in Gao and colleagues' experiments, which indicates that the equilibrium metallic phase is reached within about 100 ps. Because conductivity correlates with crystal symmetry, the low-symmetry intermediate structure is more like an insulator than a metal.

Recent years have also seen tremendous success in the use of time-resolved X-ray diffraction to obtain atomic-level views of transient phenomena in inorganic, molecular and even biomolecular systems[10], notably with the emergence of X-ray free-electron lasers[11]. Gao and colleagues' work demonstrates that laboratory-scale, ultrafast electron-diffraction set-ups represent an attractive alternative to synchrotrons or X-ray free-electron lasers — massive installations that require electron accelerators kilometres in length. At present, however, the temporal resolution of the authors' apparatus is limited to about 400 fs, and so it could not catch the faster, coherent molecular motion (previously evidenced by optical spectroscopy[2]) that drives the system to the transient intermediate state itself. Nevertheless, their study represents an experimental tour de force.

Femtosecond electron diffraction opens up new possibilities for investigating weakly diffracting systems composed of light elements, such as organic materials and two-dimensional protein crystals, or for studying systems for which laser penetration is too small to perform X-ray studies. More broadly, Gao and colleagues' work adds to the growing range of advanced structural studies, be they performed with electrons or X-rays, that are pushing the boundaries of experiments towards the limits of spatial and temporal resolution, opening the way towards greater understanding and control of molecular dynamics and material properties. ■

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BIOGEOCHEMISTRY

# Nitrogen deposition and forest carbon

**Human activity, such as agricultural fertilizer use, has increased the amount of nitrogen deposited onto forests from the atmosphere. The photosynthetic response to this in evergreen needleleaf forests has been quantified globally.**

### BEVERLY LAW

Nitrogen-containing compounds deposited from the atmosphere can affect the amount of carbon that is absorbed into ecosystems by photosynthesis. Writing in *Global Biogeochemical Cycles*, Fleischer *et al.*[1] reveal that photosynthesis by boreal and temperate evergreen forests rises with increased atmospheric nitrogen deposition, but levels out when a threshold value of 8 kilograms of nitrogen per hectare per year is reached. These findings highlight the need to clarify the connections between carbon and nitrogen in the environment, and to disentangle the effects of climate from those of nitrogen deposition on forests.

The terrestrial biosphere is thought to take up about 30% of human-produced carbon dioxide from the atmosphere annually, lessening the greenhouse effect of fossil-fuel emissions[2]. However, estimates of the size of this terrestrial sink are uncertain because of major gaps in our knowledge of the magnitude of the effects of the factors involved. One of these factors is the variation in human-caused additions of nitrogen to the atmosphere over time and space. Climate change and atmospheric fertilization of plants by human sources of nitrogen and $CO_2$ probably affect plant growth rates all over the world, but our understanding of these effects is likely to remain incomplete for the foreseeable future[3].

Most plants cannot use nitrogen gas in the atmosphere for growth. They require it to be converted to usable forms, such as ammonia — a process that forms part of the nitrogen cycle. However, the natural nitrogen cycle has been heavily influenced by human activities, which produce highly unstable forms of nitrogen known collectively as reactive nitrogen. The deposition of reactive nitrogen from the atmosphere to forests occurs mainly as a result of agricultural fertilizer use and fossil-fuel combustion, and has increased from 15 million tonnes of human-produced reactive nitrogen per year in the 1860s to 187 million tonnes by 2005 (ref. 4). Nitrogen deposition is expected to continue to increase in many regions, and has been predicted[5] to almost double globally by 2050.

The addition of reactive nitrogen to the atmosphere by humans affects climate, and the composition and function of terrestrial and aquatic ecosystems[4]. High levels of nitrogen deposition have many damaging effects on ecosystems, but small additions can be beneficial for otherwise nitrogen-limited ecosystems, because they increase the uptake of $CO_2$ from the atmosphere by photosynthesis. The effect of nitrogen deposition on carbon sequestration by soil is less clear. Most studies suggest that the net effect is between 35 and 65 kilograms of carbon sequestered per kilogram of nitrogen[6,7]. Much of the variation can be attributed to different patterns of growth and to the availability of other resources for growth.

Although low levels of nitrogen deposition might mitigate the effects of increased atmospheric $CO_2$ to some degree, 53–76% of this coincidental benefit is itself estimated to be offset globally[7]. This is because nitrogen deposition can stimulate net emissions of other greenhouse gases (methane and nitrous oxide) that are products of microbial activity in the soils of many ecosystems. Thus, the relative contribution of nitrogen deposition to the strength of the terrestrial carbon sink remains uncertain.

To address this problem, near-continuous atmospheric observations have been made from towers above vegetation canopies to provide estimates of $CO_2$ uptake (photosynthesis) and release (respiration) from and to the atmosphere, respectively. Many of these sites have been running for more than a decade, and the data are summarized by the FLUXNET Project[8]. In combination with biological and environmental data, such information has been used by researchers to examine the effect of factors such as climate variability on carbon processes at the whole-ecosystem scale at many sites around the world.

Fleischer *et al.* used FLUXNET data from 80 sites that had sufficient information about nitrogen and carbon fluxes for their analysis. They found that, for evergreen needleleaf forests in temperate and boreal zones, maximal photosynthesis under optimal environmental conditions increased with continuous nitrogen-deposition rates up to a threshold of about 8 kg of nitrogen deposition per hectare per year. Above this value, no further increase in photosynthesis was observed.

Forests above the threshold are therefore at an intermediate stage of nitrogen saturation — a stage at which nitrogen availability exceeds microbial and plant demands, and can result in some nitrogen leaching from the ecosystem. Prolonged availability of excessive nitrogen can lead to more leaching, decreased growth and nutrient imbalances. By contrast, the evergreen needleleaf forests that responded most strongly to nitrogen deposition are in a nitrogen-limited range, within which photosynthetic capacity increases with deposition. The observed threshold is a small fraction of the nitrogen that farmers would use annually in fertilizers.

The authors also found that boreal evergreen needleleaf forests had a slightly lower photosynthetic response overall to nitrogen deposition. For both boreal and temperate evergreen forests, this translates to roughly 25 kg of carbon sequestered per kilogram of nitrogen, less than the estimated global average[6,7,9] of 35–65.

The results are confounded by the effects of climate on photosynthesis: the nitrogen-deposition effect may be larger or smaller than Fleischer and colleagues' findings because part of the observed response is probably a result of climate. However, there is no evidence to suggest that the contribution of nitrogen deposition is zero. Although the authors attempted to determine the thresholds for other forest types, they were limited by the availability of biological data on both carbon and nitrogen processes. More comprehensive measurements of nitrogen stocks and cycling at the global network of carbon monitoring sites are required to separate the effects of climate and nitrogen deposition on forests.

The net emissions of all greenhouse gases — including $CO_2$, methane and nitrous oxide — should be considered when examining the net effects of nitrogen deposition and climate on ecosystems. A better understanding of how the connections between carbon and nitrogen in the environment could change in the future is also required. Nevertheless, Fleischer and co-workers' study lays the groundwork needed to refine estimates of the effects of climate and nitrogen deposition on the terrestrial biosphere's ability to remove carbon from the atmosphere as $CO_2$ emissions increase. Such refinements will be necessary to improve predictions of the effects of these emissions on ecosystems at local, regional and continental scales. ■

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COMPLEX SYSTEMS

# Spatial signatures of resilience

**Predicting when the dynamics of a complex system will undergo a sudden transition is difficult. New experiments show that the spatial distribution of organisms can indicate when such tipping points are near.** SEE LETTER P.355

STEPHEN R. CARPENTER

The divergence of dynamics towards sharply different states occurs in complex systems in fields ranging from physics and physiology to ecology and social sciences. The thresholds for these critical transitions are often unknown until surprising shifts occur. Establishing measures of the distance to a threshold — the resilience of a system — could allow researchers to compare the stability of different systems or even anticipate an impending transition. In a paper on page 355 of this issue, Dai *et al.*[1] present a novel resilience index and use ingenious laboratory experiments to support the theory underlying it*. Their approach is based on the spatial distribution of organisms and thereby adds, quite literally, a new dimension to attempts to predict transitions.

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