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# Long-Term Trends in Ecological Systems: A Basis for Understanding Responses to Global Change



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# Chapter 7

# Cross-Site Comparisons of Ecological Responses to Long-Term Nitrogen Fertilization

#### S.L. Collins, K.N. Suding, and C.M. Clark

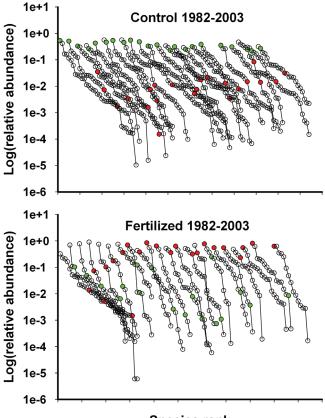
Atmospheric pollution, as either wet or dry deposition, is changing through time for many ecosystems (chapters 6, 12). The long-term effects of these changes on ecosystem structure and function are not well understood, in particular for reactive nitrogen in the forms of nitrate (NO<sub>3</sub>) and ammonium (NH<sub>4</sub>). Reactive nitrogen is an essential nutrient that limits net primary production in most terrestrial and some aquatic ecosystems (Vitousek and Howarth 1991, Elser et al. 2007). Atmospheric nitrogen deposition is considered one of the major drivers of diversity loss in ecosystems (Sala et al. 2000), though land-use change remains the most important factor.

Given that human activity has doubled available nitrogen (Vitousek et al. 1997) along with other key resources (such as phosphorus) and that net primary production is increasing globally (Nemani et al. 2003) with variable patterns in time and space at specific sites (chapters 5, 14), a more mechanistic understanding of the relationship between nitrogen availability, productivity, and species diversity is needed.

The following key questions remain unanswered:

- How do increasing resources other than nitrogen affect productivity and species diversity?
- What are the mechanisms that can cause diversity to decline as productivity increases?
- Does an increase in productivity directly or indirectly through other environmental variables (such as pH) affect species diversity?
- How do microbial communities and processes respond as resource availability increases?
- Can plant functional trait responses provide a mechanistic understanding to the relationship between productivity and diversity?

Long-term observational and experimental data are needed to address these important research questions. For example, a long-term nitrogen fertilization study at the Cedar Creek LTER site in Minnesota (CDR) provides an interesting example of both threshold changes in species abundance and loss of diversity with addition of resources. In this experiment, about 10 g/m of nitrogen has been added annually to an abandoned agricultural field since 1982. Species diversity declined rapidly in response to nitrogen fertilization, whereas diversity in control plots fluctuated from year to year in response to interannual changes in precipitation. Consequently, the abundance of a non-native annual C<sub>2</sub> grass, Agropyron repens, increased relatively rapidly while the abundance of a long-lived clonal C<sub>4</sub> bunchgrass, Schizachyrium scoarpium, decreased relative to controls (figure 7-1). Thus, chronic environmental change can cause rapid, nonlinear transitions in local distribution and abundance of plant species.



#### Species rank

Figure 7-1. Annual rank-abundance curves for (a) control and (b) fertilized plots at the Cedar Creek Ecosystem Science site (CDR) for Field C from 1982 to 2003 show the relative ranking of a late successional, perennial  $C_4$  grass (*Schizachyrium scoparium*) (green filled circles), and an early successional, annual  $C_3$  grass (*Agropyron repens*) (red filled circles) (Collins et al. 2008). The curves show how the ranks of *Schizachyrium* and *Agropyron* remain relatively constant in control plots, but they rapidly reverse order in fertilized plots. Reprinted with permission from the Ecological Society of America.

Extrapolating cause and effect relationships from one ecosystem to another is often challenging, whereas multisite analyses of similar fertilization experiments across systems can provide greater generality. In a multisite analysis of plant community responses to experimental addition of nitrogen (100 kg/ha in most cases), plant species richness declined by about 30 percent and aboveground net primary production (ANPP) increased by about 50 percent across a range of sites with different initial productivity potentials (figure 7-2). This loss of diversity also occurs along natural productivity gradients (Stevens et al. 2004). Despite these common responses across sites and systems, the mechanisms causing this decline in diversity as productivity increases are still being debated, and longterm responses have not been evaluated.

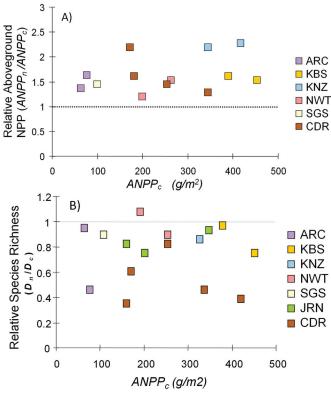


Figure 7-2. Response ratios for the last year of data for seven grassland sites receiving long-term N additions of 9 to 13 g/  $m^2$ /yr. (A) ANPP<sub>n</sub> in fertilized plots over ANPP<sub>c</sub> in control plots versus mean ANPP<sub>c</sub> of control plots. (B) species richness in fertilized plots (D<sub>n</sub>) over species richness in control plots (D<sub>c</sub>) versus mean ANPP<sub>c</sub> of control plots. Dashed lines indicate a response ratio of 1, meaning the N fertilization plots show no difference from control plots. (Redrawn from Gough et al. 2000.)

Functional traits may provide mechanistic insights into a plant community's response to fertilization (Bai et al. 2004). Species traits reflect evolutionarily derived strategies for resource capture and interspecific interactions, which influence community structure and ecosystem processes (Diaz and Cabido 2001). An analysis of more than 900 species responses from 34 nitrogen fertilization experiments across North America showed that both trait-neutral mechanisms (for example, rarity) and trait-based mechanisms (such as plant height) operated simultaneously to influence diversity loss as production increased (Suding et al. 2005). Thus, rarity, species identity, and functional traits affect species responses to increasing productivity in long-term nitrogen fertilization experiments. Because these responses may be highly dependent on context, they challenge our ability to predict how communities will change as the amount of reactive nitrogen continues to increase globally.

## Conclusions

Human activities have greatly altered the nitrogen cycle. As a consequence, net primary production has increased globally and biodiversity has decreased in many herbaceous plant communities. Trait-based analyses may provide insight into the mechanisms behind biodiversity loss in response to increased nitrogen availability. Long-term studies are needed to document these patterns under variable climatic conditions.

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