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Extent of localized tree mortality influences soil biogeochemical response in a beetle-infested coniferous forest

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ABSTRACT

Recent increases in the magnitude and occurrence of insect-induced tree mortality are disrupting evergreen forests globally. To resolve potentially conflicting ecosystem responses, we investigated whether surrounding trees exert compensatory effects on biogeochemical signatures following beetle infestation. To this end, plots were surveyed within a Colorado Rocky Mountain watershed that experienced beetle infestation almost a decade prior and contained a range of surrounding tree mortality (from 9 to 91% of standing trees). Near-surface soil horizons under plot-centered live (green) and beetle-killed (grey) lodgepole pines were sampled over two consecutive summers with variable moisture conditions. Results revealed that soil respiration was 18–28% lower beneath beetle-infested trees and correlated to elevated dissolved organic carbon aromaticity. While certain edaphic parameters including pH and water content were elevated below grey compared to green trees regardless of the mortality extent within plots, other biogeochemical responses required a higher severity of surrounding mortality to overcome compensatory effects of neighboring live trees. For instance, C:N ratios under grey trees declined with increased severity of surrounding tree mortality, and the proportion of ammonium displayed a threshold effect with pronounced increases after surrounding tree mortality exceeded ~40%. Overall, the biogeochemical response to tree death was most prominent in the mineral soil horizon where tree mortality had the largest affect on carbon recalcitrance and the enrichment of nitrogen species. These results can aid in determining when and where nutrient cycles and biogeochemical feedbacks to the atmosphere and hydrosphere will be observed in association with this type of ecological disturbance.

1. Introduction

Biogeochemical cycling in montane and subalpine forest soils has important implications for water quality, ecosystem resilience, and atmospheric feedbacks in a warming climate (Jandl et al., 2007; Lal, 2005). While a critical component in climate forecasting (Falkowski et al., 2000), knowledge gaps exist due to the highly heterogeneous, interdependent, and biological variances in natural systems (Schimel and Bennett, 2004). Forests globally are facing threats that are expected to intensify in a changing climate, including deforestation, drought, disease, insect infestations, and wildfire (Dale et al., 2001). Of particular relevance to the work herein, bark beetle infestations have increased in magnitude and severity as a result of warming temperatures and water limitations (Carroll et al., 2003; Mitton and Ferrenberg, 2012). The current mountain pine beetle infestation has affected more than 10 Mha (100,000 km^2) of coniferous forest in the western United States and British Columbia over the past two decades (Meddens et al., 2012). In extreme instances, bark beetle-induced tree mortality has the potential to change forests from carbon sinks to sources, potentially intensifying climatic feedback loops that will persist after impact (Kurz et al., 2008; Wear and Coulston, 2015). Furthermore, in some watersheds, large-scale beetle-induced forest disturbances have been shown to affect water quantity (Bearup et al., 2014; Bethlahmy, 1974; Biederman et al., 2014, 2015) and quality

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(Brouillard et al., 2016; Mikkelson et al., 2013b) while altering terrestrial carbon (C) and nitrogen (N) cycling (Clow et al., 2011; Mikkelson et al., 2013a; Morehouse et al., 2008; Norton et al., 2015; Trahan et al., 2015).

Soil biogeochemical parameters such as N and C pools, pH, and water content are affected by tree mortality after bark beetle infestation; however, there is significant variability in the magnitude of these responses (Mikkelson et al., 2013a). After bark beetles infest and kill a tree, C and N inputs to the soil system are altered. Initially, as transpiration ceases and photosynthesis stops, root exudates are no longer excreted and a source of labile C in the subsurface is lost (Grayston et al., 1997). After several years in the dead "red" phase, beetle-killed trees drop their needles and progress to the "grey" phase, during which there is a large increase in recalcitrant organic matter input as fallen needles and coarse woody material from dead trees degrade (Edburg et al., 2012). Needle litter from beetle-killed trees is also N-enriched relative to naturally-senesced litter (Griffin et al., 2011; Morehouse et al., 2008) potentially increasing the terrestrial contribution to the subsurface N-pool. These litter inputs then decay and transformed compounds are leached and transported over time from the litter horizon downward through the organic and mineral horizons.

These C and N cycling shifts resulting from beetle-induced tree mortality can create notable secondary effects that have implications for altered gaseous and aqueous flux to the atmosphere and hydrosphere. For example, the flux of greenhouse gases such as CO_2 and N_2O may change as root respiration ceases, heterotrophic respiration from root-associated microbial communities declines, or shifts to abiotic processes and changing C-N pools occur (Barrena et al., 2013; Moore et al., 2013). In addition, aqueous outputs including nutrients and dissolved organics can be transported to water sources with downstream effects on ecological processes and drinking water quality; however, the magnitude of these detrimental impacts varies across beetle-impacted ecosystems. For instance, watersheds with high levels of beetle-induced mortality in the Colorado Rocky Mountains were linked to increased organic carbon and disinfection byproduct formation potential at downstream water treatment plants while watersheds with lower levels of mortality did elicit the same response (Brouillard et al., 2016; Mikkelson et al., 2013b). The nitrogen biogeochemical response in bark beetle-impacted forests has shown similar variability as beetle-killed forests in the Czech Republic have been linked to increased nitrate runoff, threatening water sources with eutrophication (Huber, 2005; Zimmermann et al., 2000) while other beetle-killed forests in the Rocky Mountains have a more muted nitrogen response where both compensatory uptake (Rhoades et al., 2013) and riparian zone removal (Biederman et al., 2016) have been proposed as mitigating mechanisms.

While past studies have investigated seasonal and inter-annual variability of terrestrial biogeochemical cycling during forest recovery (Ferrenberg et al., 2014; Mikkelson et al., 2016b; Norton et al., 2015; Štursová et al., 2014), few have investigated variability due to the severity of beetle infestation (Cigan et al., 2015). Some studies have compared biogeochemical response between an unimpacted versus a beetle-impacted plot (Bearup et al., 2014; Brouillard et al., 2016; Mikkelson et al., 2016b); however, geographic biases can occur from differences in elevation, soil type, vegetation, and aspect between sites. In this study, we aim to better understand and resolve variable and potentially conflicting biogeochemical responses after beetle infestation to enhance predictions of soil respiration and nutrient shifts following this form of forest mortality. Previous observations following logging disturbance suggest that geochemical responses are muted until a threshold of surrounding tree mortality is surpassed (Parsons et al., 1994; Prescott et al., 2003), presumably because adjacent live trees exert a compensatory effect on ecosystem disruption. While tree harvesting impacts hydrologic and biogeochemical processes in different ways compared to mortality caused by bark beetles (Adams et al., 2012; Mikkelson et al., 2013a), we anticipate a similar compensatory effect from surviving vegetation. To this end, we hypothesized that compensatory effects from surrounding live trees mute changes to soil biogeochemical processes and microbial respiration under dead, beetle-impacted trees until a certain threshold of surrounding tree mortality is surpassed. This response will be most visible in the soil layer where decaying needle inputs from above and the cessation of root exudation converges thus creating a larger impact on signatures. To enable this inquiry, we focused our study on lodgepole pines (*Pinus contorta*) infested by bark beetles in the Colorado Rocky Mountains. Plots were surveyed that contained a range of beetle-induced tree mortality ranging from 9 to 91% of standing trees affected. A suite of soil biogeochemical parameters (i.e. soil respiration, C and N species, pH) were then compared to mortality phase (healthy vs. deceased) and related to the severity of surrounding tree mortality within each plot. Our findings provide a foundation to better understand how and when terrestrial biogeochemical processes may change in association with this type of large-scale ecosystem disruption.

2. Methods

2.1. Site selection and characterization

The study was performed in the White River National Forest approximately 5 km southwest of Frisco, Colorado (39.5427° N, 106.1460° W) in the summer of 2015 and 2016. This site was chosen for its range of localized tree mortality severity, accessibility, relative homogeneity of vegetation, and uniform slope and aspect (Table S1). The forest is dominated by lodgepole pine (*Pinus contorta*) (USDA, 2017), which experienced mountain pine beetle infestation beginning between 2007 and 2008. This study focused on comparisons between the 'green' phase, when a tree is alive, healthy, and transpiring, and the 'grey' phase, with an onset 3–5 years after initial infestation when the dead tree has dropped its needles (Mikkelson et al., 2013a). No recent anthropogenic or natural forest disturbance aside from bark beetle infestation has occurred at the site.

Thirty-eight, 8-m radius plots were established, each centered on a green phase ($n = 7$) or grey phase ($n = 31$) sample tree. Plot-level severity of tree mortality was defined as percentage of dead trees relative to total number of trees in the plot and ranged from 9 to 91%. In the northern Rocky Mountains, lodgepole pine roots may extend 4 m from the trunk (Parsons et al., 1994); therefore, an 8-m radius plot size was selected to include trees that may partially overlap with the root system of the sample tree. Plots centered on green phase trees were carefully selected to contain lower levels of surrounding tree mortality (<35%) to better represent a healthy, unimpacted forest. Only trees with diameter at breast height >7 cm were included in mortality measures. Surveyed neighboring trees were primarily lodgepole pine with an occasional aspen (Figure S1). All plots were located on the same hillslope and care was taken to account for and reduce heterogeneity in slope, aspect, soil type, land cover, tree circumference, and sun exposure while capturing a range of surrounding tree mortality (Table S1). The aspect at each sample tree was East-Southeast with slopes ranging from 8 to 27%. While the average slopes are similar when binning plots by tree phase (Table S1), we do recognize this large range of slopes may impact infiltration rates, vadose zone groundwater movement (Mikkelson et al., 2013c), and thus, possibly the biogeochemical contributions from neighboring trees.

To confirm temporal reproducibility and investigate whether