortality and increase total nitrogen uptake following a beetle outbreak. The current data suggest that, for a tree mortality of 50%, surviving trees increase foliar nitrogen concentrations by approximately 22%. The allocation of nitrogen to the leaves is about 65% of total annual nitrogen uptake (Schoettle 1993). Foliar nitrogen is thus representative of a large portion of the total plant nitrogen uptake of lodgepole. Consequently, a 22% increase in foliar nitrogen concentrations suggests that these trees are quite responsive to increased nitrogen availability, allocating significantly more nitrogen to their leaves than would otherwise be available due to severe competition for nitrogen under pre-disturbance conditions. Although an increase in foliar nitrogen concentrations from 1% to 1.5% in response to neighboring tree mortality is seemingly minor, the latter increase may be indicative of a large increase in nitrogen uptake of the entire tree. An increase of 0.5% per gram dry mass equates to 500 grams of nitrogen for every 10 kilograms of leaf biomass. In a system as nitrogen poor as the lodgepole forest, increases in nitrogen uptake of this magnitude could attenuate nitrogen that might otherwise be mobile and leach into groundwater.

Similar to the apparent increase in nitrogen uptake of resilient trees, productivity of resilient trees does increase following a beetle outbreak (Romme et al. 1986). Foliar nitrogen concentrations are correlated to photosynthetic capacity of trees (Field and Mooney 1986). Essential proteins of photosynthesis are nitrogen-rich. Increases in nitrogen uptake are closely coupled to increased photosynthetic capacity and growth rates. The results of the present study are, therefore consistent with increased production of resilient trees following pine beetle outbreaks. The increased growth rate and nitrogen
uptake of resilient trees suggests that these trees might be essential to forest regeneration following a beetle outbreak. Increased production and nitrogen uptake may also cause increased uptake of water and other soil nutrients by these trees. Resilient trees unaffected by the beetle are potentially very important to forest regeneration and biogeochemical cycling post-disturbance. Increased nitrogen uptake, growth and the prevalence of trees that survive a mountain pine beetle outbreak is suggestive of a system that is potentially resilient and responsive to the biogeochemical changes resulting from the current mountain pine beetle epidemic.

*Future directions*

Despite the apparent increase in the nitrogen uptake of resilient trees, further research is needed to confirm the relative role of these trees in nitrogen retention, and the total fraction of available nitrogen that the trees immobilize. Belowground measurements of nitrogen availability and the species of nitrogen present in soil are necessary to better understand the partitioning of nitrogen between plant and microbial communities in areas affected by mountain pine beetle. While an increase in the foliar nitrogen concentrations of resilient trees in response to local mortality is evident, the magnitude of the response with respect to total soil nitrogen availability in the system is unknown.
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