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Do biological legacies moderate the effects of forest harvesting on soil microbial community composition and soil respiration

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ABSTRACT

Ecological forestry is a management approach that uses natural disturbance processes as models for designing silvicultural prescriptions that restore or sustain ecosystem biodiversity and function in actively managed forests. We evaluated how a novel ecologically-based multi-cohort silvicultural treatment affects the soil microbial community (SMC) and tested whether supplemental dead wood in the form of girdled trees alters these effects. We also tested SMC function by measuring soil CO_2 flux over multiple growing seasons, and examined if these patterns were related to soil microbial groups. Our experimental harvests were conducted in second-growth northern hardwood forests in northern Wisconsin, USA. Treatments included a modified shelterwood harvest (SH), a shelterwood harvest plus dead wood supplementation (SH + CWD), and an unharvested control; here we report responses three to five years post-treatment. The SMC composition (determined using PLFA) in both harvests was significantly different from the control, a difference driven by greater bacterial abundance in the harvested areas, and particularly by gram negative bacteria in SH. Microbial community composition was not significantly different between the two harvests (SH and SH + CWD). Total soil respiration was significantly lower in SH than in the control and SH + CWD treatments, a difference most likely driven by a reduction of the autotrophic respiration component in SH treatments due to harvesting, while in the SH + CWD treatment roots from living girdled trees contributed to autotrophic soil respiration. The relationship between the SMC and soil respiration varied with treatment and season. In general, soil respiration in the unharvested controls was most significantly correlated with microbes that relate to autotrophic respiration sources, while respiration in SH + CWD was most significantly correlated with heterotrophic microbes. These results indicate that, although the SMC composition was affected by forest harvesting practices incorporating live and dead biological legacies, supplementing the number of standing dead trees through girdling and felling maintained SMC function, as measured through total soil respiration, an indicator of some important aspects of ecosystem function.

1. Introduction

Ecological forestry is a forest management approach that attempts to model silvicultural practices on patterns of natural disturbance for the purpose of increasing ecosystem complexity and biodiversity (Franklin et al., 2007). In the Great Lakes region, USA, wind-related treefalls of varying extent and severity are the primary natural disturbance structuring northern hardwood forests (Frelich and Lorimer, 1991; Schulte and Mladenoff, 2005). Simulating elements of this disturbance regime involves incorporating biological legacies that include standing live trees, standing dead trees (snags), and downed tree boles within the post-harvest stand. These residual structures have been referred to as "lifeboats" because they provide habitats for affected organisms post-disturbance (Franklin et al., 2007). Studies have addressed the effects of ecological forestry harvesting practices on the diversity of ectomycorrhizal (Luoma and Eberhart, 2008; Luoma et al., 2006) and saprotrophic fungi (Brazee et al., 2014; Junninen et al., 2007), but there has been little research of the effects on the overall

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structure of the soil microbial community (SMC). Understanding these effects is important due to the functional relationship of the SMC to ecosystem productivity through decomposition and the production of plant-available nutrients (McGuire and Treseder, 2010).

Forest harvesting, as traditionally applied, may alter soil microbial communities through its influence on the abundance of living and deadwood legacies following harvest. In particular, the removal of overstory trees directly affects the heterotrophic rhizosphere bacterial community that is dependent on labile carbon (C) inputs (Farrar et al., 2003; Myers et al., 2001; Outerbridge and Trofymow, 2009; Paterson et al., 2007), and can change the abundance of complex C decomposers, such as saprotrophic fungi (Wolf and Wagner, 2005) and actinomycete bacteria (Deslippe et al., 2012; Nakatsu, 2005) by altering the quantity and quality of litter inputs. Furthermore, both the amount of overstory tree removal and woody debris retention influence soil moisture and temperature regimes (Brais et al., 2004; Lal, 2005), which can affect microbial metabolism (Davidson and Janssens, 2006; Mentzer et al., 2006; Wixon and Balser, 2013), leading to higher organic matter mineralization and decomposition rates (Covington, 1981). Therefore, retaining live tree legacies in the form of overstory trees within a harvested stand may help to maintain belowground SMC structure, sustain ecosystem productivity, and enhance connectivity across the forested landscape (Franklin et al., 1997; Gustafsson et al., 2010; Lewandowski et al., 2016; Rosenvald and Lõhmus, 2008). At the same time, retaining greater amounts of dead wood following harvest increases substrate availability for the microbial decomposer community, which can positively affect microbial biodiversity (Bouget et al., 2012; Brazee et al., 2014).

An important indicator of the physiological activities of the SMC is respired soil CO_2. Total soil respiration is composed of autotrophic CO_2 flux due to root respiration of higher plants, and heterotrophic CO_2 flux originating primarily from soil microorganisms (Kuzyakov, 2006). Forest harvesting alters soil respiration rates by affecting both autotrophic and heterotrophic respiration sources (Jandl et al., 2007; Johnson and Curtis, 2001; Lal, 2005), contributing to an estimated 8% reduction of C stored in forest soils on average (Nave et al., 2010). Autotrophically derived CO_2 from plant roots and associated mycorrhizal fungi make up 50% or more of soil respiration (Högberg et al., 2001), and removal of overstory trees initially leads to a reduction in autotrophic soil respiration (Kurth et al., 2014; Mattson and Swank, 1989; Nakane et al., 1986; Noormets et al., 2012; Striegl and Wickland, 1998).

The SMC composition and physiological activity contributing to soil respiration are affected by seasonal variability. The abundance of different groups within the microbial community changes due to seasonal variation; single-celled bacteria proliferate in the cooler, wet spring season, while fungi, because they are filamentous, better tolerate the warm, dry summer (Schimel et al., 2007). Total respiration generally increases throughout the growing season, peaking in mid-to-late summer, and individual respiration components also shift from primarily autotrophic to heterotrophic throughout the growing season (Czimczik et al., 2006). Autotrophic respiration potentially peaks earlier in the season due to greater aboveground plant growth (Högberg et al., 2001), while heterotrophic respiration peaks during mid to late summer when soil temperature is at its greatest (Czimczik et al., 2006).

In this research, we evaluate how the retention of live trees in an ecologically based timber harvest affects characteristics of the SMC, and test whether the increased complexity created by supplementing dead wood moderates this effect. In addition, we test how these establishment harvests affect soil surface CO_2 flux throughout the growing season, and examine the relationship of microbial groups to soil C dynamics. We used an operational scale field trial that compares the ability of active silvicultural treatments to accelerate the development of late successional characteristics in second-growth northern hardwoods while still allowing sustainable timber harvests (The Managed Old-growth Silvicultural Study or MOSS project; Fassnacht et al., 2013). The experiment crosses canopy treatments with dead wood additions. While a number of studies have focused on group selection openings or gaps, this trial includes a novel irregular multi-cohort treatment akin to a modified shelterwood. The modified shelterwood treatment is based on the work of Hanson and Lorimer (2007) and was designed to simulate a moderate-intensity wind disturbance that would remove 30–60% of the basal area using two entries 6–10 years apart. The treatment has four modified shelterwoods of two different sizes (two 0.40 ha and two 1.2 ha), and lightly-thinned and heavily-thinned "reserve" zones (Fassnacht et al., 2013). Here we are focused on the 1.2 ha shelterwoods only.

Our first objective in this research is to contrast the effects of ecological harvesting treatments on the SMC, soil moisture and soil temperature during the spring versus summer, five years following harvest. We expect that the SMC in the shelterwood harvests will differ from the unharvested control due to altered microclimatic conditions and resource availability, but that there will be a greater abundance of wood-decomposing microbes, such as fungi and actinomycetes, in the combined shelterwood and dead wood addition treatment due to greater abundance and diversity of resources. Microbial responses will be moderated by seasonal variation, with more single celled bacteria in the spring season and greater abundances of filamentous microbes during the summer. Our second objective is to evaluate the effects of experimental harvests on soil CO_2 flux 3–5 years following harvest. We expect a reduction in total soil respiration in the shelterwood due to the reduced autotrophic contribution. However, we expect that in the shelterwood with dead wood additions total soil respiration rates will remain more similar to the unharvested controls due to a potential increase in the heterotrophic contribution with the greater availability of substrate for heterotrophic bacteria and fungi. Finally, we evaluate the relationship between soil respiration and the SMC, soil moisture, and soil temperature during the spring and summer of year 5. We expect that heterotrophic activity will be a more important component of total respiration during the summer relative to spring, particularly in the combined canopy and dead wood addition treatment.

2. Methods

2.1. Site description

This study focused on a subset of treatments and sites within the MOSS project. Our research was conducted in the Northern Highland American Legion (NHAL) State Forest in Vilas County, and the Argonne Experimental Forest located within the Chequamegon-Nicolet National Forest in Forest County, Wisconsin (Fassnacht et al., 2013; Fassnacht and Steele 2016). Prior to treatment implementation, stands were even-aged, second-growth 70–90-year-old northern hardwood forests with no recent management activities. Stands are composed of two of the most common, mesic northern hardwood habitat types in the region; *Acer-Osmorhiza-Caulophyllum* and *Acer-Tsuga-Dryopteris*, (Kotar et al., 2002). The overstory is dominated by sugar maple (*Acer saccharum* Marsh.), with white ash (*Fraxinus americana* L.), basswood (*Tilia americana* L.), yellow birch (*Betula alleghaniensis* Britt.) and eastern hemlock (*Tsuga canadensis* (L.) Carr.) present as well. Soils are primarily sandy and coarse-loamy Haplorthods in NHAL (Natzke and Hvizdak, 1988), and coarse-loamy Fragiorthods and Haplorthods in Argonne (Boelter et al., 1995). However, soils at both sites are highly variable because they are derived from recent glacial origins (Fassnacht et al., 2013). The regional climate is continental, with an average temperature of 5 °C that ranges from a summer maximum of 32 °C to a winter minimum of −40 °C. Average precipitation is 813 mm, which occurs mostly during the growing season (USFS Argonne Experimental Forest; www.nrs.fs.fed.us/ef/locations/wi/argonne/).