However, even if the carbon sink per unit of nitrogen deposited is not as large as originally suggested, it is still substantial. Furthermore, the variability of the carbon storage response contains a wealth of information that could improve our understanding of the interactions between the cycles of carbon and nitrogen. Three processes appear to control carbon sequestration per unit of nitrogen.

First, nitrogen additions can increase photosynthetic uptake of carbon dioxide, and thus carbon storage in the ecosystem, by stimulating leaf production or by increasing the levels of leaf photosynthetic enzymes and their capacity. In young accruing forests, the response of primary productivity to added nitrogen is particularly high (R. Oren, Duke Univ.). Likewise, in northern forests where nitrogen availability is the dominant constraint on forest productivity[8], nitrogen additions have significant effects (S. Linder and T. Persson, Swedish Univ. Agricultural Sciences). But additional nitrogen does not always increase carbon storage: where nitrogen is already sufficient or in excess relative to other resources, such as water or light, producing more leaves in response to higher nitrogen availability is unlikely to result in enhanced photosynthesis.

Second, to obtain nutrients and water, trees invest a substantial fraction of their photosynthates in roots and root symbionts. As nitrogen, the main nutrient, becomes less limiting, carbon allocation tends to shift from fine roots and mycorrhizal symbionts, with a relatively low carbon to nitrogen ratio, to woody biomass with a high ratio (P. Högberg and T. Näsholm, Swedish Univ. Agricultural Sciences). Even if photosynthesis responds very little to nitrogen deposition, this allocation shift could induce higher wood production and thus higher carbon uptake per unit of nitrogen deposited.

Finally, nitrogen addition affects the two competing components of soil carbon storage — soil carbon inputs and the consumption of the available substrate by soil microbes, which leads to the release of carbon back to the atmosphere. Microbial consumption is consistently retarded by nitrogen deposition[9,10], creating a potential for large soil carbon accumulation (S. Luyssaert and W. Dieleman, Univ. Antwerp). At the same time, however, soil carbon inputs decrease in response to the shift in carbon allocation from litter to woody tissue, and nitrogen requirements for the production of soil organic matter are high. Soil carbon sequestration by this route is therefore likely to be limited.

It is important to understand these three controlling factors better, because carbon–nitrogen interactions can offset any positive effect of increasing atmospheric carbon dioxide on ecosystem performance[11] (C. Calfapietra, CNR, Italy; R. Oren, Duke Univ.). Moreover, carbon–nitrogen interactions affect the potential for positive and negative feedbacks between the carbon cycle and the climate system, and therefore need to be incorporated in models of the Earth system (A. Cescatti, JRC, Italy).

To improve the quantification and understanding of variations in forest carbon uptake per unit of nitrogen deposition, we should focus on the spatial differences in the way that photosynthesis, carbon allocation and microbial degradation of soil carbon respond to nitrogen additions. ❐

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BIOGEOCHEMISTRY

Rising marshes

Salt marshes and tidal wetlands line many coasts, harbouring wildlife and supporting commercial fisheries. Coastal lands are vulnerable to a range of natural and anthropogenic threats. Thousands of hectares of marshes and wetlands are reclaimed by the open ocean each year through storm surges and flooding, and as increasing atmospheric carbon dioxide levels warm the Earth, rising sea levels may pose yet another threat to the survival of the marshes.

However, J. Adam Langley of the Smithsonian Environmental Research Center, Maryland, and colleagues have now shown that rising levels of carbon dioxide in the atmosphere could actually help tidal marshes keep up with the rising seas (*Proc. Natl Acad. Sci. USA* **106,** 6182–6186; 2009). They exposed patches of the Kirkpatrick Marsh, which borders Chesapeake Bay, to either ambient levels or an extra 340 ppm of carbon dioxide from 2006 to 2007. Both grass and root productivity were significantly higher in the marsh patches exposed to air rich in carbon dioxide, although this effect was muted by a severe drought in the autumn of 2007.

Overall, the patches treated with the higher carbon dioxide concentration gained about 3 mm in elevation per year, whereas the marsh patches at ambient carbon dioxide levels sank by just under 1 mm each year. The researchers attribute most of the land rise to increasing root mass, with some contribution from an accumulation of litter from the grass.

However, the experiments also revealed a destructive effect of anthropogenic nitrogen on the marsh, even within patches where growth had been enhanced with additions of carbon dioxide. Marsh patches exposed to high carbon dioxide and nitrogen showed no overall change in elevation, possibly because the nitrogen stimulated soil decomposition while hindering root productivity. So although coastal marshlands may be more resilient to the total effects of rising carbon dioxide levels in the atmosphere than we had thought, fertilizers running off from lawns and golf courses could prove to be their downfall.

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