Soil Organic Matter Formation:
Insights from Chronic Manipulations of Plant Inputs to Soils.

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Soil organic matter (SOM) content strongly influences key soil properties such as aeration, moisture holding capacity, and cation retention in terrestrial ecosystems. SOM also plays a central role in regulating plant growth by immobilizing and releasing nutrients for plant uptake as it is transformed from fresh litter to well-decomposed humus. In addition to its importance within individual ecosystems, SOM constitutes the largest carbon (C) pool in the terrestrial biosphere and is an integral part of the global C cycle (Schlesinger 1977, Schimel 1995). Therefore, changes in SOM formation and decomposition due to climate change, land management, disturbance or other factors can feed back to the climate system by either sequestering CO_2 into organic forms or releasing it to the atmosphere (e.g. (Cox et al. 2001)). The balance between detritus ("litter") inputs to soils and outputs from soils as respired CO_2, dissolved inorganic carbon (DIC), dissolved organic matter (DOM), and erosional losses of particulate organic matter (POM) determines the amount of SOM present in soils within individual ecosystems (Figure 1).

Despite the pivotal roles played by SOM within individual ecosystems and the global C cycle, the factors that determine its formation and dynamics are not well understood. To address this gap, we established a long-term study in of controls on soil organic matter formation in 1990 at the Harvard Forest LTER site in Petersham, Massachusetts, USA. We refer to this experiment as the DIRT (Detritus Input Removal and Transfer) project. Our project **goal** is to ***assess how rates and sources of plant litter inputs control the accumulation and dynamics of organic matter and nutrients in soils***.

The DIRT treatments at Harvard Forest consist of chronically altering above- and belowground litter inputs to permanent plots in a mid-successional oak-maple-birch forest (Fig. 2). The experimental design is derived from a project started in 1957 in forest and grassland ecosystems at the University of Wisconsin Arboretum (Nielsen and Hole 1963). Plots are 3m × 3m plots (n = 3) and are treated (n = 3) as follows:

Treatment	**Method**
CONTROL	*Normal litter inputs are allowed.*
NO LITTER	*Aboveground inputs are excluded from plots by raking.*
DOUBLE LITTER	*Aboveground inputs are doubled by adding litter removed from* NO LITTER *plots.*
NO ROOTS	*Roots are excluded by inserting impenetrable barriers in backfilled trenches to the top of the C horizon.*

NO INPUTS	*Aboveground inputs are prevented as in* NO LITTER *plots; Belowground inputs are prevented as in* NO ROOTS *plots.*
O/A-LESS	*Organic and A horizons are replaced with B horizon soil at the start. Normal inputs are allowed thereafter.*

The DIRT project is developing into a long-term, inter-site experiment. To that end we have forged linkages with similar experiments at sites in a nutrient-rich maple forest in Pennsylvania, at the Allegheny College Bousson Environmental Research Reserve (USA), a temperate coniferous forest at the H. J. Andrews Experimental Forest in Oregon (USA), and a temperate deciduous forest in a region with elevated nitrogen deposition Síkfõkút (Hungary). We hope to develop additional linkages to similar experiments located across climate and soil texture gradients with new sites proposed in a boreal (Cedar Creek, Alaska), a tropical (Luquillo Experimental Forest, Puerto Rico) and southern temperate forest (Coweeta, North Carolina). We anticipate that results from this emerging network of similar experiments will allow an assessment of the importance of physical-climatic as well as biological factors in controlling soil organic matter accumulation. Here we present selected results from the first decade of DIRT manipulations at Harvard Forest to illustrate how chronically altering aboveground litter and belowground root inputs to soils can provide useful information about ecosystem processes at short- and long-term timescales.

Although the DIRT project addresses processes of soil formation operating at time scales ranging from a single decade to centuries, during the initial years of the study we learned much about processes operating at shorter time scales. Some of these processes include root production, temperature sensitivities of rhizosphere (fine roots and closely associated microbes) respiration versus bulk soil respiration, and shifts in belowground community structure.

Selected Results

We used soil respiration budgets based on measurements done during the second year of treatments to estimate carbon inputs to soils from fine roots (Bowden et al. 1993). This analysis suggested that about that yearly C inputs to soils from roots (110 g C ha^{-1} yr^{-1}) at this site were, on average, about equal to C inputs from aboveground litter (138 g C ha^{-1} yr^{-1}). Moreover, CO_2 emissions from the soils due to live root respiration (123 g C ha^{-1} yr^{-1}), root decomposition, and fine litter decomposition were all roughly equivalent.

We found that root+rhizosphere respiration was much more sensitive to seasonal variations in temperature that was bulk soil respiration (Boone et al. 1998). Soil respiration measurements made across growing seasons on plots where roots were allowed to grow (CONTROL, NO LITTER, DOUBLE LITTER) and on plots where root growth was prevented (NO ROOTS, NO INPUTS) showed that Q_{10} values for bulk soils were about 2.4, values for rhizosphere were about 4.6. These findings have important implications for large scale carbon cycling and climate models.

Forest floor structure and function were influenced by treatments as well. For example, C and N concentrations in Oe+Oa horizons (not including fresh litter) had decreased with decreasing inputs after 5 years of treatments (Fig. 3). Treatment related differences in forest floor respiration (Fig. 4) under constant temperature and moisture were even greater than were differences in percents C and N. Information such as this, particularly if collected into the coming decades, will provide valuable information about the proportions of root and leaf litter that are eventually incorporated into soil organic matter (or "humus"). Net N mineralization potentials of forest floor samples incubated in the laboratory also differed according to treatment (Nadelhoffer et al. accepted).

Dissolved organic C (DOC) exports from forest floors to mineral soils varied with the amount and source of litter inputs (Aitkenhead and McDowell). By year 7 of manipulations DOC concentrations were significantly higher in the solutions collected from beneath forest floors in DOUBLE LITTER plots and were significantly lower in O/A-LESS plots (also DOUBLE LITTER > CONTROL = NO LITTER = NO ROOTS > NO INPUTS > O/A-LESS). There were no significant differences in DOC concentrations between treatments in the soil solution collected from the mineral horizon, however. Such information can allow us to quantify the importance of forest floor processes in regulating organic matter retention and accumulation in mineral soils.

Soil community measurements that these plots are dominated by fungi rather than by bacteria, particularly in the organic horizons (Fig. 5). Total fungal biomass varied with leaf litter input, with the highest values in DOUBLE LITTER and the lowest in NO LITTER and NO INPUTS plots. The presence of roots, however, appears not to have changed fungal biomass. Forest floor total bacterial biomass appears to have varied inversely with fungal biomass across treatments, except in DOUBLE LITTER in which both fungal and bacterial biomass were high. Active biomass of both fungi and bacteria were remarkably similar across treatments in forest floors. The strong effects of manipulations on mineralization and respiration (above) suggest that the activities of microbial functional types were influenced by treatments Clearly, neither total, nor active bacterial population size is a good predictor of soil processes. Active fungal biomass did not differ among treatments in forest floors. However, was a strong (but non-significant) trend of lower active fungal biomass in DOUBLE LITTER plots.

Summary

Our manipulations of litter and root inputs to forest soils are aimed at [1] quantifying the proportions of aboveground litter and root inputs that become stored as organic matter with long residence times, [2] quantifying how organic matter formation influences soil properties such as nutrient and water retention, and [3] characterizing how the nutrient supplying capacities of soils are influenced by plant litter and root inputs. These goals will require decades of manipulations to be achieved. We have, however, used results from the first years of the experiment to address important questions about forest ecosystem function. Thus, although the overarching goals are long-term, we have exploited the experiment for short-term benefit as well. This is a key to sustaining the interest necessary for justifying the continued maintenance of the plots. Another important feature of long-term experiments is that the manipulations themselves be simple and require a minimum of effort to maintain. This is the case for the DIRT plots, which require several days of activity to remove and add litter annually to subsets of the plots. More effort is required to establish the plots and to re-trench plots from which roots are excluded (every 8 to 12 years).

Measurements thus far indicate that in our temperate deciduous forest site—

- Inputs to soils from roots are approximately equal to aboveground litter inputs.
- Roots + rhizosphere metabolism is more temperature sensitive than is bulk soil respiration.
- Dissolved organic carbon exports from forest floors are about 10 percent of CO2-C gas losses and are important for driving mineral soil processes.

- Fungal biomass was much greater than bacterial biomass on all plots. However, aboveground litter inputs may be more important substrates for fungi than are roots.
- Effects of above- and belowground inputs on activities microbial functional groups are large, as evidenced by differences in processes among samples from differently treated plots. However, microbial populations are poor predictors of process rates.

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Figures

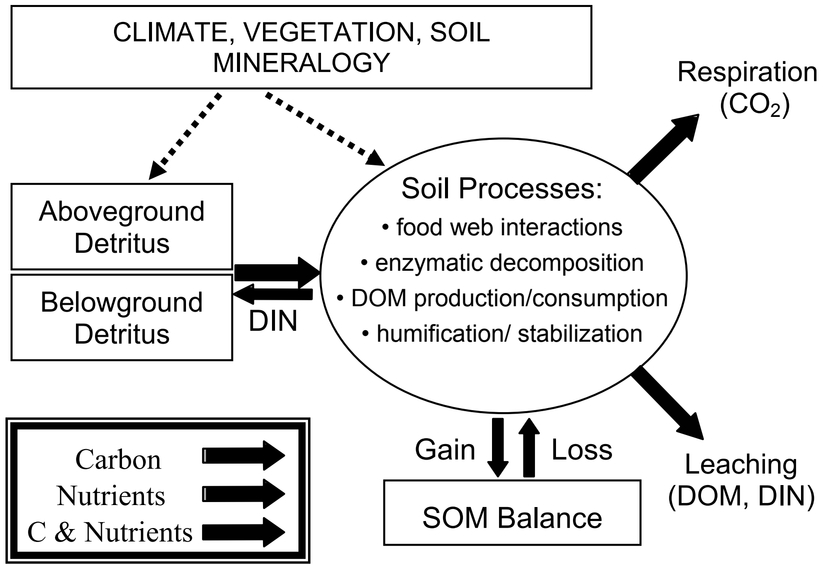

Figure 1. A conceptual model of controls on SOM balances. Dotted arrows show physical influences on detritus production and soil processes. Other arrows represent fluxes as indicated. Organic carbon and nutrients are transferred as detritus and processed in soils. Soil processes, in turn, mineralize organic C to CO_2, organic nutrients to dissolved inorganic nutrients (DIN, which can be leached or taken up by vegetation to influence detritus production), and transform detritus to SOM and dissolved organic matter (DOM). SOM can be further processed by organisms to mineral and dissolved forms.

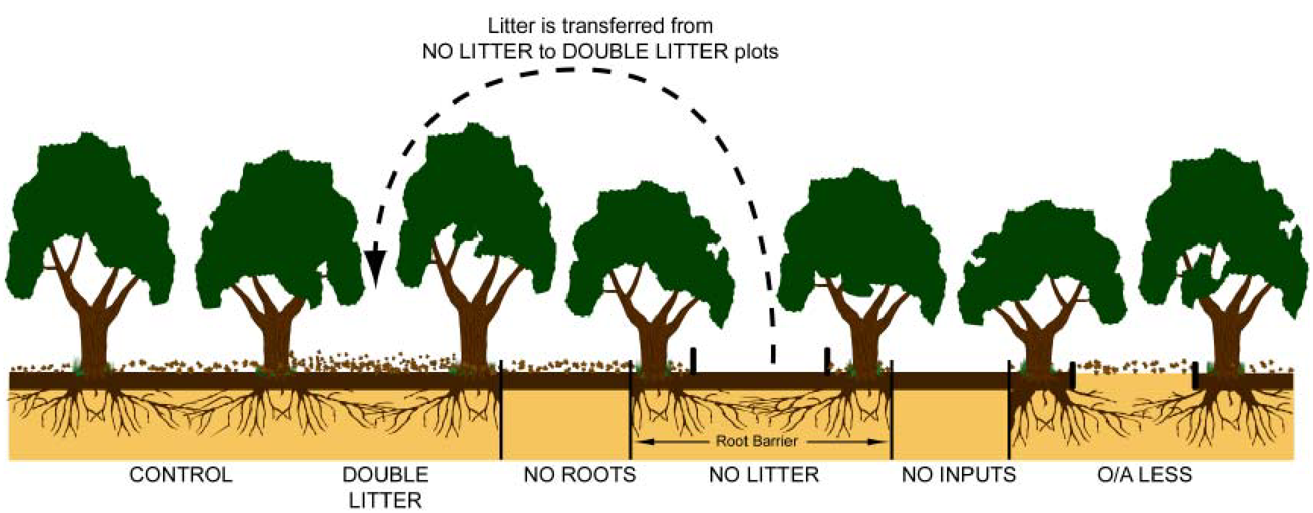

Figure 2. Schematic description of chronic treatments at the Detritus Input Removal and Transfer (DIRT) experiment at the Harvard Forest LTER site. The surface organic horizon (Oea) is shown in dark brown. Mineral soils are shown in aggregate in light brown. From Nadelhoffer et al. *in press*

Figure 3. Percents C and N in forest floor (O horizons) and 0-10cm mineral soil after 5 years of litter and root manipulations on the DIRT plots. Bars show means (n = 9). From Nadelhoffer et al. *in press.*

1991

1995

Figure 4. Cumulative respiration of forest floor materials (Oea horizons) collected from the DIRT plots (A) 1 year and (B) 5 years after the start of manipulations in 1990. Samples were incubated at 22 ºC and -66 kPa moisture. Symbols show means and standard errors (n = 9).). From Nadelhoffer et al. *in press.*

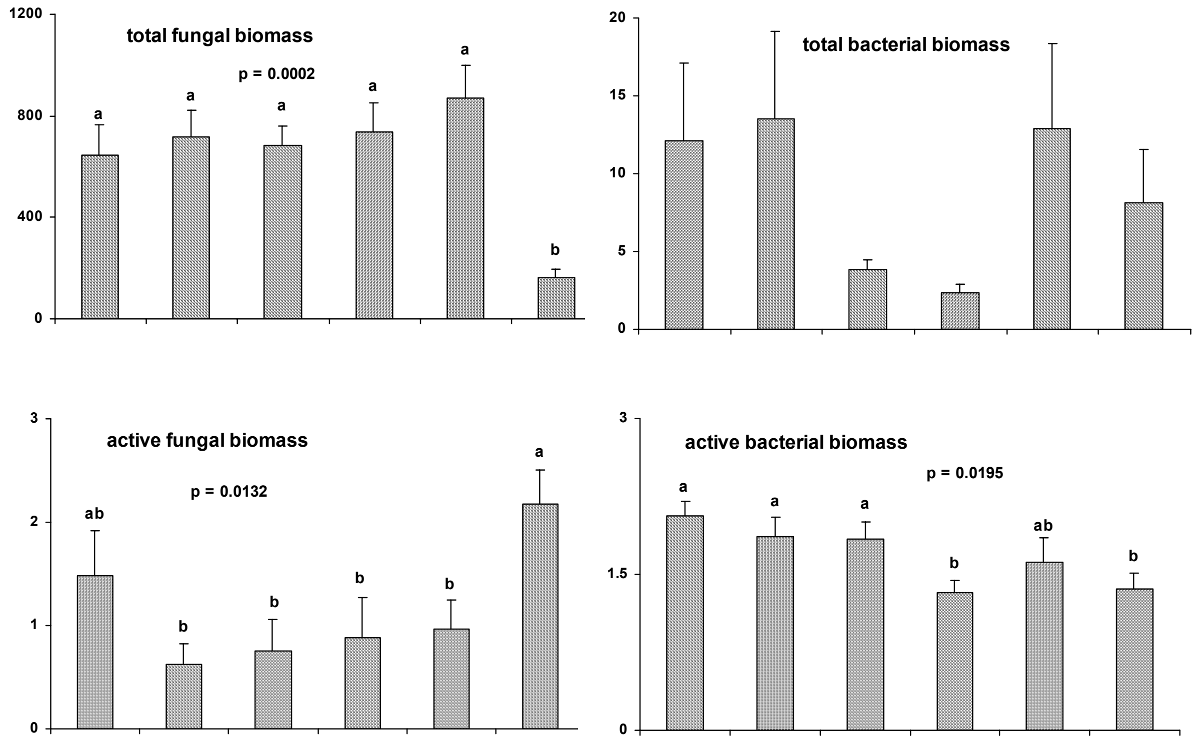

Figure 5. Fungal and Bacterial Biomass in Forest Floors at Year 5 of the Harvard Forest DIRT Manipulations. From Nadelhoffer et al., *in press.*