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Long-term litter decay in Canadian forests and the influence of soil microbial community and soil chemistry

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ABSTRACT

Long-term rates of litter decay have been shown to be primarily influenced by temperature, moisture and litter quality. However, while decomposition is a biological process, the relative importance of microbial communities and other soil chemistry factors is not well understood. Our analysis examined long-term litter decay parameters, microbial community composition via phospholipid fatty acid (PLFA) analysis, and soil organic horizon chemistry at 14 upland forested sites. Data were collected as part of the Canadian Intersite Decomposition Experiment (CIDET), a 12-year national litter decomposition experiment. Residual errors from a two-pool exponential decay model with decay rates modified by mean annual air temperature and moisture stress were compared to PLFA marker groups and chemistry variables. Residual errors were not well explained by soil PLFA marker group abundance or concentration, soil pH, nor soil C:N ratios. The best predictor of residual error was soil carbon percent (%C), with higher %C associated with slower than predicted decomposition.

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1. Introduction

The terrestrial biosphere holds large carbon (C) pools, and the decomposition of plant detritus and soil organic matter releases more carbon dioxide (CO_2) to the atmosphere annually, than fossil fuel and industrial sources (IPCC, 2007). Despite the critical role of decomposition in the global C balance, our understanding of decomposition is rudimentary in comparison to our current understanding of C inputs through primary production (Adair et al., 2008). Decomposition is a key ecosystem process that influences the recycling of nutrients and thus ecosystem fertility and it is also the main return pathway to the atmosphere of CO_2 fixed during photosynthesis. Decomposition is mediated by microbes that use plant primary production from above- and belowground litter and soil as their sources of C (Brant et al., 2006). During decomposition, the microbial community controls the partitioning of litter- and dead root-C between CO_2 via respiration and storage in semi-permanent soil-C pools (Moore-Kucera and Dick, 2008; Prescott, 2010). The size and composition of the soil microbial community has been related to complex interactions with tree species (Hobbie et al., 2012), climate (Fierer et al., 2009), disturbances (Brant et al., 2006; Moore-Kucera and Dick, 2008), soil nutrients (Leckie, 2005; Lauber et al., 2008), soil chemistry (Nilsson et al., 2005; Högberg et al., 2007), and net primary production (Brant et al., 2006).

Studies comparing the influences of several edaphic variables on microbial community structure and composition have identified different dominant drivers of the microbial community. Högberg et al. (2007) found that soil chemistry had a larger influence than tree species on the soil microbial community, but Mitchell et al. (2010) found that plant community composition better predicted changes in microbial community composition than soil properties. You et al. (2014) found that soil water, soil organic C, soil temperature, soil clay content, fine root mass, and soil C to N ratio were all significant drivers of variations in soil microbial community structure.

Although past research has shown that temperature, precipitation, and litter chemistry strongly control rates of litter decomposition (e.g. Aber et al., 1990; Aerts, 1997), how these factors indirectly or interactively influence the soil microbial community, and hence litter decay, across large spatial and temporal scales remains unclear. Decomposition studies are most often local or regional in scale, use a low diversity of litter types, and do not consider the microbial community. Extrapolating to continental scales, or non-represented litters, or different ecosystems is therefore problematic. Similarly, because most studies are conducted for less than 5 years, there are few data available to define what factors control long-term or late-phase decomposition (Trofymow et al., 2002; Hobbie et al., 2012).

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The Canadian Intersite Decomposition Experiment (CIDET) was a national litterbag experiment that examined decomposition over 12 years for a range of litter types and ecosystems. Data from this experiment has been used for quantitative assessment of model parameters in three dynamic C models (Palosuo et al., 2005; Zhang et al., 2007; Smyth et al., 2010), for testing of several combined C and nitrogen models (Manzoni et al., 2008; Zhang et al., 2008; Manzoni and Porporato, 2009) and for studying the effects of climate and litter quality on decomposition processes (Trofymow et al., 2002; Moore et al., 2006).

In this paper we present results from the 12-year C-remaining time series and examine the relationships between decomposition, climate, soil organic horizon chemistry and microbial community. We used phospholipid fatty acid (PLFA) analysis to measure soil microbial biomass and community composition. The PLFAs extracted from soils represent living microorganisms and indicator PLFA are used as markers for taxonomic groupings (Zelles, 1999; Bååth and Anderson, 2003). This method is quantitative, and multivariate statistical procedures can be used to determine significant differences in abundance and composition of soil microbial communities (Frostegård et al., 1991, 1993). PLFA analyses are economical and allow relatively high sample throughput compared to nucleic acid-based methods, which is an advantage for large scale field based studies (Moore-Kucera and Dick, 2008). This method has been shown to be proportional to other microbial biomass measures for forest soils (Fritze et al., 2000; Fierer et al., 2003; Leckie et al., 2004).

We predicted C-remaining time series from a two-pool model with decay rates modified by temperature and water stress and compared it to measured C-remaining time series (Smyth et al., 2011). Then we compared the residuals to estimates of PLFA marker groups to understand the influence of bacterial and fungal groups on residual errors. Our hypothesis was that residual errors in the litter decomposition, which reflect decomposition that is faster or slower than predicted, are significantly related to soil PLFA marker group abundance or concentration. We also assessed the relationships between soil PLFA marker groups and soil chemistry variables to determine which variables were significant drivers of variations in community composition.

2. Materials and methods

2.1. The CIDET study and sample selection

The CIDET study is a 12-year litter decomposition experiment in which roughly 11 000 litterbags were surface-placed at 21 sites (18 upland, three wetland) that represented the major forested eco-climatic provinces of Canada (Ecoregions Working Group, 1989). Litterbags were 20 × 20 cm constructed from polyproplylene mesh with 0.5 mm openings, each containing 10 g (dry weight) of one of 11 different standard litter types. All litterbags were placed in contact with litter layers just before or during litterfall in autumn 1992 on four replicate plots on each site. Litterbags were collected annually each autumn until 2000, and biennially for the last two collections (2002, 2004). Further details of site descriptions, plot layouts, details of litter collection, sample processing, and initial litter and soil chemistry were published previously (Trofymow and CIDET Working Group, 1998; Trofymow et al., 2002). For this analysis we included initial and exposed samples of eight tree foliar litters (trembling aspen: *Populus tremuloides*, American beech: *Fagus grandifolia*, Douglas-fir: *Pseudotsuga menziesii*, white birch: *Betula papyrifera*, jack pine: *Pinus banksiana*, black spruce: *Picea mariana*, tamarack: *Larix laricina*, western redcedar: *Thuja plicata*) from 14 upland forested sites for which we had PLFA data (Table 1). Two of the sites (MAR, TER) had predominantly deciduous stands, while the remaining sites had predominantly coniferous stands.

Table 1
CIDET sites, locations, climate variables and soil organic horizon %C. Climate variables are mean annual air temperature (T), water stress (W) total annual precipitation (P).

Site	Location	Latitude (N)	Longitude (W)	T (°C)	W	P (mm)	Soil %C
INU	Inuvik, NT	68° 19′	133° 32′	−7.64	0.60	237	37.5
SCH	Schefferville, QC	54° 52′	66° 39′	−4.16	0.90	830	16.5
GI1	Gillam, MB	56° 19′	94° 51′	−3.77	0.69	482	32.0
NH1	Nelson House, MB	55° 55′	98° 37′	−2.88	0.70	471	22.2
WHI	Whitehorse, YT	60° 51′	135° 12′	0.01	0.47	241	24.6
TOP	Topley, BC	54° 36′	126° 18′	1.50	0.66	557	35.0
KAN	Kananaskis, AB	51° 00′	115° 00′	3.62	0.65	625	34.0
TER	Termundee, SK	51° 50′	104° 55′	3.68	0.43	370	17.0
GAN	Gander, NL	48° 55′	54° 34′	4.18	0.87	1265	52.5
CBR	CB Rocky Harbour, NL	49° 32′	57° 50′	4.49	0.85	1258	43.0
HID	Hidden Lake, BC	50° 33′	118° 50′	6.55	0.67	717	49.6
MAR	Morgan Arboretum, QC	45° 25′	73° 57′	6.70	0.76	978	34.2
PMC	Port McNeill, BC	50° 36′	127° 20′	8.72	0.82	1912	53.2
SHL	Shawnigan Lake, BC	48° 38′	123° 42′	9.33	0.64	1266	19.2

2.2. Climate indicators

Climate data were from nearby Meteorological Services Canada (MSC) climate stations (http://www.msc-smc.ec.gc.ca) and ANUCLIM interpolated climate data (McKenney et al., 2001). Climate indicators were mean annual temperature (T), total annual precipitation (P) and water stress (W), which is defined in the decomposition model section.

2.3. Litter measurements

As described previously (Trofymow et al., 1995; Trofymow and CIDET Working Group, 1998), litters were removed from litterbags after each fall collection, oven-dried at 55 °C, weighed, and ground to 0.2 mm mesh in a Wiley mill. Weighted composite samples were prepared from four replicate litter types for each site and analyzed for total C by dry combustion on a LECO CR-12 analyzer or a LECO CNS2000 Combustion Analyzer (*LECO* Corporation, St. Joseph, MI).

Carbon remaining at time t was estimated for all litters as:

$$C_r(t) = 100\frac{C_c(t)M(t)}{C_c(0)M(0)} \quad (1)$$

where C_c is the carbon concentration (%), M is the mass of the sample, $C_c(0)$ is the initial carbon concentration, and $M(0)$ is the initial mass.

2.4. Soil measurements

2.4.1. Soil organic horizon chemistry

In 2004, samples of the surface soil organic horizon were collected immediately adjacent to the string of litterbags in three to four replicate plots at each site. After removing the litter layer and green material, a 10 × 10 cm sample was excavated to the mineral horizon and composited into a single sample bag. The field moist soils were kept at 2 °C and shipped to the laboratory within 5 days, where they were sieved to 8 mm, gently homogenized, and portioned into subsamples for analysis.

Soil pH was measured with Ag/AgCl pH electrode using 1:2 ratio of soil to calcium chloride solution (0.01 M) and settling time of

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