



Does flexible carbon allocation relieve nitrogen limitation? - Theory and observations for a resource economics paradigm to model carbon-nitrogen cycle interactions in terrestrial ecosystems

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Nitrogen (N) limitation of plant growth and carbon (C) sequestration appears to be widespread in terrestrial ecosystems, yet a substantial global sink of photosynthesis-derived C has persisted in recent decades where CO₂ has continuously increased. This appears paradoxical in view of Liebig's conceptual model of the Law of the Minimum, which posits that plant growth is ultimately limited by the most limiting resource. It also poses a challenge for process-based Dynamic Vegetation Models (DVMs) that simulate a strong N limitation of the land C sink. The interpretation of phenomena observed in field studies and the formulation of DVMs commonly conceptualise N limitation as a mismatch between supply (from the soil) and demand (by the plant) of reactive N. However, C allocation is highly flexible and plants thereby control mechanisms by which a shortage of N supply may be relieved. Mechanisms include symbiotic N fixation, plant-soil interactions stimulating N availability to plants, and the aversion of N losses from the ecosystem through effective scavenging of available N.

Here, we propose a resource economics paradigm to account for the energetic (C) cost of these adaptations and contend that eco-evolutionary optimality of plant functioning leads supply and demand to ultimately balance. A parsimonious model of optimal root and shoot allocation to balance C and N acquisition predicts that a leaf-level enhancement of photosynthesis under elevated CO₂ leads to a shift towards relatively more belowground C allocation. This shift may set in motion a cascade of feedbacks that ultimately accelerates the rate of N cycling, increases net primary productivity and reduces the openness of the N cycle, albeit at an increasing C cost of N acquisition.

We investigate observations from CO₂ manipulation experiments to test the predicted shift towards relatively more belowground C allocation and the existence of a feedback cascade that counters progressive N limitation and tends to relieve N limitation at longer time scales. This provides key mechanistic insights to reveal whether tight N constraints on CO₂ fertilisation and the land C sink may be overestimated when flexible allocation and its effects on C-N cycling are ignored in models. We argue that process-based DVMs should be re-formulated to account for C-N tradeoffs and plant adjustments to balance N supply and demand.