



## The detrital input and removal treatment (DIRT) network: Insights into soil carbon stabilization



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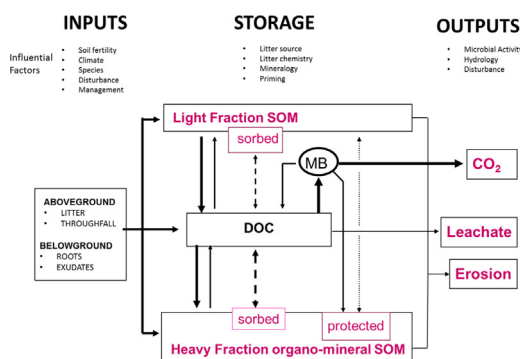
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### HIGHLIGHTS

- The DIRT Project assess how rates and sources of plant litter inputs influence stabilization of soil organic matter.
- SOM pools decreased in response to exclusion of aboveground litter, but responded only slightly to doubling of litter.
- There was limited evidence that belowground litter contributed more to stable SOM pools than aboveground litter.
- Partitioning of belowground contributions to soil respiration were predictable based on soil C and N.
- Soil fertility was negatively related to % root respiration but positively related to % aboveground litter respiration.

### GRAPHICAL ABSTRACT



### ARTICLE INFO

#### Article history:

Received 26 May 2017

Received in revised form 30 May 2018

Accepted 31 May 2018

Available online xxxx

#### Keywords:

Soil organic matter  
SOM  
Soil carbon  
Litter  
DIRT  
Respiration

### ABSTRACT

Ecological research networks functioning across climatic and edaphic gradients are critical for improving predictive understanding of biogeochemical cycles at local through global scales. One international network, the Detrital Input and Removal Treatment (DIRT) Project, was established to assess how rates and sources of plant litter inputs influence accumulations or losses of organic matter in forest soils. DIRT employs chronic additions and exclusions of aboveground litter inputs and exclusion of root ingrowth to permanent plots at eight forested and two shrub/grass sites to investigate how soil organic matter (SOM) dynamics are influenced by plant detrital inputs across ecosystem and soil types.

Across the DIRT network described here, SOM pools responded only slightly, or not at all, to chronic doubling of aboveground litter inputs. Explanations for the slow or even negative response of SOM to litter additions include increased decomposition of new inputs and priming of old SOM. Evidence of priming includes increased soil respiration in litter addition plots, decreased dissolved organic carbon (DOC) output from increased microbial activity, and biochemical markers in soil indicating enhanced SOM degradation. SOM pools decreased in response to

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Priming  
Density fractionation  
Detritus

chronic exclusion of aboveground litter, which had a greater effect on soil C than did excluding roots, providing evidence that root-derived C is not more critical than aboveground litter C to soil C sequestration. Partitioning of belowground contributions to total soil respiration were predictable based on site-level soil C and N as estimates of site fertility; contributions to soil respiration from root respiration were negatively related to soil fertility and inversely, contributions from decomposing aboveground litter in soil were positively related to site fertility. The commonality of approaches and manipulations across the DIRT network has provided greater insights into soil C cycling than could have been revealed at a single site.

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## 1. Introduction

Globally, soils contain more than three times more carbon than the atmosphere, and four and a half times more carbon than the world's biota (Lal, 2004). Despite their importance, however, soil carbon stocks have been reduced through land use change and unsustainable forest management practices (Lal, 2004; Vagen et al., 2005). It has been proposed that management efforts to increase forest productivity can result in increased C storage within living forest biomass and thereby slow the rate of atmospheric CO<sub>2</sub> increase (Pan et al., 2011; Post et al., 2012). Forest fertilization studies have shown that forest growth, and hence biomass carbon pools, can be increased as a result of active management (e.g. Chen et al., 2011a; Harrington et al., 2001). Elevated plant inputs to soils associated with higher primary productivity should lead to increased C inputs to soils, which could, in turn, lead to increased C storage in SOM. As such, forest managers are increasingly pressed to manage existing forests in ways that will increase soil carbon storage (Lal, 2005; Post et al., 2012). However, the extent to which forests can be manipulated to enhance C sequestration in soil remains unclear (Jandl et al., 2007; Schöning et al., 2013). Sources of carbon that may potentially be sequestered in soils, and long-term controls of carbon stability in soils are poorly understood (Marín-Spiotta et al., 2014; Schmidt et al., 2011; von Lützow et al., 2006, 2008).

Many factors affect SOM carbon accumulation and stabilization, including mineralogy and soil aggregation (Rasmussen et al., 2005; Torn et al., 1997; Spielvogel et al., 2008), land use and forest harvest (Yanai et al., 2003; Nave et al., 2010; Paul et al., 2003; Grandy and Robertson, 2007), and climate (Craine et al., 2010; Fissore et al., 2008; Giardina et al., 2014). Although forest type and vegetation strongly influence biomass carbon balance, the direct role of plant litter inputs on SOM C status is less well known and is neither linearly nor directly linked to rates of input. Due to climate change, net primary productivity (NPP) and thus litterfall are predicted to change in many ecosystems (Melillo et al., 1993; King et al., 1997; Raich et al., 2006), but it is not clear whether parallel changes in SOM stores will accompany changes in NPP. Models of ecosystem C balance generally assume a strong relationship among NPP, litter inputs, and soil C accumulation (Liski et al., 2002; Gottschalk et al., 2012), but there is little direct experimental evidence for these relationships. Net accumulation needs to consider the balance between aboveground (litterfall, throughfall) and belowground (root turnover, exudation of organic compounds from roots) plant detrital inputs and outputs (soil respiration, aqueous loss during leaching, physical loss via erosion).

Numerous factors contribute to non-linear relationships between litter inputs and soil C sequestration. Soils have finite capacities to sequester C and eventually become saturated (Chung et al., 2008; Stewart et al., 2009; Six et al., 2002; Mayzelle et al., 2014), effectively decoupling litter inputs and C accumulation rates; saturation levels might be more dependent on climate and soil mineralogy than on the biochemical composition and quantity of C inputs. Furthermore, additions of simple and complex organic detrital substrates to soil can increase turnover rates of native SOM, a process known as the 'priming effect' (Kuzyakov et al., 2000). Enhanced microbial respiration in response to additional plant litter inputs or increased rhizodeposition could lead to destabilization of stored SOM, paradoxically decreasing soil C sequestration.

Litter quality has often been suggested as a driver of potential accumulation rates of SOM (e.g. Berg and Meentemeyer, 2002). Litter constituents are structurally and functionally variable, ranging from soluble low molecular weight organic compounds that decompose rapidly (e.g. sugars), to complex organic compounds (structural and defensive compounds) that are relatively resistant to microbial processing (Berg and McLaugherty, 2007). Hence, litter is often described by its biochemical decomposability, and is thus quantified by a set or sets of properties meant to characterize the ease by which carbon and nitrogen within SOM can be mineralized (Bosatta and Ågren, 1999; Rovira et al., 2008; Aber et al., 1990; Talbot et al., 2012). However, such indices speak more to the decomposability of litter, and less to the dynamics and retention of C within SOM— the end product of litter and root tissue decomposition. Increasingly it is recognized that chemical interactions between SOM and mineral soil particles play perhaps the most significant role in C retention; clay surfaces and aluminum and iron oxides stabilize organic matter, and physical protection within soil aggregates decreases accessibility to microbes (Sollins et al., 1996; von Lützow et al., 2006; Marschner et al., 2008; Schmidt et al., 2011). However, in response to altered environmental conditions, SOM quality can change even if total SOM content does not (Feng et al., 2008; Feng et al., 2010; Simpson and Simpson, 2012).

The Detrital Input and Removal Treatment (DIRT) Project assesses the role of plant detritus input amounts and quality on the accumulation and dynamics of organic matter in forest soils. DIRT uses an experimental approach of chronically adding aboveground litter, excluding litter, and preventing root ingrowth to long-term experimental plots to assess the importance of plant detrital sources and loading rates on SOM formation and accumulation or loss. The prototype for the DIRT network was established in 1956 by Francis Hole in the University of Wisconsin Arboretum in two forest and two prairie sites (here referred to as WISC), where the manipulations included doubling and removal of aboveground litter inputs annually (Nielsen and Hole, 1963; Nadelhoffer and Fry, 1988; Lajtha et al., 2014b) (Fig. 1). The current DIRT network protocol includes doubled aboveground litter inputs (Double Litter), Double Wood, root exclusion by trenching (No Root), No (aboveground) Litter via screening, and complete litter and root exclusion (No Inputs) (Table 1). The Harvard Forest, MA, site (HF) was established in 1990 in a transition/mixed hardwood-forest dominated by Northern red oak (*Quercus borealis* Michx. F.), red maple (*Acer rubrum* L.), and paper birch (*Betula papyrifera* Marsh.). The Bousson Experimental Forest, PA, site (BEF) was established in 1991 in a mixed deciduous stand dominated by black cherry (*Prunus serotina* Ehrh.) and sugar maple (*Acer saccharum* Marshall), with American beech (*Fagus grandifolia* Ehrh.) and red oak (*Quercus rubra* L.) constituting most of the remainder. The H.J. Andrews, OR, site (HJA) was established in 1997 in a mid-growth conifer forest dominated by western hemlock (*Tsuga heterophylla* (Rafinesque) Sargent) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). The Síkfökút forest site in Hungary (SIK) was established in 2000 in a dry oak forest (Fekete et al., 2014; Kotrocó et al., 2014), and a site in Germany (SK) was established in a beech/oak forest in 1999 (Klotzbücher et al., 2013). A DIRT site that was crossed with an N fertilization experiment was established at the University of Michigan Biological Station (UMBS) in 2004 in a dry deciduous forest that is dominated by bigtooth aspen

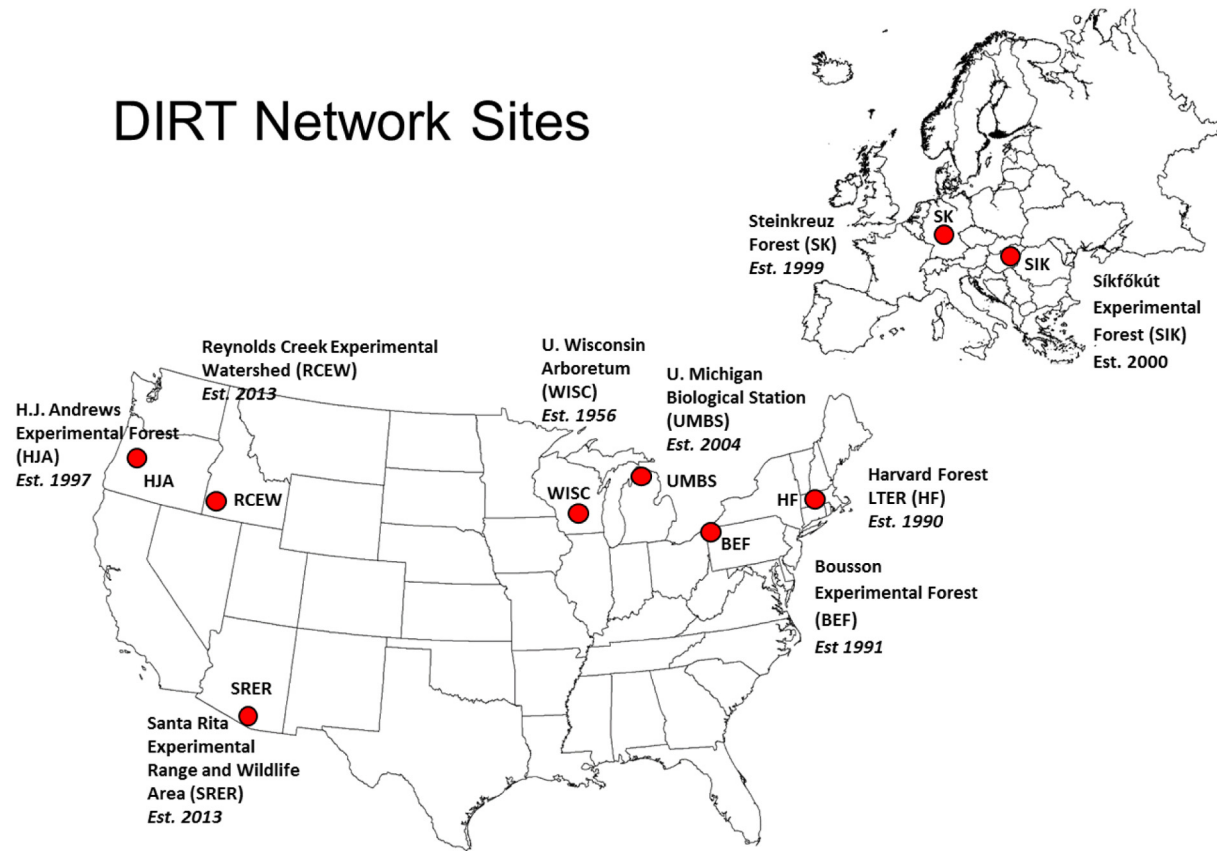


Fig. 1. Location of sites within the Detritus Input and Removal Treatments (DIRT) project.

(*Populus grandidentata* Michx.), and secondarily by red maple (*Acer rubrum* L.), red oak (*Quercus rubra* L.), paper birch (*Betula papyrifera* Marsh.), eastern white pine (*Pinus strobus* L.), sugar maple (*Acer saccharum* Marsh.), American beech (*Fagus grandifolia* Ehrh.), and trembling aspen (*Populus tremuloides* Michx.). More recently, DIRT sites were established in grassland/shrub systems in the Santa Rita Experimental Range and Wildlife Area, AZ (SRER) and in the Reynolds Creek Experimental Watershed, ID (RCEW), both in 2013.

Here we synthesize research in the international DIRT network and show how the DIRT network has contributed to understanding of the role of both above- and belowground plant inputs to soil carbon stabilization and destabilization, as well as the likelihood of increased productivity in mature forests contributing to enhanced soil C sequestration.

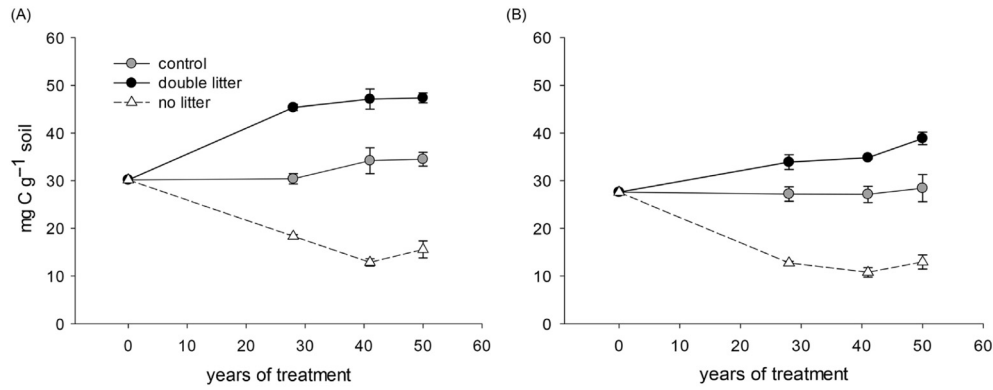
**Table 1**  
Description of litter treatments at the DIRT Plots.

Treatment	Description
Control	Natural above and belowground litter inputs are allowed. Coarse woody debris >1 cm dia is excluded. Seedlings and herbaceous material are removed.
Double Litter	Above ground leaf or needle inputs are doubled by adding litter removed annually and allocated proportionately from the No Litter plots.
Double Wood	Above ground wood inputs are increased by adding chipped wood in an amount such that total C additions are approximately equal to the Double Litter treatments. This treatment occurs only at Síkfokut and Andrews.
No Litter	Aboveground inputs are removed from plots during autumn senescence and periodically throughout the year.
No Roots	Roots are excluded with trenching that extends from the soil surface to 140 cm depth.
No Inputs	Aboveground inputs are excluded as in No Litter plots; belowground inputs are prevented as in No Roots plots.
OA-less	~Top 30 cm of soil (O and A Horizons) was replaced with mineral soil.

Responses of total soil C and density fractions to detrital manipulation: SOM resilience.

Soil carbon content is expected to change in response to detrital manipulation only gradually with time, thus our collections were timed at 5 and 10 year intervals, with major sampling efforts made at decadal anniversaries. Density fractionation (Sollins et al., 2009) to identify free particulate, labile vs. mineral-associated SOM pools has also been measured at decadal intervals.

Because most models of soil organic matter composition assume a direct relationship between litter inputs and soil C accumulation (Gottschalk et al., 2012), we initially predicted that treatments with litter additions (Double Litter and Double Wood) would show relatively rapid increases in surface soil C content and that treatments with litter removals (No Litter, No Roots, No Inputs) would show similar decreases in surface soil C content. Indeed, the trajectory of C concentration from the original DIRT site in Wisconsin clearly exhibited this pattern, although the first analyses of soils were not done until 28 years after the experiment began (Lajtha et al., 2014b; Fig. 2). However, analyses from the other forested DIRT sites that were sampled within the first 20 years showed little response to Doubled Litter inputs, and in fact showed remarkably similar trends of slight, but not significant decreases in both C concentration and total profile C content (Fig. 3). We were surprised that even after 20 years, density fractionation data also showed little to no increase in free light fraction material with litter additions (Lajtha et al., 2014a, 2014b; Klotzbücher et al., 2013). However, all sites showed significant decreases in surface soil C concentration with litter removals. In contrast to reports suggesting that root-derived C is preferentially stabilized over aboveground inputs (Rasse et al., 2005; Bird et al., 2008), aboveground litter exclusion had an effect on C levels similar to that of root exclusion, thus we did not see evidence that root-derived C is more critical to soil C



**Fig. 2.** Soil Organic Carbon (SOC) concentrations in the top 10 cm (A Horizon) for Noe Woods (A) and Wingra Woods (B) in the WISC Detrital Input and Removal Treatments plots in 1984, 1997 and 2006 (Lajtha et al., 2014b). Values are means  $\pm$  1 standard error ( $n = 4$ ). Significant differences in values among treatments within a site in 2006 (yr 50) are shown in Table 2. When SE bars are not shown it is because the SE was smaller than the symbol.

sequestration. Across sites, in fact, aboveground litter exclusion had a slightly greater negative effect, although not significantly so at any site, than root exclusion.

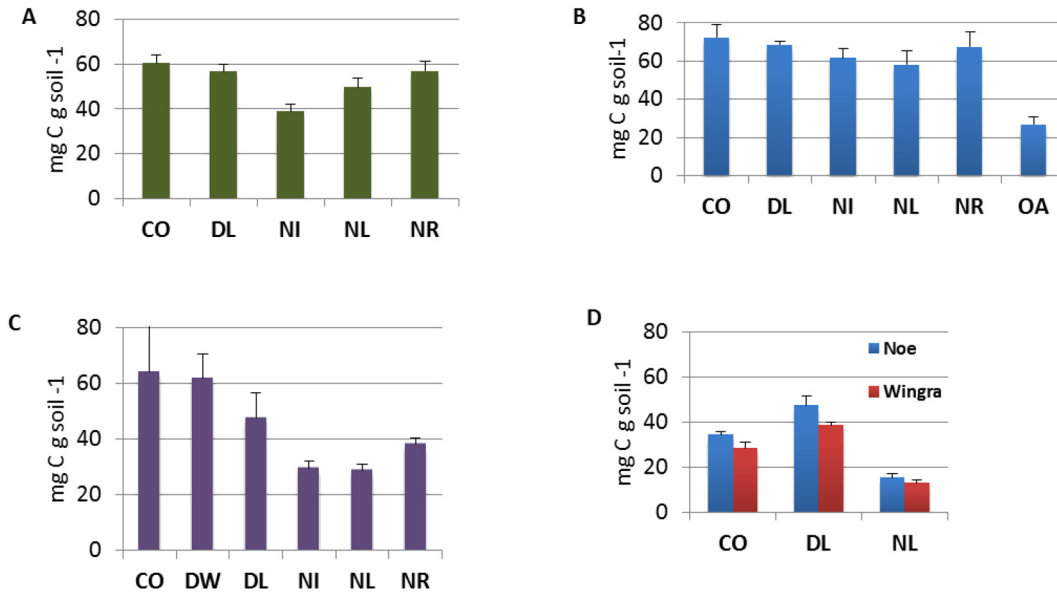
**2. Soil respiration**

Soil respiration, or CO<sub>2</sub> released from soil into the atmosphere, includes CO<sub>2</sub> released during microbial decomposition of soil organic matter, and CO<sub>2</sub> respired by live roots and soil fauna. Over the last two decades, important insights have been gained in understanding both biotic and abiotic factors that control soil respiration, which is a critical controller of SOM stocks, given that the rate of SOM accumulation depends on a balance between inputs and outputs. Recognizing that soil respiration is the main output of C from soil, the DIRT network provides first-hand evidence of the effects of increased OM inputs on soil C outputs, nuances on effects of soil moisture on respiration, and the role of site fertility in controlling sources that contribute to total soil respiration.

The Double Litter treatment enables us to examine the response of increased litterfall in response to accelerated rates of forest productivity. Certainly, doubling of aboveground litterfall is not likely to occur across most existing mature forests. Nonetheless, it was surprising that we detected limited changes in total soil C in response to doubled litter inputs.

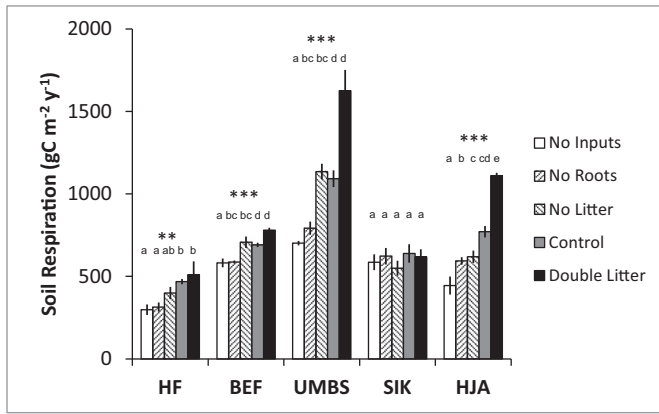
At four of five sites (Fig. 4), we found that annual soil respiration increased in the double litter plots. Our work does not yet allow us to identify the sources – root respiration or SOM decomposition – of CO<sub>2</sub> contributing to the elevated soil respiration following increased litter additions. We do know that at Bousson (Bowden et al., 2014) and the Harvard Forest (Lajtha et al., 2014a), roots did not increase in the Double Litter plots (Fig. 5), and preliminary results from the UMBS site also suggest that the root masses in the Control and DL treatments are also similar. Although we cannot rule out the possibility that root activity was enhanced, or that root turnover was also increased, it seems most likely that decomposition of the additional aboveground litter caused the increase in soil respiration. This enhanced decomposition, then, contributes to the lack of C accretion in the Double Litter plots - the microbial community responded to the additional inputs, either in enhanced activity of the existing microbial population, or in an increased microbial population. The SIK and WI plots did display an increase in C, but this was detectable only in the surface soils, and in the case of WI, only after 50 years.

These results, then, speak directly to ecological processes that will influence management efforts to increase forest productivity as a means to increase C storage in SOM pools. Enhancing productivity may well increase litter inputs from leaves, bark, branches and reproductive tissues, but the microbial community responds rapidly to



**Fig. 3.** Surface soil (0–10 cm) C concentration in (A) BEF (B) HF (C) HJA and (D) WISC DIRT sites. Error bars denote 1 SE. Data for BEF (Bowden et al., 2014) and HF (Lajtha et al., 2014a) are after 20 years of treatment; data for HJA (Crow et al., 2009b) are after 10 years; data for WISC (Lajtha et al., 2014b) are after 50 years.

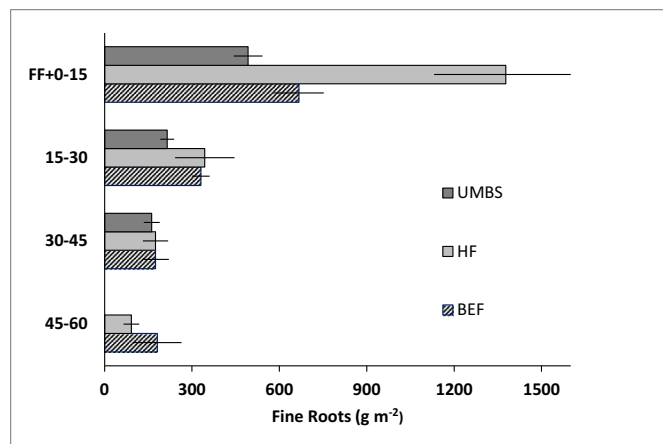




**Fig. 4.** Annual soil respiration (mean  $\pm$  SE) among treatments at DIRT sites. ANOVA (\*\*,  $p < 0.01$ ; \*\*\*,  $p < 0.001$ ) and Student-Newman-Keuls Method used to determine treatment effect, and pairwise comparisons, respectively. Soil respiration was measured using a soda-lime technique (Bowden et al., 1993; Fekete et al., 2014) at BEF, HF, and SIK and a LICOR system at UMBS and HJA (Sulzman et al., 2005). The first six months following trenched plot construction were excluded from annual flux estimates to allow time for the initial rapid decomposition of roots killed by the trenching process (Bowden et al., 1993). Respiration values are for the first full years at HF (Bowden et al., 1993) and BEF (unpublished), and UMBS (unpublished), years 2–7 at SIK (Fekete et al., 2014) and years 3–5 at HJA (Sulzman et al., 2005).

these additional inputs, respiring away these C inputs that could have been potentially stored in soil. Certainly, over time, small amounts of C are added each year to the pool of SOM, but any such inputs are small and incremental, and are not easily detectable given the variability of soils.

Although the DIRT experiment was not designed explicitly to quantify factors that control soil respiration, it has provided insights into soil respiration responses to conditions of the soil environment. The US sites are located in mesic environments where soil moisture is not usually limiting, where temperature is the dominant controller of soil respiration (Chen et al., 2000; Davidson and Janssens, 2006; Knorr et al., 2005; Kotrocó et al., 2008; Bond-Lamberty and Thomson, 2010; Smith and Fang, 2010) and where moisture effects are limited (Bowden et al., 1998). This is important because the No Roots and No Inputs treatments reduce living roots, thus reducing water uptake by tree roots. Nonetheless, we have observed at best small changes in soil moisture between control and either No Roots or No Inputs treatments. The Sikkokut site, however, is located in a moderate continental climate, where average annual precipitation is 553 mm (Fekete et al., 2014), compared to the US sites, which range from 817 mm at UMBS to 2200 mm at HJA. Here, removal of roots significantly increased soil



**Fig. 5.** Fine root content from control plots at the UMBS (unpublished data), HF (Lajtha et al., 2014a), and BEF (Bowden et al., 2014) DIRT sites. Mean  $\pm$  SE.

moisture such that during drier periods, when soil moisture content in control plots was  $<16\%$  (v/v), soil  $\text{CO}_2$  emissions in No Roots and No Inputs plots were significantly greater than the rates in control plots, even in the absence of root respiration. During wetter periods, however, when the soil moisture content in control plots was  $>16\%$  (v/v), emission rates were not significantly different among treatments. In moisture-stressed forest environments, therefore, soil respiration is unlikely to increase even when soil temperature and nutrient supply are favorable for microbial processing of soil organic matter (Sardans and Peñuelas, 2005; Fekete et al., 2012), and will lead to retention of soil C. Our data support this finding – at the SIK site, soil respiration rates in the DL and Control plots did not differ (Fig. 4), and after eight years, surface SOM concentrations increased in the DL plots (Fekete et al., 2014).

The DIRT experiment has been instrumental in assessing the relative contribution of autotrophic and heterotrophic respiration to total soil respiration. Accurate estimates of these contributions are important to understanding C budgets and to modelling forest C dynamics. Previous work has shown that the total allocation of carbon to roots is driven by aboveground productivity (Raich and Nadelhoffer, 1989), but the relative contributions of autotrophic and heterotrophic respiration to total soil respiration in temperate forests vary considerably (Bond-Lamberty et al., 2004; Ryan and Law, 2005; Chen et al., 2011b). Furthermore, the causes of this variability are not well known. One factor that may control the partitioning of soil respiration between autotrophic and heterotrophic sources is soil nitrogen availability, which is often a resource limitation in temperate ecosystems. It has been postulated that as soil nitrogen increases, increased ecosystem productivity will result in increased rates of aboveground litter production, reduced fine root biomass, and faster fine root turnover, subsequently resulting in greater inputs of root litter to the SOM pool (Nadelhoffer et al., 1985; Hendricks et al., 1993). Conversely, in a forest ecosystem of lower productivity, relative aboveground litter production is lower, fine root biomass is increased due to the need by trees to explore soil for limited stores of nitrogen, and fine root turnover is reduced. Because we have a range of soil N content and relative availability across our sites, the DIRT treatments allow us to test the hypothesis that the relative contributions to total soil respiration from aboveground litter will be proportional to soil nutrient status, but that relative contributions from root respiration will be inversely proportional to soil nutrient status.

Contributions to total soil respiration by aboveground litter, belowground litter, and root respiration were assessed by assuming that on an annual basis, soil C stores are at steady state, and that annual aboveground litter inputs at steady state are equal to total respiration losses due to decomposition of newly deposited and previously deposited leaf litter. We acknowledge that total SOM may show interannual variation, but such changes will be small in comparison the autotrophic and heterotrophic respiration. Autotrophic and heterotrophic contributions to total soil respiration were thus estimated using the following calculations (Bowden et al., 1993):

$$\text{Total Soil Respiration} = \text{Annual flux from Control Plots}$$

$$\text{Aboveground Litter Respiration} = \text{Aboveground (AG) Litterfall C}$$

$$\text{Root Respiration} = \text{Control Plot} - \text{No Roots}$$

$$\text{Belowground (BG) Litter Respiration} \\ = \text{Control Plot} - \text{No Roots} - \text{AG Litterfall}$$

Site-level soil C and N, and calculated site-level soil CN ratios, which serve as strong indicators of nitrogen availability (e.g. Taylor et al., 1989), were used as estimators of site fertility.

At the hardwood sites (we excluded H.J. Andrews, which is an old-growth conifer stand, and Wisconsin for which we had neither have soil respiration nor site-level soil C and N data) we found that the proportion of total soil respiration from root respiration ranged from 8%

at Sikfokut to 38% at UMBS (Table 2) and the proportion of soil respiration derived from AG litter ranged from 15 to 46%. We found that contributions from root respiration were negatively related to soil C and N (Fig. 6) and site-level soil CN (UMBS: 25.7, HF: 18.4, BEF: 13.8, SIK:13.3) and that contributions from AG litter are positively related to site fertility. These relationships are consistent with our hypothesis. Hence, in the sites with the lowest fertility, forests invest a very high proportion of annual production into root biomass and rhizospheric respiration due to the need for soil nutrient exploration and uptake. Interestingly, we found that the UMBS site had the lowest root mass (Fig. 5), yet the highest rates of soil respiration. We also know that at this site, nearly half of annual net primary production is used to grow roots (Gough et al., 2008). The roots support most of the hyphal production at UMBS, and mycorrhizae are responsible for much of the uptake of nitrogen, thus hyphal production may rival litterfall C inputs (Nave et al., 2013). Ectomycorrhizae also comprise over a third of soil fungi at UMBS (Castillo, unpublished data), with nearly all roots infected with either ectomycorrhizal or arbuscular mycorrhizal fungi. Thus, the combination of root and microbial respiration within the rhizosphere may be contributing to the high rates of total soil respiration at this site.

Soil fertility exerts a strong control over the sources of soil CO<sub>2</sub>, and this relationship is likely to be dynamic as anthropogenic alterations, such as climate warming and nitrogen deposition (Hicks Pries et al., 2017; Janssens et al., 2010), continue to alter soil fertility – soil respiration relationships. With soil respiration comprising such a large component of ecosystem and global C fluxes, models of ecosystem or global C budgets must account for differences in the relative contributions of aboveground and belowground sources of soil respiration to best quantify how potential changes in soil respiration may be driven by heterotrophic respiration of SOM that can lead to transfer of C from soil to atmospheric pools.

### 3. Priming: the DIRT perspective

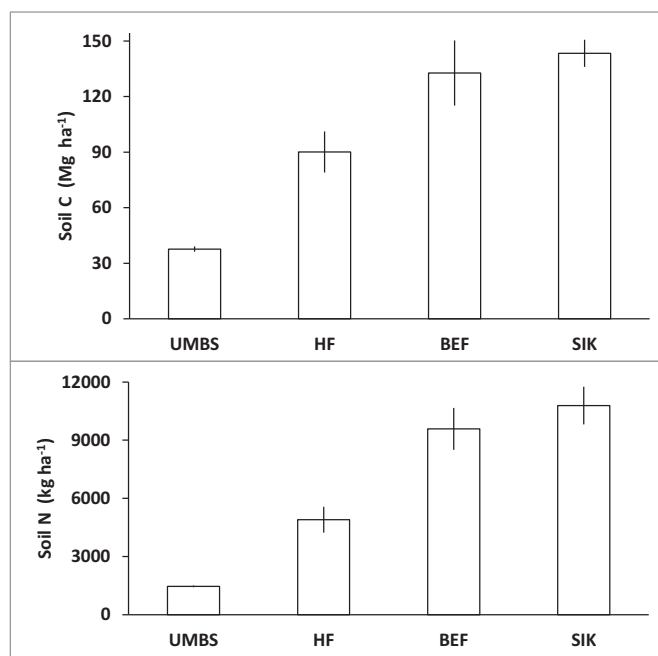
Soil priming, defined as the accelerated decomposition of existing SOM in response to increased litter inputs, is an interaction between the live and dead components of the soil ecosystem, specifically the living soil microbial community and dead soil organic matter (SOM) (Kuzyakov, 2010; Cheng et al., 2014). Generally, priming is a sequence of soil processes initiated by elevated litter inputs that result in increased microbial biomass, higher respiration, and greater extracellular enzyme production, and which, over time, alters soil microbial community structure (Kuzyakov, 2011) and increases SOM decomposition, thus decreasing soil C stocks. Importantly, even if drivers of primary productivity such as temperature, atmospheric CO<sub>2</sub>, and rainfall together stimulate ecosystem productivity, and in doing so increase litter and root organic matter inputs to soils, the net effect of priming may be that soil C stores are unchanged or even diminished.

The components of DIRT that we hypothesize to induce aspects of a priming effect include 1) pulse additions of aboveground litter following field maintenance days when litter transfers were made from the No Litter to Double Litter plots, 2) continuous effects of the additional litter decay over time (both of which induce litter-derived priming,

**Table 2**

Proportion of total soil respiration due to root respiration and decomposition of aboveground and belowground litter. Data sources are: SIK (Fekete et al., 2014); HF: (Bowden et al., 1993); HJA: (Sulzman et al., 2005). Data from BEF and UMBS are unpublished.

Site	Vegetation type	Soil respiration component			
		Root respiration	AG litter	BG litter	Total belowground
SIK	Hardwood	8	46	46	54
BEF	Hardwood	15	30	55	70
HF	Hardwood	33	29	37	70
UMBS	Hardwood	38	15	48	86
HJA	Conifer	22	19	59	81



**Fig. 6.** Soil C and N in upper 60 cm at hardwood DIRT sites. Mean  $\pm$  SE. Data source are: HF: (Lajtha et al., 2014a); BEF: (Bowden et al., 2014); SIK (Fekete et al., 2014); data for UMBS are unpublished.

without rhizosphere priming effects associated with increased NPP), 3) continuous effects of double wood addition, that may induce a strong C:N-derived competition between microbes and trees and may result in long-term C losses, and 4) a pulse of belowground inputs with the death of roots following trenching.

A compelling example of priming occurred in the coniferous H.J. Andrews DIRT site after nine years of treatments: litter-induced priming occurred in response to the Double Litter treatment, and was detected because total soil respiration rates were well in excess of rates that could be expected from the freshly added, additional litter (Sulzman et al., 2005). Here, because aboveground NPP of this treatment was not different from the Control, we can distinguish litter-induced priming from rhizosphere priming (Sulzman et al., 2005; Crow et al., 2009a, 2009b). Doubling needle input at H.J. Andrews stimulated mineralization of in situ SOM, accounting for 11.5–21.6% of annual CO<sub>2</sub> flux, leaving less labile, more degraded soil (Crow et al., 2009a). Evidence for priming included 1) lower DOC outputs from the mineral soil in Double Litter than Control plots and 2) DOC in Double Litter plots having higher concentrations of compounds associated with microbial degradation, and 3) high root and fungal activity in the O horizon (Crow et al., 2009b), which may serve as a biotic link to mineral soil and priming (Brant et al., 2006). Evidence of accelerated decomposition in the organic horizon of the double litter plots was also detected - DOM in O horizon became more degraded with added litter.

Whereas the HJA site showed demonstrable evidence of priming, other forests may have differences in climate, nutrient status, and forest type that may influence whether or not additional organic matter inputs promote priming. For example, the first eight years of DIRT at Sikfokut Double Litter showed no increase in soil respiration, but an increase in C content at 0–5 cm (Fekete et al., 2014). In this case, low precipitation and high temperature during summer likely inhibited decomposition, thus promoting soil C increases (Fekete et al., 2014). Furthermore, atmospheric nitrogen deposition, which is high at Sikfokut (15 kg N ha<sup>-1</sup> yr<sup>-1</sup>) (Holland et al., 2004) may have further inhibited decomposition at the Hungary site (Frey et al., 2014). Similarly, the SK site, after eight years of treatment, showed an increase in soil C, but no increase in indicators of enhanced lignin degradation (Klotzbücher et al., 2013).

More subtle evidence for priming and its transitory nature was found at the Bousson site (Bowden et al., 2014; Mayzelle et al., 2014), and the Harvard Forest (Lajtha et al., 2014a). As evidence, we found that after 20 years at Bousson, coarse particulate organic matter within small mineral soil macroaggregates (>250  $\mu\text{m}$ ) had decreased in the Double Litter treatment (Mayzelle et al., 2014), rather than increased, as had been expected. Further evidence is derived from recent molecular-level assessments. At Bousson, we observed evidence of accelerated degradation of SOM and lignin in the Double Litter plots (Wang et al., 2017), providing evidence of enhanced decomposition. At the Harvard Forest, the amount of solvent-extractable and lignin-derived compounds did not change significantly with doubled litter inputs (Pisani et al., 2016). Likewise, this is evidence priming because two decades of enhanced inputs should have increased these compounds; a lack of increase is consistent with accelerated decomposition. Furthermore, even after 20 years of doubled litter inputs, cutin-derived biomarkers did not increase significantly at either Bousson or the Harvard Forest, as would have been expected from doubled leaf litter inputs; this suggests strongly that these compounds were indeed degraded. During laboratory incubations of the Bousson soils, there was no change in total carbon content or cumulative  $\text{CO}_2\text{-C}$  respired, but the Double Litter soils were proportionally enriched with lipids (58.3%) versus ambient soils (19.5%) and these lipids were preferentially lost (49.9%) during incubation (Reynolds et al., 2018). The proportional increase in lipids under Double Litter may be the result of turnover in the heavy, older fraction due to priming followed by the incorporation of younger, less degraded carbon, as indicated by the relative mineralizability of these lipids during laboratory incubation.

Although induction of apparent priming is real and informative in the DIRT experiments, from an ecosystem perspective our experimental litter-doubling manipulations do not and were not meant to mimic long-term changes in forest productivity. Instead, “real” priming effects in forests may be delayed by days, weeks, or months, depending upon the timing and rate of extra litter inputs (Fontaine et al., 2004; Blagodatsky et al., 2010). For example, natural short-term, high input pulses may come during fall senescence in temperate deciduous and boreal forests or senescence in dry subtropical regions, or in bursts associated with storm events or other disturbances. These stochastic pulses of OM inputs could lead to priming that occurs immediately following litterfall inputs, as long as decomposition conditions are suitable, and which then declines as energetic gains from those inputs are depleted.

Efforts to enhance forest productivity could also lead to greater pulses of aboveground OM inputs, and enhanced rhizospheric priming may also occur if increases in productivity also increase rhizodeposition of exudates and cell wall sloughage (Dijkstra et al., 2013). Quantifying the timing of priming remains elusive. The HJA site showed that we could quantify priming on an annual basis (Sulzman et al., 2005), as the HF and BEF sites showed evidence of priming over longer time frames through intensive characterization of physical and biochemical characteristics. Detecting short-term pulses of priming, however, remains challenging.

Taken together, The DIRT experiment has used examination of soil respiration measurements, soil aggregate analysis, soil biochemistry characterizations, and laboratory incubations to collectively suggest that soil OM degradation was indeed primed via stimulation of microbial activity. It is important to note that despite clear evidence of priming at HJA, Bousson, and the Harvard Forest, none of these sites showed reductions in total SOM. Although priming negated potential increases in SOM due to added inputs, accelerated SOM losses were balanced by two decades of additional litter inputs that had apparently been stabilized. Clearly, forest production produces both the aboveground and belowground OM that leads ultimately to SOM. However, to understand linkages between productivity and carbon cycling, and to model changes in biomass pools and SOM pools, above and belowground components of the priming effect need to be considered (Kuzyakov, 2011). Our ability to accurately predict terrestrial carbon cycle responses to changing productivity will be limited by not including priming effects on SOM storage (Cheng et al., 2014).

#### 4. Conclusions and the Future of DIRT

Numerous factors influence the quantity and quality of SOM inputs, outputs, and storage (Fig. 7), thus soil carbon pools in forests may not respond linearly or immediately to aboveground or belowground litter inputs. Aboveground and belowground inputs have different biochemical characteristics, and can operate at different time scales. Multiple factors influence both the rates and quality, as well as relative proportion of inputs, as well. On the output side, SOM losses can be gaseous, physical, or hydrological, and can be driven by biological and physical factors, as well as chronic or stochastic events. For decades, SOM storage was thought to be driven primarily by the sources and inherent biochemistry of OM inputs; in recent years, however, we have learned that soil

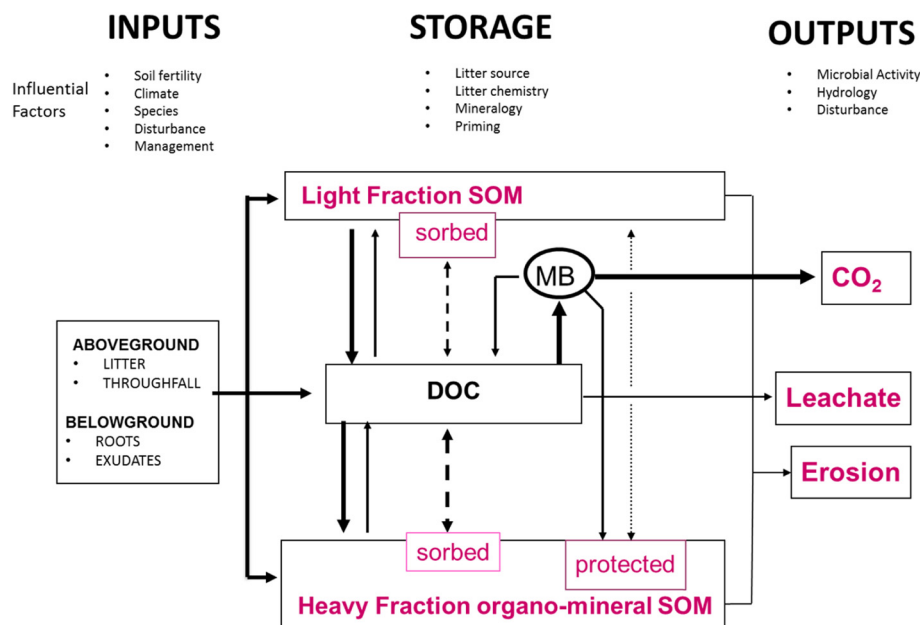


Fig. 7. Conceptual model of factors and processes influencing soil organic matter quantity and quality.



mineralogy exerts important controls through protection of SOM, including pools considered to be both recalcitrant and labile. Recent understanding of priming also indicates our growing appreciation of microbial biology, and how this process can produce non-linear relationships between inputs and SOM sequestration and stability.

Efforts to sequester carbon by managing productivity and associated litter inputs will not likely result in increased carbon storage over short time frames. Conversely, SOM is sensitive to litter additions, thus management activities or environmental changes that may reduce OM inputs may also threaten SOM storage. Our work at DIRT sites also underscores the importance of collaboration at multiple sites, especially for processes that cannot be understood within short study periods. Future goals are to expand the DIRT network to more sites to understand the generalizability and drivers of variability among sites, and to increase molecular- and microbial-level understanding that will help to better understand factors of SOM stabilization and destabilization.

## Acknowledgements

MJS thanks the Natural Sciences and Engineering Research Council (NSERC) of Canada for funding via a Discovery Grant (#2015-05760) and a Discovery Accelerator Supplement (#478038-15). The Canada Foundation for Innovation, Ontario Research Fund, and University of Toronto are thanked for support of the Environmental NMR Centre. KL was supported by NSF grants 0817064 and 1257032. RDB thanks the Shanbrom and Wells foundations, and Sam Reese and numerous Allegheny College undergraduates for invaluable field and laboratory assistance. IF and ZK were supported under the KH<sub>17</sub> funding scheme of the National Research, Development and Innovation Fund of Hungary, projects 125688 (IF) and 126478 (ZK). Serita Fry has been instrumental in work at the Harvard Forest DIRT site. We acknowledge grants NSF 1237491 to the Harvard Forest LTER research program and NSF 1440409 to the H.J. Andrews LTER research program, and OKTA funds to the Sikfokut ILTER program.

## References

- Aber, J.D., Melillo, J.M., McLaugherty, C.A., 1990. Predicting long-term patterns of mass loss, nitrogen dynamics, and soil organic matter formation from initial fine litter chemistry in temperate forest ecosystems. *Can. J. Bot.* 68, 2201–2208.
- Berg, B., McLaugherty, C., 2007. *Plant Litter: Decomposition, Humus Formation, Carbon Sequestration*. 2nd Ed. Springer, Berlin (338 p).
- Berg, B., Meentemeyer, V., 2002. Litter quality in a north European transect versus carbon storage potential. *Plant Soil* 242, 83–92.
- Bird, J.A., Kleber, M., Torn, M.S., 2008. <sup>13</sup>C and <sup>15</sup>N stabilization dynamics in soil organic matter fractions during needle and fine root decomposition. *Org. Geochem.* 39, 465–477.
- Blagodatsky, S., Blagodatskaya, E., Yuyukina, T., Kuzyakov, Y., 2010. Model of apparent and real priming effects: linking microbial activity with soil organic matter decomposition. *Soil Biol. Biochem.* 42, 1275–1283.
- Bond-Lamberty, B., Thomson, A., 2010. Temperature-associated increases in the global soil respiration record. *Nature* 464, 579–582.
- Bond-Lamberty, B., Wang, C., Gower, S.T., 2004. A global relationship between the heterotrophic and autotrophic components of soil respiration? *Glob. Chang. Biol.* 10, 1756–1766. <https://doi.org/10.1111/j.1365-2486.2004.00816.x>.
- Bosatta, E., Ågren, G.I., 1999. Soil organic matter quality interpreted thermodynamically. *Soil Biol. Biochem.* 3, 1889–1891.
- Bowden, R.D., Nadelhoffer, K.J., Boone, R.D., Melillo, J.M., Garrison, J.B., 1993. Contributions of aboveground litter, belowground litter, and root respiration to total soil respiration in a temperate mixed hardwood forest. *Can. J. For. Res.* 23, 1402–1407.
- Bowden, R.D., Newkirk, K.M., Rullo, G., 1998. Carbon dioxide and methane fluxes by a forest soil under laboratory-controlled moisture and temperature conditions. *Soil Biol. Biochem.* 30, 1591–1597.
- Bowden, R.D., Deem, L., Plante, A.F., Peltre, C., Nadelhoffer, K., Lajtha, K., 2014. Litter input controls on soil carbon in a temperate deciduous forest. *Soil Sci. Soc. Am. J.* 78, S66–S75.
- Brant, J., Sulzman, E., Myrold, D., 2006. Microbial community utilization of added carbon substrates in response to long-term carbon input manipulation. *Soil Biol. Biochem.* 38, 2219–2232.
- Chen, H., Harmon, M.E., Griffiths, R.P., Hicks, W., 2000. Effects of temperature and moisture on carbon respired from decomposing woody roots. *For. Ecol. Manag.* 138, 51–64.
- Chen, B., Coops, N.C., Black, A., Jassal, R.S., Chen, J.M., Johnson, M., 2011a. Modeling to discern nitrogen fertilization impacts on carbon sequestration in a Pacific Northwest Douglas-fir forest in the first-postfertilization year. *Glob. Chang. Biol.* 17 (Issue 3): 1442–1460. <https://doi.org/10.1111/j.1365-2486.2010.02298.x>.
- Chen, G., Yang, Y., Guo, J., Xie, J., Yang, Z., 2011b. Relationships between carbon allocation and partitioning of soil respiration across world mature forests. *Plant Ecol.* 212, 195–206.
- Cheng, W., Parton, W., Gonzalez-Meler, M., Phillips, R., Asao, S., McNickle, G., Brzostek, E., Jastrow, J., 2014. Synthesis and modeling perspectives of rhizosphere priming. *New Phytol.* 201, 31–44.
- Chung, H., Grove, J.H., Six, J., 2008. Indications for soil carbon saturation in a temperate agroecosystem. *Soil Sci. Soc. Am. J.* 72, 1132–1139.
- Craine, J.M., Fierer, N., McLaughlan, K.K., 2010. Widespread coupling between the rate and temperature sensitivity of organic matter decay. *Nat. Geosci.* 3, 854–857.
- Crow, S.E., Lajtha, K., Bowden, R.D., Yano, Y., Brant, J., Caldwell, B.A., Sulzman, E., 2009a. Increased coniferous needle inputs accelerate decomposition of soil carbon in an old-growth forest. *For. Ecol. Manag.* 258, 2224–2232.
- Crow, S.E., Lajtha, K., Filley, T.R., Swanston, C.W., Bowden, R.D., Caldwell, B.A., 2009b. Sources of plant-derived carbon and stability of organic matter in soil: implications for global change. *Glob. Chang. Biol.* 15, 2003–2019.
- Davidson, E.A., Janssens, I.A., 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature* 440 (165–173), 2006.
- Dijkstra, F., Carrillo, Y., Pendall, E., Morgan, J., 2013. Rhizosphere priming: a nutrient perspective. *Front. Microbiol.* <https://doi.org/10.3389/fmicb.2013.00216>.
- Fekete, I., Zs, Kotrocó, Cs, Varga, Hargitai, R., Townsend, K., 2012. Variability of organic matter inputs affects soil moisture and soil biological parameters in a European detritus manipulation experiment. *Ecosystems* 15, 792–803.
- Fekete, I., Kotrocó, Z., Varga, C., Nagy, P.T., Tóth, J.A., Bowden, R.D., Várbió, G., Lajtha, K., 2014. Alterations in forest detritus input influence soil carbon concentration and soil respiration in a Central-European deciduous forest. *Soil Biol. Biochem.* 74:106–114. <https://doi.org/10.1016/j.soilbio.2014.03.006>.
- Feng, X., Simpson, A.J., Wilson, K.P., Dudley Williams, D., Simpson, M.J., 2008. Increased cuticular carbon sequestration and lignin oxidation in response to soil warming. *Nat. Geosci.* 1, 836–839.
- Feng, X., Simpson, A.J., Schlesinger, W.H., Simpson, M.J., 2010. Altered microbial community structure and organic matter composition under elevated CO<sub>2</sub> and N fertilization in the duke forest. *Glob. Chang. Biol.* 16, 2104–2116.
- Fissore, C., Giardina, C.P., Kolka, R.K., Trettin, C.C., King, G.M., Jurgensen, M.F., Barton, C.D., McDowell, S.D., 2008. Temperature and vegetation effects on soil organic carbon quality along a forested mean annual temperature gradient in North America. *Glob. Chang. Biol.* 14, 193–205.
- Fontaine, S., Bardoux, G., Abbadie, L., Mariotti, A., 2004. Carbon input to soil may decrease soil carbon content. *Ecol. Lett.* 7, 314–320.
- Frey, S.D., Ollinger, S., Nadelhoffer, K., Bowden, R., Brzostek, E., Burton, A., Caldwell, B., Crow, S., Goodale, C., Grandy, S., Finzi, A., Kramer, M., Lajtha, K., LeMoine, J., Martin, M., McDowell, W., Minocha, R., Sadowsky, J.J., Templer, P., Wicking, K., 2014. Chronic nitrogen additions suppress decomposition and sequester soil carbon in temperate forests. *Biogeochemistry Letters* 121, 305–316.
- Giardina, C., Litton, C., Crow, S.E., Asner, G., 2014. Warming-related increases in soil CO<sub>2</sub> efflux are explained by increased below-ground carbon flux. *Nat. Clim. Chang.* <https://doi.org/10.1038/NCLIMATE2322>.
- Gottschalk, P., Smith, J.U., Wattenbach, M., Bellarby, J., Stehfest, E., Arnell, N., Osborn, T.J., Jones, C., Smith, P., 2012. How will organic carbon stocks in mineral soils evolve under future climate? Global projections using RothC for a range of climate change scenarios. *Biogeosciences* 9, 3151–3171.
- Gough, C.M., Vogel, C.S., Schmid, H.P., Su, H.-B., Curtis, P.S., 2008. Multi-year convergence of biometric and meteorological estimates of forest carbon storage. *Agric. For. Meteorol.* 148:158–170. <https://doi.org/10.1016/j.agrformet.2007.08.004>.
- Grandy, A.S., Robertson, G.P., 2007. Land-use intensity effects on soil organic carbon accumulation rates and mechanisms. *Ecosystems* 10 (59–57).
- Harrington, R.A., Fownes, J.H., Vitousek, P.M., 2001. Production and resource use efficiencies in N- and P-limited tropical forests: a comparison of responses to long-term fertilization. *Ecosystems* 4 (7), 646–657.
- Hendricks, J.J., Nadelhoffer, K.J., Aber, J., 1993. Assessing the role of fine roots in carbon and nutrient cycling. *TREE* 8 (5), 174–178.
- Hicks Pries, C.E., Castanha, C., Porras, R.C., Torn, M.S., 2017. The whole-soil carbon flux in response to warming. *Science* 355, 1420–1423.
- Holland, E., Braswell, B., Sulzman, J., Lamarque, J.-F., 2004. Nitrogen Deposition Onto the United States and Western Europe. ORNL DAAC, Oak Ridge <http://www.daac.ornl.gov>.
- Jandl, R., Lindner, M., Vesterdal, L., Bauwens, B., Baritz, R., Hagedorn, F., Johnson, D.W., Minkinen, K., Byrne, K.A., 2007. How strongly can forest management influence soil carbon sequestration? *Geoderma* 137:253–268. <https://doi.org/10.1016/j.geoderma.2006.09.003>.
- Janssens, I.A., Dieleman, W., Luysaert, S., Subke, J.-A., Reichstein, M., Ceulemans, R., Ciais, P., Dolman, A.J., Grace, J., Matteucci, G., Papale, D., Piao, S.L., Schulze, E.-D., Tang, J., Law, B.E., 2010. Reduction of forest soil respiration in response to nitrogen deposition. *Nat. Geosci.* 3, 315–322.
- King, A.W., Post, W.M., Wullschlegel, S.D., 1997. The potential response of terrestrial carbon storage to changes in climate and atmospheric CO<sub>2</sub>. *Clim. Chang.* 35, 199–227.
- Klotzbücher, T., Strohmeier, S., Kaiser, K., Bowden, R., Lajtha, K., Ohm, H., Kalbitz, K., 2013. Lignin properties in topsoils of a beech/oak forest after 8 years of manipulated litter fall: relevance of altered input and oxidation of lignin. *Plant Soil* 367, 579–589.
- Knorr, W., Prentice, I.C., House, J.I., Holland, E.A., 2005. Long-term sensitivity of soil carbon turnover to warming. *Nature* 433, 298–301.
- Kotrocó, Z., Fekete, I., Tóth, J.A., Tóthmérész, B., Balázsy, S., 2008. Effect of leaf- and root-litter manipulation for carbon-dioxide efflux in forest soil. *Cereal Res. Commun.* 36, 663–666.



- Kotroczo, Z., Veres, Z., Fekete, I., Krakomperger, Z., Tóth, J.A., Lajtha, K., Tóthmérész, B., 2014. Soil enzyme activity in response to long-term organic matter manipulation. *Soil Biol. Biochem.* 70, 237–243.
- Kuzyakov, Y., 2010. Priming effects: interactions between living and dead organic matter. *Soil Biol. Biochem.* 42, 1363–1371.
- Kuzyakov, Y., 2011. Ecology: prime time for microbes. *Nat. Clim. Chang.* 1, 295–297.
- Kuzyakov, Y., Friedel, J.K., Stahr, K., 2000. Review of mechanisms and quantification of priming effects. *Soil Biol. Biochem.* 32, 1485–1498.
- Lajtha, K., Bowden, R.D., Nadelhoffer, K., 2014a. Litter and root manipulations provide insights into soil organic matter dynamics and stability. *Soil Sci. Soc. Am. J.* 78, S261–S269.
- Lajtha, K., Townsend, K., Kramer, M., Swanston, C., Bowden, R., Nadelhoffer, K., 2014b. Changes to particulate versus mineral-associated soil carbon after 50 years of litter manipulation in forest and prairie experimental ecosystems. *Biogeochemistry* 119, 341–360.
- Lal, R., 2004. Soil carbon sequestration impacts on global climate change and food security. *Science* 304, 1623–1627.
- Lal, R., 2005. Forest soils and carbon sequestration. *For. Ecol. Manag.* 220 (Issues 1–3), 242–258.
- Liski, J., Perruchoud, D., Karjalainen, T., 2002. Increasing carbon stocks in the forest soils of western Europe. *For. Ecol. Manag.* 169, 159–175.
- von Lützow, M., Kogel-Knabner, I., Ekschmitt, K., Matzner, E., Guggenberger, G., Marschner, B., Flessa, H., 2006. Stabilization of organic matter in temperate soils: mechanisms and their relevance under different soil conditions - a review. *Eur. J. Soil Sci.* 57, 426–445.
- von Lützow, M., Kogel-Knabner, I., Ludwig, B., Matzner, E., Flessa, H., Ekschmitt, K., Guggenberger, G., Marschner, B., Kalbitz, K., 2008. Stabilization mechanisms of organic matter in four temperate soils: development and application of a conceptual model. *J. Plant Nutr. Soil Sci.* 171, 111–124.
- Marín-Spiotta, E., Gruley, K.E., Crawford, J., Atkinson, E.E., Miesel, J.R., Greene, S., Cardona-Correa, C., Spencer, R.G.M., 2014. Paradigm shifts in soil organic matter research affect interpretations of aquatic carbon cycling: transcending disciplinary and ecosystem boundaries. *Biogeochemistry* 117, 279–297.
- Marschner, B., Brodowski, S., Dreves, A., Gleixner, G., Gude, A., Grootes, P.M., Hamer, U., Heim, A., Jandl, G., Ji, R., Kaiser, K., Kalbitz, K., Kramer, C., Leinweber, P., Rethemeyer, J., Schäffer, A., Schmidt, M.W.I., Schwark, L., Wiesenberger, G.L.B., 2008. How relevant is recalcitrance for the stabilization of organic matter in soils? *J. Plant Nutr. Soil Sci.* 171, 91–110.
- Mayzelle, M.M., Krusor, M.L., Lajtha, K., Bowden, R.D., Six, J., 2014. Effects of detrital inputs and roots on carbon saturation deficit of a temperate forest soil. *Soil Sci. Soc. Am. J.* 78, S76–S83.
- Melillo, J.M., McGuire, A.D., Kicklighter, D.W., Moore, B., Vorosmarty, C.J., Schloss, A.L., 1993. Global climate change and terrestrial net primary production. *Nature* 363, 234–240.
- Nadelhoffer, K.F., Fry, B., 1988. Controls on natural N-15 and C-13 abundances in forest soil organic-matter. *Soil Sci. Soc. Am. J.* 52 (6), 1633–1640.
- Nadelhoffer, K.J., Aber, J.D., Melillo, J.M., 1985. Fine root production in relation to net primary production along a nitrogen availability gradient in temperate forests: a new hypothesis. *Ecology* 66, 1377–1390.
- Nave, L.E., Vance, E.D., Swanston, C.W., Curtis, P.S., 2010. Harvest impacts on soil carbon storage in temperate forests. *For. Ecol. Manag.* 259, 857–866.
- Nave, L.E., Nadelhoffer, K.J., Le Moine, J.M., van Diepen, L.T.A., Cooch, J.K., Van Dyke, N.J., 2013. Nitrogen uptake by trees and mycorrhizal fungi in a successional Northern temperate forest: insights from multiple isotopic methods. *Ecosystems* 16, 590–603.
- Nielsen, G.A., Hole, F.D., 1963. A study of the natural processes of incorporation of organic matter into soil in the University of Wisconsin Arboretum. *Wisconsin Acad. Sci. Arts Lett.* 52, 213–227.
- Pan, Y., Birdsey, R.A., Fang, J., Houghton, R., Kauppi, P.E., Kurz, W.E., Phillips, O.L., Shvidenko, A., Lewis, S.L., Canadell, J.G., Ciais, P., Jackson, R.B., Pacala, S.W., McGuire, A.D., Piao, S., Rautiainen, A., Sitch, S., Hayes, D., 2011. A large and persistent carbon sink in the world's forests. *Science* 333:988–993. <https://doi.org/10.1126/science.1201609>.
- Paul, K.I., Polglase, P.J., Richards, G.P., 2003. Predicted change in soil carbon following afforestation or reforestation, and analysis of controlling factors by linking a C accounting model (CAMFor) to models of forest growth (3PG), litter decomposition (GENDEC) and soil C turnover (RothC). *For. Ecol. Manag.* 177, 485–501.
- Pisani, O., Lin, L.H., Lun, O.Y., Lajtha, K., Nadelhoffer, K.J., Simpson, A.J., Simpson, M.J., 2016. Long-term doubling of litter inputs accelerates soil organic matter degradation and reduces soil carbon stocks. *Biogeochemistry* 127, 1–14.
- Post, W.M., Izaurralde, R.C., West, T.O., Liebig, M.A., King, A.W., 2012. Management opportunities for enhancing terrestrial carbon dioxide sinks. *Front. Ecol. Environ.* 10: 554–561. <https://doi.org/10.1890/120065>.
- Raich, J.W., Nadelhoffer, K.J., 1989. Belowground carbon allocation in forest ecosystems: global trends. *Ecology* 70, 1346–1354.
- Raich, J.W., Russell, A.E., Kitayama, K., Parton, W.J., Vitousek, P.M., 2006. Temperature influences carbon accumulation in moist tropical forests. *Ecology* 87, 76–87.
- Rasmussen, C., Torn, M.S., Southard, R.J., 2005. Mineral assemblage and aggregates control carbon dynamics in a California Conifer Forest. *Soil Sci. Soc. Am. J.* 69, 1711–1721.
- Rasse, D.P., Rumpel, C., Dignac, M.-F., 2005. Is soil carbon mostly root carbon? Mechanisms for a specific stabilisation. *Plant Soil* 269, 341–356.
- Reynolds, L.L., Lajtha, K., Bowden, R.D., Tfaily, M., Johnson, B.R., Bridgman, S.D., 2018. Insights into soil C cycling from long-term input-manipulation and high-resolution mass spectroscopy. *JGR-Biogeosci.* (in press).
- Rovira, P., Kurz-Besson, C., Couteaux, M.M., Vallejo, V.R., 2008. Changes in litter properties during decomposition: a study by differential thermogravimetry and scanning calorimetry. *Soil Biol. Biochem.* 40, 172–185.
- Ryan, M.G., Law, B.E., 2005. Interpreting, measuring, and modeling soil respiration. *Biogeochemistry* 73 (1), 3–27.
- Sardans, J., Peñuelas, J., 2005. Drought decreases soil enzyme activity in a Mediterranean *Quercus ilex* (L.) forest. *Soil Biol. Biochem.* 37, 455–461.
- Schmidt, M.W.I., Torn, M.S., Abiven, S., Dittmar, T., Guggenberger, G., Janssens, I.A., Kleber, M., Kogel-Knabner, I., Lehmann, J., Manning, D.A.C., Nannipieri, P., Rasse, D.P., Weiner, S., Trumbore, S.E., 2011. Persistence of soil organic matter as an ecosystem property. *Nature* 478, 49–56.
- Schöning, I., Grüneberg, E., Sierra, C., Hessenmöller, D., Schruppf, M., Weisser, W., Schulze, E.-D., 2013. Causes of variation in mineral soil C content and turnover in differently managed beech dominated forests. *Plant Soil* 370, 625–639.
- Simpson, M.J., Simpson, A.J., 2012. The chemical ecology of soil organic matter molecular constituents. *J. Chem. Ecol.* 38, 768–784.
- Six, J., Conant, R.T., Paul, E.A., Paustian, K., 2002. Stabilization mechanisms of soil organic matter: implications for C-saturation of soils. *Plant Soil* 241, 155–176.
- Smith, P., Fang, C., 2010. A warm response by soils. *Nature* 464, 499–500.
- Sollins, P., Homann, P., Caldwell, B.A., 1996. Stabilization and destabilization of soil organic matter: mechanisms and controls. *Geoderma* 74, 65–105.
- Sollins, P., Kramer, M., Swanston, C., Lajtha, K., Filley, T., Aufdenkampe, A.K., Wagai, R., Bowden, R.D., 2009. Sequential density fractionation across soils of contrasting mineralogy: evidence for both microbial- and mineral-controlled soil organic matter stabilization. *Biogeochemistry* 96, 209–231.
- Spielvogel, S., Prietzel, J., Kogel-Knabner, I., 2008. Soil organic matter stabilization in acidic forest soils is preferential and soil type-specific. *Eur. J. Soil Sci.* 59, 674–692.
- Stewart, C.E., Paustian, K., Conant, R.T., Plante, A.F., Six, J., 2009. Soil carbon saturation: implications for measurable carbon pool dynamics in long-term incubations. *Soil Biol. Biochem.* 41, 357–366.
- Sulzman, E., Brant, J., Bowden, R., Lajtha, K., 2005. Contribution of aboveground litter, belowground litter, and rhizosphere respiration to total soil CO<sub>2</sub> efflux in an old growth coniferous forest. *Biogeochemistry* 73, 231–256.
- Talbot, J.M., Yelle, D.J., Nowick, J., Treseder, K.K., 2012. Litter decay rates are determined by lignin chemistry. *Biogeochemistry* 108 (1–3), 279–295.
- Taylor, B.R., Parkinson, D., Parsons, W.J., 1989. Nitrogen and lignin content as predictors of litter decay rates: a microcosm test. *Ecology* 70, 97–104.
- Torn, M.S., Trumbore, S.E., Chadwick, O.A., Vitousek, P.M., Hendricks, D.M., 1997. Mineral control of soil organic carbon storage and turnover. *Nature* 389, 170–173.
- Vagen, T.G., Lal, R., Singh, B.R., 2005. Soil carbon sequestration in Sub-Saharan Africa: a review. *Land Degrad. Dev.* 16, 53–71.
- Wang, J., Pisani, O., Lin, L.H., Lun, O.O.Y., Bowden, R.D., Lajtha, K., Simpson, A.J., Simpson, M.J., 2017. Long-term litter manipulation alters soil organic matter turnover in a temperate deciduous forest. *Sci. Total Environ.* 607–608, 865–875.
- Yanai, R.D., Currie, W.S., Goodale, C.L., 2003. Soil carbon dynamics after Forest harvest: an ecosystem paradigm reconsidered. *Ecosystems* 6, 197–212.