

How does nutrient cycling modify responses to global change?

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1) *Progressive Nitrogen Limitation*

Will nitrogen availability limit CO₂ fertilisation and C sequestration? (cf. Hungate et al 2003). The evidence so far is equivocal:

- Meta-analysis indicates that both ecosystem C and N tend to increase under increasing CO₂ although there is much variability between studies (Luo et al. 2006).
- Some high-CO₂ experiments show no reduction in NPP response over time. At Oak Ridge, the NPP increase is a sustained 25%, largely allocated to roots, which increase N uptake via increased soil exploration (Norby & Iversen 2006). At Duke, there is also a sustained NPP increase, largely allocated to stems, and supported by a widening ecosystem C:N ratio (Finzi et al. 2006a). However, there is also evidence of increased N immobilization in wood and in the O horizon, and there are shifts in microbial activity indicating increased N limitation (Finzi et al. 2006a,b). Similar responses are found in a Texas grassland: the CO₂-induced biomass increase is sustained, but soil N availability is reduced, and soil C:N ratios increase, which will likely limit C uptake in future (Gill et al. 2006).
- The Florida scrub-oak ecosystem (Hungate et al. 2006) showed a dramatic increase in biomass in response to elevated CO₂ but this increase slowed over time, likely due to reduced N availability; N was found to accumulate in the forest floor. In a nutrient-limited Tasmanian grassland, there was no biomass response to elevated CO₂, but nitrogen availability declined over time regardless (Hovenden et al. submitted).
- These differences among ecosystems may be due to differences in background N availability and N inputs (Hu et al. 2006). From meta-analyses, plant and soil C pools tend to increase only when fertilizer is added (de Graaff et al 2006, van Groeningen et al 2006). The activity of microbes in determining ecosystem N additions and losses (via fixation, nitrification and denitrification) may be crucial (Hu et al. 2006).

What is needed?

- Better **allocation** models. How can we account for the contrasting allocational responses between Oak Ridge and Duke ecosystems?
- A better understanding of **soil organic matter processes**. In particular: what drives **slow pool turnover**? What determines **microbial activity**?
- A better understanding of **timescales for soil feedbacks**. How long would FACE experiments need to run for, either to demonstrate PNL or to rule it out? Ecosystem can clearly respond to high CO₂ by changing C:N ratios: how flexible are these ratios?
- A better understanding of controls over nutrient inputs and outputs to ecosystems. In particular: What controls **N fixation**? What controls **N losses**?

2) *Interactions between nutrients, especially the role of P.*

- To what extent does **P availability** limit CO₂ responses (rather than just N)? Currently very few data. Further high CO₂ experimentation, at the ecosystem scale, is needed for ecosystems limited by P availability.
- **Interactions between N, P and CO₂** need to be understood. How do N and P availability interact, and how does P availability affect N fixation? Experimental evidence suggests that N fixation only responds to high CO₂ when there is adequate P (e.g. Edwards et al 2006). But Wang et al. (2007) suggest increased N fixation can improve P availability.
- **Influence of fire:** Adams (2007) argues that fire plays an important role in regulating N and P availability because N volatilizes far more readily. Fire thus changes N:P stoichiometry. Presence of N fixers after fire is also important in replacement of lost N.
- **Burning** can also modify CO₂ responses, possibly by promoting increased P availability (Henry et al 2006).

3) *Interactions with climatic factors: temperature and rainfall*

We should not investigate impacts of CO₂ alone, since changes in CO₂ will be accompanied by changes in temperature and rainfall and these also modify nutrient availability. For example, Hovenden et al. (submitted) show that the CO₂-induced reduction in nitrogen availability in a Tasmanian grassland does not occur when the plots are also warmed.

Impacts of temperature on ecosystems cannot be understood without taking nutrient cycling into account. Evidence for this:

- Rustad et al (2001) meta-analysis of soil warming experiments which showed significant positive effects on N mineralization and plant productivity
- Kerkhoff et al. (2005) demonstrate that ANPP is invariant with temperature and argue that nutrient feedbacks offset temperature effects on kinetics of photosynthesis and respiration
- Modelling studies also demonstrate the importance of nutrient cycling in modulating ecosystem response to temperature (e.g. Medlyn et al 2000, Pepper et al 2005).
- Equally, nutrient cycling is strongly affected by precipitation and soil moisture availability (e.g. Austin & Vitousek 1998).

What is needed?

- Experimental studies of nutrient cycling and primary productivity in response to temperature and precipitation: both gradient studies and manipulative experiments required
- Studies of interactions between CO₂ and climatic factors

- Such studies must be underpinned by a modelling framework that incorporates nutrient cycling, and particularly, plant acclimation and adaptation to changes in nutrient availability

4) *Community composition*

- Global change (e.g. CO₂, T, rainfall, N deposition, etc) is likely to modify community composition. Changes in nutrient availability may drive the change in competitive relations, although these changes may also be caused by other factors.
- However caused, changes in community composition may alter nutrient cycling due to species differences in nitrogen content, litter decomposability, rooting depth, etc (e.g. King et al. 2004, Gill et al. 2006).
- Changes in functional type are of particular importance e.g. abundance of N-fixers, or competition between woody plants and grasses.
- We need a better understanding of how nutrient availability determines community composition.
- We also need to know how changes in species composition (driven by other processes, CO₂, T, water, etc) affect nutrient relations.

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