

SPECIAL FEATURE

Does Nitrogen Constrain Carbon Cycling, or Does Carbon Input Stimulate Nitrogen Cycling?¹

The concept that nitrogen (N) availability can limit plant productivity is well established based on (1) N fertilization that stimulates productivity and (2) increases in productivity along gradients of soil fertility. Nitrogen limitations to plant productivity are regulated by processes such as mineralization, immobilization, and plant physiological adjustments. However, this production-centric perspective might not fully explain patterns in carbon (C) sequestration in terrestrial ecosystems. Carbon sequestration involves both plant and soil pools. The plant pool, which is the main concern of production research, can be much smaller than the soil pool. To quantify terrestrial C sequestration, therefore, we have to develop an ecosystem perspective to examine how C and N interact in both plant and soil pools.

Due to fossil fuel burning and deforestation, atmospheric CO₂ concentration has increased by approximately 35% since the Industrial Revolution. In general, elevated CO₂ enhances photosynthesis and stimulates initial C sequestration in terrestrial ecosystems. How sustainable the CO₂-induced C sequestration can be depends, in part, on ecosystem N availability and supply. Thus, the interdependence of C and N cycles is an issue that is not only interesting to ecologists, but also has important implications for global change policy.

Increased C influx into an ecosystem under elevated CO₂ generally requires more N to support plant growth than is required at ambient CO₂ and, in turn, sequesters N into long-lived plant biomass and soil organic matter pools. This N sequestration can decrease soil N availability for plant uptake and lead to progressive N limitation (PNL) over time. The PNL hypothesis states that N sequestration in long-term organic matter pools will, without new N input and/or decreases in N losses, lead to a decline in mineral N availability over time at elevated CO₂ compared to ambient CO₂. On the other hand, increased plant N demand and/or sequestration could induce changes in N supply. When elevated CO₂ increases N use efficiency (NUE) and stimulates N transfer from the soil organic pools with narrow C:N ratios to plants with broad C:N ratios, PNL may be delayed. If additional C input at elevated CO₂ stimulates capital gain of N through fixation, decreased losses, increased forage for soil N, or any combinations of them, PNL may not occur. If it does, CO₂-induced C sequestration in ecosystems declines over time. In short, N will constrain C sequestration over time unless additional C input at elevated CO₂ stimulates N gain in ecosystems.

This Special Feature consists of six papers that examine various aspects of PNL against field data collected from ecosystems that have been exposed to elevated CO₂ treatments. The first two papers show sustained CO₂ stimulation of net primary production (NPP) in forest ecosystems. Norby and Iversen present data from a sweetgum forest stand in Oak Ridge, Tennessee, that has been exposed to free-air CO₂ enrichment (FACE) for six years. The sustained CO₂ stimulation of NPP was associated primarily with increased N uptake, since NUE did not change significantly under elevated CO₂. Sufficient N supply from soil at Oak Ridge may help delay or even avoid PNL as elevated CO₂ substantially stimulated root growth to explore N sources in deeper soil layers. At the Duke Forest FACE site, Finzi and colleagues demonstrate that the CO₂ stimulation of NPP was sustained at 18–24% during the first six years of the experiment. Sustained NPP stimulation occurred together with significantly more N uptake by trees and higher NUE at elevated than at ambient CO₂. Their mass balance analysis shows that significantly more N accumulated at elevated CO₂ in plants and in forest floor litter. The forest ecosystem accrued N capital at an average rate of 12 g N·m⁻²·yr⁻¹, perhaps due to N uptake from deeper in the soil profile.

¹ Reprints of this 73-page Special Feature are available for \$11.00 each, either as PDF files or as hard copy. Prepayment is required. Order reprints from the Ecological Society of America, Attention: Reprint Department, 1707 H Street, N.W., Suite 400, Washington, DC 20006 (esaHQ@esa.org).

However, PNL of plant growth and C sequestration appears to occur in a scrub-oak ecosystem, Florida (Hungate et al.), and a C₃/C₄ grassland, Texas (Gill et al.) in response to elevated CO₂. Initial CO₂ stimulation of plant biomass growth was supported by more N uptake from soil in the scrub-oak ecosystem. As N was accumulated in plant biomass and litter layers in the O horizon in years 4–7, soil N availability progressively declined, as did the CO₂ stimulation of plant growth. Initially, PNL of plant growth was avoided by increased N uptake from the soil and alleviated later through increased NUE. Elevated CO₂ did not change total ecosystem N content but caused a redistribution of N from the mineral soil to plants and litter. In the Texas grassland, increased CO₂ along a gradient from 200 to 560 μmol/mol also caused reallocation of N from soil to plant and from more recalcitrant to more labile fractions within the soil. The N reallocation alleviates PNL and allows plant production to increase with increasing CO₂. However, it does not support much long-term C sequestration in the soil at elevated CO₂, since the C gained from increased plant production can be rapidly lost through decomposition.

Results at experimental sites are often highly variable. To synthesize results from multiple sites, Luo et al. conducted a meta-analysis of data from 104 published papers and found significant increases in C and N contents on average in all the plant and soil pools under elevated CO₂. The net N accumulation in plant and soil pools at least helps prevent complete down-regulation of, and likely supports, long-term CO₂ stimulation of C sequestration. The net C and N accumulations under elevated CO₂ are consistent with C and N dynamics during succession over hundreds to millions of years, suggesting that ecosystems may have intrinsic capabilities to stimulate N accumulation by C input. Johnson reviews the early nutrient cycling literature related to PNL during forest stand development and more recent studies on C and N interactions under elevated CO₂. In general, trees can “mine” N from soils over the long term, but PNL will constrain CO₂ stimulation of plant growth unless external inputs of N are increased by N fixation or atmospheric deposition.

The six papers in this Special Feature provide experimental evidence on ecosystem C and N interactions but do not fully resolve the issue of whether N constrains the C cycle or additional C input stimulates the N cycle in response to elevated CO₂. Against the backdrop of diverse responses in nature, the challenge is how we can incorporate the diverse mechanisms of C and N interactions into models to predict future C sequestration. In the end, we hope this Special Feature will stimulate research to test the PNL hypothesis further and advance our understanding of the biogeochemical coupling of C and N cycles.

—YIQI LUO
Guest Editor
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—CHRISTOPHER B. FIELD
Guest Editor
Carnegie Institution of Washington
—ROBERT B. JACKSON
Special Features Editor
Duke University

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