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 CO_2 concentration has increased by approximately 35% since the Industrial Revolution. In general, elevated CO_2 enhances photosynthesis and stimulates initial C sequestration in terrestrial ecosystems. How sustainable the CO_2-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 CO_2 generally requires more N to support plant growth than is required at ambient CO_2 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 CO_2 compared to ambient CO_2. On the other hand, increased plant N demand and/or sequestration could induce changes in N supply. When elevated CO_2 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 CO_2 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, CO_2-induced C sequestration in ecosystems declines over time. In short, N will constrain C sequestration over time unless additional C input at elevated CO_2 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 CO_2 treatments. The first two papers show sustained CO_2 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 CO_2 enrichment (FACE) for six years. The sustained CO_2 stimulation of NPP was associated primarily with increased N uptake, since NUE did not change significantly under elevated CO_2. Sufficient N supply from soil at Oak Ridge may help delay or even avoid PNL as elevated CO_2 substantially stimulated root growth to explore N sources in deeper soil layers. At the Duke Forest FACE site, Finzi and colleagues demonstrate that the CO_2 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 CO_2. Their mass balance analysis shows that significantly more N accumulated at elevated CO_2 in plants and in forest floor litter. The forest ecosystem accrued N capital at an average rate of 12 $g\ N \cdot m^{-2} \cdot yr^{-1}$, 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 C_3/C_4 grassland, Texas (Gill et al.) in response to elevated CO_2. Initial CO_2 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 CO_2 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 CO_2 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 CO_2 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 CO_2. However, it does not support much long-term C sequestration in the soil at elevated CO_2, 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 CO_2. The net N accumulation in plant and soil pools at least helps prevent complete down-regulation of, and likely supports, long-term CO_2 stimulation of C sequestration. The net C and N accumulations under elevated CO_2 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 CO_2. In general, trees can ''mine'' N from soils over the long term, but PNL will constrain CO_2 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 CO_2. 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.

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