The Detrital Input and Removal Treatment (DIRT) Network

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Introduction

Globally, soils contain at least three times more carbon than the atmosphere, and four and a half times more carbon than the world's biota. Despite their importance, however, soil carbon stocks have been degraded through land use change and unsustainable forest management practices. 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_2 increase. Forest fertilization studies have shown that forest growth, and hence biomass carbon pools, can be increased as a result of active management. 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. However, the extent to which forests can be manipulated to enhance C sequestration soil remains questionable.

Many factors affect SOM carbon accumulation and stabilization, including mineralogy and soil aggregation, land use and forest harvest, and climate. 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. Due to climate change, changes in net primary productivity (NPP) and thus litter fall are predicted in many ecosystems, but it is not clear whether parallel changes in SOM stores will accompany changes in NPP.

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 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 (Nielsen and Hole, 1963; Lajtha et al., 2014b). 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 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 payrifera* Marsh.). The Bousson Experimental Forest, PA, site was established in 1991 in a mixed deciduous stand dominated by black cherry (*Prunus serotina* hrh.) 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 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 Síkfőkút forest site in Hungary was established in 2000 in a dry oak (*Quercetum petraea-cerris*) forest, and a site in Germany was established in a beech/oak (*Fagus sylvatica* L., *Quercus petraea* (Matt.) Liebl.) forest in 1999. A DIRT site that was crossed with an N fertilization experiment was established at the University of Michigan Biological Station in 2004 in a dry deciduous forest that is dominated by bigtooth aspen (*Populus grandidentata*), and secondarily by red maple (*Acer rubrum*), red oak (*Quercus rubra*), paper birch (*Betula paperifera*), eastern white pine (*Pinus strobus*), sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), and trembling aspen (*Populus tremuloides*).

In this article, we synthesize research in the international DIRT network and show how the DIRT network has contributed to the study of the role of both above- and belowground plant inputs to soil carbon stabilization and destabilization.

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Table 1 Description of litter treatments for DIRT experiment

Treatment	*Description*
Control	Natural above and belowground litter inputs are allowed.
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 only at Síkfőkút 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.
O/A-less	Top 30 cm of soil was replaced with mineral soil.

Responses of Total Soil C and Density Fractions to Detrital Manipulation: SOM Resilience

Because most models of soil organic matter composition assume a direct relationship between litter inputs and soil C accumulation, it would be reasonable to assume that treatments with litter additions (Double Litter and Double Wood) would show relatively rapid increases in surface soil C concentration and that treatments with litter removals (No Litter, No Roots, No Inputs) would show similar decreases in surface soil C concentrations. Indeed, the trajectory of C content from the original DIRT site in Wisconsin clearly exhibited this pattern (Lajtha et al., 2014b; Fig. 1). 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 C concentration (Fig. 2). However, all sites showed significant decreases in surface soil C content with litter removals. In addition, aboveground litter exclusion had an effect on C levels similar to that of root exclusion, thus there was no evidence that root-derived C was more critical shoot-derived C to soil C sequestration.

Priming: The DIRT Perspective

Soil priming, defined by the accelerated decomposition of existing SOM in response to increased litter inputs, is a sequence of soil processes initiated by elevated litter loading which results in increased microbial biomass, higher respiration, and greater extracellular enzyme production. Overall, priming effects may lead to a lack of increase or even small decreases in SOM storage with increased organic inputs.

In the coniferous H.J. Andrews DIRT site after 9 years of treatments, priming occurred in response to the Double Litter treatment. Doubling needle input at H.J. Andrews stimulated mineralization of in situ SOM, accounting for 11.5–21.6% of annual CO_2 flux, leaving less labile, more degraded soil (Crow et al., 2009a). Evidence for priming included: (1) lower DOC flux from the mineral soil in Double Litter than Control plots; (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. In contrast, the first eight years of DIRT at Síkfőkút Double Litter resulted in no

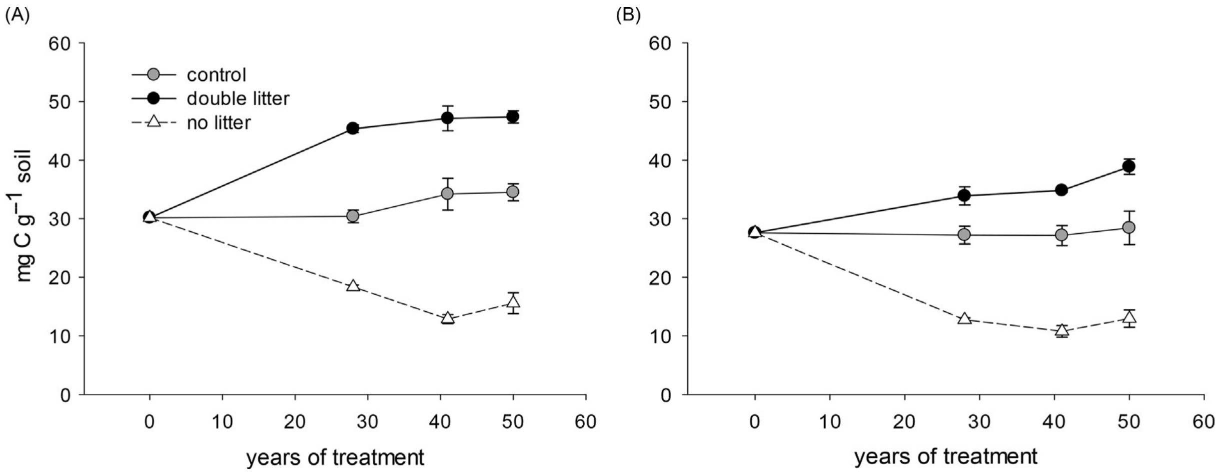

Fig. 1 Soil organic carbon (SOC) concentrations for NOE Woods (A) and Wingra Woods (B) in the Wisconsin Detrital Input and Removal Treatments (DIRT) plots in 1984, 1997, and 2006. Values are means ±1 standard error, $n = 4$. Significant differences in values between treatments within a site in 2006 are shown in Table 2. When SE bars are not shown it is because the SE was smaller than the symbol.

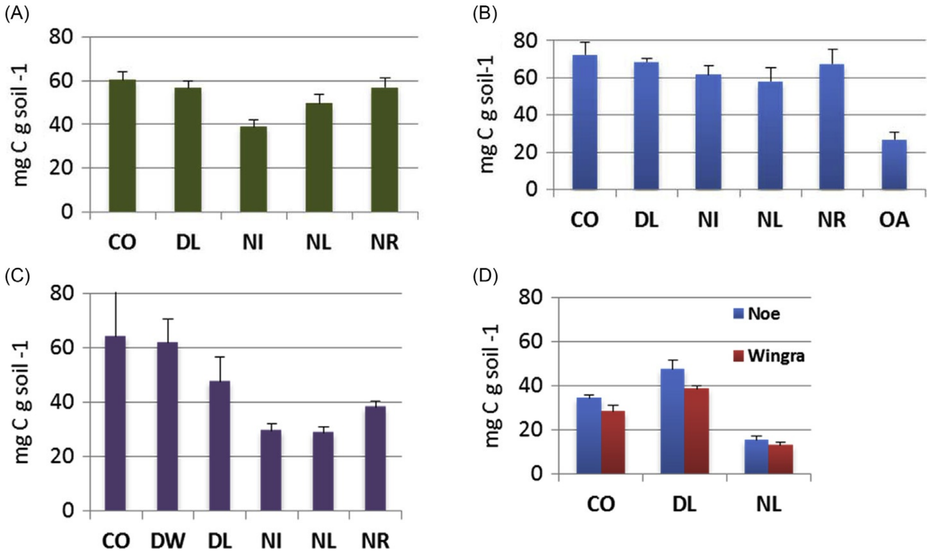

Fig. 2 Surface soil (0–10 cm) C concentration in (A) Bousson, (B) Harvard Forest, (C) H.J. Andrews, and (D) Wisconsin DIRT sites.

increase in soil respiration and an increase in C content at 0–5 cm (Fekete et al., 2014). At H.J. Andrews, priming was greatest during the hottest and driest months of summer (Crow et al., 2009b), while at Síkfőkút low precipitation and high temperature inhibited decomposition and promoted C stabilization rather than priming (Fekete et al., 2014). Nitrogen deposition, which is extremely low at H.J. Andrews (1.6 kg N per hectare per year) and high at Síkfőkút (15 kg N per hectare per year), may have further inhibited decomposition and priming at the Hungary site. This example highlights that differences in climate, nutrient status, and forest type may drive differences in ecosystem dynamics that promote priming.

Soil Respiration

Soil respiration, or CO_2 released from soil into the atmosphere, includes CO_2 released by the soil food web during decomposition of soil organic matter (heterotrophic respiration) and CO_2 respired by live roots (autotrophic respiration). At all the sites (Fig. 3), soil respiration increased in the Double Litter plots, with consistent differences among treatments throughout the year. Thus, in response to increased litter C inputs, microbial activity also increased, helping explain the lack of response of soil C pools to added litter. It is likely that a good portion of this increased respiration is due to microbial use of the recently added litter, but priming of older organic matter decomposition must also occur to explain the large increases in respiration.

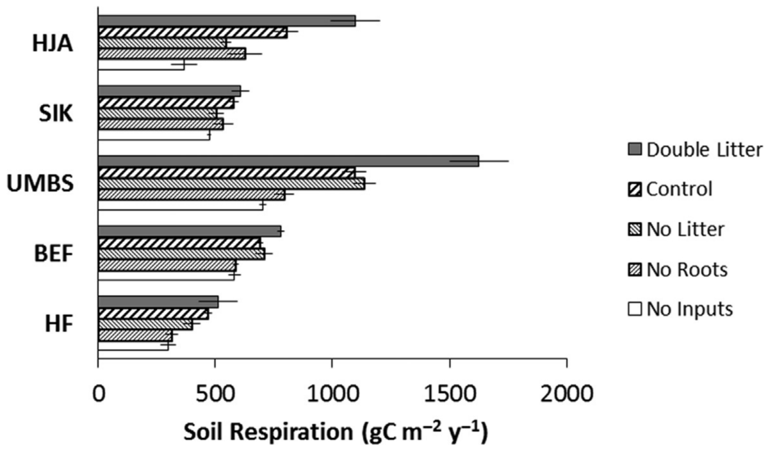

Fig. 3 Annual soil respiration in the different litter manipulation treatments at 5 DIRT sites. *HJA* = Andrews Forest, OR; *SIK* = Síkfőkút, HU; *UMBS* = Michigan Biological Station, MI; *BEF* = Bousson Forest, PA; *HF* = Harvard Forest, MA. Mean ± SE.

Previous work has shown that the total allocation of carbon to roots is driven by aboveground productivity, but the relative contributions of autotrophic and heterotrophic respiration to total soil respiration in temperate forests vary considerably. 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 and reduced fine root biomass. Conversely, in a forest ecosystem of lower productivity, relative aboveground litter production is lower, but fine root biomass is increased due to the need by trees to explore soil for limited stores of nitrogen. We would thus expect 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 steady-state soil C conditions on an annual basis. Autotrophic and heterotrophic contributions to total soil respiration were estimated using the following calculations:

Total Soil Respiration	Annual flux from Control Plots
Aboveground Litter Respiration	Aboveground (AG) Litter fall C
Root Respiration	Control Plot – No Roots
Belowground (BG) Litter Respiration	Control Plot – No Roots - AG Litter fall

Table 2 Proportion (%) of total soil respiration due to root respiration and decomposition of aboveground and belowground litter

		Soil respiration component			
Site	*Vegetation type*	*Root Respiration*	*AG litter*	*BG litter*	*Total belowground (BG litter + root respiration)*
Síkfőkút, HU	Hardwood	8	46	46	54
Bousson, PA	Hardwood	15	30	55	70
Harvard Forest, MA	Hardwood	33	29	37	70
UMBS, MI	Hardwood	38	15	48	86
Andrews, OR	Conifer	22	19	59	81

We assumed that over the short term, 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.

At the hardwood sites we found that the proportion of total soil respiration from root respiration ranged from 8% at Síkfőkút to 38% at UMBS (Table 2) and the proportion of soil respiration derived from AG litter ranged from 15% to 46%. Using site-level soil C and N as estimates of site fertility, contributions from root respiration are negatively related to soil fertility (Fig. 4) and contributions from AG litter are positively related to site fertility. These relationships are consistent with our hypothesis. Total belowground CO_2 sources (root respiration plus belowground litter) were responsible for 54–86% of total soil respiration in agreement with estimates that belowground sources contribute 70–80% of total soil respiration across a wide range of forests. 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.

Responses of Soil C Quality and Stability to Detrital Manipulation

Composition and Function of SOM Based on Molecular-Level Insight from NMR Analysis

Solid-state ^{13}C NMR spectroscopy is an excellent tool for assessing the overall composition of SOM and over the past few decades has emerged as one of the most commonly applied NMR techniques to study SOM. In DIRT treatments at the Harvard Forest (Pisani et al., 2016), both variation in the composition of SOM and differences in the relative degree of degradation are observed with notable changes in the proportion of alkyl and O-alkyl carbon for all treatments with the exception of root exclusion (Fig. 5, Table 3). With root exclusion, an increase in alkyl carbon was observed suggesting the preferential accumulation of plant lipids and preferential degradation of more labile constituents, such as carbohydrates and peptides, which is consistent with the decrease in the O-alkyl region. A slight decrease in aromaticity was also observed which is likely due to the lack of suberin-derived root inputs relative to the other treatments as well as degradation of other aromatic SOM constituents such as lignin. Similarly, no inputs and no litter both exhibited increases in alkyl carbon and decreases in O-alkyl carbon. This suggests that microbes are using labile SOM stocks as substrates. The analogous trend is also observed when the O and A horizons are removed (O/A Less). Native microbes likely use labile carbon stocks to sustain activity which results in an overall decline in O-alkyl carbon. Interestingly, doubling the litter inputs did not necessarily increase NMR signatures that would be consistent with fresh plant inputs. In Double Litter plots, the NMR spectrum reveals lower O-alkyl carbon in the Double Litter mineral soil samples suggesting that increases in litter fall may have resulted in soil priming and a concomitant decrease in labile SOM stocks. It is also important to note that the alkyl carbon did

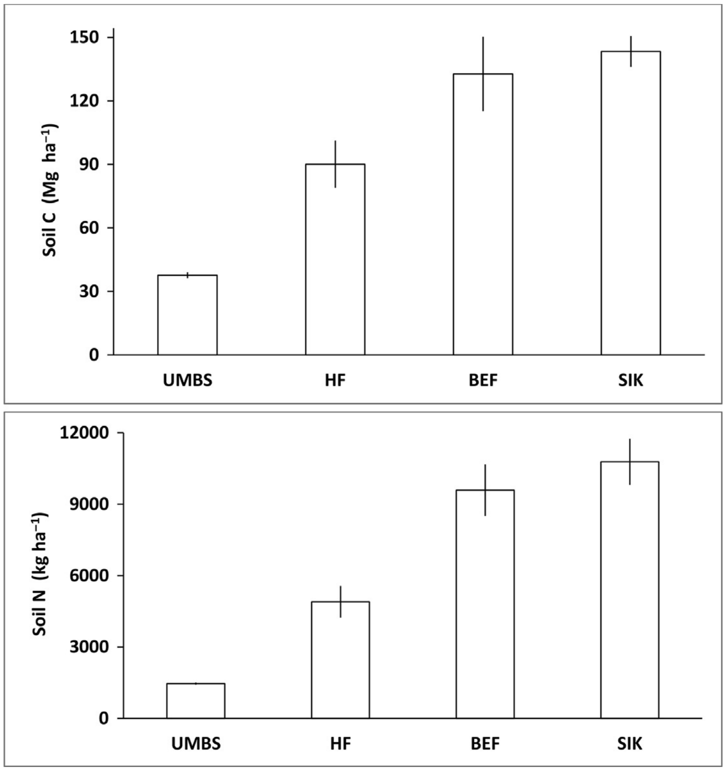

Fig. 4 Soil C and N at the hardwood (*UMBS* = MI; *HF* = Harvard Forest, MA; *BEF* = Bousson, PA; *SIK* = Síkfőkút, HU) DIRT sites. Mean ± SE.

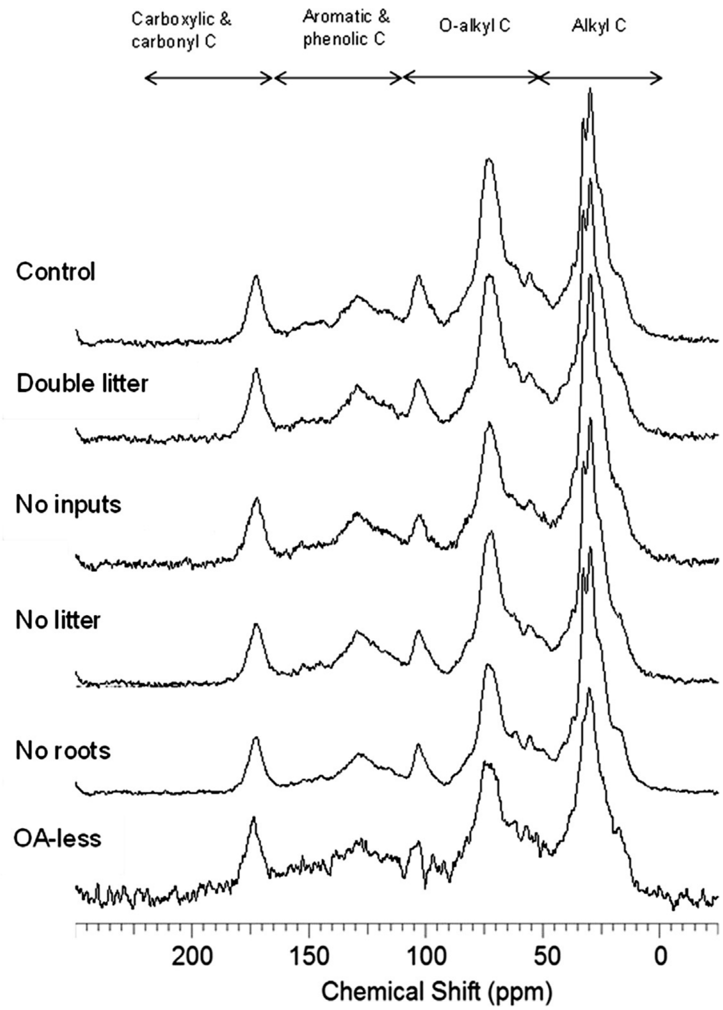

Fig. 5 Solid-state ^{13}C NMR spectra of Harvard Forest mineral soil samples showing the variation in carbon chemistry with DIRT.

Table 3 Solid-state ^{13}C NMR integration results and alkyl/O-alkyl ratios for mineral soil samples from the Harvard Forest DIRT plots.

Treatment	*Alkyl C (0–50 ppm)*	*O-alkyl C (50-10 ppm)*	*Aromatic and phenolic C (110–165 ppm)*	*Carboxylic and carbonyl C (165–215 ppm)*	*Alkyl/ O-alkyl C*
Control	38	39	14	9	0.97
Double Litter	39	36	15	10	1.08
No Inputs	45	31	14	10	1.45
No Litter	43	33	14	10	1.30
No Roots	47	32	12	9	1.47
O/A-less	42	34	14	10	1.24

Values are expressed as percentage of the total ^{13}C signal.

not increase suggesting that plant waxes, which are hypothesized to be biochemically recalcitrant, may have also been susceptible to biodegradation.

Conclusion

Numerous factors influence the quantity and quality of SOM inputs, outputs, and storage, thus soil carbon pools in forests may not respond linearly or immediately to aboveground or belowground litter inputs. Efforts to sequester carbon by managing productivity and associated litter inputs will not likely result in increased carbon storage over short time frames. Research at the DIRT sites also underscores the importance of collaboration at multiple sites, especially for processes that cannot be understood within short study periods.

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Further Reading

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