Final Technical Report
Mechanisms Controlling Soil Carbon Sequestration Under Atmospheric Nitrogen Deposition (DE-FG02-03ER63591)

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Abstract: Increased atmospheric nitrogen (N) deposition can alter the processing and storage of organic carbon in soils. In 2000, we began studying the effects of simulated atmospheric N deposition on soil carbon dynamics in three types of northern temperate forest that occur across a wide geographic range in the Upper Great Lakes region. These ecosystems range from 100% oak in the overstory (black oak-white oak ecosystem; BOWO) to 0% overstory oak (sugar maple-basswood; SMBW) and include the sugar maple-red oak ecosystem (SMRO) that has intermediate oak abundance. The leaf litter biochemistry of these ecosystems range from highly lignified litter (BOWO) to litter of low lignin content (SMBW). We selected three replicate stands of each ecosystem type and established three plots in each stand. Each plot was randomly assigned one of three levels of N deposition (0, 30 & 80 kg N ha^{-1} y^{-1}) imposed by adding $NaNO_3$ in six equal increments applied over the growing season. Through experiments ranging from the molecular to the ecosystem scales, we produced a conceptual framework that describes the biogeochemistry of soil carbon storage in N-saturated ecosystems as the product of interactions between the composition of plant litter, the composition of the soil microbial community and the expression of extracellular enzyme activities. A key finding is that atmospheric N deposition can increase or decrease the soil C storage by modifying the expression of extracellular enzymes by soil microbial communities. The critical interactions within this conceptual framework have been incorporated into a new class of simulations called guild decomposition models.

Project History:

With support from the DOE Carbon Sequestration Program (ER 62998 0006115), we initiated a landscape-level study to better understand the biochemical mechanisms by which atmospheric nitrogen (N) deposition could alter soil carbon (C) storage. Our rationale for this work was observations that elevated levels of inorganic N in soil solution can slow the decomposition of litter and humus (Fog 1988, Berg and Matzer 1997) and that this effect is linked to the suppression of microbial oxygenase and peroxidase activities (Carreiro et al. 2000, Saiya-Cork et al. 2002). We hypothesized that atmospheric N deposition has ecosystem-specific effects on soil C storage, because of the varying biochemical composition of plant litter and the varying effects of N on the physiology of soil microorganisms. Our central hypothesis was that N deposition would alter decomposition by suppressing the oxidative decomposition of plant secondary compounds (lignin, tannin) and their diagenetic products (humus) by fungi, thereby shifting this rate-limiting process to less efficient prokaryotes. Such a response should promote accumulation of soil organic matter in ecosystems dominated by highly lignified litter, a prediction first proposed by Berg and Ekbohm (1991). Conversely, greater soil N availability could accelerate decomposition in ecosystems with plant litter low in lignin, because the degradation of cellulose is a N-limited process (Sinsabaugh et al. 2002).

In 2000, we began evaluating these hypotheses, using a variety of approaches, in three types of northern temperate forest that occur across a wide geographic range in the Upper Lake States region. These ecosystems range from 100% oak in the overstory (black oak-white oak ecosystem; BOWO) to 0% overstory oak (sugar maple-basswood;

SMBW); the sugar maple-red oak ecosystem (SMRO) has intermediate oak abundance. These ecosystems span a range of litter biochemistry from highly lignified litter (BOWO) to litter of low lignin content (SMBW). In each ecosystem type, we studied three replicate stands, which allow us to generalize responses to experimental N deposition by these three widely occurring forest types.

In April 2000, we established three plots in each stand, and randomly assigned them to three levels of N deposition (0, 30 & 80 kg N ha^{-1} y^{-1}). Nitrate is the dominant form of N entering these ecosystems (Burton et al. 1991), and we imposed our N deposition treatments using six equal increments of $NaNO_3$ applied over the growing season. Our treatments were designed to simulate chronic rates of NO_3^- deposition in the northeastern U.S. (30 kg N ha^{-1} y^{-1}) and Europe (80 kg N ha^{-1} y^{-1}; Bredemeier et al. 1998).

Results:

With support from the DOE Office of Science (BER) Carbon Sequestration Program, we have made substantial progress understanding *how* and *why* atmospheric N deposition alters leaf litter decomposition, the degradation of lignin and cellulose, the metabolic activity of soil fungi and bacteria, and, ultimately soil C sequestration. Our key finding is that atmospheric N deposition can *increase or decrease the soil C storage by modifying the expression o f extracellular enzymes by soil microbial communities* (Gallo et al. 2003, Waldrop et al. 2003a). From experiments ranging from the molecular to the ecosystem scales, we have established a conceptual framework that describes the biogeochemistry of soil carbon storage in N-saturated ecosystems as the product of interactions between the composition of plant litter, the composition of the soil microbial community and the expression of extracellular enzyme activities. This framework allows us to understand the basis of ecosystem-specific responses to increased atmospheric N deposition that lead to changes in soil carbon sequestration. The key interactions within this framework have been incorporated into a new class of simulations called guild decomposition models.

The principal elements of our synthesis are:

(1) Increased atmospheric N deposition alters the extracellular enzyme activity (EEA) of soils in an ecosystem-specific manner.

(2) Within litter and mineral soil horizons, increased N deposition tends to increase cellulase and phosphatase activities and decrease oxidative enzyme activity (laccase, peroxidase).

(3) The magnitude of EEA responses is a function of microbial community composition and litter biochemistry.

(4) Opportunistic microorganisms growing on low lignin or newly senescent plant material respond to increased N availability by increasing expression of cellulose-degrading enzymes, contributing to faster rates of mass loss and organic matter transformation.

(5) Microorganisms that degrade lignocellulose (defined as the Decomposer guild) or humus (defined as the Miner guild) respond to N enrichment by decreasing expression of oxidases and peroxidases needed for the degradation of

aromatic carbon, contributing to the slowing of decomposition and an accumulation of soil organic matter.

(6) At the ecosystem scale, the magnitude of the oxidative EEA responses is tied to the abundance of Basidiomycota.

(7) Within ecosystems, the abundance and diversity of laccase (a broadly distributed class of phenol oxidase enzymes) genes does not respond to increased N deposition, indicating the changes in these activities are the result of altered gene expression rather than changes in microbial community composition.

(8) Long term increases in N deposition rate may lead to changes in microbial community composition, but these changes are small in comparison to the differences across ecosystem types.

(9) Because the biochemical composition of plant litter inputs and the composition of soil microbial communities varies across ecosystem types, the net effects of increased N deposition on decomposition and carbon sequestration also vary.

(10) Changes in EEA expression as a result of increased N deposition alters the composition of soil organic matter and its distribution within the soil matrix. These effects include increased concentrations of dissolved organic carbon and phenolic carbon.

(11) The relationships between EEA, decomposition rates and organic matter composition are strongest in the litter and coarse soil fractions.

(12) Our modeling approach includes many of these nonlinear and threshold responses of the decomposer-decomposition system and thus generates many of the divergent patterns of system behavior in response to N regime.

(13) Modeling results suggest that the state of the system with respect to many dynamic features (e.g., amount and composition of litter chemistry, amount and composition of decomposer community, N availability) influence both the magnitude and direction of system response to N addition.

In summary, increased N deposition alters EEA within the O and A horizons of soil. The magnitude of these effects depends on microbial community composition. The net effect of EEA changes on the decomposition process depends on the biochemical composition of litter inputs. The ultimate effect these biogeochemical changes on soil carbon sequestration depends on soil texture and the size distribution of organic matter within the soil matrix.

Scientific Training:

This project has trained three postdoctoral fellows (Mark Waldrop, Kirsten Hofmockel, Chris Blackwood), four graduate students (Marcy Gallo, Christian Lauber, Martina Stursova, Tom Weicht), and it has provided nine undergraduate students with summer/academic year research experiences.

Abstracts/Presentations:

Moorhead, D.L. and R.L. Sinsabaugh. 2007. Modeling C dynamics with measurable biological and SOM parameters. Annual meeting of Soil Science Society of America, New Orleans, 4-8, November.

Findlay, SEG, RL Sinsabaugh, DR Zak, GM Lovett, K Smemo, B Dail. 2006. Increased carbon leaching from soils: cause and consequence for aquatic ecosystems. Annual meeting of American Society of Limnology and Oceanography, Victoria, 4-9 June.

Blackwood, C., M. Waldrop, N. Seleno, R.L. Sinsabaugh, D.R. Zak. 2005. Poster presentation at Soil Science Society of America annual meeting. Salt Lake City, 6-8 November.

Moorhead, D. L. 2005. Modeling transitions between microbial versus litter control of decomposition. Soil Ecology Society meeting, Argonne National Lab, May.

Gallo, M.E., Sinsabaugh, R.L., Lauber C.L., Stursova, M., and Zak, D.R. 2005. Extracellular enzyme activities differ in distribution and response to simulated N deposition in northern hardwood forests and a semi-arid grassland. Biannual meeting of the Soil Ecology Society, Argonne National Lab, May.

Moorhead, D. and R. Sinsabaugh. 2005. Linking microbial guilds to decomposition: A new modeling approach. Annual meeting of the Ecological Society of America, Montreal, 2-6 August.

Moorhead, D.L. and R.L. Sinsabaugh. 2003. Modeling impacts of N- and polyphenolic inhibition on litter decay. Talk, Annual meeting of Ecological Society of America, Savannah, 5 August.

Sinsabaugh, R.L., D.R. Zak, M. Waldrop, M.E. Gallo. 2003. N deposition, microbial community organization and soil carbon dynamics in north temperate forests. Talk, Soil Ecology Society biannual meeting, Palm Springs, 12 May.

Gallo, M., R. Amonette, C. Lauber, R.L. Sinsabaugh, D.R. Zak. 2003. Microbial community responses to N amendment in north temperate forest soils. Poster, Soil Ecology Society biannual meeting, Palm Springs, 13 May.

Antibus, R.K., C. Lauber, R. L. Sinsabaugh and D.R. Zak. 2003. The impact of nitrogen amendment on glomalin content in soils in three forest communities in lower Michigan, USA. Talk, 4th International Conference on Mycorrhizae. August.

Waldrop, M.W., D.R. Zak, R.L. Sinsabaugh. 2002. N deposition alters C flow in soils through shifts in microbial community composition and function. Talk, annual meeting, Soil Science Society of America, Indianapolis, 12 November.

Peer-reviewed Publications:

Grandy, A.S., R.L. Sinsabaugh, J.C. Neff, M. Stursova, and D.R. Zak. 2008. Carbon Chemistry and Enzyme Activities in Soil Fractions: Ecosystem-Specific Responses to N Fertilization. Submitted.

Lauber, C.L., R. L. Sinsabaugh and D.R. Zak. 2008. Basidiomycete laccase genes in soils from N-amended oak forest ecosystems in northern Michigan USA. Submitted.

Blackwood, C.B., M.P. Waldrop, D.R. Zak, R.L. Sinsabaugh. 2007. Response of basidiomycete lignin-degraders and general fungal community composition to nitrogen deposition in three forest ecosystems. Environmental Microbiology 9(5):1306-1316.

Antibus, R., R.L. Sinsabaugh, D.R. Zak. 2006. The impact of nitrogen amendment of Bradford reactive soil proteins in three forest communities in northern lower Michigan. Plant and Soil 288:173-187.

Stursova, M., C. Crenshaw, R.L. Sinsabaugh. 2006. Microbial responses to long term N deposition in a semi-arid grassland. Microbial Ecology 51(1):90-98.

Moorhead, D.L. and R.L. Sinsabaugh. 2006. A theoretical model of litter decay and microbial interaction. Ecological Monographs 76(2):151-174.

Waldrop, M.P, and D.R. Zak. 2005. Microbial mechanisms controlling dissolved organic carbon production in response to elevated atmospheric nitrogen deposition. Ecosystems 9: 921–933.

Gallo, M.E., C.L. Lauber, S.E Cabaniss, M. Waldrop, R.L. Sinsabaugh, D.R. Zak. 2005. Soil organic matter composition in response to experimental N deposition in northern temperate deciduous forest ecosystems. Global Change Biology 11(9):1514-1521.

Sinsabaugh, RL, ME Gallo, C Lauber, M Waldrop, DR Zak. 2005. Extracellular enzyme activities and soil carbon dynamics for northern hardwood forests receiving simulated nitrogen deposition. Biogeochemistry 75(2):201-215.

Waldrop, M.P., D.R. Zak, R.L. Sinsabaugh. 2004. Microbial community response to nitrogen deposition in northern forest ecosystems. Soil Biology & Biochemistry 36:1443-1451.

Waldrop, M. P., D.R. Zak, R.L. Sinsabaugh, M.E. Gallo and C. Lauber. 2004. Nitrogen deposition modifies soil carbon storage through changes in microbial enzyme activity. Ecological Applications 14:1172-1177.

Sinsabaugh, R.L., D.R. Zak, M. Gallo, C. Lauber, R. Amonette. 2004. Nitrogen deposition and dissolved organic matter production in northern temperate forests. Soil Biology & Biochemistry 36:1509-1515.

Gallo, M, R. Amonette, C.. Lauber, R.L. Sinsabaugh, D.R. Zak. 2004. Short-term changes in oxidative enzyme activity and microbial community structure in nitrogen-amended north temperate forest soils. Microbial Ecology 48:218-229.