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Rapid soil organic matter loss from forest dieback in a subalpine coniferous ecosystem

Yanmei Xiong^{a,b}, Justin J. D'Atri^a, Shenglei Fu^b, Hanping Xia^b, Timothy R. Seastedt^{a,*}

^a Institute of Arctic and Alpine Research and Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, CO 80309-0334, USA ^b South China Botanical Garden, Chinese Academy of Sciences, Guangzhou 510650, China

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ABSTRACT

Forest dieback caused by climate-change associated stresses and insect outbreaks has emerged as a global concern, and the biogeochemical consequences of this phenomenon need to be elucidated. We measured biological and chemical traits of soil beneath live trees or trees recently killed by a mountainpine-beetle outbreak in a subalpine coniferous forest in the Front Range of Colorado. We focused on the top 5 cm of mineral soil just beneath the O horizon and measured microbial biomass, soil invertebrate abundance and composition, and soil chemical characteristics. With the termination of inputs from rhizodeposition, mycorrhizal fungal turnover and fine root turnover, soil total carbon (C) and total nitrogen (N) in the mineral soil at three sites decreased by 38–49% and 26–45%, respectively. Tree mortality was associated with reduced soil microbial biomass but soil nematode and microarthropod densities were unchanged. Nematode trophic structure was altered with an increased proportion of bacterial feeders. Soil inorganic N concentrations were inversely correlated to microbial C:N ratios. Tree death was associated with increased soil pH, a possible loss of calcium (Ca^{2+}), but an accumulation of soil inorganic N, largely as NH⁴₄. Our results suggest that forest dieback results in rapid C and N loss from surface mineral soils and that the accumulation of soil inorganic N, the reduction in microbial biomass, and the more bacterial-based soil food web increase the potential of enhanced N loss from affected ecosystems.

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1. Introduction

Forest dieback in which high rates of landscape to regional-scale tree mortality occur has emerged as a global issue and has been related to drought and heat stresses associated with climate change (Breshears et al., 2005, 2009; van Mantgem et al., 2009; Allen et al., 2010). In the past, forest dieback has been reported to occur mainly in semi-arid regions; however, this phenomenon has recently been documented from all wooded continents and from diverse forest types around the world (Allen et al., 2010). Climate-induced drought and warmer temperatures not only act as a direct stress to cause tree mortality, but also trigger many extensive forest insect and disease outbreaks that kill trees as well (Desprez-Loustau et al., 2006; Raffa et al., 2008; Breshears et al., 2009).

Native bark beetles outbreaks have killed millions of hectares of trees spanning the entire range of the Rocky Mountains from Alaska to Mexico (Raffa et al., 2008; Lundquist and Bentz, 2009; Allen et al.,

2010), and these outbreaks over the last decade have been unprecedented in the extent of frequency, impact and range. Since 1999, 47 million hectares of conifer forests along the Rocky Mountains have been affected by bark beetles (Raffa et al., 2008). The tree mortality within a single year ranges from individual trees to most of a stand (Kurz et al., 2008). Climate change, including warmer minimum winter temperature, increased summer temperatures, and reduced summer precipitation are considered as contributors to the severe outbreaks (Williams and Liebhold, 2002; Kurz et al., 2008). With continued warming, coniferous forests are expected to suffer from beetle infestation and will continue to be at risk of regional-scale tree mortality.

Forest dieback not only causes large economic loss but also can have severe consequences to ecosystems and ecosystem services not often factored into cost-benefit analyses. Trees grow relatively slowly but can die within a few months, and the abrupt forest dieback can result in rapid ecosystem changes more quickly than the gradual transitions that occur from tree regeneration and growth (Allen et al., 2010). Among the studies investigating the ecological impacts of forest dieback, most attention is paid to the loss of forest carbon (C) sequestration and the effects on wildlife





^{*} Corresponding author. Tel.: +1 303 492 3302; fax: +1 3034926388. *E-mail address:* timothy.seastedt@colorado.edu (T.R. Seastedt).

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inhabiting the affected forests (Kurz et al., 2008; van Mantgem et al., 2009; Albani et al., 2010). However, potential changes in other biotic and chemical properties, especially in belowground processes of these forests remain poorly known, except that increased nitrogen (N) mineralization and nitrification rates have been reported (Jenkins et al., 1999; Yorks et al., 2000).

Dieback produces a distinct alteration in both the inputs to soil and the feedbacks of soil to the canopy. The linkages between aboveground-belowground interactions in community organization and ecosystem processes have only recently been emphasized (Wardle et al., 2004; Bardgett et al., 2005; van der Putten et al., 2009) and beetle-killed trees provide opportunities to examine the individual role of rhizosphere activities. Plant-derived C input to soil in forms of leaf- and root-litter and root exudates are the most important C sources fueling the soil decomposer food web (Ruf et al., 2006; Pollierer et al., 2007), and drive soil biogeochemical processes. Moreover, turnover of mycorrhizal mycelium was reported to be another major contributor to dissolved organic C (DOC) in soil and could support a large portion of soil microbial biomass (Högberg and Högberg, 2002; Godbold et al., 2006). Since termination of rhizodeposition as well as mycorrhizal turnover is an immediate result from tree death while canopy litterfall is delayed, the coupling of above- and belowground C sources is released and an assessment of this loss on soil biological and chemical properties is possible. Termination of rhizodeposition and mycorrhizal turnover by tree girdling has been shown to substantially alter a series of soil processes, such as decreased soil respiration. DOC and microbial biomass, but increased soil N mineralization (Högberg et al., 2001; Högberg and Högberg, 2002; Weintraub et al., 2007; Zeller et al., 2008). Although it is logical to assume that beetle killing may have similar effects as tree girdling on rhizosphere soil processes given the similar responses of trees to beetle killing and girdling, direct evidence from beetle outbreak studies is scarce and more assessments are needed.

Colorado is among the areas severely affected by the recent bark beetle infestation. As of 2006, about 700,000 ha of forest had been impacted (USFS, 2007). In 2009, we selected three sites in a beetleaffected pine forest in Colorado Front Range and measured a series of soil biological and chemical properties to evaluate the impacts of tree death on soil processes in the first few years following beetle kill. We envisioned that soil labile C would decline following tree death due to the termination of root exudates and mycorrhizal turnover, but labile N and soil organic matter (SOM) would increase because of the termination of root uptake of N and increased dead root input, respectively. We expected soil microbial biomass to decline because soil microorganisms are believed to be limited by C availability but not N in most soils (Ekblad and Nordgren, 2002; Demoling et al., 2007) and also because that C from root exudates can be more important in fueling soil food web than litter input (Pollierer et al., 2007). We hypothesized that soil fauna density would decline without the microbial resource. We also hypothesized that soil food web structure might change due to the shifted C source from root exudates to root litter and the altered availability of soil C and N.

2. Materials and methods

2.1. Site description and soil sampling

The study was conducted near the Mountain Research Station of University of Colorado, part of the Niwot Ridge Long-Term Ecological Research (LTER) site. The field station is approximately 25 km west of Boulder, Colorado (40°N; 105°W), at 2900 m elevation above sea level. Mean annual temperature is 4 °C and annual precipitation averages 800 mm, mostly occurring between November and April in the form of snow. Soils at these sites are of recent origin, having formed on moraines left from the most recent glaciations (ca 18,000–14,000 BP; Madole, 1976). All soils were weakly developed Inceptisols formed from Precambrian igneous materials (Burns, 1980). We noted no topographic patterns associated with patterns of living and dead trees; slope and aspect did not differ within sites sampled here.

The forest in this area is approximately 100 years old, dominated by *Pinus contorta* Douglas var. *latifolia* (lodgepole pine), *Picea engelmannii* Parry ex Engelm. (Engelmann spruce) and *Abies lasiocarpa* (Hook.) Nutt. (subalpine fir). *Pinus flexilis* James (limber pine) is locally abundant, particularly on rocky sites. More detailed description of this forest can be found in Monson et al. (2002).

Three sites were selected in our study that were experiencing beetle attacks. The sites were 2–5 km away from each other and each was on a separate hillslope. Sites 1 and 2 consisted of an interspersed matrix of live, dying and dead trees, and we used a random sampling design to obtained nine samples beneath live and dead trees in each these two sites. Beetle kill was observed at these sites first in 2007, although some may have been attacked in 2006. Site 3 consisted of discrete clusters (100–200 m² in area) of dead trees surrounded by live trees. We sampled beneath 12 living and 12 dead trees at this site. The beetle kill had been ongoing longer at Site 3, as evidenced by the dead trees observed here in 2005. Sampling area at each site was approximately 1–2 ha.

The time since tree death due to beetles can be estimated during the first few years following attack by the color and presence of the tree needles (Wulder et al., 2006; Klutsch et al., 2009). For samples in 2009, we did not attempt to age the trees except to note that sites 1 and 2 had experienced recent mortality (2-3 years or less), whereas Site 3 contained trees that appeared to have initiated dieback several years earlier (4-5 years or less). Sites 1 and 2 were near monocultures of P. contorta and Site 3 was dominated by P. contorta with clusters of P. flexilis. The canopy cover at the study sites was 75–85%, and all samples were taken beneath the canopy of either a living or dead tree. The sites have a sparse ground cover of about 15% or less, mostly represented by a low-growing shrub, Vaccinium sp. Surface litter was not measured in this study, but needle fall from beetle-kill trees does not begin until the third year following attack, and only Site 3 showed signs of needle drop in 2009.

For all measurements, only the top 5 cm of mineral soil located beneath a very distinct O horizon was sampled using a soil corer of 5 cm diameter. Four soil cores were taken and pooled as one sample for all soil analyses except for microarthropod extraction, for which a single soil core was used. While no fixed distance was used to separate samples from living and dead trees, samples from live trees were never taken within 4 m of the drip zone of dead trees.

In 2010, we measured tree diameters at breast height (DBH) and repeated pH measurements at Site 1 to test if tree size was related to beetle attack and if tree size affected soil pH. We again used the presence or absence of beetle pitch tubes to identify live and recently killed trees, and the color and presence of needles to age the time since the tree was attacked. In 2010, however, each tree was coded as live, dead 1–2 years (needles still green), dead 2–3 years (needles all present but red), dead 3–4 years (needle drop initiated) or dead longer than 4 years (needles on ground). Sample size was 9, 8, 6, 8, and 8 for each age group, respectively. As before, four 5 cm deep cores of the uppermost mineral soil were composited for each sample.

2.2. Soil analyses

Fresh soil was sieved through a 2 mm mesh for soil dissolved organic C (DOC), inorganic N and microbial biomass analyses. Soil

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