Geoderma 243–244 (2015) 141–148

Contents lists available at ScienceDirect

Geoderma

journal homepage: www.elsevier.com/locate/geoderma

Conifer litter identity regulates anaerobic microbial activity in wetland soils via variation in leaf litter chemical composition

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ARTICLE INFO

Article history:
Received 4 August 2014
Received in revised form 23 December 2014
Accepted 27 December 2014
Available online 9 January 2015

Keywords:
Anaerobic respiration
Conifer
Hemicellulose
Methanogenesis
Peat soil
Pectin
Plant species identity

ABSTRACT

Plant litter is a crucial source of energy and nutrients for soil microorganisms, and thus plant species identity may help account for variation in rates of soil microbial activity via species dependent differences in litter chemistry. This may be particularly important in forested wetlands where the composition of conifer tree species can vary. We explored the relationship between conifer litter identity and anaerobic microbial activity by adding fresh needle litter from nine conifer species to soils from two contrasting forested wetlands and quantifying rates of anaerobic respiration (CO_2 production) and methanogenesis (CH_4 production). We characterized litter chemistry as the amounts of structural polysaccharides and polymers (cellulose, hemicellulose, pectin, lignin) and examined changes in these fractions during incubation. Litter from *Pinus* species supported the largest rates of CH_4 production, whereas litter from *Picea* species supported the lowest rates. Litter from two deciduous conifers (*Metasequoia*, *Larix*) supported intermediate rates of CH_4 production. Tree species identity had less impact on rates of anaerobic CO_2 production. Rates of CH_4 production correlated with hemicellulose and with covalently bonded pectin, whereas rates of anaerobic CO_2 production showed a positive correlation with initial acid-detergent lignin concentration and with pectin. Gaining a better understanding of how hemicellulose and pectin in decomposing plant litter promote anaerobic microbial activity, especially specialized methanogenesis in soil provides insight that links plant litter identity and leaf traits to anaerobic microbial activity in the underlying soil.

1. Introduction

Woody vegetation can be a dominant feature in some peatland ecosystems (Rydin and Jeglum, 2013), and interest in the functional role of trees in peatlands has increased in concert with the recent expansion of *Pinus*, *Picea*, and *Larix* onto cool temperate peatlands in North America and in Europe (Berg et al., 2009; Heijmans et al., 2013; Pellerin and Lavoie, 2003). Because trees increase the capture of atmospheric carbon, they can, in turn, promote increased rates of heterotrophic microbial activity in soil via an added amount of litter to the soil (Jackson et al., 2002). In forested peatlands, leaf litter is the largest source of fresh carbon added to the soil (Coles and Yavitt, 2004), and thus understanding linkages between tree leaf litter and soil microbial activity is necessary if we are to fully explain carbon dynamics in peatlands. This is particularly germane to the production of methane (CH_4) and carbon dioxide (CO_2) derived ultimately from leaf litter decay, and thus consideration of tree species identity might help predict emission of these atmospheric gasses in response to current and future changes in tree species composition on peatlands.

This follows the growing body of research that links plant species aboveground to soil microorganisms belowground (Zak et al., 2003). The rationale is that plant leaves show a suite of chemical characteristics that might confer distinctiveness to soil microorganisms. For example, plant leaves can be viewed along a spectrum from long-lived, evergreen leaves that are thick, with low nutrient content, and high amounts of structural compounds to seasonally deciduous leaves that are thinner, with higher nutrient content, and fewer structural compounds (Wright et al., 2004). This spectrum has been shown to influence the rate of leaf decomposition, e.g., slower rates for evergreen leaves and faster rates for deciduous leaves (Cornwell et al., 2008). Since microbial activity generally corresponds to the rate of litter decomposition, variation in litter chemistry should provide a crucial control on microbial activity. Furthermore, while the leaf trait spectrum is familiar for angiosperms, the question whether it extends to conifers, from evergreen *Picea* and *Pinus* to deciduous *Larix* and *Metasequoia*, in peatlands is unclear. Also, under some circumstances, deciduous conifers may produce more leaf litter than evergreen conifers (Middleton and McKee, 2004; Williams et al., 2003).

Most studies of litter decomposition are prolonged, taking the first measurement of mass loss only after several months to one year, and following the residue for three or more years. As a result, we know much less about microbial colonization of fresh litter at the very earliest

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http://dx.doi.org/10.1016/j.geoderma.2014.12.023
0016-7061/

stage of decomposition (Koide et al., 2005; Moorhead and Sinsabaugh, 2006). The situation is especially acute in wetland soils where common wisdom suggests slow rates of litter decay, in particular, with little oxygen and via anaerobic metabolism (Yavitt et al., 1997).

Here we propose that the mechanistic link to soil microbial activity occurs in the suite of chemical compounds that make up plant cell walls. Plant cell walls are combinations of three dominant structural polysaccharides (cellulose, hemicellulose and pectin), the lignin polymer, and various proteins and a variety of low molecular weight soluble compounds (Berg and McClaugherty, 2003). A general model is that cellulose microfibrils are embedded in a matrix of hemicellulose, pectin, and proteins (Keegstra, 2010). In secondary cell walls, lignin surrounds the cellulose and is bound to the hemicellulose (Cosgrove, 2005). Therefore, the traditional litter decay model posits that initial decomposition of leaf litter consumes the soluble fraction and non-protected cellulose (Berg and Staaf, 1980), leaving other components to accumulate in the residue. However, recent research has shown that initial decomposition can include the hemicellulose (Delaney et al., 1996), pectin (Jenkins and Suberkropp, 1995) and lignin (Klotzbücher et al., 2011). Moreover, different components of plant cell walls are known to vary in how accessible and digestible they are to different microbial decomposers (Ding et al., 2012). Thus, variation in the relative amounts of these plant cell wall components, among different species of conifers may play a role in regulating the early stages of litter decay and the supply of substrates to the soil microbial community (Koide et al., 2005).

We examined how tree species identity might ultimately regulate microbial activity in soil. We used a common garden approach and added needle litter from nine conifer species to soils from two forested wetlands with contrasting soil types. We focused specifically on anaerobic production of CO_2 and CH_4 (methanogenesis). We expected a priori that CO_2 production would exhibit relatively weak relationships with leaf litter identity. The reason being that CO_2 comes from a plethora of decarboxylation reactions, fermentations, and anaerobic respirations, such that the net effect on CO_2 would be muted. However, for methanogenesis we expected greater fidelity with leaf litter identity, given that methanogens use only a limited number of substrates derived specifically from fermentation and that fermentation, specifically, would depend on the suite of fermentable material per plant species (Drake et al., 2009; Reith et al., 2002). This follows the finding from Bremer et al. (2007) that plant species identity influenced the microorganisms that carried out soil denitrification. Therefore, specific predictions were for greater rates of microbial activity with deciduous rather than long-lived foliage, and that variation in the plant cell wall composition of litter among species would, in part, explain variation in rates of anaerobic microbial activity.

2. Materials and methods

Soils were collected from two sites in central New York State. Average annual temperature for the region is 6.5 °C, and average annual precipitation is 1170 mm. June and July typically have the highest mean monthly precipitation.

One site, Labrador Hollow (local name; hereafter, peat soil), is a forested peatland located 8 km southeast of Tully, New York (Labrador Hollow Unique Area, 42.781932°N, 76.041628°W). The site has a closed-canopy forest composed of *Acer rubrum* L. (red maple) and several conifer species: *Pinus strobus* L. (eastern white pine), *Tsuga canadensis* (L.) Carrière (eastern hemlock), and *Larix laricina* (Du Roi) K. Koch (tamarack or larch). *Vaccinium corymbosum* L. (highbush blueberry), *Toxicodendron radicans* (L.) Kuntze (poison ivy), and a mixture of pteridophytes are common in the understory. *Sphagnum* mosses cover about 75% of the ground and include the following species: *Sphagnum squarrosum* Crome, *Sphagnum girgensohnii* Russow, *Sphagnum fimbriatum* Wilson, *Sphagnum henryense* Warnst., and *Sphagnum russowii* Warnst. Beneath *Sphagnum* is a 0 to 10 cm thick layer of dense roots overlying about 8 m of mesic Typic Medisaprists peat soil. Below that, glacial till and sand cover Devonian age shale and limestone (Fisher et al., 1970). Further details are given in Coles and Yavitt (2004).

The second site, Sapsucker Woods (hereafter, swamp soil), is a forested wetland in Ithaca, New York (42.477291°N, 76.451523°W), located 47 km to the southeast of the first site. Sapsucker is a closed canopy forest dominated by *A. rubrum*, *Alnus incana* (L.) Moench ssp. *rugosa* (Du Roi) R.T. Clausen (Grey alder), and *T. canadensis*. Trees occur on elevated hummocks surrounded by water-filled depressions. The soil (Alden series) is a mesic Mollic Endoaquept, very poorly drained in depressions and low areas. It is approximately 1 m deep with a fragipan soil horizon that prevents drainage and maintains a high water table throughout the year. Soil for the incubations was collected from the depressions between tree hummocks.

Needle litter was collected from trees growing within close proximity (ca. 1 km) of each other, on the same soil, and exposed to identical climate in the Cornell Plantations Natural Area. We collected needles from three deciduous conifers; *L. laricina*, *Metasequoia glyptostroboides* Hu and Cheng (Dawn redwood), and *Taxodium distichum* (L.) Rich. (Bald cypress); and from six evergreen conifers (*Pinus banksiana* Lamb. (Jack pine), *Pinus rigida* Mill. (Pitch pine), *P. strobus* (Eastern white pine), *Picea abies* (L.) Karst. (Norway spruce), *Picea glauca* (Moench) Voss (White spruce), and *Picea mariana* (Mill.) Britton, Sterns and Poggenb. (Black spruce)). We collected needles at the end of the growing season in October by shaking branches gently, indicating a well-formed abscission zone, and collecting the needles that landed in a plastic bag placed beneath the branches. Needles were air dried at low humidity. Sub-samples were oven dried at 105 °C to ascertain moisture content. Other portions were sampled for chemical analyses (detailed below). We constructed litterbags containing a total of 1 g dry-weight-equivalent litter using a 15-cm^2 piece of fine mesh material (0.675 mm mesh size), gathered and sealed with plastic thread.

We quantified plant litter effects on rates of soil CH_4 production and anaerobic CO_2 production using in vitro incubation studies. Five replicate soil samples were collected randomly, combined and thoroughly mixed by hand before 30-g portions of soil were placed into individual incubation jars ($N = 3$ per leaf litter type) on the date of collection. We added 20 mL of de-ionized water before we sealed the jar with a lid that had a gas-tight septum to allow sampling gas in the headspace of the sealed jar. The jar headspace was made anoxic by evacuating for several minutes using a vacuum pump and refilling with O_2-free N_2. The evacuation was repeated three times. Jars with soil were incubated for 15 days at 20 °C, and concentrations of CO_2 and CH_4 in the headspace were measured every third day in order to establish the in vitro basal rate of microbial CO_2 and CH_4 production. The pre-incubation period also reduced the amount of inherent substrate for soil microorganisms (see Wang et al., 2003), thereby increasing the impact of the added leaf litter on their activity.

Samples were analyzed by gas chromatography using a flame ionization detector for CH_4 and a thermal conductivity detector for CO_2. The gas chromatograph has a 2.75 m by 3.18 mm column of Poropak Q 80/100 mesh (Waters Chromatography, Milford, MA) maintained at 50 °C to separate the gasses. The flow rate of the He carrier gas was 30 mL min^{-1}. The injector temperature was 110 °C.

Following the pre-incubation period, we opened the jars and added a litterbag to the surface of the soil. We tapped the bag to insure contact with soil before re-sealing the jar and establishing anoxic conditions and incubating at 20 °C, as described above. We measured CH_4 and CO_2 in the headspace every three to four days for 24 days. At the end of the incubation period, the litterbag was removed, and the residue remaining was analyzed for its biochemical content.

We determined the composition of hemicellulose, cellulose, and lignin using the detergent fiber technique (Van Soest, 1994). First, we combined and thoroughly mixed material per species before being ground through a Wiley Mill. Duplicate subsamples (0.5 g) per species were subjected to sequential neutral detergent fiber (Van Soest et al., 1991), acid detergent fiber, and acid detergent lignin digestions