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Chapter 15.

The DIRT Experiment: Litter and Root Influences on Forest Soil Organic Matter Stocks and Function

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“Oh, I’m hoping for a thousand years at least.”– F. D. Hole’s reply when asked how long his Arboretum plots should be maintained after his retirement.

Rationale and Overview

Soil organic matter is a key component of forest ecosystems. Important soil properties such as moisture holding capacity, aeration, and cation retention are strongly influenced by and typically increase with organic matter content. Organic matter also constitutes major reservoirs of nutrients and fixed carbon in forests that fuel microbial processes and support complex communities of soil and forest floor organisms. Because nutrient cycles are relatively closed in most forests, trees and understory plants depend mainly on the nutrients released from decomposing organic matter to meet their nutritional requirements. Therefore, the amount and the “quality” (decomposability) of soil organic matter influence tree growth and forest dynamics. Inputs of fine litter from aboveground (leaf, twig, buds, reproductive tissues) and from belowground (mostly fine roots) feed back, in turn, to determine the amount and quality of organic matter in forest soils.

Recognition of the importance of feedbacks from plants in determining soil nutrient dynamics and carbon storage has led to a large number of litter decomposition studies. Such studies typically follow decomposition processes for two to five years, or until 40 to 20 percent of the original litter material remains. Much has been learned from such studies about the roles of litter nutrient content and carbon quality in controlling the relatively rapid cycling of nutrients through the litter layer. For example, litter types with large concentrations of soluble carbohydrates and cellulose typically decay faster and both immobilize and mineralize nutrients earlier in the decay sequence than do litter types with high concentrations of lignin and other complex polyphenolic compounds. Also, litter with relatively high nutrient concentrations tend to decompose quickly and to release nutrients to plant available pools more rapidly than do litter types with low initial nutrient concentrations. Because species and tissues often have characteristic litter chemistry, the

litter inputs to soils from various species within a forest ecosystem partially regulate the rates at which nutrients become available to plants.

Far less is known about the fate of plant litter and its role in determining soil organic matter content and function over time scales ranging from 5 years to decades and centuries. Because humus (well-decomposed organic matter) typically contains most of the growth limiting nutrients and at least half of carbon in forest ecosystems, the lack of information about how plant processes influence humus formation represents a critical gap in knowledge about forest functioning. To address this gap, we established a long-term study of controls on soil organic matter formation: the DIRT (Detritus Input Removal and Transfer) project. The **goal** of the DIRT project is to *assess how rates and sources of plant litter inputs control the accumulation and dynamics of organic matter and nutrients in forest soils over decadal time scales.*

Our project is inspired by Professor (*emeritus*) Francis D. Hole's work at the University of Wisconsin Arboretum. Unlike many arboreta, the Wisconsin Arboretum is much more than a horticultural collection. Established in the 1930s, its mission has been to recreate and manage landscapes (or ecosystems) that confronted European settlers in the 19th Century Midwest. In the early 1950s, plant ecologist and Arboretum Director John Curtis challenged a young Dr. Hole to design a long-term study of soil formation within the Arboretum. The idea was that restoration of plant communities required information about soil-forming processes and plant-soil interactions. The interest in control of organic matter accumulation in soils was later included as a core theme of the National Science Foundation's Long-Term Ecological Research (LTER) program. Dr. Hole, recognizing that the university had made a commitment to sustaining the Arboretum as a long-term research site, devised an elegant and powerful experiment to meet this challenge.

Hole sited his study in native oak forests (recovering from occasional partial cutting) and prairies (restored pasture and cropped land). His design called for simple, sustained manipulations of plant inputs to soils, coupled with periodic sampling and assessment of soil structure and properties. Treatments included altering aboveground litter and, in grasslands, root inputs to soils. Treatments at Dr. Hole's plots in the Wisconsin Arboretum's were started in 1956 in the Wingra Woods, Noe Woods, and Curtis Prairie ecosystems. They have continued into the present due to diligent efforts of Dr. Hole, Arboretum staff, students, and community volunteers over the past four decades. We were granted the privilege of sampling at the Wisconsin forest plots in 1984 and again, in grassland and forest plots, in 1997. Results from the Arboretum plots provide us with valuable long-term information against which the effects of the first decade of treatments at the Harvard Forest can be compared.

We have established the DIRT project as a long-term, intersite experiment. To that end we have developed links with similar and newly established experiments at sites in a nutrient-rich maple forest in Pennsylvania (Allegheny College Bousson Environmental Research Reserve) and temperate rain forest in Oregon (H. J. Andrews Experimental Forest USFS). Our hope is to develop additional linkages to similar experiments located across climate and soil texture gradients. This will allow an assessment of the importance of physical as well as biological factors in controlling soil organic matter accumulation.

Experimental Design

Treatments consist of chronically altering above- and belowground plant inputs to permanent plots in a mid-successional oak-maple-birch forest in Harvard Forest's Tom Swamp tract. The plot design is modified from that of an experiment started by Francis Hole in 1956 at the University of Wisconsin Arboretum (*above*) and continued through the present. Harvard Forest treatments (Fig. 1) were started in the fall of 1990 and are as follows:

| <u>Treatment</u> | <u>Manipulation</u> |
|------------------|---|
| CONTROL | (normal litter inputs) |
| DOUBLE LITTER | (twice aboveground litter inputs) |
| NO LITTER | (aboveground litter excluded from plots) |
| NO ROOTS | (roots excluded from plots by lined trenches) |
| NO INPUTS | (no aboveground litter and no roots) |
| O/A-LESS | (organic and A horizons replaced with B horizon soil, normal inputs thereafter) |

Plots are replicated (3m × 3m each, n = 3) and are located beneath an intact forest canopy. No tree boles are present on the plots and ground flora is removed as needed by clipping and occasional herbicide applications. Aboveground litter is excluded from NO LITTER plots with mesh fabric. Aboveground litter inputs are augmented in DOUBLE LITTER plots by adding litter taken from NO LITTER plots. Root growth is prevented in the NO ROOTS treatment by lining backfilled trenches (dug into the C horizon) with inert barriers. The NO INPUTS treatment is a combination of the NO LITTER and NO ROOTS treatments. In the O/A-LESS treatment, soils were experimentally impoverished by replacing the forest floor and 0-15 cm mineral soil with B horizon material. The O/A-LESS treatment does not involve manipulations beyond the initial treatment. This treatment is intended to allow estimation of 1) the fraction of total litter inputs (above-plus belowground) that are eventually transferred from litter to SOM and 2) the time course required for impoverished soils to recover to pre-disturbance conditions.

Our field measurements will allow us to quantitatively link changes in soil properties and processes to the amounts of fixed carbon (energy) and nutrients entering soils. The value of this information will increase greatly as the manipulations continue into the next millennium. Field measures include CO₂ fluxes from forest floors (LICOR and soda lime), soil moisture and soil temperature. Soil solutions are collected from beneath the forest floor (zero tension lysimeters) and at 30-40cm depth (Prenart® suction lysimeters). Solutions are analyzed for ammonium, nitrate, phosphate, dissolved organic carbon (DOC) and dissolved organic nitrogen (DON). We also collect samples periodically to track changes in forest floor and soil organic matter and nutrient contents. Soils were sampled from the plots at the inception of treatments in 1990 and again after 1 (1991) and 5 years of treatment (1995). We plan to sample after 10 years of treatment and once per decade thereafter. Samples (forest floor, 0-10cm mineral soil, 10-15cm mineral soil) are assayed for total soil organic matter, C, N, and nutrient contents and for standard soil properties (acidity, cation exchange capacity, base saturation, mineral soil

texture). We have also measured CO₂ release and net N mineralization and nitrification under constant temperature and moisture conditions and gross N fluxes using ¹⁵N pool dilution methods on the samples collected in Years 1 and 5. As with the field measures, laboratory results are used to quantify the effects of plant litter inputs treatments on biological processes and C and N dynamics.

Soil community structures were analyzed in subsamples from our Year 5 collections. Microbes (bacteria and fungi) and microfauna (protozoa and nematodes) were counted and classified into functional categories (protozoa as flagellates, ciliates, and amoebae; nematodes by feeding type) to assess the effects of litter and root inputs on forest floor and soil community structures.

Initial Results

Although DIRT addresses long-term questions about soil organic matter formation, plant-soil interactions and nutrient cycling, results from the first years of manipulations proved useful for addressing unanswered questions about important ecosystem processes. Processes investigated in the initial years of the study were fine root production, temperature sensitivities of rhizosphere (fine roots and closely associated microbes) respiration versus bulk soil respiration, and shifts in belowground community structure.

Partitioning Soil CO₂ Flux– Measuring fine root production, decomposition and respiration are among the most problematic issues in ecosystem studies. We used field measures of soil respiration in the first year after the start of manipulations and mass balances to estimate these processes. Soil respiration on control plots (371 g CO₂-C m⁻² yr⁻¹) was partitioned into contributions from live root respiration and from decomposition of ≤1-year-old aboveground litter, >1-year-old aboveground litter and root litter (Fig. 2) as follows: Live root respiration (123 g CO₂-C m⁻² yr⁻¹) was estimated as the difference between respiration on CONTROL and NO ROOTS plots. Contributions to soil respiration from aboveground litter (recent plus old) were assumed equal to annual C inputs from litterfall (138 g CO₂-C m⁻² yr⁻¹). This value was further partitioned into contributions from recent litter (43 g CO₂-C m⁻² yr⁻¹; the mean of differences in respiration between CONTROL and NO LITTER and between DOUBLE LITTER and CONTROL treatments) and older litter (95 g CO₂-C m⁻² yr⁻¹). Annual fine root production was assumed equal to CO₂-C released from decomposing organic matter derived from roots (110 g CO₂-C m⁻² yr⁻¹) which was estimated as total soil respiration on CONTROL plots minus the contributions of live root respiration and decomposing organic matter from aboveground litter (old and new).

This mass balance approach indicated that live root respiration, production of aboveground fine litter (leaf, twig and other fine litter) and fine root detritus each constituted about one-third of C inputs to soil in this stand. This suggests that fine root and leaf litter production are approximately equal in this forest type. Importantly, this finding narrows the range of uncertainty in estimating fine root production and suggests a method that can be applied elsewhere.

Temperature Regulation of Rhizosphere vs. Bulk Soil Respiration– Soil respiration is a critical process in global-scale as well as local-scale analyses of biogeochemical cycles.

Models of the global C cycle used to predict ecosystem-atmosphere interactions in warmer climates are sensitive to variations in the relationship between soil respiration and temperature. However, regional and global simulation models typically use a single exponential function (“ Q_{10} ”) to predict releases of CO_2 to the atmosphere from soil respiration. Comparisons of soil respiration on treated plots in Year 4 (Fig. 3) showed that respiration by fine roots and associated rhizosphere organisms is more responsive to temperature than is bulk soil respiration. The Q_{10} value for the roots and rhizosphere (4.6) was significantly greater ($p < .05$) than the Q_{10} values for both the Controls (3.5) and the treatments without roots (NO ROOTS = 2.5, NO INPUTS = 2.3). Q_{10} values changed little and non-significantly with either addition or exclusion of leaf litter. The findings suggest that soil respiration should be most sensitive to temperature in systems in which roots contribute a large portion of total soil CO_2 efflux. This finding has important implications for global carbon cycling models

Litter Effects on Dissolved Organic Carbon– Soil solutions were collected after each rain event during Year 4 (1994) and Year 7 (1997) growing seasons. In Year 4 there were no significant differences in DOC concentration between treatments, and within-treatment variance was large (Fig. 4). By Year 7, DOC concentrations were significantly higher in the solutions collected from DOUBLE LITTER plots and were significantly lower in O/A-LESS plots (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 in either year. Results from the forest floor lysimeters suggest that changes in organic matter availability cause changes in soil solution organic chemistry within a less than a decade. In contrast, we infer from the mineral soil data that DOC losses to surface waters are relatively insensitive to changes in forest floor organic matter dynamics. These results indicate that DOC exports from mineral soil horizons are less sensitive or respond more slowly to amounts of litter input. However, differences in DOC inputs to mineral soils relative as controlled by amounts of litter inputs are likely to influence C accumulation in mineral horizons.

Cumulative Effects on Soil Properties– Changes in processes observed in the field during the initial years of manipulations were consistent with changes in soil properties and processes observed 5 years after the start of treatments. At the 5-year time scale, for example, forest floors C and N percentages showed trends of increasing or decreasing with increases or decrease in aboveground litter and root inputs (Fig. 5). Mineral soils, however, did not show similar trends. Mineral soils are less responsive to manipulations of plant inputs because most inputs are to forest floors. Also, mineral soil organic matter is likely more stabilized than is forest floor organic matter.

Cumulative Effects on Soil Processes: Laboratory Incubations– Laboratory incubations of forest floor samples collected in Year 5 were consistent with field measures showing large effects on organic matter quality and microbial processes (Fig. 6a). Doubling aboveground litter inputs increased 6-month laboratory respiration by about 40 percent relative to respiration of samples from plots with normal (CONTROL) litter inputs. Preventing root ingrowth (NO ROOTS) on plots decreased respiration of incubations by 43 percent relative to controls. Exclusion of aboveground litter and root inputs for five

years (NO INPUTS) decreased cumulative respiration by almost two-thirds relative to controls. These patterns are consistent with field results (Fig. 2) indicating litter inputs from aboveground and from roots are approximately equal. Respiration of samples from the NO LITTER plots, however, was not reduced as much as would be expected given the large increase in respiration after doubling litter inputs. Curiously, doubling litter inputs increased respiration much more than exclusion of litter inputs decreased respiration. This suggests that additional litter inputs might stimulate or enhance decomposition of more recalcitrant organic matter. Patterns of DOC release from incubations in response to 5 years of treatment were similar to those of respiration (Fig. 7). Moreover, cumulative DOC release was about one-tenth of CO₂-C release and showed overall patterns similar to those obtained in the field from lysimeters (Fig. 4)

Net N mineralization (DIN release in sequential leachings) under laboratory conditions was also influenced by five years of plot manipulations (Fig 8a). However, differences in mineralization among incubations of samples from treated plots were not as consistent or as pronounced as were differences in respiration. Cumulative DIN releases from DOUBLE LITTER, CONTROL and NO LITTER incubations were similar. This could indicate that the source of most mineralized N is from leaf litter greater than 5-years-old. However, excluding root ingrowth from the plots, whether alone (NO ROOTS) or in combination with litter exclusions (NO INPUTS), decreased laboratory N mineralization. This suggests that root turnover, root exudation, or both processes contribute strongly over short time scales to mineralization. The absence of roots, while decreasing net N mineralization overall (Fig. 8a), increased net nitrification (Fig. 8b); nitrate-N constituted over half of the DIN released from NO ROOTS and NO INPUTS soils whereas nitrate-N release from soils collected from plots with roots was essentially zero until after 3 months of incubation. We speculate that the absence of roots and competition from mycorrhizal hyphae has allowed nitrifier populations and activity to increase in forest floors and that this activity carried over to laboratory incubations. The lack of response in net N mineralization to variation variations in aboveground litter suggests that microbial immobilization exerts strong control over soil N dynamics.

Cumulative Effects on Soil Communities— As would be expected for a forest soil, these plots are dominated by fungi rather than by bacteria, particularly in the organic horizons. Total fungal to bacterial biomass ratios averaged 200 across all treatments and horizons, with the mean ratios for mineral soils (114) significantly lower than for organic soils (305). The lowest ratios were found in the O/A-LESS mineral soils, where total fungal to bacterial biomass ratios averaged 20. This suggests that the fungal:bacterial ratios decline with increasing recalcitrance of soil carbon.

Total fungal biomass was much greater than total bacterial biomass in forest floors (Fig. 9) under all treatments. 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, there was a strong (but non-significant) trend of lower active fungal biomass in DOUBLE LITTER plots.

Fungal biomass was also greater than bacterial biomass in mineral soils (Fig. 10). Total fungal biomass partially followed patterns of C and N content (Fig. 5): values were significantly lowest in O/A-LESS plots (Fig. 10). In contrast, active fungal biomass was significantly greatest in O/A-LESS plots. This is surprising given that the C content of this B-horizon material is quite low and is presumably more recalcitrant than the C of the 0-10cm mineral soils (mostly A-horizons) in the other plots. The most likely explanation is that disturbance of the soil profile from plot installation broke up soil aggregates, exposing previously physically protected organic matter. Total bacterial biomass was highly variable within treatments, except when roots were excluded (Fig. 10). In the NO ROOTS and NO INPUTS plots, total biomass values and variances were low. This is probably because rhizospheres harbor larger microbial communities than do bulk soils. In contrast, patterns of active bacterial biomass in mineral soils followed patterns of easily degradable organic matter: the O/A-LESS had the lowest C and N contents, followed by the NO INPUTS soils (Fig.5), both of which had low active bacterial biomass (Fig 9).

Protozoan numbers were extremely variable and there were few significant differences among treatments (Fig. 11). Patterns of microbial abundance only loosely matched patterns of protozoan populations. Although protozoa are grazers of both bacteria and fungi, patterns of protozoa numbers appeared more to follow trends in total fungal biomass rather than trends in bacterial biomass. This might be expected in these soils where fungal biomass dominates the microbial community. In organic horizons fungal biomass was greatest in the DOUBLE LITTER and lowest in the NO LITTER treatments; total protozoan numbers were higher in the DOUBLE LITTER treatment than in either NO LITTER or NO INPUTS treatments, but were greatest in the NO ROOTS treatment. This did not correspond to patterns of microbial abundance, and none of these trends were statistically significant. In mineral soils, protozoan numbers were low in the O/A-LESS treatment, corresponding to low total fungi and low C content, but other patterns in protozoa abundances did not match microbial abundance across treatments. Nematode numbers (not shown) were quite variable in organic soils, but were greatest in DOUBLE LITTER and NO ROOTS treatments, closely matching patterns of protozoa. In mineral soils, numbers of nematodes per g soil were very low, but were lowest in the O/A-LESS and in NO ROOTS treatments. Again, patterns again matched those of total protozoa numbers. Nematodes graze on fungi and bacteria as do protozoa. They can also graze protozoa.

The relationships between microbial predators and their prey are complex, and experimental results in the literature have shown that grazers such as nematodes and protozoa can either increase or decrease microflora abundances; these effects appear to be dependent on the particular species of grazer present. However, even where microbial populations have decreased in the presence of a protozoan or nematode predator, rates of

N or C cycling often increase. This makes it difficult to infer ecosystem process from patterns of soil organisms. In the DIRT experiment, patterns of microflora appeared to follow patterns in carbon availability and recalcitrance, with less of a clear pattern seen in higher trophic levels.

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).

As the end of the first decade of manipulations nears, we have learned much.

- Inputs to soils from roots are approximately equal to inputs from aboveground litter.
- Metabolism of roots and rhizosphere organisms are more temperature sensitive than are bulk soil organisms.
- Changes in dissolved organic carbon fluxes from organic to mineral horizons required at least 5 years of litter manipulation.
- Dissolved organic carbon losses from forest floors could be about 10 percent of CO₂-C gas losses and are important for driving mineral soil processes.
- The effects of preventing root ingrowth on microbial processes were greater than the effects of either doubling or preventing aboveground inputs during the first years of the experiment. However, the effects of aboveground and belowground inputs converged somewhat after 5 years of treatment.
- Although net N mineralization rates were lower in samples collected from plots with no roots, nitrification rates were much higher when roots were absent from plots.
- 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.

Acknowledgements

Chance encounters in the early 1980s between Francis Hole and the senior author on bus rides between our east Madison neighborhood and the University of Wisconsin campus motivated the DIRT project. Soils were often the topic of discussion on these rides, but any subject was game. Fellow passengers doubtlessly learned much from Dr. Hole. Our project was inspired by his work. We also thank large numbers of students, Harvard Forest staff, and short-term “volunteers” who helped us set up and maintain the plots. Drs. John Aber and David Foster provided valuable editorial advice. Suzanne Donovan assisted with graphics. In addition to the NSF-LTER program, this project has been funded by the USDA Competitive Grants Program and the US-DOE’s National Institute for Global Environmental Change.

Figures

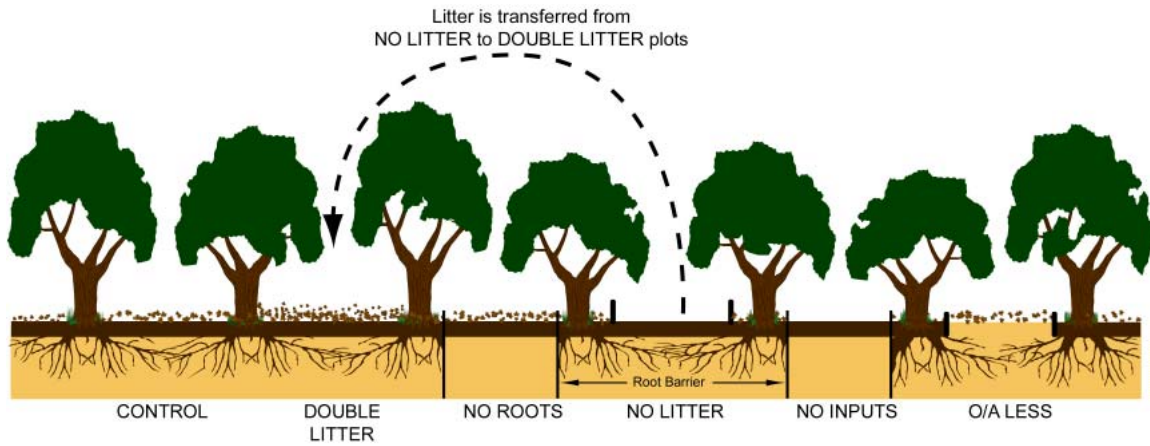


Figure 1. A conceptual diagram of long-term Detritus Input Removal and Transfer (DIRT) experiment at the Harvard Forest LTER site. The surface organic horizon (Oea) is shown in dark brown. Mineral soils are shown in aggregate in light brown.

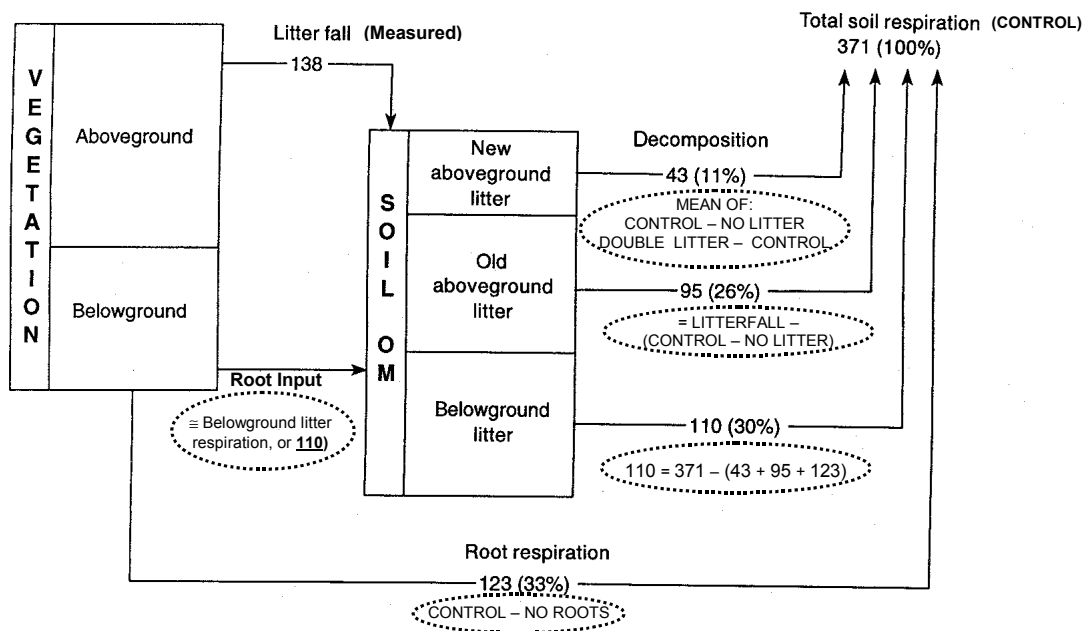


Figure 2. Soil respiration budget for a hardwood forest (the DIRT site) at the Harvard Forest LTER. Ellipses show how live root respiration and decomposition of aboveground litter, both new (previous fall) and old, and decomposition of belowground (mostly fine root) litter were estimated from seasonal CO₂ fluxes made under different treatments. Respiration from decomposing above- and belowground (new + old) litter are assumed equal to annual inputs. Flux measurements were made during the first full year following the start of treatments (See text.). Numbers are fluxes (g C m⁻² yr⁻¹) and percentages of total soil respiration for each component. (Modified from Bowden et al. 1993.)

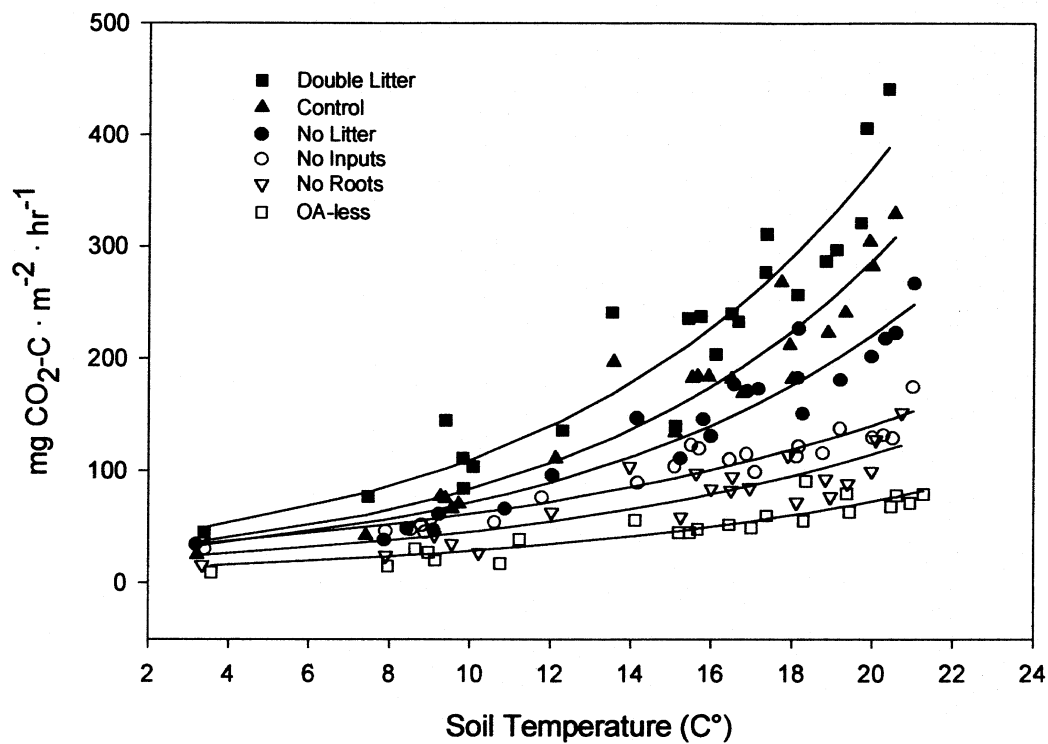


Figure 3. Relationship by treatment between mean daily soil CO₂ flux and soil temperature at 5cm soil depth from 16 June 1994 through 14 June 1995. An exponential function of the form $y = \beta_0 e^{\beta_1 T}$, where y = flux, β_0 and β_1 are fitted constants, and T = temperature, was fitted to the data. Reprinted from Boone et al. (1998).

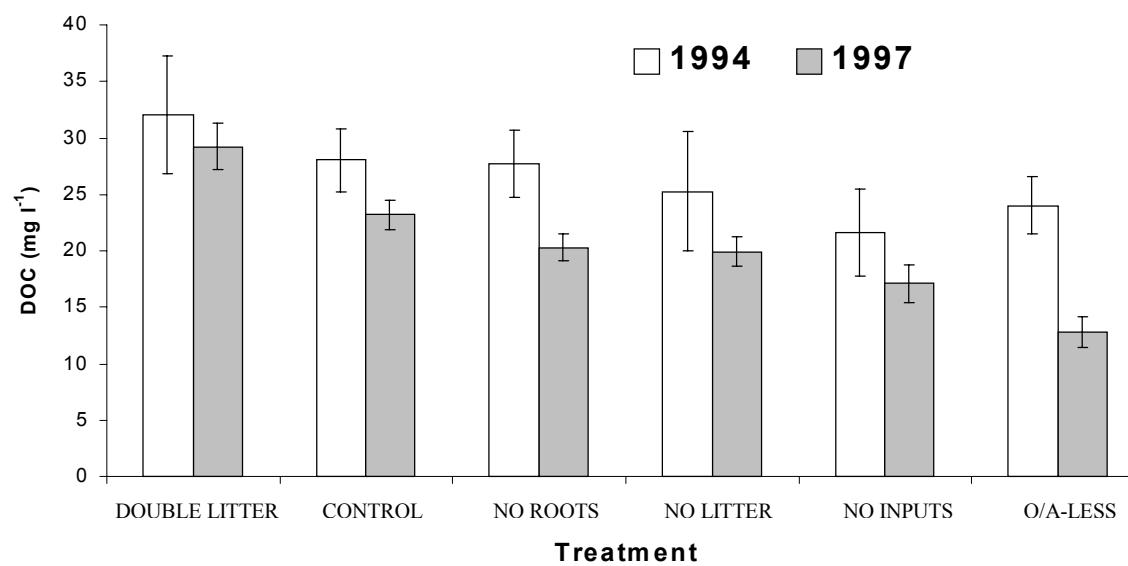


Figure 4. Mean concentrations of DOC (± 1 SE) in solutions collected beneath forest floors in 1994 and 1997. From Aitkenhead and McDowell, *in prep.*

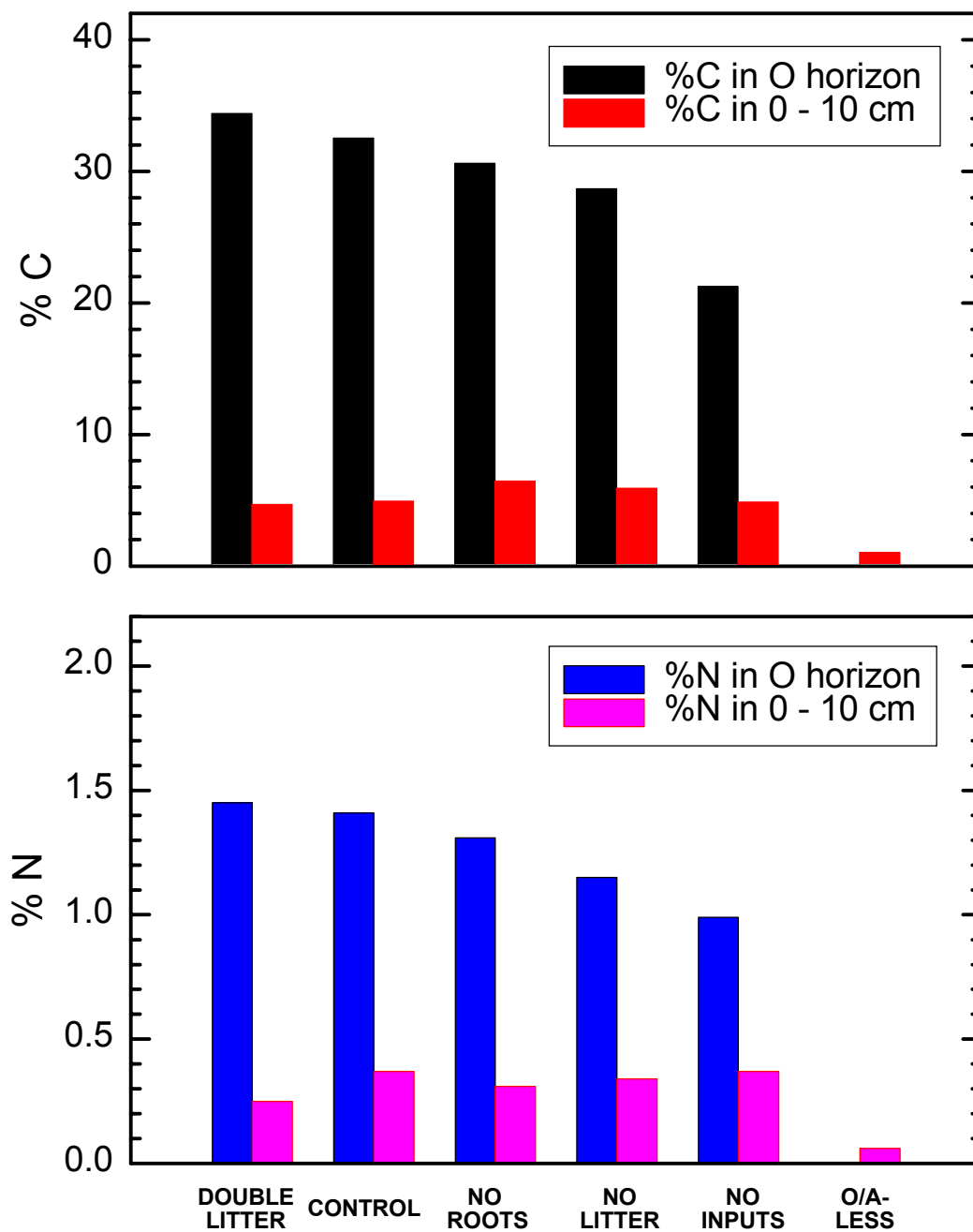


Figure 5. Percents C and N in forest floor (O horizons) and 0-10cm mineral soil after 5 years of litter and root manipulations on the DIRT plots. Bars show means ($n = 9$).

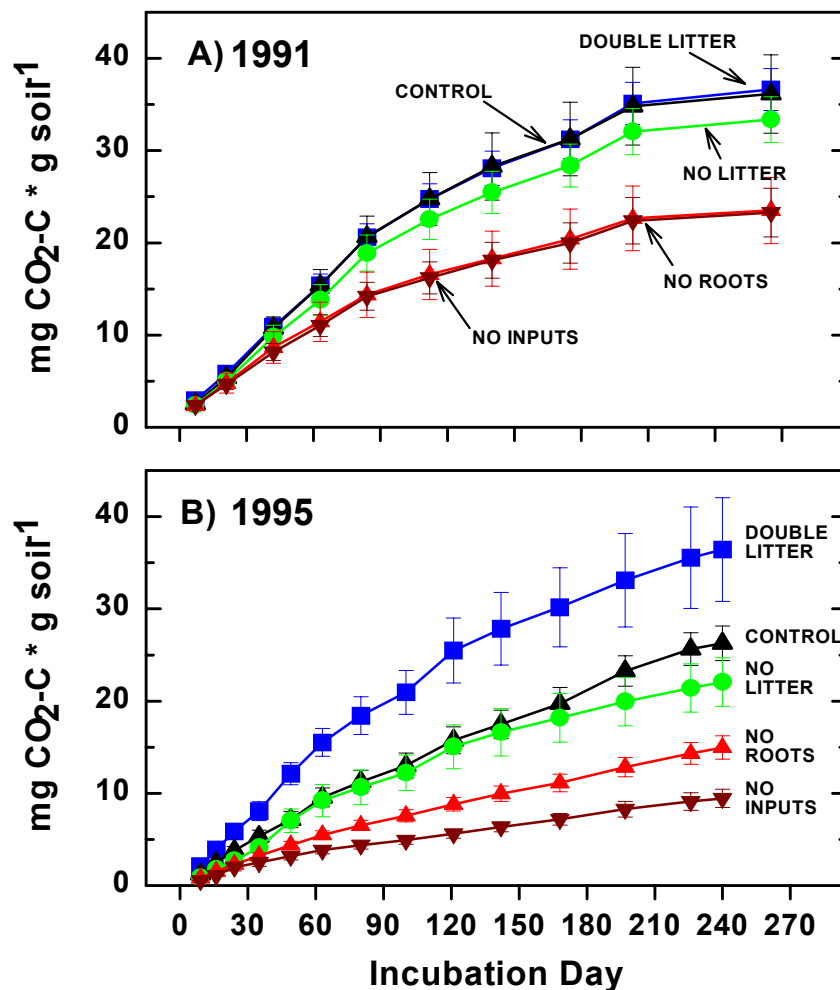


Figure 6. Cumulative respiration of forest floor materials (Oea horizons) collected from the DIRT plots (A) 1 year and (B) 5 years after the start of manipulations in 1990. Samples were incubated at 22 °C and -66 kPa moisture. Symbols show means and standard errors ($n = 9$).

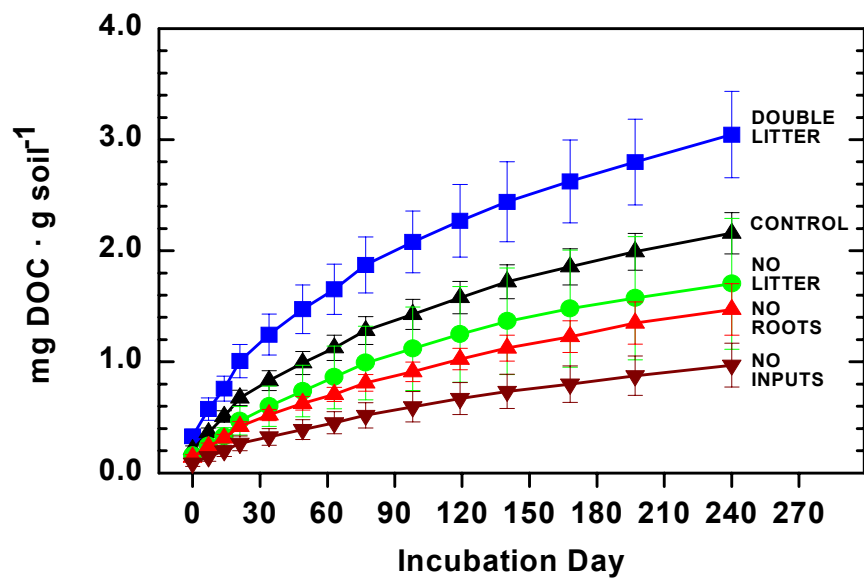


Figure 7. Cumulative dissolved organic carbon (DOC) release from forest floor materials (Oea horizons) collected from the DIRT plots 5 years after the start of manipulations in 1990. Samples were incubated at 22 °C and -66 kPa moisture. Symbols show means and standard errors ($n = 3$ to 4).

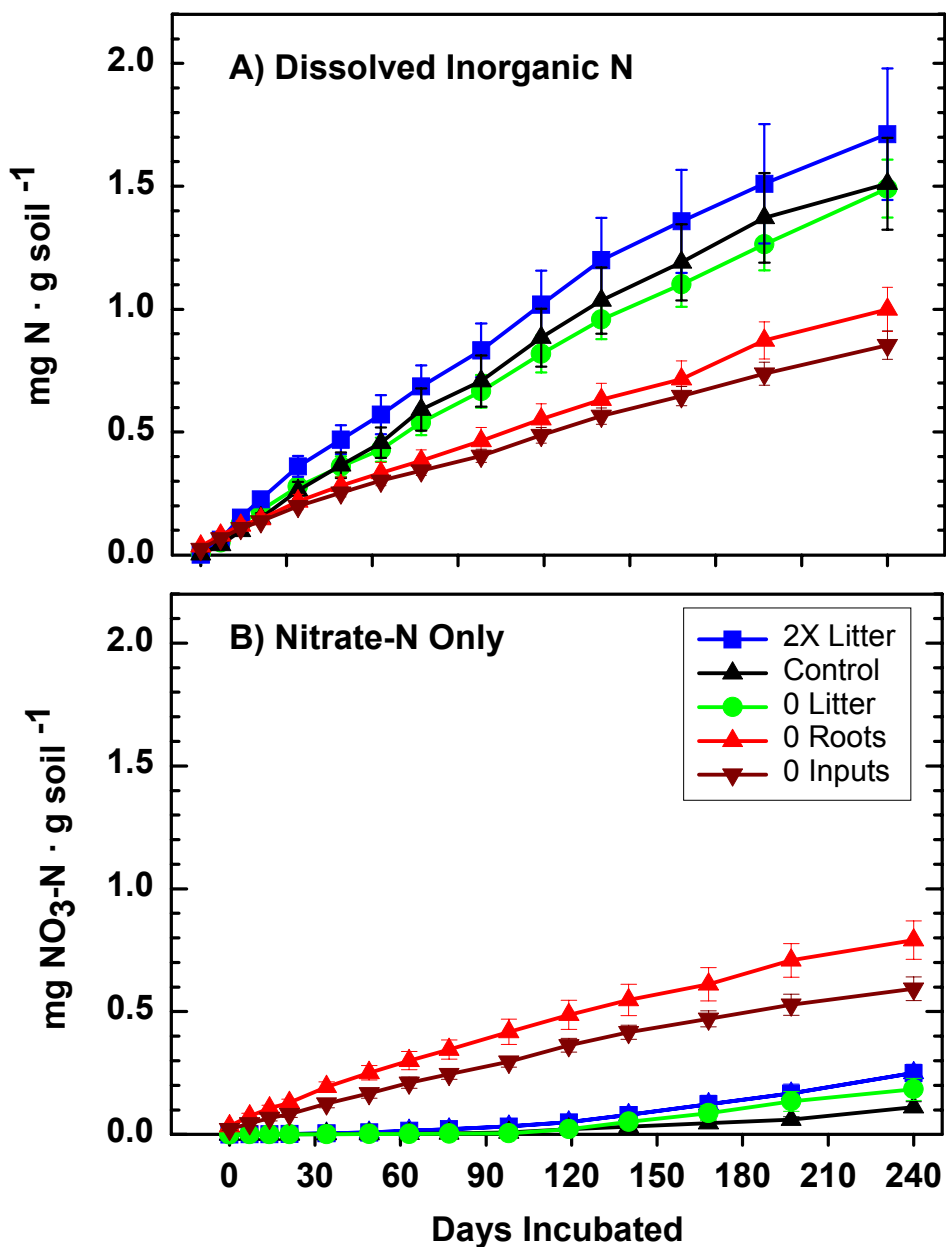


Figure 8. Cumulative (A) dissolved inorganic N (DIN: NH_4+NO_3) and (B) nitrate-N leached from incubations (22°C , -66 kPa moisture tension) of forest floor samples (Oea horizons) collected from DIRT plots after 5 years of manipulations. Symbols show means and standard errors ($n = 9$).

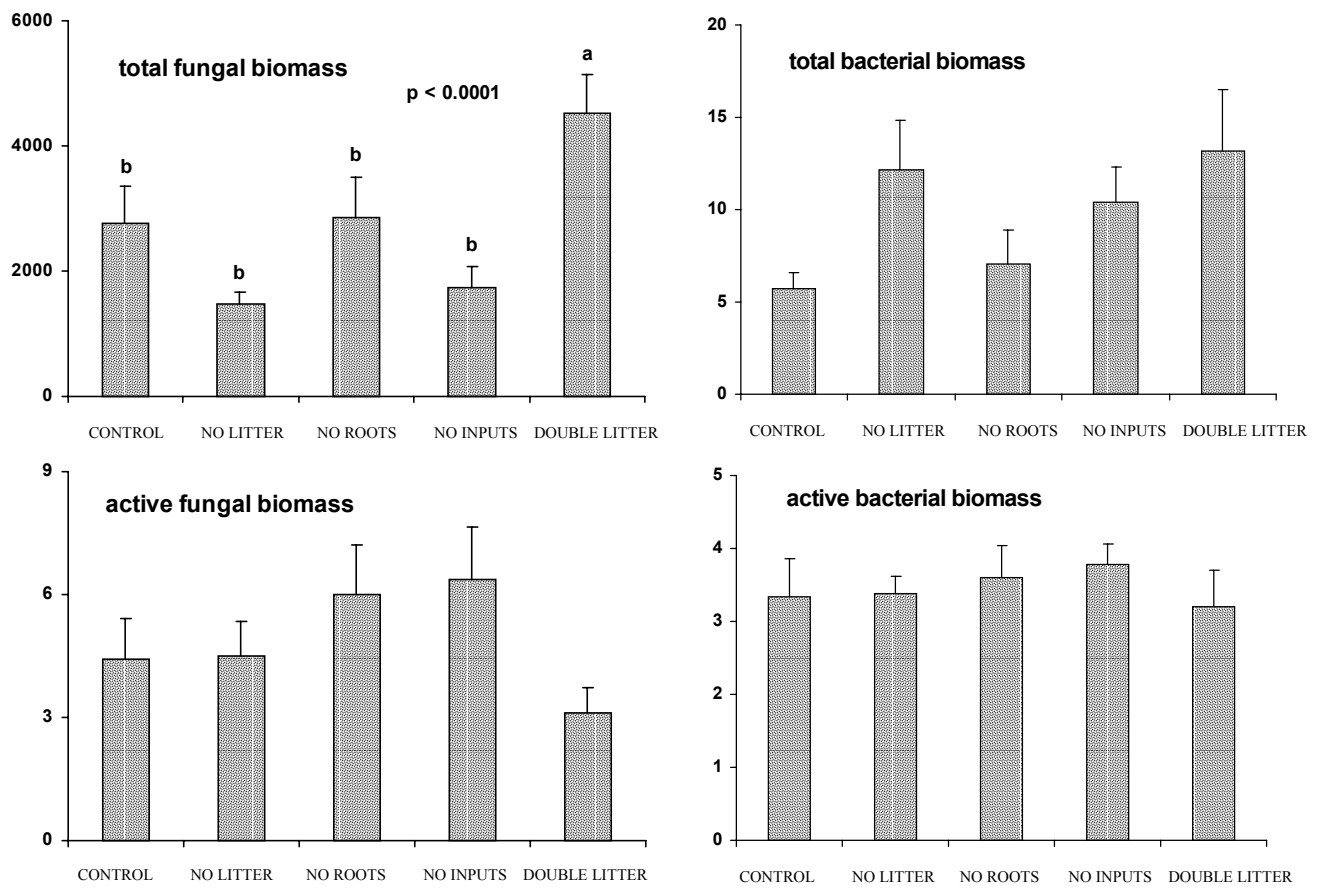


Figure 9. Fungal and Bacterial Biomass in Forest Floors at Year 5 of the DIRT Manipulations.

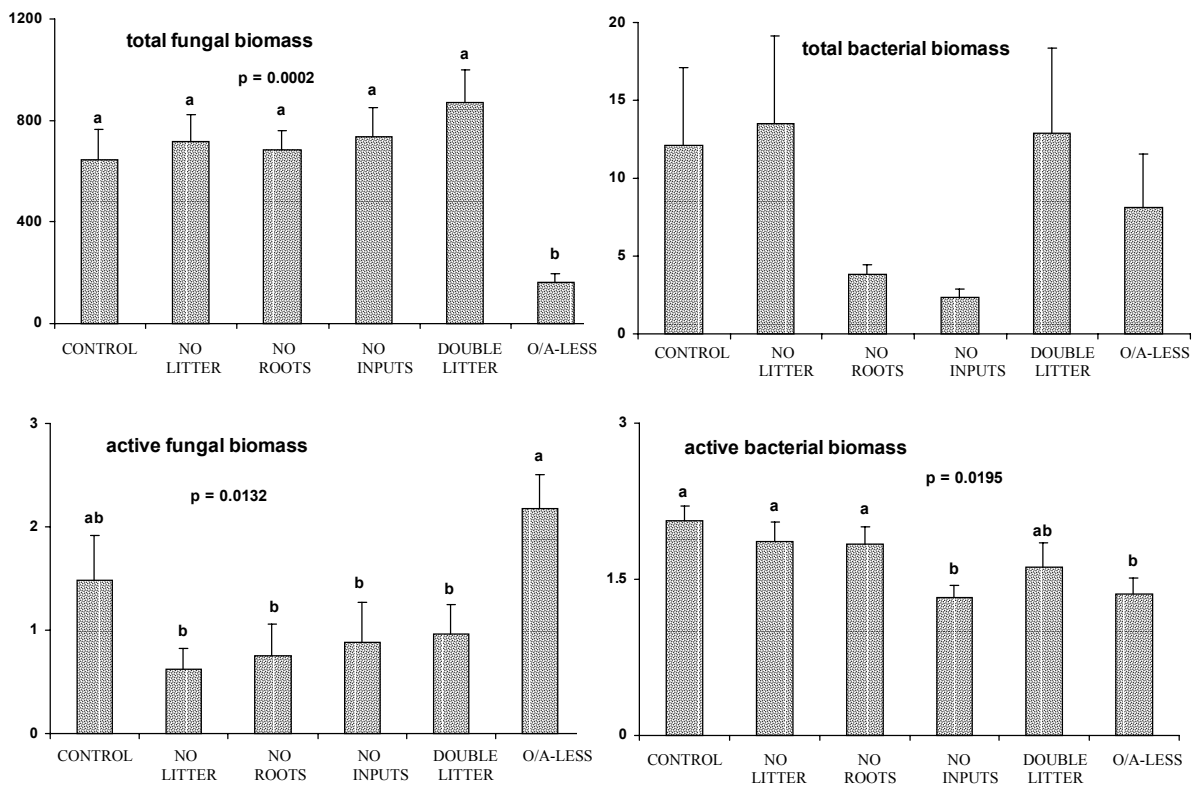


Figure 10. Fungal and Bacterial Biomass in 0-10cm Mineral Soils at Year 5 of the DIRT Manipulations.

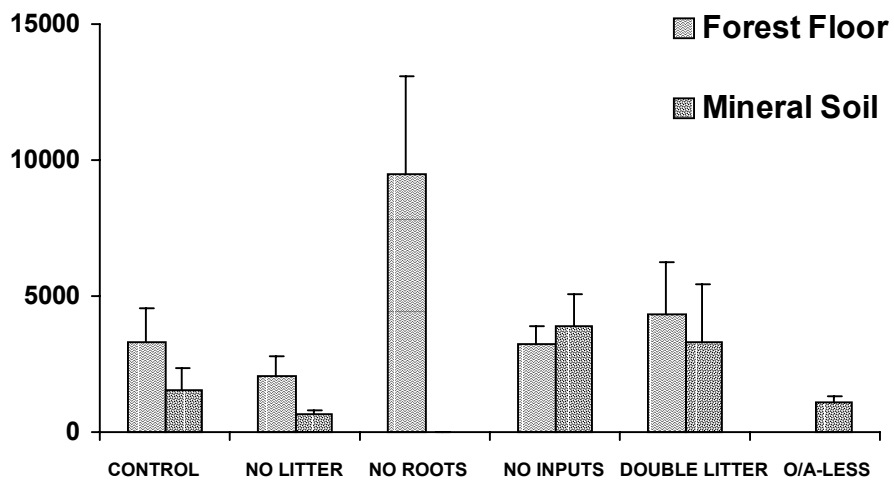


Figure 11. Protozoan Populations at Year 5 of the DIRT Manipulations.