

CHAPTER 10

LANDSCAPE AND REGIONAL SCALE STUDIES OF NITROGEN GAS FLUXES

PETER M. GROFFMAN, RODNEY T. VENTEREA, LOUIS
V. VERCHOT, AND CHRISTOPHER S. POTTER

10.1 INTRODUCTION

Nitrogen (N) gas fluxes have great relevance to soil fertility, water quality and air quality. Analysis of these fluxes presents several conceptual and practical scaling challenges because they are mediated by microorganisms at the scale of microns and seconds but have relevance at relatively large spatial (meters to kilometers and larger) and temporal (years, decades) scales. In this chapter, we evaluate three scaling issues that arose as part of an analysis of the effects of N deposition on gaseous N loss from temperate forest ecosystems in the northeastern U.S.

How does this chapter fit into the context of this book and the topic of “scaling and uncertainty analysis in ecology?” It occurs to us that there are three main groups of scientists grappling with scaling issues: (1) those with an inherent conceptual interest in scaling, (2) those interested in micro-scale processes (e.g., N gas fluxes) that are relevant at large scales and (3) those interested in solving large scale problems (e.g., nitrate delivery to coastal waters) that are regulated by micro-scale processes. We fall solidly in the second group, researchers who have been struggling to measure N gas fluxes at micro-scales being asked to evaluate the importance of our results to large-scale problems such as the fate of atmospheric N deposition or nitrate delivery to coastal waters (these knotty problems are defined below). Given that N gas fluxes are miserable to measure at micro-scales (lousy methods, absurd variability over small spatial and temporal scales), we, and most other micro-scale researchers, are uncomfortable scaling our miserable data to larger scales. That is, if you take a bad number measured at a small scale and extrapolate it to a very large scale, do you end up with a “very bad number” or a “big bad number” or what? So, be warned gentle reader, that landscape and regional scale studies of N gas fluxes are “not for the squeamish.” But, given the difficulty of our challenge, we are pleased to contribute to a book that includes representatives from all three scaling

motivation groups. In our view, exchange of ideas and challenges among these groups is the key to making progress in this critically important area of environmental science.

Our case study addresses three distinct scaling challenges: (1) how to account for landscape scale variability in regional studies – an experimental design issue, (2) how to account for the episodic nature of gas flux – a temporal scaling issue, and (3) how to validate landscape and regional scale flux estimates – an uncertainty and validation issue. The experimental design issues that we address are also discussed in the chapters by Wu and Li (Chapters 1 and 2), Bradford and Reynolds (Chapter 6), and Peters et al. (Chapter 7). Li and Wu (Chapter 3) provide a relevant discussion of uncertainty and error analysis that is relevant to our third challenge.

10.2 N GAS FLUXES AND ATMOSPHERIC DEPOSITION – SOME BACKGROUND

Soil-atmosphere N gas fluxes are the most poorly characterized component of the terrestrial N cycle (Mooney et al. 1987, Schlesinger 1997). There are three gases that are produced; nitric oxide (NO), nitrous oxide (N₂O) and dinitrogen (N₂), as a by-product of multiple N transformations that occur in soil (Firestone and Davidson 1989). The most important transformations that lead to gas flux are nitrification, an aerobic process, and denitrification, an anaerobic process. Given that these processes have complex regulating factors and high variability in time and space, N gas fluxes often exhibit extreme variation (Folorunso and Rolston 1984, Parkin 1987, Robertson et al. 1988). Moreover, it is difficult to measure gas fluxes without disturbing the physical soil environment and/or the biological transformations that produce the fluxes, leading to frequent concerns that observed results are artifacts of a particular method (Groffman et al. 1999).

Fluxes of N gases influence several ecosystem (10 m), landscape (100m), regional (>100 km) and global scale processes. At the ecosystem scale, N gas fluxes can deplete soil stocks of inorganic N, an essential, and frequently limiting (to plant growth) nutrient (Vitousek and Howarth 1991). At the landscape scale, these fluxes can prevent or mitigate the movement of excess inorganic N from terrestrial environments (e.g., highly fertilized agricultural fields) into water bodies where they can cause overgrowth of aquatic plants and eutrophication (Lowrance 1998). At regional and global scales, N₂O is a “greenhouse” gas that can influence the earth’s radiative budget and plays a role in stratospheric ozone destruction (Prather et al. 1995). Nitric oxide is a highly reactive gas that is a precursor to tropospheric ozone formation and is readily converted to reactive N and deposited back to the earth’s surface in precipitation (NRC 1992).

In addition to the greenhouse effect, an additional regional scale phenomenon affected by N gas fluxes is atmospheric deposition. Human activities have greatly increased the global production of reactive nitrogen through fertilizer use and fossil fuel combustion, leading to enrichment of the atmosphere and increased rates of reactive N deposition to the earth’s surface (Vitousek et al. 1997). There is concern that enriched deposition can create a series of adverse consequences in the environment, resulting in N “saturation” or an N “cascade” affecting forests,

groundwater and freshwater and coastal aquatic ecosystems (Aber et al. 1989, Galloway et al. 2003). One of these effects may be to enhance N gas fluxes, contributing to the greenhouse effect (N_2O) or increasing ozone levels and N deposition (NO).

The fate of N deposition in terrestrial ecosystems is one of the greatest current mysteries in environmental science. Many studies have found that a very high percentage (>90%) of the N deposited on terrestrial ecosystems is retained, i.e., not exported from the ecosystem via hydrologic pathways (Boyer et al. 2002, van Breemen et al. 2002). The specifics of this vast retention, which consists of N storage in soils and vegetation and gaseous losses, are not well characterized. Quantifying the contribution of N gas fluxes to this retention is of great interest because this N is removed from the ecosystem while N stored in soils and plants remains available for cycling within, and export from, the ecosystem. There is also interest in determining if N gas fluxes could be a sensitive indicator, or early warning symptom of the onset of N saturation.

Previous studies have suggested that N gas fluxes in northeastern forest soils are low (Bowden 1986, Bowden et al. 1991), but only a small number of sites have been studied. Moreover, these studies have, for the most part, only measured N_2O . Fluxes of NO have recently been shown to be much higher than those of N_2O in forest plots receiving long-term experimental N additions (Venterea et al. 2003a). Fluxes of N_2 are basically unknown, but could be an important component of ecosystem retention of atmospheric deposition, with no negative environmental impact.

10.3 A REGIONAL SCALE STUDY OF THE IMPORTANCE OF N GAS FLUXES TO THE FATE OF ATMOSPHERIC N DEPOSITION

We received funding from the US Environmental Protection Agency's Science To Achieve Results (STAR) program on Regional Scale Analysis and Assessment to investigate the "effects of N deposition on gaseous N loss from temperate forest ecosystems." Our project has four objectives: (1) to determine the importance of gaseous loss of N from temperate forest ecosystems, (2) to determine the impacts of N deposition on gaseous loss of N from these ecosystems, (3) to test a mechanistic model that relates N gas emissions to N availability and soil moisture content, and (4) to develop a new and more mechanistic version of the daily NASA-CASA ecosystem model for N gas emissions that can be applied at the regional level using satellite remote sensing and other spatial data sets in a geographic information system (GIS) format. This new simulation model will be used to assess trends in N cycling over gradients of N deposition in the northeast US and to project changes in N gas fluxes with changing air pollution.

The project takes advantage of an N deposition gradient in the northeastern US that runs from West Virginia (high deposition - $\sim 12 \text{ kg N ha}^{-1} \text{ y}^{-1}$) north and east to Maine (low deposition - $\sim 5 \text{ kg N ha}^{-1} \text{ y}^{-1}$). Our approach was to make monthly *in situ* measurements of gas fluxes using chamber ($\sim 0.10 \text{ m}^2$) methods (Venterea et al. 2003a) along with measurements of ancillary N cycle processes at five sites along the gradient: Fernow Experimental Forest, WV, Catskill Preserve, NY, Harvard Forest, MA, Hubbard Brook, NH, and Bear Brook, ME. We then used the

data to modify existing process (hole in the pipe) and ecosystem (NASA-CASA) scale models and then use regional data sets to run the models at the regional scale.

The project presents three distinct scaling challenges: (1) how to account for landscape scale variability at each point along the regional gradient, i.e., how to determine the “representative flux” at each site, (2) how to account for the episodic nature of gas flux, e.g., bursts of flux in response to rainfall events, given a monthly sampling program, and (3) how to validate the landscape and regional scale estimates of flux that we produce given that we have no large-area, independent way to measure flux at landscape and regional scales. In the sections below we discuss how we have addressed each of these scaling challenges.

10.3.1 Challenge #1 – How To Account for Landscape Variability along a Regional Gradient

This challenge arises from the fact that although our five sites are aligned along a marked N deposition gradient, there is considerable natural variability in N dynamics and gas flux at each site due to variation in soils, vegetation, geology, elevation, aspect, and land use history. To establish a “representative flux” at each of our five sites, it was necessary to account for these factors in the selection of our monthly sampling locations.

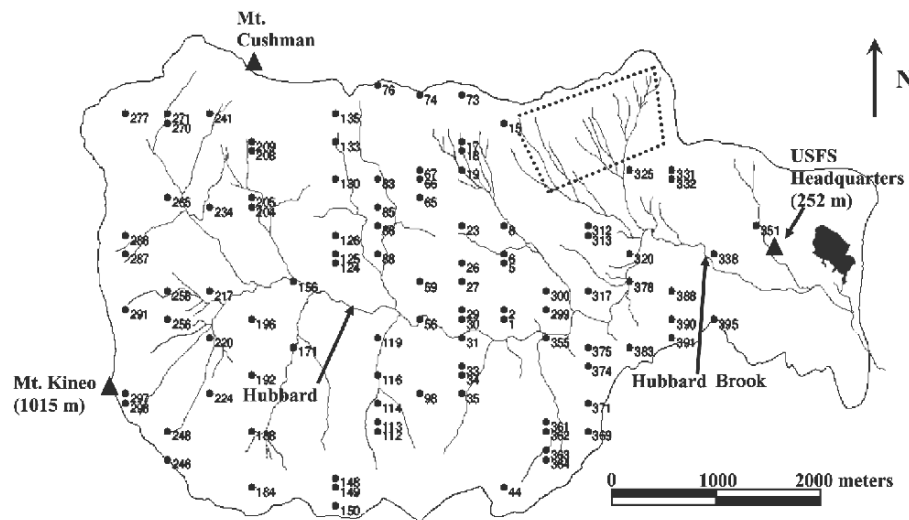


Figure 10.1. The Hubbard Brook Experimental Forest, showing 100 plot locations utilized in the “valley-wide” study. Numbers are plot designations previously established by Schwarz *et al.* (2003). Dashed lines are approximate boundaries of areas used in previous watershed-scale studies (Likens and Bormann 1995). From Venterea *et al.* (2003b).

At the Hubbard Brook Experimental Forest in New Hampshire, we designated the Hubbard Brook valley, a 3,160-ha catchment within the White Mountain

National Forest of central New Hampshire, USA (43° 56' N, 71° 45' W), as the representative landscape unit for this location along our regional N deposition gradient. While the HBEF has been the site of numerous watershed/ecosystem scale studies (Likens and Bormann 1995), the vast majority of these studies have taken place in a series of small watersheds in the northeast corner of the Hubbard Brook valley. For this study, we participated in a multi-investigator effort to characterize variation in ecosystem properties across the entire valley. To accomplish this, we sampled 100 randomly selected plots, a subset of 400 plots that had been established for an earlier valley-wide vegetation study (Figure 10.1, Schwarz et al. 2003), incubated samples in the laboratory, and measured potential net N mineralization and nitrification and N₂O production (Venterea et al. 2003b). We then examined relationships between these N cycle variables, which have been shown to be strongly related to N gas fluxes (Davidson et al. 2002, Venterea et al. 2003a) and landscape parameters (elevation, aspect, dominant tree species).

Our hypothesis was that there were not going to be strong landscape scale patterns in N cycling at Hubbard Brook. The forest is relatively uniform northern hardwood forest composed of yellow birch (*Betula alleghaniensis* Britton), sugar maple (*Acer saccharum* Marsh.), red spruce (*Picea rubens* Sarg.) and American beech (*Fagus grandifolia* Ehrh.) with small amounts of paper birch (*Betula papyrifera* Marsh.), balsam fir (*Abies balsamea*), red maple (*Acer rubrum*), Eastern hemlock (*Tsuga canadensis*), white ash (*Fraxinus americana*), and striped maple (*Acer pensylvanicum* L.) (Schwarz et al. 2003). Soils are acidic (pH 3.5 - 5.5) and consist of well-drained, Typic Haplorthods of sandy loam texture derived from glacial till (USDA 1996). The implications of this hypothesis for our regional project were profound – if sustained, it meant that we could sample anywhere (or at least randomly), e.g., in a nice flat site close to the road, rather than have to establish sites “all over the damn place . . .”

Somewhat surprisingly (given the relative uniformity of soils and vegetation described above), we observed strong, coherent landscape patterns of N cycling across the landscape of the Hubbard Brook valley. All process rates were higher on south facing than on north facing slopes, and at high elevation than at low elevation (Figure 10.2). These patterns were driven by the effects of aspect and elevation on soil moisture and the distribution of vegetation. The results are consistent with many other studies that have found strong patterns in N cycling with elevation and aspect (Schimel et al. 1985, Burke 1989, Groffman and Tiedje 1989, Bohlen et al. 2001).

The nitrification and N₂O fluxes were higher than we expected, with nitrification representing over 50% of net mineralization and N₂O flux representing more than 0.70% of net nitrification. These results suggest that N cycling at Hubbard Brook is relatively dynamic, and that the potential for N gas fluxes is relatively high. These results were surprising given that this site is towards the low end of our regional N deposition gradient and that streamwater nitrate losses at this site are low (Aber et al. 2002).

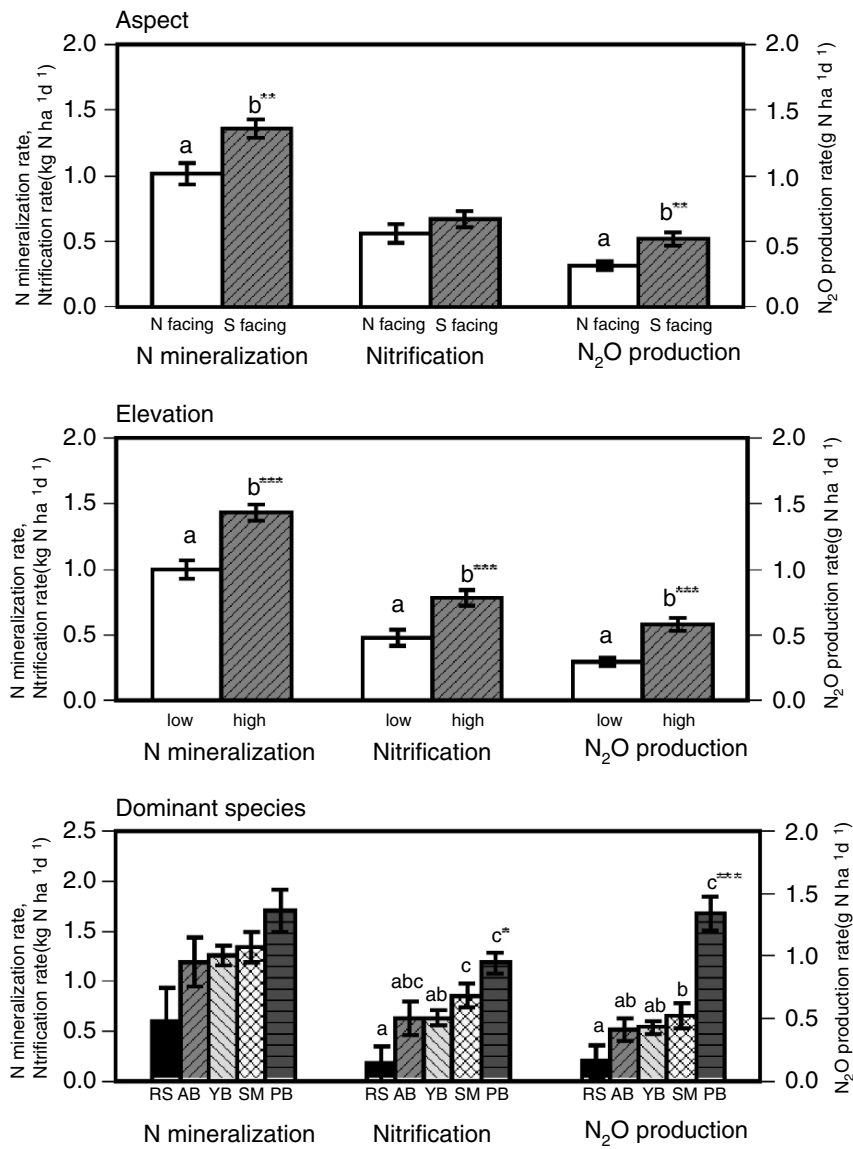


Figure 10.2. Landscape patterns in N cycle processes at the Hubbard Brook Experimental Forest: Top – Aspect, Middle – Elevation (< or > 600 m), and Bottom – Vegetation type (> 50% basal area). Mineralization and nitrification data from Venterea et al. (2003b). RS = red spruce, AB = American beech, YB = yellow birch, SM = sugar maple, and PB = paper birch.

The results from our “valley-wide” study were used as a basis for picking sites for our monthly measurements of *in situ* gas fluxes. They increased our confidence

that we were measuring representative fluxes at this point along our regional N deposition gradient because we had evidence that our design encompassed the major landscape-scale factors influencing flux at this location. This confidence depends on the idea that the laboratory-based potential fluxes that we measured are indicative of field fluxes, which is well supported conceptually and practically (Davidson et al. 2002, Venterea et al. 2003a), and that we have not missed any key landscape-scale factors influencing flux at this point along the gradient e.g., dead moose carcasses may be hotspots of N gas flux. The intensive sampling that we did (100 plots) suggests that this is not the case, but this is impossible to verify (see discussion of our third scaling challenge below; also see Wu and Li, Chapters 1 and 2, Bradford and Reynolds, Chapter 6, Peters et al., Chapter 7, and Wagenet 1998 for discussions of landscape scale experimental designs). We were also left to grapple with questions about the number of sites and measurements necessary to produce well-constrained estimates of flux. Unfortunately, few of our sites for monthly flux measurements were able to be located in flat locations near the road!

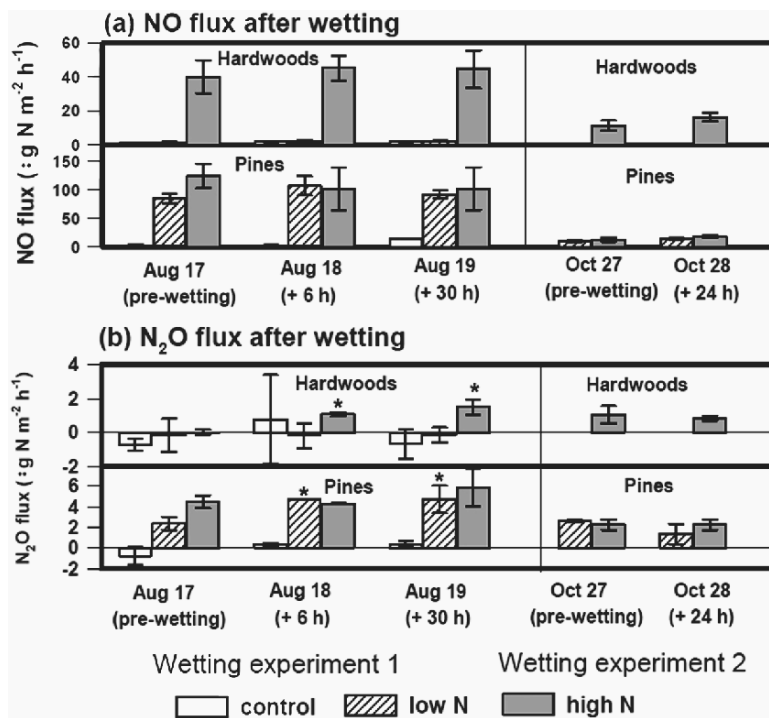


Figure 10.3. Response of (a) NO flux and (b) N₂O flux to 25-mm of water added on August 17 and October 27 of 2001 to control, low N (50 kg N ha⁻¹ y⁻¹) and high N (150 kg N ha⁻¹ y⁻¹) plots at the Harvard Forest, MA. Asterisks indicate if post-wetting fluxes are significantly different from pre-wetting fluxes at $p < 0.05$. From Venterea et al. (2003a).

It is important to note that Hubbard Brook was only one of the five points along our regional N deposition gradient. At the other points on the gradient, analyses of landscape-scale controls on flux and site selection were based on previous work at the sites by other investigators. Our regional study was greatly aided by the fact that numerous N cycling studies have been carried out at these sites.

10.3.2 Challenge #2 – How to Account for the Episodic Nature of N Gas Fluxes?

N gas fluxes are notoriously episodic, with short bursts of production occurring following rainfall or thawing events accounting for a high percentage of annual flux (Groffman et al. 2000). The best way to produce accurate evaluations of flux is to make continuous (greater than daily) measurements (Papen and Butterbach-Bahl 1999, Groffman et al. 2000). However, continuous monitoring of flux is difficult and expensive even at one site, and it is certainly not possible at landscape and regional scales. We approached this challenge with a mixture of field campaigns to assess the episodic nature of flux and simulation modeling to accomplish temporal scaling.

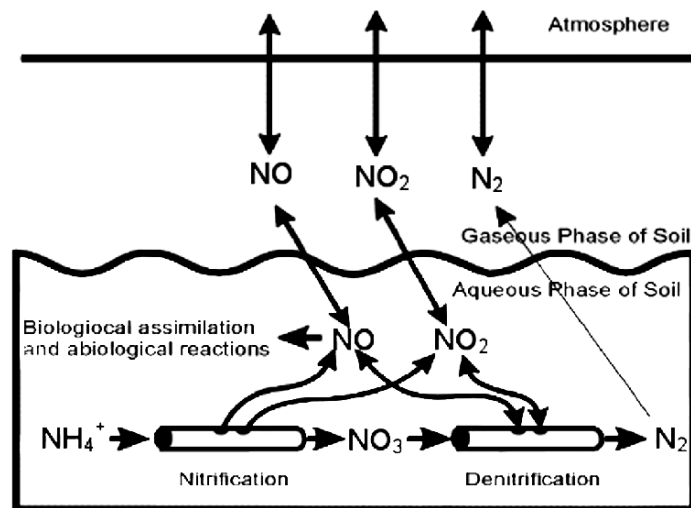


Figure 10.4. The “hole-in-the-pipe” conceptual model of N gas fluxes. From Firestone and Davidson (1989).

At the Harvard Forest, MA site, we assessed episodic fluxes of NO and N₂O associated with wetting events (Figure 10.3), diurnal temperature changes and N additions. Data from these assessments, combined with data from our monthly sampling allow us to parameterize flux models for these gases based on the “hole-in-the-pipe” formulation devised by Firestone and Davidson (1989). In this model, the overall rate of N transformation is depicted as the flow of water through a pipe, and N gases leak out through holes in the pipe (Figure 10.4). The overall rate of N transformation is controlled by soil and organic matter quality variables and is

represented by measurements of gross and/or net N mineralization and nitrification. The size of the holes is controlled by more transient soil conditions such as pH, temperature and water content. The hole-in-the-pipe model can be run at a daily time step and is thus capable of depicting the episodic nature of N gas fluxes. We suggest that process models, carefully calibrated with site-specific field data, are useful tools for depicting the episodic nature of N gas fluxes. Until we have technology that allows for continuous measurement of fluxes, at multiple sites, these models will continue to be important tools in landscape and regional scale studies of these fluxes.

It is interesting to note that the fluxes of NO at the Harvard Forest site were high, up to 8% of inputs, while N₂O fluxes were much lower. Previous studies at this site also found low N₂O fluxes (Bowden et al. 1991, Magill et al. 1997). Our new NO data suggest that N gas fluxes are larger, and more responsive to N deposition, than previously thought. Fluxes of NO were not responsive to wetting events, but N₂O fluxes were.

10.3.3 Challenge #3 – How to Validate Landscape and Regional Scale Estimates of Flux

In addition to serving as tools for depicting the episodic nature of N gas fluxes, i.e., for temporal extrapolation, we use models as spatial extrapolation tools to produce landscape and regional scale estimates of flux. We are in the process of linking our process models with the NASA-CASA model (Figure 10.5), which is an aggregated representation of major ecosystem C and N transformations (including gas fluxes) that can be run at regional scales when driven by a set of gridded coverages at 1-km spatial resolution (Potter et al. 1996, 1997).

The N gas emission components of the NASA-CASA model have been re-evaluated in the context of our field measurements. Revisions are underway in the CASA framework, based in part on recent validation/comparison studies (Davidson et al. 2000, Parton et al. 2001). Regional driver data sets that will be used for extrapolation include nitrogen deposition isopleth maps, daily climate drivers, soils and satellite-based estimates of leaf area index, and land cover and vegetation type. The NASA-CASA model will generate predicted nitrification rates in forest soils, which will in turn be used to predict NO and N₂O emission fluxes from soil surfaces as a function of simulated soil water content, temperature, pH, bulk density, and texture. Field measurements of these parameters at our five experimental sites will be used to make model calibration checks of the trace gas algorithms.

While the NASA-CASA model will produce landscape and regional scale estimates of flux, we have no way to directly validate these estimates because there is no way to independently assess flux at these scales. While we feel that our models are conceptually sound and empirically robust, it is possible that we have overlooked critical controlling factors at the landscape and regional scale, e.g., dead moose carcasses that may be hotspots of N gas flux in our northern sites. Given our inability to truly validate our estimates, some alternative approaches are possible. First, it is possible to predict fluxes for new sites within our region and then validate these predictions with field measurements. Second, we can evaluate our flux

estimates in the context of what is known about other fluxes at these well-studied sites. For example, if our estimates of gas flux are much higher than precipitation inputs and/or streamwater outputs of N, we will suspect that our estimates are too high. Finally, we can develop and apply other, independent modeling/extrapolation approaches to the region and see if estimates are similar. Clearly, none of these alternative validation approaches is very satisfying, but it is currently the best we can do. We can also apply standard methods of uncertainty analysis to our model results (reviewed by Li and Wu, Chapter 3), but again, these do not allow for true validation of our landscape and regional scale flux estimates.

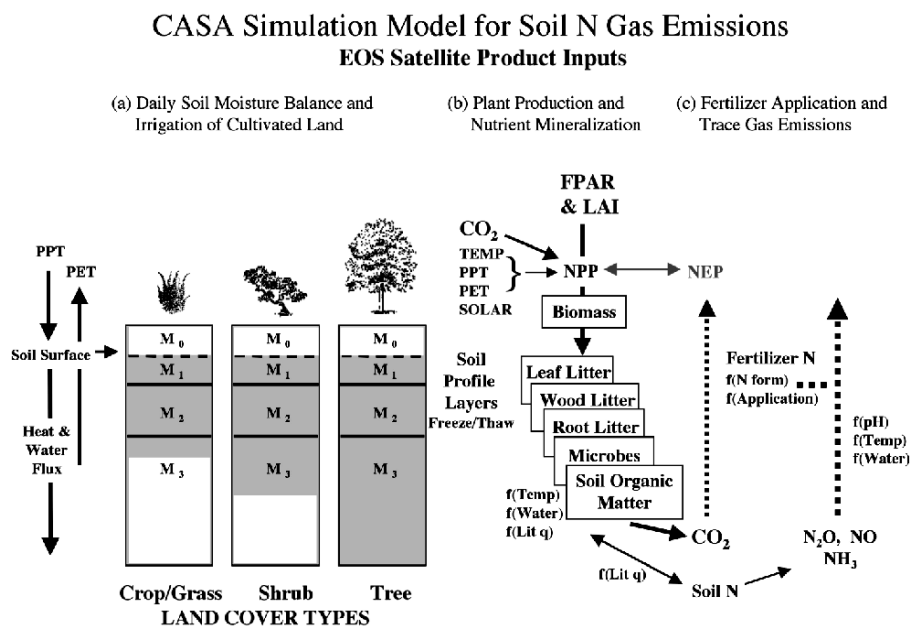


Figure 10.5. The NASA-CASA ecosystem carbon and nitrogen process model showing how landscape and regional scale data can be used to drive ecosystem process (including N gas fluxes) models.

10.4 CONCLUSIONS

Landscape and regional scale studies of N gas fluxes are difficult. Are the scaling challenges inherent in these studies insurmountable? One way to evaluate this is to ask if we have successfully addressed the objectives of our project. We have met our first objective (i.e., to determine the importance of gaseous loss of N from temperate forest ecosystems) with data suggesting that N gas fluxes, especially NO, are more important in northeastern forest soils than previously thought. For our second objective, we have evaluated the response of N gas fluxes to N deposition, with fertilization studies and by comparison of sites along our regional deposition

gradient (still underway). This comparison is greatly facilitated by our landscape experimental designs, which allow us to establish representative fluxes for each site along the regional gradient. These designs will also allow us to evaluate the importance of deposition as a driver of flux compared to “local factors” such as elevation, aspect and vegetation type.

Our third objective, to develop models of N gas fluxes, has also been achieved, by collection of data to parameterize flux models for our sites. It is important to note that hole-in-the-pipe type modeling is ongoing at many sites around the world, providing many opportunities for comparison and synthesis (Verchot et al. 1999, Davidson et al. 2000).

We will also achieve our fourth objective, producing regional scale estimates of N gas fluxes. However our ability to validate these estimates is indirect and incomplete and therefore our confidence in their accuracy is low. We will compare our estimates of flux with regional deposition estimates and budgets (Boyer et al. 2002, Driscoll et al. 2003) and will carry out spatial validation, i.e., prediction of flux at new sites. However, true validation will await the development of new methods (e.g., micrometeorological towers, aircraft-based measurements, new isotope approaches) that allow for independent measurement of fluxes at ecosystem, landscape and regional scales.

ACKNOWLEDGEMENTS

This work was funded by grants from the EPA (NCERQA Grant R827674), the National Science Foundation (Grant NSF DEB-9810221, Hubbard Brook LTER) and the Andrew W. Mellon Foundation. Special thanks to Jianguo Wu for organizing the workshop and book of which this chapter is a part.

REFERENCES

- Aber, J. D., K. J. Nadelhoffer, P. Steudler, and J. M. Melillo. 1989. Nitrogen saturation in northern forest ecosystems. *Bioscience* 39:378-386.
- Aber J. D., S. V. Ollinger, C. T. Driscoll, G. E. Likens, R. T. Holmes, R. J. Freuder, and C. L. Goodale. 2002. Inorganic N losses from a forested ecosystem in response to physical, chemical, biotic and climatic perturbations. *Ecosystems* 5:648-658.
- Bohlen, P., P. Groffman, C. Driscoll, T. Fahey, and T. Siccama. 2001. Plant-soil-microbial interactions in a northern hardwood forest. *Ecology* 4:965-978.
- Bowden, R., J. Melillo, P. Steudler, and J. Aber. 1991. Effects of nitrogen additions on annual nitrous oxide fluxes from temperate forest soils in the northeastern United States. *Journal of Geophysical Research-Atmospheres* 96:9321-9328.
- Bowden, W. B. 1986. Gaseous nitrogen emissions from undisturbed terrestrial ecosystems: an assessment of their impact on local and global nitrogen budgets. *Biogeochemistry* 2:249-279.
- Boyer E. W., C. L. Goodale, N. A. Jaworski, and R. W. Howarth. 2002. Anthropogenic nitrogen sources and relationships to riverine nitrogen export in the northeastern USA. *Biogeochemistry* 57:137-169.
- Burke, I. C. 1989. Control of nitrogen mineralization in a sagebrush steppe landscape. *Ecology* 70:1115-1126.
- Davidson, E. A., M. Keller, H. E. Erickson, L. V. Verchot, and E. Veldkamp. 2000. Testing a conceptual model of soil emissions of nitrous and nitric oxides. *Bioscience* 50:667-680.
- Driscoll, C., D. Whitall, J. Aber, E. Boyer, M. Castro, C. Cronan, C. Goodale, P. Groffman, C. Hopkinson, K. Lambert, G. Lawrence, and S. Ollinger. 2003. Nitrogen pollution in the northeastern United States: sources, effects and management options. *BioScience* 53:357-374.

- Firestone, M. K., and E. A. Davidson. 1989. Microbial basis for N₂O and NO production and consumption. Pages 7-21 in M. O. Andreae and D. S. Schimel, editors. *Exchange of Trace Gases Between Ecosystems and the Atmosphere*. Wiley, New York.
- Folorunso, O. A., and D. E. Rolston. 1984. Spatial variability of field-measured denitrification gas fluxes and soil properties. *Soil Science Society of America Journal* 49:1087-1093.
- Galloway, J. N., J. D. Aber, J. W. Erisman, S. P. Seitzinger, R. W. Howarth, E. B. Cowling, and B. J. Cosby. 2003. The nitrogen cascade. *BioScience* 53:341-356.
- Groffman, P. M., and J. M. Tiedje. 1989. Denitrification in north temperate forest soils: relationships between denitrification and environmental factors at the landscape scale. *Soil Biology and Biochemistry*. 21:621-626.
- Groffman, P. M., R. Brumme, K. Butterbach-Bahl, K. E. Dobbie, A. R. Mosier, D. Ojima, H. Papen, W. J. Parton, K. A. Smith, and C. Wagner-Riddle. 2000. Evaluating annual nitrous oxide fluxes at the ecosystem scale. *Global Biogeochemical Cycles* 14:1061-1070.
- Groffman, P. M., E. Holland, D. D. Myrold, G. P. Robertson, and X. Zou. 1999. Denitrification. Pages 272-288 in G. P. Robertson, C. S. Bledsoe, D. C. Coleman, and P. Sollins, editors. *Standard Soil Methods for Long Term Ecological Research*. Oxford University Press, New York.
- Likens, G. E., and F. H. Bormann. 1995. *Biogeochemistry of a Forested Ecosystem*, 2nd edition. Springer-Verlag, New York.
- Lowrance, R. 1998. Riparian forest ecosystems as filters for nonpoint-source pollution. Pages 113-141 in M. L. Pace and P. M. Groffman, editors. *Successes, Limitations and Frontiers in Ecosystem Science*. Springer-Verlag, New York.
- Magill, A. H., J. D. Aber, J. J. Hendricks, R. D. Bowden, J. M. Melillo, and P. A. Steudler. 1997. Biogeochemical response of forest ecosystems to simulated chronic nitrogen deposition. *Ecological Applications* 7:402-415.
- Mooney, H. A., P. M. Vitousek, and P. A. Matson. 1987. Exchange of materials between terrestrial ecosystems and the atmosphere. *Science* 238:926-932.
- National Research Council (NRC). 1992. *Rethinking the Ozone Problem in Urban and Regional Air Pollution*. National Academy Press, Washington, D.C.
- Papen, H., and K. Butterbach-Bahl. 1999. A 3-year continuous record of nitrogen trace gas fluxes from untreated and limed soil of a N-saturated spruce and beech forest ecosystem in Germany: 1. N₂O emissions. *Journal of Geophysical Research* 104:18487-18503.
- Parkin, T. B. 1987. Soil microsites as a source of denitrification variability. *Soil Science Society of America Journal* 51:1194-1199.
- Parton, W. J., E. A. Holland, S. J. Del Grosso, M. D. Hartman, R. E. Martin, A. R. Mosier, D. S. Ojima, and D. S. Schimel. 2001. Generalized model for NO_x and N₂O emissions from soils. *Journal of Geophysical Research – Atmospheres* 106:17403-17419.
- Potter, C. S., P. A. Matson, P. M. Vitousek, and E. A. Davidson. 1996. Process modeling of controls on nitrogen trace gas emissions from soils worldwide. *Journal of Geophysical Research* 101:1361-1377.
- Potter, C. S., R. H. Riley, and S. A. Klooster. 1997. Simulation modeling of nitrogen trace gas emissions along an age gradient of tropical forest soils. *Ecological Modelling* 97:179-196.
- Prather, M., R. Derwent, D. Ehhalt, P. Fraser, E. Sanhueza, and X. Zhou. 1995. Other trace gases and atmospheric chemistry. Pages 73-126 in J. T. Houghton, L. G. Meiro Filho, B. A. Callander, N. Harris, A. Kattenburg, and K. Maskell, editors. *Climate Change*. Cambridge University Press, New York.
- Robertson, G. P., M. A. Huston, F. C. Evans, and J. M. Tiedje. 1988. Spatial variability in a successional plant community: patterns of nitrogen availability. *Ecology* 69:1517-1524.
- Schimel, D. S., M. A. Stillwell, and R. G. Woodmansee. 1985. Biogeochemistry of C, N and P in a soil catena of the shortgrass steppe. *Ecology* 66:276-282.
- Schlesinger, W. H. 1997. *Biogeochemistry: An Analysis of Global Change*. Academic Press, New York.
- Schwarz, P. A., T. J. Fahey, and C. E. McCulloch. 2003. Factors controlling spatial variation of tree species abundance in a forested landscape. *Ecology* 84:1862-1878.
- U.S. Department of Agriculture Forest Service. 1996. *Hubbard Brook Ecosystem Study: Site Description and Research Activities*. USDA Forest Service NE-INF-96-96R.
- Van Breemen, N., E. W. Boyer, C. L. Goodale, N. A. Jaworski, K. Paustian, S. P. Seitzinger, K. Lajtha, B. Mayer, D. Van Dam, R. W. Howarth, K. J. Nadelhoffer, M. Eve, and G. Billen. 2002. Where did all the nitrogen go? Fate of nitrogen inputs to large watersheds in the northeastern U.S.A. *Biogeochemistry* 57/58:267-293.

- Venterea, R. T., P. M. Groffman, L. V. Verchot, A. H. Magill, J. D. Aber, and P. A. Steudler. 2003a. Nitrogen oxide gas emissions from temperate forest soils receiving long-term nitrogen inputs. *Global Change Biology* 9:346-357.
- Venterea, R. T., G. M. Lovett, P. M. Groffman, and P. A. Schwarz. 2003b. Landscape patterns of soil nitrate production in a northern hardwood-conifer forest. *Soil Science Society of America Journal*. 67:527-539.
- Verchot, L., E. Davidson, J. Cattanio, I. Ackerman, H. Erickson and M. Keller. 1999. Land use change and biogeochemical controls of nitrogen oxide emissions from soils in eastern Amazonia. *Global Biogeochemical Cycles* 13:31-46.
- Vitousek, P. M., and R. W. Howarth. 1991. Nitrogen limitation on land and in the sea: how can it occur. *Biogeochemistry* 13:87-115.
- Vitousek, P. M., J. D. Aber, R. W. Howarth, G. E. Likens, P. A. Matson, D. W. Schindler, W. H. Schlesinger, and D. G. Tilman. 1997. Human alteration of the global nitrogen cycle: sources and consequences. *Ecological Applications* 7:737-750.
- Wagenet, R. J. 1998. Scale issues in agroecological research chains. *Nutrient Cycling in Agroecosystems* 50:23-34.