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Litter decay controlled by temperature, not soil properties, affecting future soil carbon

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Abstract

Widespread global changes, including rising atmospheric CO_2 concentrations, climate warming and loss of biodiversity, are predicted for this century; all of these will affect terrestrial ecosystem processes like plant litter decomposition. Conversely, increased plant litter decomposition can have potential carbon-cycle feedbacks on atmospheric CO_2 levels, climate warming and biodiversity. But predicting litter decomposition is difficult because of many interacting factors related to the chemical, physical and biological properties of soil, as well as to climate and agricultural management practices. We applied ^{13}C-labelled plant litter to soil at ten sites spanning a 3500-km transect across the agricultural regions of Canada and measured its decomposition over five years. Despite large differences in soil type and climatic conditions, we found that the kinetics of litter decomposition were similar once the effect of temperature had been removed, indicating no measurable effect of soil properties. A two-pool exponential decay model expressing undecomposed carbon simply as a function of thermal time accurately described kinetics of decomposition. (R^2 = 0.94; RMSE = 0.0508). Soil properties such as texture, cation exchange capacity, pH and moisture, although very different among sites, had minimal discernible influence on decomposition kinetics. Using this kinetic model under different climate change scenarios, we projected that the time required to decompose 50% of the litter (i.e. the labile fractions) would be reduced by 1–4 months, whereas time required to decompose 90% of the litter (including recalcitrant fractions) would be reduced by 1 year in cooler sites to as much as 2 years in warmer sites. These findings confirm quantitatively the sensitivity of litter decomposition to temperature increases and demonstrate how climate change may constrain future soil carbon storage, an effect apparently not influenced by soil properties.

Keywords: agriculture, carbon cycling, climate change, litter decomposition, temperature

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Introduction

Rising atmospheric CO_2 concentrations, climate warming and loss of biodiversity are some of the global changes predicted for this century (Rockstrom *et al.*, 2009; Steffen *et al.*, 2011). These changes are expected to affect terrestrial ecosystem processes through, for example, alterations to the terrestrial C cycle, changes in community composition and potential resulting feedbacks (Bardgett, 2005; Hector & Bagchi, 2007). Hence, there is urgency to develop better understanding of carbon cycling in terrestrial ecosystems; of particular importance is the decomposition of plant litter and soil organic matter, a process mediated mostly by soil biota. This process roughly balances annual net primary productivity, thus emitting an amount of CO_2 almost five to six times that from current rates of fossil fuel combustion (Smil, 2013; Le Quéré *et al.*, 2014; Davidson, 2015). Consequently, any influence on rate of decomposition can have pronounced and lasting effect on atmospheric CO_2, with important ramifications for global climate. For example, acceleration of

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decomposition by warming temperatures could conceivably create a positive feedback that would amplify climate change (Davidson & Janssens, 2006; Kirschbaum, 2006; Conant *et al*., 2011).

The decomposition process also has a critical influence on the health of terrestrial ecosystems, which are sustained by the continual influx of carbon-rich plant litter, invested with the sun's energy via photosynthesis and enriched with nutrients absorbed from the soil (Pelletier *et al*., 2011; Haberl *et al*., 2014; Amundsen *et al*., 2015). Some of this biomass is harvested or consumed by humans or other biota, but most – as much as 90% of net primary productivity – enters the soil, where it gradually decays to mineral constituents, including CO_2 and soluble nutrients (Jenkinson, 1981; Gessner *et al*., 2010). The rate of this process affects many ecosystem functions: conserving biodiversity, ensuring plant nutrition, maintaining air and water quality and preserving soil resilience (Swift *et al*., 1979; Joffre & Ågren, 2001; Handa *et al*., 2014; Steffen *et al*., 2015; Turmel *et al*., 2015).

Understanding litter decomposition well enough to predict its rates with reliable models is therefore an urgent objective, both for mitigating climate change and preserving ecosystem function (Lin, 2014). The development of such models, however, is constrained by the influences of many interwoven and often fluctuating factors. Intrinsic soil properties such as pH, salinity and texture may influence decomposition by affecting microbial activity or by stabilizing substrates (Jenkinson, 1977a,b), often in multiple direct and indirect ways. For example, some research suggests that clay mineralogy and quantity regulate decay (Saggar *et al*., 1996) both directly, by absorbing and thereby shielding carbonaceous intermediates from decomposition (Oades, 1988; Hassink, 1997; Krull *et al*., 2003; Dungait *et al*., 2012; Lützow *et al*., 2006), and also indirectly, by controlling soil water content through structural effects (Thomsen *et al*., 1999).

Land management practices such as tillage also influence the rate of plant litter decomposition. Kinetic analysis of decomposition has shown that litter managed under ploughed systems sometimes decomposes faster than under no-tillage (Beyaert & Voroney, 2011). Ploughing mixes litter into soil, allowing better microbial access, and dampening extreme, fluctuating temperature and moisture conditions that occur on the surface (Burgess *et al*., 2002). Climatic conditions such as temperature and precipitation regulate decomposition by governing the size, activity and composition of microbial communities that mediate decomposition (Parr & Papendick, 1978; Jenkinson, 1981; Sanderman & Amundson, 2014).

Given this multitude of factors and the complexity of their interactions, litter decomposition is often highly variable among sites and can be adequately studied only by taking into account conditions in local ecosystems (Beyaert & Voroney, 2011; Cunningham *et al*., 2013). The relative importance of the environmental and edaphic factors regulating decomposition *in situ* is still unclear, in part because of the paucity of data from a wide range of sites, spanning many of the aforementioned variables. Even small variations in local environmental conditions and soil properties, and their complex interactions, will affect the short- and long-term dynamics of decomposition.

In this study, we explore the effects of soil properties and environmental conditions on litter decomposition. To evaluate the importance of these variables at a broadscale, we measured decomposition at ten sites chosen to represent a cross section of Canadian agricultural zones, spanning a transcontinental range of climate and soil properties (Fig. 1). Our experiment was designed to mimic, as much as possible, natural decomposition processes *in situ* and was established in cropped fields to include the effects of growing plants. Using ^{13}C-labelled litter and applying it to diverse soils across a wide range of climatic environments, our objective was to evaluate long-term litter decomposition as influenced by soil and environmental conditions.

Materials and methods

Production of ^{13}C-labelled litter

Barley (*Hordeum vulgare* cv. AC Metcalfe) was planted in coarse-textured soil in 10 cm diameter × 30 cm cylindrical pots and grown to maturity in a greenhouse equipped with supplemental lighting. After germination, plants were thinned to three per pot, and medical-grade silicone was applied at their base to allow sealing of soil from atmosphere during exposure to $^{13}CO_2$. Twice weekly, a cohort of plants was enclosed for six hours in a sealed temperature-controlled acrylic chamber (2.1 m long × 1.1 m width × 1.4 m tall) and exposed to $^{13}CO_2$ at 60 atom% (Fig. 2a). During the labelling events, a fixed pulse of $^{13}CO_2$, from pressurized cylinders, was delivered whenever atmospheric CO_2 concentration in the chamber fell below a threshold (~350 ppmv). In this way, the number of pulses (and cumulative $^{13}CO_2$ administered) per labelling session was directly proportional to the rate of photosynthesis, ensuring uniform labelling of tissues. The number of pulses ranged from one to 20 per 6-h labelling period, depending on photosynthetic rate, and each of three cohorts of plants was exposed to 21 or 22 labelling sessions, from shortly after germination until shortly before harvest (total number of pulses per cohort = 162–168). At maturity, the plants were subdivided into five components: seeds, chaff, stems, leaves and roots. The litter (plant parts excluding seed) was cut into < 1.5 cm lengths, and aliquots were prepared by

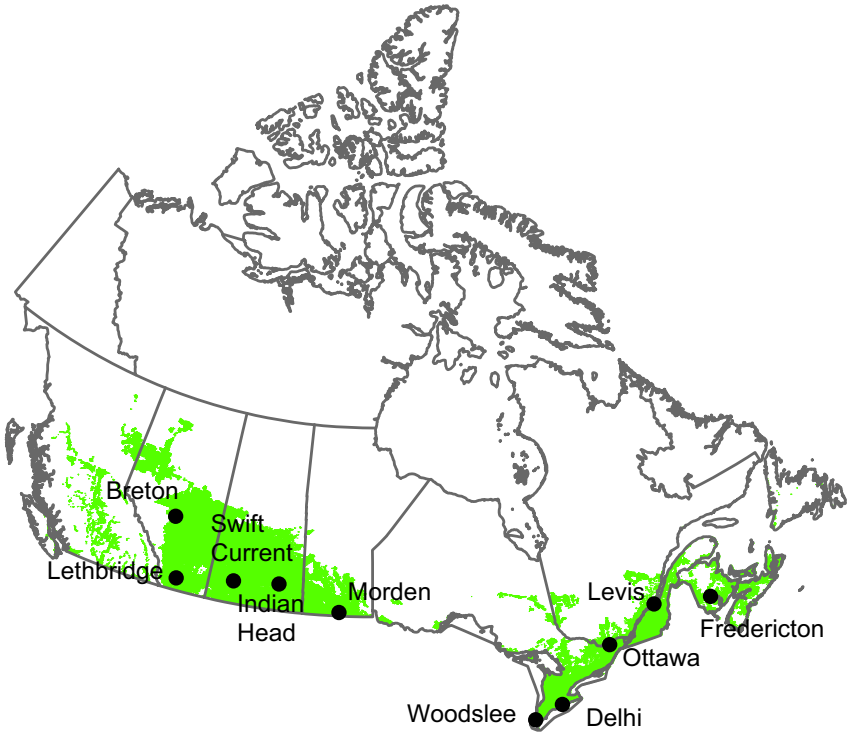

Fig. 1 Location of the 10 experimental litter decomposition study sites within the agricultural areas (shaded in green) in Canada.

weighing proportionate amounts of each component into envelopes (total weight: 3.6 g dry matter). Representative subsamples of these litter cohorts were analysed for ^{13}C abundance (10.38 atom%) and carbon concentration (405 mg C g^{-1}).

Application of labelled plant litter

Ten experimental sites were selected across southern Canada to span the climate typical of Canadian arable lands (Table S1) and encompass diverse soil properties (Tables 1 and S2). In the fall of 2007, labelled barley litter was applied to microcosms at a rate equivalent to 2 Mg C ha^{-1} (200 g C m^{-2}; 3.6 g air-dry matter per microcosm). The litter consisted of stems, leaves and roots mixed in proportion to relative harvest weights. Open-ended microcosms (PVC pipe, 15 cm long, 10 cm diameter), four replicates for each sampling time, were inserted 10 cm into the soil. This depth confined the applied litter, but allowed access from below by roots of adjacent rows of crop plants (Fig. 2b). The litter was mixed into the soil by inserting the microcosm, removing the soil to a depth of 9 cm and mixing the soil and litter in a plastic bag. The soil/labelled litter mixture was carefully returned to the microcosm and repacked to the original depth in the microcosm. After applying the litter, the microcosm was covered with fibreglass screen (1-mm mesh openings), secured by a PVC collar, to contain litter but allow air and water exchange. Every fall thereafter, to simulate litter input and tillage, a fresh quantity of unlabelled barley litter was similarly incorporated, at the same rate as the first pulse of labelled litter, into all remaining microcosms. Nitrogen fertilizer was added annually in spring to all microcosms (ammonium nitrate, 40 kg N ha^{-1}).

At each site, soil temperature loggers (Tinytag™, Gemini Data Loggers, Chichester, UK), programmed to record hourly temperature, were placed inside a microcosm with the sensor at a depth of 5 cm. All sites were located near a weather station that provided daily precipitation data for modelling soil water content.

Soil moisture modelling

We used the Versatile Soil Moisture Budget (VSMB) model (Baier *et al.*, 1979; Akinremi *et al.*, 1996) to simulate soil moisture at experimental sites and assess its influence on litter decay. In this model, the soil profile was divided into six layers, with each layer characterized by a saturation, field capacity and permanent wilting point. In the modified VSMB (Akinremi *et al.*, 1996), water from precipitation cascaded from upper to lower layers when the upper ones reached field capacity; vertical redistribution of soil water was simulated using an algorithm adapted from the CERES-Wheat model (Ritchie & Otter, 1985). The rate of water uptake was simulated using depth-dependent crop coefficients (Baier *et al.*, 1979) that changed with crop growth stage. The soil moisture budget was adjusted for surface run-off (Akinremi *et al.*, 1996) and snowfall (Baier *et al.*, 1979). Planting dates of wheat or barley were estimated according to procedures of Bootsma and De Jong (Bootsma & De Jong, 1988); crop growth was defined by a biometeorological time scale model (*49*); and

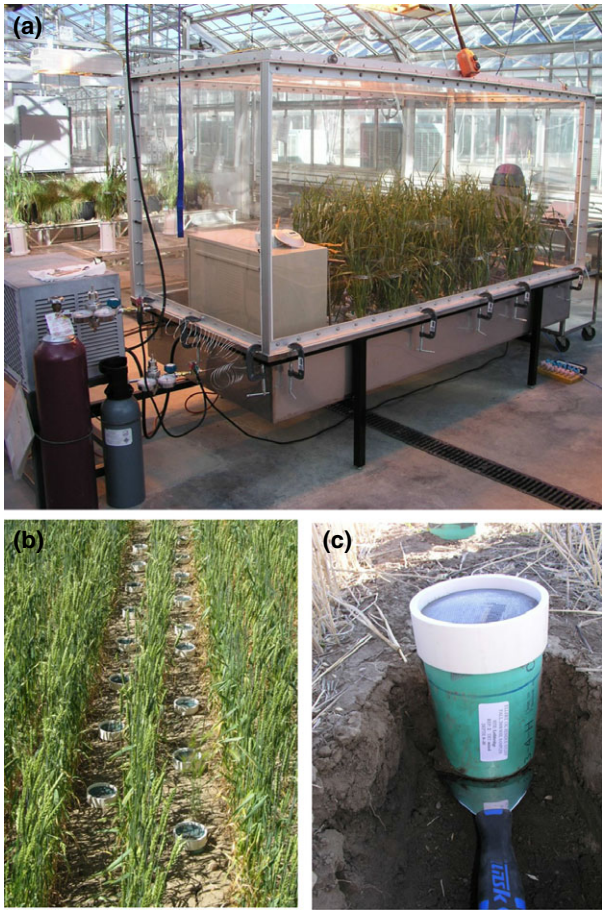

Fig. 2 Digital images of (a) the acrylic chamber used to enclose barley plants for labelling with 60 atom% $^{13}CO_2$, (b) location of microcosms within a cropped environment and (c) collection of intact microcosm.

harvest dates were assumed to occur one week after ripening. Soil moisture was simulated for a continuous 7-year period, beginning with an assumed soil water content of 75% of the maximum on 15 April 2006. Modelled daily soil water content in the top 15-cm layer at the Ottawa site was evaluated with soil water content measured on site inside the microcosms (0–10 cm). Results from a paired *t*-test indicated that the modelled soil water content was not significantly different from those measured.

Collection and analysis of soil

Four replicate microcosms of each litter treatment were collected at time zero in fall of 2007, spring of 2008 (approximately 6 months after application of labelled litter), and fall of 2009, 2010, and 2012 (Fig. 2c). The microcosms were collected intact and kept cool until processed in the laboratory. Soil below the microcosms (10–20 and 20–25 cm depths) was also collected using a hand corer (7 cm diameter) and analysed for organic C and ^{13}C abundance to measure possible C leaching (Table S3).

For consistency, all samples were processed and analysed in the same laboratory. There, the soil was removed from the cylinder, placed in a drying tray, weighed, subsampled to estimate field soil water content and bulk density and air-dried. Soils were then crushed to pass a 2-mm sieve, and subsamples were finely ground (<0.25 mm) for elemental and isotopic analysis. Total N and C concentrations in finely ground soil were determined by automated flash combustion-gas chromatography using a NC-2100 analyzer (CE Instruments, Milan, Italy). Soil organic C and ^{13}C enrichment were determined using a similar analyser interfaced to an isotope ratio mass spectrometer (IRMS model: Optima; Micromass, Manchester, UK), after pre-acidification to remove carbonates (Ellert & Rock, 2008). The presence of large ^{13}C-enriched litter fragments within samples at time zero posed a challenge for obtaining representative subsamples, as evident in high variability in ^{13}C abundance among subsamples from the same microcosm. This high initial heterogeneity was minimized by manually removing and separately analysing visible litter samples, and by collecting multiple relatively large subsamples (~60 g) of soil for analysis, and grinding them in successive stages to obtain representative subsamples. Over time, with diminution and redecay of labelled litter, the variability declined.

Calculations and statistical analysis

Recovery of litter-derived C in the microcosm (0–10 cm depth) was calculated as follows:

$$R = \frac{\text{molC}_{\text{soil}}(^{13}\text{Cat\%}_{\text{soil}} - ^{13}\text{Cat\%}_{\text{na}})}{\text{molC}_{\text{res}}(^{13}\text{Cat\%}_{\text{res}} - ^{13}\text{Cat\%}_{\text{na}})}$$

where: R = recovery (molar fraction)

$\text{molC}_{\text{soil}}$ = moles of soil C (moles microcosm^{-1})
= mol C g^{-1} C * g C g^{-1} soil * g soil microcosm^{-1} in 0–10 cm layer

molC_{res} = moles of litter-derived C added (moles microcosm^{-1})
= mol C g^{-1} C * g C g^{-1} litter * g litter added microcosm^{-1}

$^{13}\text{Cat\%}_{\text{soil}}$ = ^{13}C abundance of C in soil (atom%) with enriched litter

$^{13}\text{Cat\%}_{\text{res}}$ = ^{13}C abundance of C in enriched litter (atom%)

$^{13}\text{Cat\%}_{\text{na}}$ = natural ^{13}C abundance of C in soil (atom%).

Atomic mass of carbon (inverse of mol C g^{-1} C) was adjusted for varying enrichment with ^{13}C. (For example, if ^{13}C abundance = 10.38 atom%, then mean atomic mass = 12 (1−0.1038) + 13.0034(0.1038) =12.104 atom%). In cases where litter had been manually extracted, recovery in these litter samples was calculated in the same way and added to the recovery in the mineral soil alone.

Temporal patterns of decay were described using nonlinear regression (SAS Institute, Cary, NC, USA), to fit the following general equation (Jenkinson, 1977a,b, 1990):

$$R = ae^{-ct} + be^{-\text{dt}}$$

where a = fraction of original C in a 'fast' pool, with decay coefficient of c

b = fraction of original C in a 'slow' pool, with decay coefficient of d

Table 1 Soil classification, texture, organic carbon concentration and pH at the 10 experimental sites

Site	Soil classification (WRB)	Sand (%)	Clay (%)	Organic C (%)	pH	Mean annual air temperature (°C)	Mean annual precipitation (mm)
Fredericton, NB	Humic Podzol	53	9	1.70	6.2	6.6	1157
Levis, QC	Mollic, Umbric, Calcic Gleysol	60	15	2.23	5.0	5.6	1231
Ottawa, ON	Cambisol, Eutric Cambisol	67	12	1.79	6.2	7.4	926
Delhi, ON	Albic Luvisol, Haplic Luvisol	85	6	0.84	6.5	8.9	970
Woodslee, ON	Mollic, Umbric, Calcic Gleysol	41	27	2.88	7.1	10.0	875
Morden, MB	Chernozem	32	36	2.86	6.3	4.1	533
Indian Head, SK	Chernozem	10	48	2.06	7.8	2.5	431
Swift Current, SK	Kastanozem (Aridic)	33	29	1.17	6.0	4.2	397
Lethbridge, AB	Kastanozem (Haplic)	53	23	1.52	7.7	6.5	467
Breton, AB	Albic Luvisol, Gleyed Luvisol	36	22	1.66	5.8	3.5	506

t = time.

By definition, $a+b = 1$, so that:

$$R = ae^{-ct} + (1-a)e^{-\mathrm{dt}}.$$

Calculation of thermal time

The concept of thermal time has been used as a way of adjusting time to account for temperature effects on the rate of biological processes (Smith *et al.*, 1998; Trudgill *et al.*, 2005; Yousefi *et al.*, 2014). We calculated thermal time based on accumulated degree-days (base temperature 0 °C) from the date of initial ^{13}C-labelled litter application, using either *in situ* soil temperatures or air temperature from nearby meteorological stations. Accumulated degree-days were converted to degree-years (1 degree-year = 365.25 degree-days), from which we calculated thermal years (1 thermal year = 10 degree-years), based on the average degree-year per calendar year ratio observed across all our sites. That is, on average, a calendar year accumulated about 10 degree-years. In effect, this approach – plotting recovery against thermal years – adjusts the duration of a calendar year, based on temperature: for cooler sites (e.g. Breton), a year of thermal time is less than a calendar year; for warmer sites (e.g. Delhi), a year of thermal time is greater than a calendar year.

Modelling litter decomposition under different climate change scenarios

To illustrate the implications of our findings, we used the two-pool equation describing ^{13}C recovery as a function of thermal time to consider possible effects of climate change on litter decomposition for a 30-year period: 2041–2070 (Table 2). Five experimental sites were selected, representing the range of temperature and soil textures, and two future climate scenarios were applied to these sites. The climate change scenario was based on the most recent Canadian Regional Climate Model of the Canadian Centre for Climate Modelling and Analysis (CCCma). The model was driven by the CCCma second Earth System Model, for projections under two representative concentration pathways, 4.5 and 8.5 W m^{-2} (van Vuuren *et al.*, 2011). Temperature data for grid cells relevant to our study sites were corrected for bias (Qian *et al.*, 2015) before input to our kinetic model.

Table 2 Predicted number of days for decay of 50%, 80% and 90% of litter at five of the experimental sites under baseline climate and projected changes under two future climates based on the Canadian Region Climate Model 4 (CanRCM4)

Site	Baseline (1971–2000)	RCP4.5* (2041–2070)	RCP8.5
50% decayed			
Fredericton	283	−31†	−41
Woodslee	239	−86	−117
Ottawa	271	−31	−41
Swift Current	290	−25	−33
Lethbridge	274	−31	−42
80% decayed			
Fredericton	1355	−296	−328
Woodslee	1030	−258	−284
Ottawa	1118	−121	−180
Swift Current	1412	−331	−355
Lethbridge	1332	−291	−320
90% decayed			
Fredericton	2294	−465	−534
Woodslee	1782	−338	−379
Ottawa	2124	−379	−536
Swift Current	2494	−550	−655
Lethbridge	2348	−444	−502

*Representative concentration pathway in W m^{-2}.

†Negative values indicate the reduction in the number of days projected from the baseline climate.

To assess the consistency of our projections, we also included a set of climate scenarios from the North American Regional Climate Change Assessment Program (NARCCAP (Mearns *et al.*, 2012; http://www.narccap.ucar.edu/data/model-info.html) for the period 2041–2070 under the GHG

emission scenario IPCC SRES A2 (Nakićenović *et al.*, 2000). We used three NARCCAP scenarios:

- CRCM (Caya & Laprise, 1999), a Canadian RCM driven by the third-generation Canadian global climate model (CGCM3) (Kim *et al.*, 2002, 2003);
- HRM3 (Gordon *et al.*, 2000), the third-generation RCM of the Hadley Centre, UK Met Office, driven by its third-generation global climate model (HadCM3); and
- WRFP (Michalakes *et al.*, 2004), the Weather Research & Forecasting model of the US Pacific Northwest National Lab driven by the Community Climate System Model (CCSM3) (Collins *et al.*, 2006).

All projections (Table S4) were based on 30-year mean values (baseline or projected for 2041–2070) with a starting date of September 1.

Results

The climate across the 10 experimental sites was highly variable, reflecting conditions typical for Canadian arable lands, with mean annual temperature ranging between 2 and 10 °C. Mean annual precipitation varied threefold across sites and was lower in western Canada (397–533 mm for five sites) than in eastern Canada (857–1231 mm for five sites) (Table 1). The experimental sites encompassed diverse soil types, including Podzols, Gleysols, Luvisols, Chernozems and Kastanozems (Table 1). Soil properties were also highly variable across the experimental sites; sand content varied between 10% and 85% and pH was between 5.0 and 7.8.

Recovery of ^{13}C at all sites followed a similar temporal pattern: a rapid initial rate of loss, slowing progressively with time. About 20–40% of litter-derived C was lost within about 0.5 years, over the winter period. Within one year, 50–70% of litter-derived C applied was lost and after five years only about 10–20% of the added C remained (Fig. 3). Almost all of the losses could be ascribed to decomposition because only traces of ^{13}C enrichment were detected in the soil below the microcosms at all sites (Table S3). Thus, while leaching was sometimes discernible, estimated losses by this route were a minuscule fraction of the amount applied.

A two-pool exponential decay model described the decomposition of litter over time reasonably well. This model, however, had several consistent discrepancies from measured values (Fig. 3): it overestimated early overwinter decay (measured litter-derived C recovery at 0.5 years was on average about 70%, whereas the predicted recovery at that time was 62%) and underestimated decomposition after 1 year (average litter-derived C recovery measured was 38%, and predicted recovery was 46%). The model also did not account for clear differences among sites for most sampling times.

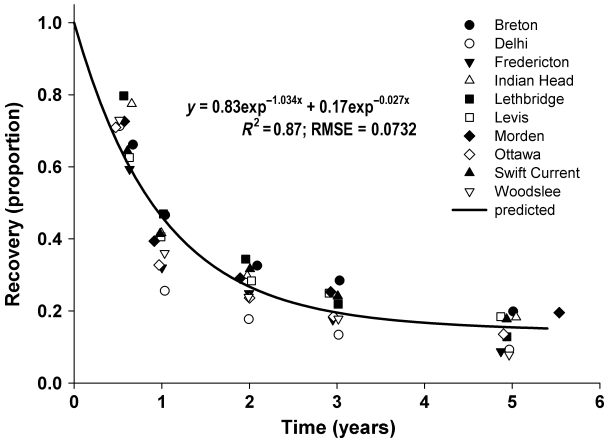

Fig. 3 Recovery of litter-derived ^{13}C over five years at ten sites across Canada. Each plotted value is the mean recovery in the 0–10 cm layer of four replicate microcosms, destructively sampled.

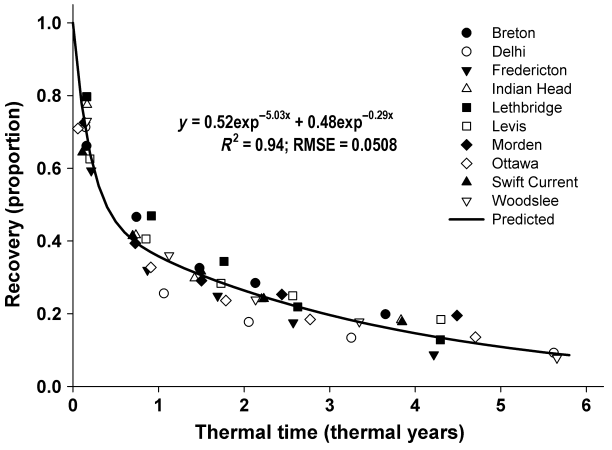

Fig. 4 Recovery of litter-derived ^{13}C over five years of thermal time at ten sites across Canada. Thermal time adjusts for varying temperature, based on calculation of cumulative degree-days above 0 degrees C: thermal years = cumulative degree-days/3652.5 (see Materials and methods).

For example, the model consistently underestimated loss at Delhi, a relatively warm site, and overestimated loss at Breton, a relatively cool site (Fig. 3).

To test whether these departures might reflect differences in temperature among sites, we plotted recovery against thermal time (Trudgill *et al.*, 2005; Yousefi *et al.*, 2014), calculated from the cumulative degree-days (daily soil temperature >0 °C; see Materials and methods). In effect, this adjusts time elapsed for differences in temperature: a day at warm temperatures is biologically 'longer' than a day at cool temperature. This approach resulted in an improved relationship (Fig. 4; R^2 = 0.94; RMSE = 0.0508) that diminished the discrepancies of the absolute-time model. Prediction of

recovery after about 0.5 year was improved because thermal time adjusted for slower decomposition over the winter period and differences among sites were mostly eliminated (Fig. 4).

Daily soil temperature data may not always be available, so we evaluated whether air temperature could be used in its place. Thermal time calculated from air temperature, assuming the same partitioning of litter derived earlier (Fig. 4), resulted in the following equation:

$$y = 0.52e^{-4.89x} + 0.48e^{-0.31x} (R^2 = 0.95; \mathrm{RMSE} = 0.0470),$$

where y = proportion of litter-derived C remaining, x = thermal years.

Thus, air temperature, which is commonly available, is as effective as soil temperature in describing decomposition accurately.

To consider possible effects of moisture on decomposition, we simulated soil moisture at all sites for the experimental period using the Versatile Soil Moisture Budget model (Baier *et al*., 1979; Akinremi *et al*., 1996). We applied a generalized soil moisture effect on decomposition (Bonan, 2008) derived from a terrestrial ecosystem model (Raich *et al*., 1991; McGuire *et al*., 1992) to modify the thermal time calculated from soil temperature. Including this simulated soil moisture in a modified expression of thermal time did not improve the relationship describing decomposition (R^2 = 0.92; RMSE = 0.0561), even though precipitation varied more than threefold across sites.

We conducted further analysis to see whether other soil variables could account for any remaining differences in decomposition among sites. The two-pool model was fitted individually for each of the sites and used to predict recovery after four thermal years; this, in effect, normalizes decomposition for temperature. When these predicted values were regressed against various soil properties (organic C, sand, clay, cation exchange capacity, pH and mean annual precipitation), only the relationship with clay content was significant, and then only weakly (P = 0.10; Fig. S1). This implies that decay was slowed only slightly by increasing clay content, presumably by stabilizing reactions (Voroney *et al*., 1989; Saggar *et al*., 1996).

Discussion

Some researchers have argued that current models of decomposition are constrained by the lack of field data (Burke *et al*., 2003), and others have suggested that laboratory incubations may not accurately reflect decomposition occurring under field conditions (Beyaert & Voroney, 2011). In laboratory studies, soils are usually incubated at optimum, unvarying temperature and water conditions, whereas in the field, these are rarely both at optimum levels and fluctuate wildly, with important impacts on the rate and extent of decomposition (Parr & Papendick, 1978). Furthermore, laboratory studies also exclude the strong effect of growing crops on decomposition (Fuhr & Sauerbeck, 1968; Jenkinson, 1977a,b). Our field studies, conducted at many sites for long time periods, allowed measurement of residue decay under the diverse and fluctuating conditions observed in the field, as opposed to the controlled conditions of laboratory incubations. In agreement with other studies, a two-pool exponential model described the decomposition of litter over time reasonably well (Jenkinson, 1977a,b, 1990; Aita *et al*., 1997; Beyaert & Voroney, 2011). This model implies carbon pools of varying turnover time, partly from innate biochemical differences in litter applied (Voroney *et al*., 1989), but probably largely reflecting microbial effects: as the litter decays through successive stages of microbial activity, the lingering products become progressively more resistant to further breakdown (Cotrufo *et al*., 2013; Kögel-Knabner & Amelung, 2014; Sanderman & Amundson, 2014). But there were consistent discrepancies between modelled and measured values; these were mostly related to temperature because plotting recovery against thermal time resulted in an improved relationship that diminished the discrepancies of the absolute-time model. Thus, one equation, adjusting time for soil temperature differences, effectively described litter decomposition over five years at ten diverse sites across Canada.

Across all 10 experimental sites, there were variations of up to ninefold in soil texture, tenfold in CEC and 3 pH units, but these had little discernible effect on litter decomposition. Including soil moisture in a modified expression of thermal time did not improve the relationship describing decomposition. From this, we infer that although soil moisture may affect short-term decomposition rates, temperature evidently overwhelms these effects in the long run, perhaps through bursts of decay previously delayed by dry conditions.

Our intention in this study was to evaluate, in a simple but robust way, the effects of soil properties and environmental conditions on litter decomposition at a broadscale. Various composite climatic indices (e.g. actual evapotranspiration, potential evapotranspiration) have been proposed to assess the impact of environmental conditions on decomposition (Burke *et al*., 2003; Adair *et al*., 2008). These generally performed adequately, but most are composite indices with temperature as the main driver. Our approach in determining which factors play a key role in decomposition was to reduce complexity as much as possible and use the simplest model that accurately describes litter decay.

Our study demonstrates an overriding predominance of temperature in governing the rate of residue decay, superseding that of extreme differences in soil properties and moisture in temperate climates across southern Canada. This finding has several widely useful implications. Firstly, it offers a robust, consistent way of comparing decay rates across diverse sites and climates, even among time periods within the same site. For example, the thermal time approach provides a way of comparing decay measured in seasons or years differing in climate. Secondly, the use of thermal time may advance the development of simplified soil C models, by consolidating the influences of many soil and climatic variables, some of which are not easily measured, into a single cumulative parameter based on readily available soil or air temperature data. Thirdly, the thermal time approach provides quantitative insight into consequences of projected climate warming. To illustrate, we used our kinetic model to simulate decomposition under climate scenarios (2041–2070) for five of the experimental sites that span the range of climate across all locations. Using the two-pool model based on thermal time calculated from air temperature, we predicted the number of days required for decay of 50%, 80% and 90% of litter under baseline and projected climates at these sites. Based on our calibrated kinetic model, 1417 degree-days (DD) are required for 50% (i.e. mostly the labile fraction) of applied litter to decay, 10100 DD are required for 80% to decompose, and 18175 DD are required for 90% (including recalcitrant fractions) to decompose. The time required to reach these amounts at each site depends on the temperature regime in the region. Under baseline climate (30-year mean), the predicted time required for 50% of litter to decay was, on average, 239 days at Woodslee (a relatively warmer site) versus 290 days at Swift Current (a relatively cooler site) (Table 2). Under the projected future climate for 2041–2070 (30-year mean), the predicted time to reach 50% decomposition would be shortened by almost four months at Woodslee and by less than one month at Swift Current (Table 2). The time required to reach 90% decay would be reduced by about one year at Woodslee and by about two years at Swift Current. These projections, although approximate, have clear repercussions for storing additional soil carbon, derived from decomposing plant litter inputs, as a way of preserving productivity and removing atmospheric CO_2 (Davidson & Janssens, 2006; Kirschbaum, 2006; Conant *et al*., 2011; Dungait *et al*., 2012).

Decomposition of plant litter, the source of energy for soil biota and recycled nutrients for succeeding plants, is a process fundamentally tied to the functioning of ecosystems. It is important especially in agricultural systems, where litter inputs are usually reduced by harvest and export of plant biomass. The fate of remaining litter is therefore critical for future productivity and soil health. We have shown here, in an extensive, long-term network using ^{13}C-labelled litter that decomposition can be accurately and succinctly described using a simple concept – thermal time. Projections using the kinetic model derived from this approach confirmed the sensitivity of litter decomposition to temperature, demonstrating how warming temperatures would accelerate decay, thereby further enhancing CO_2 release and exacerbating climate change.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Mean annual climate data for the 10 sites over the experimental period, 2007–2012.
Table S2. Soil properties at the ten experimental sites.
Table S3. Atom $\%^{13}C$ of soil in the 0–10, 10–20 cm layers of soil at the time of last sampling during the experimental period (2012).
Table S4. Predicted number of days for decay of 50%, 80%, and 90% of litter at five of the experimental sites under baseline climate and projected changes under three future climates for the IPCC SRES A2 scenario (Nakićenović *et al*., 2000) from the North American Regional Climate Change Assessment Program.
Figure S1. Relationship between soil clay content and the predicted recovery of litter-derived ^{13}C after four thermal years for ten sites across Canada.