27th New Phytologist Symposium

Stoichiometric flexibility in terrestrial ecosystems under global change

Biosphere 2, Oracle, AZ, USA
25–28 September 2011

Programme, abstracts and participants

New Phytologist

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Scientific Organizing Committee

Richard Norby *(Oak Ridge National Laboratory, USA)*

Amy Austin *(University of Buenos Aires, Argentina)*

Jeff Dukes *(Purdue University, USA)*

Travis Huxman *(University of Arizona, USA)*

Yiqi Luo *(University of Oklahoma, USA)*

Gaius Shaver *(The Ecosystems Center, Marine Biological Laboratory, USA)*

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Programme, abstracts and participant list compiled by Jill Brooke
'Stoichiometric flexibility in terrestrial ecosystems under global change' illustration by A.P.P.S., Lancaster, UK

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Meal locations
Breakfast will be served daily from 7:00–8:15 in the ‘Snack Shop’.
Lunches and the **Welcome Reception** will also be in the ‘Snack Shop’ at the times indicated above.
Dinners on Monday and Tuesday evening will be held in the Biosphere Exhibit Hall.

Speaker Abstracts

Session 1: **Principles of stoichiometry in biological systems**
Chair: Rich Norby

1.1 Stoichiometry and coupled global biogeochemical cycles

WILLIAM H. SCHLESINGER
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The chemical characteristics of Earth have carried the imprint of biology since the first appearance of life more than 3.5 billion years ago, defining the science of biogeochemistry. On Earth, the movements of about 30 chemical elements essential to life are coupled, so that the behavior of one element can often be used to predict the behavior of other elements - in both the natural and human-perturbed settings. The coupling of biochemical elements stems from basic stoichiometry (the relative quantities of chemical elements in living tissue), the oxidation-reduction or "redox" reactions (in which one substance is oxidized [loses electrons] while another is reduced [gains electrons]) during metabolic activity, and chelation (in which a metal ion binds to an organic compound). In land plants, for instance, leaf tissues carry N and P in a predictable ratio of about 15, and deviations can be used to recognize N or P deficiencies. A similar, Redfield, ratio is seen in the biomass of marine phytoplankton.

In contrast, the biomass of land plants typically carries an N-to-P ratio of about 8.5, which is perhaps more flexible among varying environmental circumstances. Many anthropogenic environmental problems - climate change, eutrophication, acid precipitation, nitrogen saturation, and metal pollution - originate from the release of non-stoichiometric quantities of chemical elements to the environment. Geoengineering as a solution to certain global environmental problems, such as fertilizing ocean waters or agricultural soils, must be consistent with the underlying constraints of stoichiometry that characterizes coupled biogeochemical cycles.

1.2 Element cycling in a changing world

PETER VITOUSEK
Department of Biology, Stanford University, Stanford, CA 94305, USA

Multiple stochiometries meet and interact in ecosystems. The fascinating and variable stochiometries of life play out in the context of a number of geochemical stoichiometries that affect living organisms; in terrestrial ecosystems, some of these geochemical stoichiometries are independent of biological processes, at least in the short term. Major sources of element inputs to terrestrial ecosystems include atmospheric deposition, which is little affected by organisms in the receiving system in either magnitude or element ratios; rock and soil weathering, which organisms strongly influence in magnitude but not clearly in element ratios; biological nitrogen fixation, which is controlled by organisms and responds to their stoichiometries. Human-caused inputs of elements can occur by any of these pathways, or others. Element losses from ecosystems more frequently are strongly influenced – even regulated – by biological processes; however, they too include components (eg erosion) for which the stoichiometries of living organisms exert little influence. Human activities change element inputs to ecosystems on a very large scale, in both space and magnitude; they cause novel conditions in both the rates and ratios of elements entering and leaving ecosystems.

Session 2: Stoichiometric control of ecosystem responses to atmospheric and climatic change in different biomes

Chair: Amy Austin

2.1 Constraints on arid ecosystem response to a changing climate

TRAVIS E. HUXMAN

Ecology and Evolutionary Biology, Biosphere 2 & B2 Earthscience, University of Arizona, Tucson, AZ 85721-0088, USA

While soil water availability strongly controls the temporal dynamics of biological activity in arid systems, soil and plant nutrient status can modify the response of different ecosystem components to the major abiotic drivers of global change. Because of the ephemeral nature of water input, the timing of nutrient uptake and investment in active growing tissues controls the magnitude of a production response to rainfall. Interestingly natural selection has influenced the coordination of leaf exchange surfaces and nutrient concentrations such that species-specific responses to fertilization may mimic responses to changes in water status. Because of the pulsed nature of rain driving plant versus soil microbial processes, and differences in the population growth rates, how plant or microbial production processes may feed back and constrain either ecosystem response to abiotic drivers. What is not so clear is how novel atmospheric conditions may alter the relationship between production and other biogeochemical processes, or how changes in species composition may affect the distribution of nutrients on the landscape and the resulting constraints on change to novel drivers.

2.2 Stoichiometric flexibility in terrestrial ecosystems at physiological, community and ecosystem scales

ADRIEN FINZI
Dept. of Biology Graduate Prog. in Biogeoscience, Boston University, Boston, MA 2215, USA

Nearly ten years ago, Sterner and Elser suggested that ecological stoichiometry serves as a unifying principle for understanding coupled biogeochemical cycles. Since that time a great deal of research in terrestrial ecosystems has found both strong support and substantial variation from the basic tenets outlined in their book. In this talk, I examine the flexibility of ecological stoichiometry at physiological, community and ecosystem scales. This presentation draws from work conducted in tropical, temperate, boreal and arctic ecosystems. The basic conclusion at the time of writing this abstract is that shifts in community composition dominate stoichiometric flexibility, but that physiological plasticity and ecosystem-scale "constraints" also play an important role in stoichiometric controls over biogeochemical cycles.

2.3 Patterns in foliar nutrient resorption at multiple scales: driving factors and ecosystem consequences

SASHA C. REED, CORY C. CLEVELAND, ERIC A. DAVIDSON, ALAN R. TOWNSEND
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Foliar nutrients are transported away from leaves during senescence, and here we investigated patterns of nitrogen (N) and phosphorus (P) resorption at multiple scales to assess how the stoichiometry of resorption is related to ecosystem properties and nutrient limitation. We assessed resorption in six rainforest tree species in Costa Rica, explored N and P resorption patterns in an Amazon forest regeneration chronosequence where data previously suggested a transition from plant N to P limitation and, finally, analyzed published global resorption datasets to assess nutrient resorption patterns over large spatial scales. In the Costa Rica forest, N and P resorption varied significantly by tree species and resorption patterns were directly correlated with species-specific footprints in leaf litter and soil N and P. On average, canopy trees resorbed significantly more P than N (31 vs. 20%), consistent with previous data suggesting P constraints on ecosystem processes at this site. Data from the Amazon forest chronosequence suggested that, while canopy leaf N:P ratios did not vary systematically with forest age, resorption N:P changed in concert with transitioning nutrient limitation. At larger scales, data suggested that N:P resorption ratios were <1 in tropical forests, where P is commonly believed to limit plant growth, and >1 in temperate forests where N may more often be limiting. Together, these data suggest that, while N and P resorption patterns vary on multiple scales, resorption N:P ratios could offer an alternative foliar metric with which to consider nutrient limitation.

2.4 The role of soil stoichiometry in regulating vegetation response to elevated CO_2: N versus P limited forests

MEGAN MCGRODDY
Department of Environmental Sciences, University of Virginia, Charlottesville, VA 22904, USA

Experimental manipulations of atmospheric CO_2 have resulted in positive, negative and no response of forest vegetation. The ability of forest communities to increase their biomass in response to elevated atmospheric CO_2 is strongly dependent on nutrient availability. In a number of temperate studies increased root exudates resulted in increased rates of mineralization of organic nitrogen pools. The resulting increase in plant-available nitrogen supported an increase in plant biomass much larger than the amount of carbon released from the soil during mineralization. Mineralization of organic nutrients is a microbially mediated process and is regulated in part by the difference between microbial and soil carbon: limiting nutrient ratios. A survey of reported values for soil and microbial stoichiometric ratios showed that microbial C:N was globally very consistent and just over half the mean value of C:N in surface soils (8.2 vs 14.5). Given a microbial efficiency of 50% this suggests that microbes are generally slightly C limited with respect to N and C additions and are likely to respond to C additions. In contrast microbial C:P values were three-fold lower than those reported for soils (74.0 vs 211.7) suggesting that carbon additions could stimulate immobilization of P rather than mineralization. Here we compare the dynamics of P and N dynamics in soil organic matter and the results from temperate forest studies may or may not predict responses of P-limited forests to CO_2 enhancement

2.5 N:P ratios under climate change in grassland are regulated by indirect effects of soil moisture

FEIKE A. DIJKSTRA[1], ELISE PENDALL[2], YOLIMA CARRILLO[2], DANA BLUMENTHAL[3], JACK A. MORGAN[3]

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While most terrestrial ecosystems are more limited by nitrogen (N) than by phosphorus (P), future climates could change this situation. We tested whether increasing atmospheric [CO_2] (to 600 ppm) and/or temperature (1.5/3.0˚C day/night) altered the relative pools of N and P in plants, soil microbes and absorbed to resin probes in a semi-arid grassland. Elevated CO_2 decreased N:P ratios because of relative decreases in N pools (plants, resin probes) or relative increases in P pools (microbes). Warming often increased N:P ratios because of relative increases in N pools (plants, resin probes) or relative decreases in P pools (microbes). Decreased N:P ratios under eCO_2 and increased N:P ratios with warming could be explained by soil wetting effects of eCO_2 and soil drying effects of warming. Overall N:P ratios were higher in dry than in wet years. Our results suggest that grassland systems become more N limited under elevated CO_2 alone, but the balance between N and P limitation is restored with warming and drying.

2.6 Stoichiometric constraints on the response of northern peatlands to global environmental change

RIEN AERTS
Institute of Ecological Science, VU University Amsterdam, the Netherlands

Global environmental change includes a wide array of changes, including elevated CO_2 concentrations, increased atmospheric N deposition and higher temperatures. All these changes affect directly or indirectly stoichiometric relations in ecosystems and thereby their responsiveness. Northern peatlands are particularly important in this context as they play a pivotal role in the global carbon budget and any constraints on their responsiveness to global change have direct repercussions for the C budget. Fertilization studies have shown that plant growth in northern peatlands is usually N-limited (as corroborated with the generally low leaf N/P ratios). Given the great potential range in plant N/P ratios and the relatively moderate effects of global environmental change on N and P supply rates in northern peatlands, this implies that it is not the stoichiometric constraints in plants that limit their responses, but rather the relative net supply rates of N and P in the soil. The scarce data from sub-arctic and Antarctic warming studies show that the responsiveness of soil N and P dynamics to global environmental change is largely determined by secondary constraints such as microbial immobilization of nutrients, low pH, low temperatures and chemical interactions with secondary plant compounds. Therefore, future studies should concentrate more on the effects of global environmental change on soil N and P dynamics and the underlying mechanisms.

2.7 Stoichiometry and change in carbon balance of the arctic landscape

GAIUS R SHAVER
The Ecosystems Center, Marine Biological Laboratory, Woods Hole, MA 02543, USA

The arctic landscape is a heterogeneous mosaic of contrasting ecosystems, dominated by a diverse array of plant functional types and varying by more than two orders of magnitude in productivity, organic matter accumulation, and rates of element cycling. The properties of this landscape mosaic are also changing rapidly, driven by rapid change in the arctic environment including warmer temperatures, a changing disturbance regime, and corresponding changes in vegetation composition, structure, and function.

Despite this apparent patchiness of the arctic landscape, a growing body of evidence indicates that diverse arctic vegetation types follow very similar allometric and stoichiometric “rules” of canopy development and biomass accumulation. These common rules can be used effectively to scale up predictions of large-area C exchange, based on fine-scale measurements and without detailed knowledge of species or functional type composition of the vegetation. The same rules can be used to explain changes in vegetation function on disturbed or experimentally manipulated sites where the vegetation composition is changing or has changed. This talk will provide several examples of these empirical rules, focusing on controls of Gross Primary Production and Net Ecosystem Production in relation to leaf area and canopy N content.

Session 3: **Stoichiometric limitations across scales**
Chair: Yiqi Luo

3.1 Coupling of metabolism with chemical composition in leaves

OWEN ATKIN
Division of Plant Sciences, Research School of Biology, The Australian National University, Canberra, ACT, Australia

Analyses of leaf phenotypes from a wide range of biomes have shown that interspecific variations in leaf carbon exchange rates can be predicted using scaling relationships linking leaf photosynthesis (A) and respiration (*R*) to the underlying chemistry of leaves, and that these scaling relationships are important for predicting vegetation patterns and plant-atmosphere carbon fluxes. Crucially, however, considerable scatter occurs around predicted log-log scaling relationships in field-sampled data sets, particularly when plants are sampled at environmentally contrasting sites (e.g. sites differing in growth temperature, nutrient availability and/or soil moisture). In this talk, I will discuss the underlying metabolic and developmental factors responsible for this scatter, with focus being placed on the impact of acclimation of plant carbon metabolism, and environment-mediated changes in leaf chemistry, on predicted log-log scaling relationships.

3.2 The interplay between soil N availability, forest C partitioning, and ecosystem C storage in a CO_2-enriched sweetgum plantation

COLLEEN M. IVERSEN, RICHARD J. NORBY
Environmental Sciences Division, Oak Ridge National Laboratory, One Bethel Valley Road, Oak Ridge, TN 37831-6301, USA

Rising atmospheric CO_2 concentrations are expected to increase carbon (C) storage in long-lived plant biomass and soil organic matter pools in forested ecosystems. However, the long-term fate of C in forests depends on the amount of tree C uptake under elevated [CO_2], and the subsequent partitioning of photosynthates among different plant tissues. In turn, these processes are limited by, and respond to, plant-available soil nitrogen (N).
An N-limited sweetgum plantation in eastern Tennessee, USA, responded to 12 years of CO_2-enrichment with increased C uptake, which was mainly partitioned belowground to fine roots in order to mine the soil for N. Short lifespans of fine-roots resulted in increased C storage in soil but not plant biomass. While flexibility in C partitioning facilitated increased N uptake, this response was not sustainable over the long-term, as most of the additional N acquired under elevated [CO_2] was needed to support the production of N-rich root tissue. Ultimately, N-limitation precluded a sustained increase in stand production under elevated [CO_2].
A future goal of data-model synthesis should be to capture the interplay between C partitioning among plant biomass compartments in response to soil nutrient availability, and the subsequent effects on long-term ecosystem C storage.

3.3 Does carbon get in the way? Stoichiometric controls on litter decomposition and nutrient release in terrestrial ecosystems

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Climatic and plant chemistry controls on litter decomposition and nutrient mineralization in terrestrial ecosystems have been explored extensively, and while carbon:nutrient ratios have been shown to be important as predictors of mass loss and nutrient release, the general nature of stoichiometric controls on litter decomposition is not clear. Due to the recalcitrant nature of many of the carbon compounds in senescent plant material, particularly, lignin and its monomer components, straightforward controls of C:N:P ratios are often obscured in empirical litter decomposition studies. In some ecosystems, particularly aridlands, these are unrelated to rates of mass loss. We explore modeling and empirical efforts that have tried to elucidate these relationships and ask the following questions: 1) How important is litter carbon chemistry in modulating stoichiometric controls on litter decomposition? 2) Do C:N:P controls dominate only in ecosystems where microbial decomposition is most important? 2) Will the relative importance of stoichiometric controls on litter decomposition be altered by global change? New models which incorporate the relative importance of multiple controls on litter decomposition could be important in extending our understanding of ecological stoichiometry on the key process of decomposition in terrestrial ecosystems.

3.4 Stoichiometric homeostasis of dominant plant species: Impacts of global change and implications for community dynamics and productivity

MELINDA D. SMITH
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Recent studies suggest dominant plant species have greater stoichiometric homeostasis - that is, the ability to maintain their elemental composition of nitrogen and phosphorus despite variation in the elemental composition of available resources - than those that are uncommon in the community. Furthermore, ecosystems dominated by homeostatic plant species have been shown to be more productive and stable. However, it is unclear the extent to which dominant species within a community may vary in their stoichiometric homeostasis, whether aspects of global change, such as climate change and eutrophication, may differentially alter stoichiometric homeostasis of dominant plant species, and what consequences these alterations may have for community structure and function over time. Here, I address these gaps in our understanding by first assessing variation in stoichiometric homeostasis of the key dominant plant species in the tallgrass prairie ecosystem of the central US. I then utilize several ongoing experiments in intact tallgrass prairie to determine whether multiple aspects of climate change (altered precipitation, warming and climate extremes) and long-term nutrient additions alter stoichiometric homeostasis of these dominant species. Finally, I explore the implications of alterations in stoichiometric homeostasis of dominant plant species for plant community structure and function.

3.5 Microbial growth efficiency influences ecological stoichiometry and nutrient cycling from soils downstream to seas

P. G. TAYLOR, A. R. TOWNSEND
Institute of Arctic and Alpine Research and Department of Ecology and Evolutionary Biology, University of Colorado – Boulder, 1560 30th Street, Boulder, CO. 80303, USA

Heterotrophic microbes are the primary engines of decomposition and their respiration is the largest sink for organic matter. The balance between carbon storage and loss depends in part on the share of organic carbon converted into biomass (anabolism) versus respiration (catabolism), termed growth efficiency (GE). Decades of research show that microbial metabolism is highly responsive to temperature and nutrient availability, and can vary from <1 to 80%, but few studies have investigated these controls on GE across Earth's ecosystems. We begin with showing differential dependence of anabolic and catabolic metabolism on temperature and nutrient availability. The difference between growth and respiration is highest at cold and hot temperatures, and these processes converge in warm environments. This divergent response drives a strong "hump-shaped" curve in GE with the apex near to 25°C. Collectively, these patterns closely mimic physiological responses of leaf metabolism to temperature. Nutrients also play a role, where at any given temperature variations in GE can be explained by differences in nutrient availability. Lastly, we integrate our findings into stoichiometric theory, and demonstrate that shifts in GE alter system-level nutrient accumulation by shifting the stoichiometric breakpoints of nutrient uptake and recycling.

3.6 The stoichiometric imprint of land use and production

ESTEBAN G. JOBBÁGY
Grupo de Estudios Ambientales, CONICET & Universidad Nacional de San Luis, Argentina

Productive land uses influence the stoichiometry of terrestrial ecosystems through (i) biomass harvest, (ii) replacement of plant and animal communities, and (iii) addition of fertilizers and soil amendments. I examine the range of stoichiometric imprints left by these three types of interventions on ecosystems and discuss some of their recent trends. The stoichiometry of nutrient exports respond not only to the final target product (e.g. protein, starch, timber, energy) but also with the organism/tissue in which it is embedded. For example, the N:P ratio of protein exports from farming land grow as we switch from cereal (milk) to pulse (beef) to poultry, indicating decreasing P costs per unit of protein along this sequence. Animal pathways, however, create a strong P redistribution within farms and high disposal and local P pollution when fed with grains in confined systems. In the case of bioenergy harvests, although C is the principle export, high exports of N and P also occur (when biomass is grain-based) or K (when sucrose-based, exported from sap) or Ca (when wood-based). Even under no harvesting scenarios, the vegetation transformations that come with land uses can alter the stoichiometry of ecosystems. The transitions of natural forests to pastures and natural grasslands to tree plantations produce opposing imprints in the Ca:K composition of the exchange complex of soils (and their acidity as well) that mirror the contrasting cycling ratios of these two elements by woody and herbaceous plants. These same systems show that in relatively short periods the stoichiometry of the top soil and the new vegetation converge. In agricultural systems, fertilizer inputs aimed to sustain or increase harvesting rates, do not necessarily track the stoichiometry of outputs. Cross-national comparisons and decadal statistics suggest that, as agriculture intensifies, the N:P ratios of these inputs raise beyond those of product outputs, explaining raising N:P ratios of field-borne pollution.

3.7 Stoichiometry as an ingredient of invasive species' success

JEFF DUKES
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A variety of mechanisms have been invoked to explain why some species become invasive when introduced to new regions. Stoichiometric differences between introduced and native species are likely to play a role in many systems. For instance, invasive plant species that thrive in disturbed and nutrient-rich areas often have lower C:nutrient ratios than natives, and grow and take up nutrients more quickly. Introduced species that become problematic in resource-poor habitats are sometimes better adapted to nutrient-limited conditions, with higher resource-use efficiencies than many of the native species. In both environments, invasive species tend to have high trait plasticity, which can include flexible stiochiometry. Other mechanisms may combine with stoichiometric differences to favor introduced species. For instance, in resource-rich areas, which are becoming more widespread as rates of N deposition continue to increase in many regions, stoichiometric differences may combine with enemy release to favor invasive plant species. That is, invasive species that are pre-adapted to high-resource conditions often have many natural enemies in their home ranges, and so may experience large reductions in herbivory and pathogen attack in their new range, which could disproportionately favor them over natives. Consequences of invasions for rates of carbon and nutrient cycling will depend on initial resource conditions in the local environment, as well as the extent of stiochiometric differences between invasives and common natives. These consequences will also depend on a variety of other ecosystem processes and properties that influence the nature of trait-ecosystem feedbacks, such as aridity and disturbance regimes.

Session 4: **Stoichiometric limits to C sequestration**
Chair: Travis Huxman

4.1 Effect of increased atmospheric [CO_2] on C:N:P ratios of litter and soils at plantations in Italy and Wales

MARCEL R. HOOSBEEK
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At the POP-EuroFACE experiment in central Italy (1999–2004), N concentrations of leaf litter (*Populus euramericana, P. alba, P. nigra*) were lower under increased atmospheric [CO_2]. The C:N ratio of L (Oi) litter was larger under increased [CO_2], while C:N ratios of the F (Oe) and H (Oa) layers were not affected due to N immobilization during decomposition. In the mineral soil C:N ratio increased linearly from 9.3 in 1999 to 10.7 in 2003, but decreased in 2004 to 10.0. Monitoring of microbial biomass revealed that in 2004 increased N immobilization took place under increased [CO_2]. At the BangorFACE experiment in north-west Wales (2004–2008), C:N ratios of *Alnus* and *Betula* leaves increased under increased atmospheric [CO_2]. C:N ratios of the mineral soil decreased in 2005, increased in 2006, and decreased again in 2007. The increase in 2006 was due to a priming effect. During the total experiment soil C:N ratios decreased, although there was no significant [CO_2] treatment effect. Increased N-use efficiency was found to be the major mechanism at both sites sustaining increased NPP under increased [CO_2]. Currently (July 2011), litter and soil samples are analyzed for total and available P after which the role and fate of P will be explored.

4.2 Stoichiometric controls on terrestrial biological nitrogen fixation

CORY C. CLEVELAND[1], **SASHA C. REED**[2], **BENJAMIN Z. HOULTON**[3]
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Biological di-nitrogen (N_2) fixation is a lynchpin biogeochemical process that brings nearly all new N into natural ecosystems. Despite the fact that the potential biota of the vast majority of ecosystems includes organisms that possess the ability to fix atmospheric N_2, low N availability still constrains plant productivity and carbon (C) storage throughout much of the terrestrial biosphere. A number of mechanisms have been postulated to explain this paradox (energy, climate, herbivory, etc.) with recent research pointing to strong biogeochemical regulation. In particular, N, phosphorus (P) and trace metal availability have all been linked to N fixation rates, both directly and indirectly. Further, substrate stoichiometry (e.g. N:P ratios), is widely held to be a control on marine N fixation and probably influences N fixation on land as well. In this presentation, I will synthesize existing data of stoichiometric (C, N, P and micronutrient) constraints on N fixation, and describe how such constraints are likely to respond to both climate and atmospheric change. In addition, while the response of the terrestrial C cycle to climate and atmospheric change (e.g. atmospheric CO_2 enrichment), is directly linked to ecosystem N availability – with some models suggesting that N fixation responses to global change will strongly influence the future C cycle – most current models do not include nutrient-N fixation interactions. Thus, I will also outline a framework for incorporating stoichiometric controls on N fixation into prognostic earth system and climate change models.

4.3 Microbial element-use efficiencies drive the stoichiometry of mineralization processes

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We investigated the regulation of microbial homeostasis by physiological adaptations of the microbial community during litter decomposition, i.e. the adjustments of the microbial assimilation efficiencies of carbon (C), nitrogen (N) or phosphorus (P) to variations in resource stoichiometry in order to maintain constant biomass stoichiometry. We conducted a 6-month mesocosm experiment with beech (*Fagus sylvatica*) litter of varying C:N:P ratios and measured gross rates of N (protein depolymerisation and ammonification), P and C mineralization. Our results demonstrate that microbial N and P cycling processes are strongly affected by litter C:nutrient ratios and that microbial communities in the decomposing litter were physiologically N limited, resulting in constraints on the stoichiometry of mineralization fluxes (microbial C, N and P mineralization). Our findings provide empirical and mechanistic support that the extent of C and nutrient losses is strongly determined by the C, N and P assimilation efficiencies of decomposer communities and that the limiting element controls the rate of C sequestration and nutrient recycling during litter decomposition. We suggest that adjustments in microbial element-use efficiencies, due to changes in litter stoichiometry, should be included into ecosystem models to accurately predict litter decomposition in the context of climate change.

4.4 Stoichiometry of an oak woodland in response to twelve years of CO_2 treatment

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Increased carbon dioxide concentration in the atmosphere stimulates photosynthesis and could increase rates at which ecosystems accumulate carbon. Increased carbon gain could dilute concentrations of other elements, promote their increased acquisition from external sources, and alter their distribution within ecosystems, moving elements from ecosystem compartments with naturally low ratios of carbon to other elements to compartments where those ratios are higher. Limits on these stoichiometric solutions could modulate the nature and magnitude of ecosystem carbon gain as atmospheric carbon dioxide (CO_2) continues to increase. We exposed a sub-tropical oak woodland to elevated Co_2 for twelve years and monitored the masses and concentrations of 27 elements in plant and soil pools at the end of the experiment. The elements measured were: Al, As, Ba, C, Ca, Cd, Co, Cu, Cr, Fe, K, Mg, Mn, Mo, N, Na, Ni, P, Pb, S, Se, Sr, Ti, U, V, W, and Zn, and thus include macronutrients, micronutrients, and potentially toxic elements. Solutions to the stoichiometric challenges imposed by elevated CO_2 included dilution and redistribution (from soil to plants), with little evidence for accumulation. These results suggest stoichiometric constraints to ecosystem carbon gain in response to elevated CO_2, though the boundaries and generality of those constraints require further testing in a broader array of ecosystems.

Session 5: Incorporating stoichiometric principles into models

Chair: Gaius Shaver

5.1 Flexibility of key parameters in determining carbon-nitrogen coupling under elevated CO_2 in Duke and Oak Ridge Forests: Results from inverse analysis

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Carbon (C) sequestration in terrestrial ecosystems is strongly regulated by nitrogen (N) processes. However, key parameters that determine the degree of N regulation on terrestrial C sequestration have not been well quantified. We have used a Bayesian probabilistic inversion approach to estimate 14 target parameters related to ecosystem C and N interactions from 19 datasets obtained from Duke, and 13 data sets from Oak Ridge Forests under ambient and elevated carbon dioxide (CO_2). Our results indicated that 8 of the 14 target parameters (such as C:N ratios in most ecosystem compartments, plant N uptake and external N input) were well constrained by available datasets whereas the others (such as N allocation coefficients, N loss and the initial value of mineral N pool) were poorly constrained. Our analysis showed that elevated CO_2 in Duke Forest led to increases in C:N ratios in foliage, fine roots and litter. Moreover, elevated CO_2 stimulated plant N uptake and increased ecosystem N capital in Duke Forests by 25.2% and 8.5%, respectively. In addition, elevated CO_2 resulted in the decrease of C exit rates (i.e., increases in C residence times) in foliage, woody biomass, structural litter and passive soil organic matter, but the increase of C exit rate in fine roots. In comparison, elevated CO_2 in Oak Ridge Forest increased C turnover in foliage and fine roots and did not significantly increase ecosystem N capital. Our results demonstrated that CO_2 enrichment substantially altered key parameters in determining terrestrial C and N interactions, which have profound implications for model improvement and predictions of future C sequestration in terrestrial ecosystems in response to global change.

5.2 The effects of long-term warming on tundra soil enzyme dynamics: linking empirical data with modeled microbial N-limitation

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Globally, Arctic soils are among the largest stores of terrestrial organic carbon (C), and there is substantial interest in developing mechanistic descriptions of Arctic systems' C dynamics as they respond to predicted warming. Recent research suggests that nitrogen (N) - limitation regulates both plant and microbial growth in tundra soils during the summer growing season, but microbes may become C-limited during the winter and spring thaw period. However, there is a paucity of information on the impact of warming on the seasonality of Arctic biogeochemical dynamics. To address this knowledge gap, we are using a combination of modeling and empirical approaches to explore the consequences of long-term warming on seasonal permafrost soil biogeochemical cycling using a greenhouse experiment initiated in 1988 at the Toolik, AK Long Term Ecological Research site. We have correlated potential extracellular enzymatic activity with concurrently collected biogeochemical measurements using soils harvested across seasons and horizons. Our study suggests that warming has stimulated hydrolytic enzyme activity, with the greatest increase correlated with a spike in dissolved N occurring during the spring thaw. Mechanistically modeled scenarios that incorporate the potential for explicit microbial nutrient limitation support these empirical results. This project highlights the potential for the seasonal timing of warming to be a significant factor in regulating stoichiometric constraints on microbial dynamics and thus the potential magnitude of tundra soils' decomposition response to climatic warming.

5.3 Modelling the effects of stoichiometric constraints on global ecosystem responses to global change

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The first generation of coupled carbon-cycle climate models (C4-models) suggested that there is a strong terrestrial carbon-climate interaction, effectively accelerating the rate of anthropogenic climate change. This is compensated for by an even stronger carbon-concentration interaction due to the CO_2-fertilisation of vegetation that leads to enhanced terrestrial carbon sequestration and thereby slows the rate of anthropogenic climate change. The often made criticism that these models ignore the consequences of ecosystem stoichiometry for ecosystem dynamics has sparked the development of a second generation of C4-models that account for nitrogen, and in some cases also phosphorous dynamics. The first global studies of these new models generally show a substantially smaller carbon-concentration interaction, and also a reduced (if not inversed) carbon-climate interaction, that, when combined, lead to a larger rate of anthropogenic climate change than predicted by the first-generation C4-models.

In this talk I will discuss the key assumptions made in global carbon-nitrogen (-phosphorous) cycle models for estimating the effects of ecosystem stoichiometry (and its flexibility) on ecosystem responses, and potential data sources for constraining global stoichiometric models. I will further explore the consequences of these assumptions to step-wise and transient perturbations of the nitrogen-carbon cycle induced by enhanced atmospheric N deposition and atmospheric CO_2 concentration for different ecosystem types. Based on these examples I will draw out the uncertainty in global carbon-cycle climate system interactions due to uncertainty in representing the effects of ecosystem stoichiometry on land carbon cycling.

5.4 Stoichiometry and global change from a modeling perspective

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The C:N:P stoichiometry of organisms is well understood. In plants it can be explained by the links from P-rich RNA to production of N-rich enzymes and to biomass production. A consequence is that increasing relative growth rates imply increasing element concentrations, linear in N and quadratic in P. No similar mechanistic relations have been proposed for other elements. It seems, however, that stochiometrically P, S and probably Mn closely follow N in plants although another group of elements (K, Ca, Mg) follow biomass or C development more closely. The behaviour of other elements seems to be in-between these two groups.
What is causing stoichiometrical differences? I suggest that the major driver is differences in the environment. Differences between individuals of the same genotype can be as large as between different genotypes when growing in the same environment. Variations between, for example, leaves on the same individual can also be considerable. Together with the uncertainty of the extent and role of uptake beyond what is required for growth (excess uptake), this is a challenge for the interpretation of stoichiometrical differences.

Poster Abstracts

Listed alphabetically by first author, presenting author is underlined.

1. Exploring the missing processes contributing to the Amazon Basin phosphorus budget.

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The Amazon Basin is one of the world's largest organic carbon reservoirs. Due to the humid climate and slow tectonic uplift, soils are strongly weathered and poor in phosphorus (P). It is hypothesized that the availability of P strongly depends on atmospheric inputs. However, recent studies have shown that the atmospheric input of P is smaller than the atmospheric export. These lines of evidence raise the question about which unidentified biogeochemical processes provide P to the rainforest. We hypothesized that animals, as P vectors of nutrient transfer, are essential to keep the productivity in the terra firme Amazonian lowland forest. We tested our hypothesis modeling terra firme and flooded forest dynamics separately using Buendia *et al.* (2010) model and then coupling the two systems though P biotic fluxes. Our sensitivity experiments suggest that the biotic redistribution of P can sustain the long-term forest productivity. Alterations of this ecosystem function (e.g., a loss of biodiversity) may, therefore, affect productivity in the Amazon. Although our model is minimalistic it allows synthesizing multiple processes contributing to the terra firme Amazonian P budget. As such, this model serves as an explorative tool generating quantitative predictions and hypotheses, which may stimulate further studies of Amazonian P dynamics.

2. The quality of rhizodeposits can alter the effects of elevated CO_2 on SOM decomposition

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Elevated CO_2 (eCO_2) has been associated with altered soil organic matter (SOM) decomposition (positive or negative priming), but the mechanisms underlying this effect are not understood. We evaluated the interactive effects of the C-N stoichiometry of rhizodeposits and eCO_2 on priming. We grew two grass species (C_4 *Bouteloua gracilis,* C_3 *Pascopyrum smithii*) in growth chamber conditions under ambient and eCO_2. The C/N of rhizodeposits was manipulated by repeated foliar application of K_2NO_3. Plants were grown from seed in a ^{13}C-labeled atmosphere, which allowed us to quantify SOM decomposition via isotopic partitioning of respiration.

eCO_2 increased plant biomass and soil microbial biomass C and N but it decreased soluble organic C. Foliar N addition did not alter biomass but it increased soil mineral N and decreased the ratio of soluble C to N. Presence of plants increased SOM decomposition under ambient CO_2, but decreased it under eCO_2. In soils with *B. gracillis,* foliar N addition enhanced the negative effect of eCO_2 but it increased decomposition under ambient CO_2. We conclude that the effect of eCO_2 on SOM decomposition is dependent on the stoichiometry of root-derived inputs and that this effect is species-specific.

3. Stoichiometric shifts of soil carbon, nitrogen and phosphorus in response to prescribed burning regimes

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A well-replicated, 33 year old experiment was selected to investigate the effect of repeated burning on the biogeochemical cycling of carbon (C), nitrogen (N) and phosphorus (P) in a native wet sclerophyll forest dominated by *Eucalyptus pilularis*. The treatments included: unburnt, biennially burnt and quadrennially burnt. Results showed that topsoil C and N contents were significantly lower but the P content was higher in the biennial burnt treatment than the unburnt and quadrennially burnt, while there were no significant differences between the unburnt and quadrennially burnt treatments. This led to lower soil C:P and N:P ratios in the biennially burnt treatment than in the unburnt and quadrennially burnt treatments, while the soil C:N ratio remained unchanged across treatments. This indicated that biennial burning modified the biogeochemical cycling, while the quadrennial burning allowed the recovery of biogeochemical processes. However, over the 33 year period of the experiment, the soil N:P ratio increased with time regardless of burning regimes, implying that leaching loss of P from the ecosystem would continue in the long term despite P returning to the soil from burning of the plant materials and/or N inputs will increase due to biological N fixation.

4. Direct and indirect effects of changing rainfall on tropical forest leaf litter decomposition

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Tropical forests contain huge stores of carbon (C), both aboveground and belowground, and their ability to act as a C sink depends on the balance between photosynthesis and respiration. Global climate change could influence decomposition and respiration directly by altering microbial processes or indirectly via vegetation change, which alters the quantity and quality of organic C entering the soil.

We investigated the indirect and direct effects of changing precipitation on leaf litter decomposition in lowland tropical forests. Specifically, we quantified the relative importance of leaf litter quality, soil nutrient availability and precipitation for decomposition. This was done by measuring the decomposition of senescent leaves from a range of tropical tree species, with varying functional traits, placed along a rainfall gradient in Panama.

Decomposition was affected significantly by litter species identity and soil fertility, but not rainfall. The soil fertility effect was explained by soil phosphorus (P) and C: nitrogen (N) ratio, and extracellular soil enzyme activities, while the litter species effect was not explained by C:N:P ratios alone. These results suggest that precipitation change will affect decomposition in lowland tropical forests indirectly via shifts in plant community composition, and that the responses will vary with soil fertility.

5. How to make a beetle out of wood: stoichiometric determinants of the life history of xylophages

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Xylophages and their diet differ drastically in element composition which may result in prolonged development time. We used *Stictoleptura rubra* (Coleoptera, Cerambycidae) to learn how this xylem-feeding beetle can match its life history to dietary constraints. The composition of *S. rubra* does not differ much from other Coleoptera in N, P and Cu contents, but the ratios C:N, C:P and C:Cu in the beetles are 408, 298 and 107 times lower respectively than in clean pine wood, thus causing severe nutritional imbalance. The discrepancy is less drastic for the samples of wood taken at larval corridors (102, 70 and 71), and even less so for rotting wood (59, 26 and 22 respectively). Simulations using data on life history show that feeding on the clean wood could increase development time to improbable values, while feeding on wood heavily infested with fungi may balance nutritional budgets during the usual development period. Further enquiry needs to focus on how *S. rubra* can thrive on its usual diet of wood that is only slightly enriched in nutrients by fungi.

6. Experimental manipulation of N-to-P ratio had contrasting effects in plant growth and decomposition

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Recent increases in atmospheric Nitrogen (N) deposition in forest ecosystems in the northern hemisphere have changed plant diversity, plant growth and nutrient cycling. Chilean temperate ecosystems have not historically been exposed to high inputs of atmospheric N, and are likely phosphorous (P) depleted because of high rainfall regimes. If ecosystem responses to N addition are predominantly determined by initial soil nutrient stoichiometry (i.e. N:P) then, increases in soil N in Chilean temperate ecosystems could lead to P-limitation. We experimentally tested the potential effects of future N-deposition on the growth and decomposition of five dominant tree species from southern Chile by soil N- and P-fertilization. We found that higher N increased soil N:P reducing mean plant growth by 25%. Soil P-addition increased plant growth by 13.5%. In contrast, decomposition did not change significantly with any treatment. Our study suggests that in Chilean temperate forests nutrient limitation on plant growth and microbial activity differ and could respond differentially to future global change scenarios.

7. The changing roles of N and P limitation on land carbon uptake in projections with a global model

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Globally, the most common nutrients limiting plant growth and soil carbon (C) storage are nitrogen (N) and phosphorus (P). The N and P cycles have different geophysical controls and therefore the effects of climate change and increasing atmospheric CO_2 concentrations on N and P cycling differ. To investigate the influence of N and P limitation on land C cycling, we incorporate a P cycle into the land surface model JSBACH. Model results show that P limitation differs from N limitation in its geographic occurrence and temporal evolution, resulting in a strong additive effect of N and P limitation on land C uptake in the 21st century. Besides increasing atmospheric CO_2, the temporal evolution of N and P limitation is strongly influenced by warming and N deposition. The positive effect of warming on mineralization rates is less pronounced for P than for N. In combination with high N deposition rates warming shifts the today's N-limited ecosystems of higher latitudes to P limitation under high atmospheric CO_2. These findings suggest that land C uptake could be less than expected from C and CN models.

8. Leaf-level gas exchange response to nitrogen addition in Arctic tundra species

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Consequences of global climate change are detectable in the historically nitrogen and phosphorus limited Arctic tundra landscape, and pose implications for the terrestrial carbon cycle. Photosynthesis and respiration, the main components of autotrophic carbon cycling, are influenced both directly through increased temperatures and indirectly through increased soil nutrient availability by higher rates of microbial activity. This study examines leaf-level gas exchange and related leaf traits in two dominant tundra species, *Betula nana* (woody shrub) and *Eriophorum vaginatum* (tussock sedge), under a gradient of nitrogen and phosphorus fertilization in the North Slope of Alaska. Respiration increased with increasing N and P addition ($p<0.10$ in *B. nana*); the highest rates of respiration corresponded to the highest concentrations of leaf N in both species. Similarly, the degree of inhibition by light (Kok-effect) generally decreased with increasing fertilization. Rates of photosynthesis did not significantly or linearly increase with fertilization, perhaps exhibiting an acclimation effect. At the cellular level, both chloroplast and mitochondrial densities exhibited species and treatment effects ($p<0.01$). Results from this study indicate a species-specific decoupling of responses in respiration and photosynthesis under N and P fertilization, implying an alteration of the carbon balance of the tundra ecosystem under future climatic conditions.

9. TRY – a global database of plant traits

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We present the global database initiative named TRY, which has united a wide range of the plant trait research community worldwide, and gained an unprecedented buy-in of trait data: so far 93 trait databases have been contributed. The data repository currently contains almost three million trait entries for 69,000 out of the world's 300,000 plant species, with a focus on 52 groups of traits. A first analysis of the data shows that most plant traits are approximately log-normally distributed, with widely differing ranges of variation across traits. Most trait variation is between species, but significant intraspecific variation is also documented, accounting for up to 40% of the overall variation. Plant functional types (PFTs), as commonly used in vegetation models, capture a substantial fraction of the observed variation - but for several traits most variation occurs within PFTs, up to 75% of the overall variation. In the context of vegetation models these traits would better be represented by state variables rather than fixed parameter values. The improved availability of plant trait data in the unified global database is expected to support a paradigm shift from species to trait-based ecology and enable a more realistic and empirically grounded representation of terrestrial vegetation in Earth system models.

10. Feedback regulation of photosynthesis by accumulation of non-structural carbohydrates and nitrogen nutrition

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It is well known that both the capacity for the utilization of assimilates (non-structural carbohydrates) and nitrogen content are critical to the ability of plants to sustain increased photosynthetic rates when grown at elevated CO_2 concentration. However, mechanisms for interactive effects of nitrogen content and accumulation of non-structural carbohydrates are still not well understood. Using 3-year-old *Fagus sylvatica* seedlings we have explored the interactive effects of nitrogen nutrition (leaf nitrogen content was 1.21% and 2.53%) and sink capacity (sucrose feeding) on the dynamics of accumulation of non-structural carbohydrates and photosynthetic parameters. Exponential decay ($p<0.01$) was observed in CO_2 assimilation rate and stomatal conductance when the content of non-structural carbohydrates increased. However, this relationship was modified by the nitrogen content. Accumulation of non-structural carbohydrates had relatively smaller effect on photochemical efficiency of photosystem II. Application of chlorophyll fluorescence imaging enabled us to evaluate changes in spatial distribution of photosynthesis down-regulation on the leaf-level. We can conclude that the accumulation of non-structural carbohydrates down-regulates photosynthesis mainly through the stomatal conductance, and this effect is further modified by nitrogen content.

11. The impact of elevated carbon dioxide concentration and drought on C and N metabolism in field grown *Glycine max*

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Nitrogen fixation is very sensitive to drought, and growth at elevated (e) carbon dioxide concentration ([CO_2]) commonly reduces water use. Therefore, we hypothesized that the soil moisture content under *Glycine max* (soybean) grown at e[CO_2] would remain above the threshold for inhibition of N_2-fixation, and limit the negative impact of drought on N assimilation. We grew soybean at current (c) [CO_2] and e[CO_2] using Free Air CO_2 Enrichment (FACE) technology. Within each FACE plot we created a drought sub-plot by deploying rainfall exclusion awnings to intercept nocturnal precipitation (drought). An adjacent un-manipulated sub-plot provided a control. We present metabolite levels and the activities of enzymes associated with C and N metabolism measured over two seasons. N metabolism was largely unaltered by drought at c[CO_2]. However, when drought was most severe, the leaf N content of soybeans grown at e[CO_2] was reduced. This suggests that e[CO_2] does not protect N assimilation during moderate drought, but surprisingly, has a negative impact on N assimilation during episodes of severe drought.

12. Are exotic plant invasions and species loss related to N:P stoichiometry? A test for the Brazilian Cerrado vegetation

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Plant invasions and species loss threaten terrestrial ecosystems. Both are related to nutrient enrichment, and recently vegetation N:P stoichiometry has been recognized as a potential controlling factor. Plant species loss and invasions are mostly studied in the Northern hemisphere, whereas many biodiversity hotspots are on ancient tropical soils. The Brazilian Cerrado has a high floristic diversity but has been invaded, mainly by African grasses. By measuring 60 field plots we found that endangered species and exotic invasive species showed opposite patterns with respect to aboveground biomass of the vegetation and the N:P ratio in it: i.e., endangered species occurred in sites with biomass <1200 g.m^{-2} and N:P >11, whereas alien species mainly occurred at biomass >1000 g.m^{-2} and N:P <13. The occurrence of endangered or alien species was not correlated to soil inorganic N or P. Cerrado soils are generally poor in mineral-P but rich in organic-P. Hence, plant growth may be controlled by acquisition of organic-P. Indeed, an experiment showed that phosphatase activity is an important mechanism for the success of alien plant invasions, and indicates that vegetation N:P stoichiometry reflects the actual nutrient limitation of the community, integrating information on plant physiology and soil nutrient status.

13. C:N:P stoichiometry along the leaf-litter-soil-stream continuum

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The relationships among C, N, and P are strongly constrained by biological factors in terrestrial and aquatic ecosystems. In consequence, C:N:P ratios and nutrient dynamics are highly conserved as fresh, photosynthetically active leaves senesce, enter the decomposition pathway and are degraded, returning inorganic nutrients to soils and streams. Nutrients are resorbed from senescing leaves to conserve limiting resources, increasing C:N and C:P ratios in surface litter. These plant residues are degraded by decomposers with cellular composition richer in N and P than the litter, resulting in strong stoichiometric imbalances. As C is respired and nutrients immobilized by the decomposers, C:N and C:P ratios decline, reaching values typical of soil organic matter. Here we attempt to elucidate the controlling factors on both resorption and nutrient mineralization. First, climatic and vegetation drivers of resorption are assessed. Second, global patterns of N and P mineralization during decomposition are interpreted using a decomposition model that accounts for decomposer stoichiometry. The modeling analysis suggests that respiration from nutrient-poor residues is higher than from nutrient-rich ones – a response observed in other aquatic and terrestrial organisms. The common stoichiometric rules the regulate decomposition explain the striking similarities between C:N:P ratios in terrestrial and aquatic systems worldwide.

14. Ecological stoichiometry: a better predictor for climate sensitivity of respiration in peat soils?

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Organic soils act as vital global carbon stores maintained in northern latitudes by climate and nutrient limited rates of organic matter decomposition. In peatlands, organic matter decomposition rates are sensitive to climate change. However, predicting the magnitude of respiratory response is complex due to unknown interactions between climate and substrate quality. In this work, we investigate the role of organic matter nutrient status in regulating the climate sensitivity of decomposition and CO_2 production in peat. In particular, we examine the use of carbon (C) to phosphorus (P) stoichiometry, as a proxy for P limitation and use a combination of experiments and modelling exercises to understand relationships between peat C:P ratios and temperature sensitivity. Here we present data from multi-factorial P-limitation assays made on organic soils across a gradient of ecosystem C:P ratios. Initial results from nutrient manipulation experiments indicate a linear relationship between decreasing soil C:P and increasing respiration rates. Building on these findings we are testing whether this relationship is observed across a wider range of peat soils and will investigate the potential interactions between soil C:P ratio, P limitation and the temperature sensitivity of soil microbial respiration.

15. Nutrient status and δ^{15}N values in leaves and soils: A cross-biome comparison

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Stable nitrogen (N) isotope ratios (δ^{15}N) are often assumed to provide an integrated measure of multiple nitrogen cycling processes. For instance, shifts in the bioavailability of soil N forms are thought to alter plant δ^{15}N values. Demonstrating this relationship is important as ecosystems undergo anthropogenic disturbances. We evaluated patterns and implied mechanisms of the N cycle using ecosystem δ^{15}N values from 16 plots in boreal black spruce (*Picea mariana*) forest and lowland wet tropical forest. Fertilizer N and phosphorus (P) was applied annually for five and 11 years prior to measurement of ecosystem δ^{15}N values. Full sun canopy foliage and soil extractable nitrate, ammonium, and dissolved organic N (DON) were sampled in fertilized and control plots and analyzed for δ^{15}N. In boreal forest, N fertilization reduced DON concentrations and caused a depletion of δ^{15}N in foliage and fungal sporocarps. Of four species occurring in all plots in the tropical forest, one (*Alseis blackiana*) had increased foliar δ^{15}N values following N fertilization, one (*Tetragastris panamensis*) had increased foliar δ^{15}N values following P fertilization, and one (*Oenocarpus mapora*) had increased foliar δ^{15}N following N+P fertilization. Surprisingly, soil nitrate in the boreal forest became substantially ^{15}N-enriched under P fertilization, whereas nitrate in the tropical forest soil was enriched only under N or N+P fertilization. Collectively, nitrate enrichment is likely due to enhanced rates of soil denitrification as evidenced by elevated resin extractable soil nitrate concentrations and close correlations between δ^{15}N and δ^{18}O values. On average, foliar δ^{15}N in tropical trees corresponded well with δ^{15}N in soil nitrate in control and P fertilized plots, but was 2–3‰ more enriched than DON under N and N+P fertilization. In boreal forests, N and N+P fertilization increased foliar N concentration and δ^{15}N values indicating substantial use of applied fertilizer. Taken together, these results suggest that altering soil fertility changes soil N fractionation pathways and resulting foliar δ^{15}N values, although the direction and magnitude of the changes varies by biome and species, notwithstanding soil types. The utility of δ^{15}N measurements for detecting changes in the N cycle will be discussed.

16. Crowded spruce stands increases soil N availability

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Basic principles of ecology predict that increased population density intensifies intra-specific competition for resources, reducing resource availability. Here we show that spruce forests growing in overcrowded stands increase soil N availability relatively to sparse stands due to changes in crown architecture, shifting the ratio of N-rich litter to N-poor wood at individual and ecosystem scales. We used a Siberian afforestation experiment with spruce grown for the past 30 years at different levels of density. Higher stocking density increased litter N concentration (suggesting higher soil N availability) and increased foliar ^{15}N content (suggesting a smaller role of mycorrhizae in N supply). Higher soil N availability to trees grown in high-density stands is further confirmed by higher NH_4^+ and NO_3^- concentrations in soils. Surprisingly, trees in high-density stands were not more water limited as evidenced by foliar ^{13}C, leaving light as the main limiting factor. The ability of spruce to grow in dark overcrowded stands is obviously due to highly effective photosynthesis, allowing them to survive with fewer needles than other species to support the growth. The results suggest stand-level plasticity in supplying and partitioning N, and that high-density spruce stands may have greater potential for responding to rising atmospheric CO_2 than previously thought.

17. Covariation of leaf nitrogen concentrations and specific leaf area at different scales along a fire frequency gradient

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To predict ecosystem processes, plant stoichiometry and functional trait-based approaches must be integrated. For example, specific leaf area (SLA) and leaf nitrogen (N) concentrations covary across sites, but it is unclear whether this reflects: 1) sorting of plant species with certain trait combinations among sites, 2) covariation of SLA and leaf N among species within sites, or 3) within-species-responses of SLA and leaf N to abiotic gradients. To address this uncertainty, we measured SLA and leaf N of >80 plant species and 700 individuals in an oak savanna where plant communities range from closed canopy forest to open grassland due to differences in fire frequency. By partitioning species-level variation in these traits into alpha and beta components, we showed that covariation of SLA and leaf N among species is largely due to effects of fire frequency on community assembly (i.e. SLA and leaf N covary across sites due to environmental filtering). Each trait varied more independently among species growing in similar environmental conditions, perhaps due to niche partitioning. Within-species-plasticity in SLA and leaf N contributed little to their variation across the fire frequency gradient, further emphasizing the role of species sorting in coupling SLA and leaf N across sites.

18. Seasonal C and N dynamics in *Pinus taeda* grown at elevated carbon dioxide concentration and supplemental fertilization

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To improve understanding of the interactive effects of elevated carbon dioxide concentration (e[CO_2]) and nutrient supply on C and N metabolism in forests we conducted extensive sampling of canopy, shoot, stem and root tissue at the Duke Forest Free Air CO_2 Enrichment experiment where we have measured the major C and N pools (hexoses, sucrose, starch, nitrate, free amino acids and protein) and the activity of sixteen enzymes in central C and N metabolism. Preliminary results from analysis of the canopy indicate that after 14 years of CO_2 enrichment there is no sink limitation of C utilization at e[CO_2]. Fertilization increased the availability of free amino acids at both current (c) [CO_2] and e[CO_2], particularly in developing tissue. However, trees at e[CO_2] appeared to utilize the additional N differently. Needle protein content was unaffected by N fertilization at e[CO_2], but was increased by 10% at c[CO_2], suggesting that the additional N assimilated in fertilized plots was partitioned differently at e[CO_2].

19. CO_2 enhancement of forest productivity constrained by limited nitrogen availability

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Coupled carbon cycle–climate models are sensitive to the negative feedback to atmospheric CO_2 resulting from stimulation of terrestrial productivity by rising CO_2. The representation of CO_2 fertilization in models has been consistent with experimental evidence from four free-air CO_2 enrichment (FACE) experiments, which indicated that net primary productivity (NPP) of forests was increased on average by 23% in response to CO_2 enrichment of the atmosphere to 550 ppm. However, feedbacks through the nitrogen (N) cycle are hypothesized to reduce the CO_2 stimulation of NPP. NPP and N dynamics were measured in a FACE experiment in a *Liquidambar styraciflua* plantation in which forest plots were exposed to 545 ppm CO_2 from 1998 to 2009. New evidence from this experiment shows that N limitation significantly reduced the stimulation of NPP by elevated atmospheric CO_2 concentration. The responses are consistent with a progressive N limitation related to stand development and exacerbated by eCO_2. Our results provide a strong rationale and process understanding for incorporating N limitation and N feedback effects in ecosystem and global models used in coupled carbon cycle–climate change assessments.

20. Environmental change affects the tree-grass balance in savanna and therefore C:N:P stoichiometry

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An increased atmospheric CO_2 concentration tends to favour trees over C_4-grasses, and therefore can alter the tree-grass equilibrium in savanna. Since many savanna trees and shrubs are N-fixing legumes, woody encroachment may alter C, N and P cycling and stoichiometry. We quantified annual N- and P-balances in sites dominated by tall grasses or acacia trees in Tanzanian savanna. The N-balance was negative in tall-grass vegetation and positive in acacia woodland, with both having a neutral P-balance. Our prediction that growth would be N-limited in tall-grass savanna and P-limited in acacia woodlands was confirmed in a fertilizer experiment. Soil measurements along gradients of increasing tree density at sites in Tanzania and Zambia showed that N-fixing woody species increased soil N, P and C pools. Isotopic analysis revealed that the increase in soil N was due to both N-fixation and an accumulation of soil C and P through reduced decomposition rates. Our study in Zambia showed that construction of hydro-electric dams to gain energy, and hence a possible reduction in atmospheric CO_2 emissions, will not counteract the above-mentioned effects. In contrast, altered hydrology through these dams encouraged encroachment of native and exotic N-fixing shrubs, which drastically reduced food supply for (endemic) large herbivores.

21. Effects of elevated CO_2 concentration on soil nitrogen cycle

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It has been demonstrated by experimental studies that soil nitrogen (N) availability constrains plant carbon (C) uptake in response to global change. However, how elevated CO_2 influences soil nitrogen cycle and availability is not very clear. Here, we used meta-analysis to synthesize experimental results from 273 studies so as to evaluate effects of elevated CO_2 on soil nitrogen processes. The objective of the analysis was to determine whether elevated CO2 influence nitrogen cycle in soil and if so, what the implications are for soil carbon (C) sequestration. Our results show elevated CO_2 significantly increased nitrogen fixation by 10.7%, reduce inorganic nitrogen leaching by 33.1% and N_2O fluxes by 19.3%; there is no significantly difference for net nitrogen mineralization (1.1%). In experiments with both N and CO_2 treatments, elevated CO_2 decreased N leaching by 45% and 12%, respectively, with N and without N addition, and N_2O fluxes by 19.7% and 2.4%. Net mineralization under elevated CO_2 increased by 11.1% without N addition but decreased by 26% with N addition. These results suggest that progressive nitrogen limitation is likely to be at least partially alleviated since elevated CO_2 stimulates N fixation but decreased N losses, leading to a positive effect on long-term soil N availability.

22. Stoichiometric shifts of *Erica multiflora* leaves across year seasons and under climate change and their link with metabolism.

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This study presents the C:N:P:K leaf responses of *Erica multiflora* across the contrasted Mediterranean seasons and under field climatic treatments (drought and warming). Our analyses showed a high leaf stoichiometric change among seasons. N:P and C:P leaf ratios were lowest in spring (the growing season) thus supporting the Growth Rate Hypothesis that states that fast-growing organisms need to increase P allocation to rRNA (P-rich) to support the elevated protein synthesis. In the following summer season C:K and N:K ratios reached their lowest values and K:P ratios their highest. The moderate climate change treatments (on average 19% decreased soil moisture and 1ºC warming) also altered the leaf elemental stoichiometry but less than seasons with more marked climatic changes. Drought resulted in the same trend as summer (i.e. droughted plants presented the lowest C:K and the highest P:K ratios). We also conducted ^{1}H-NMR metabolomic analyses that showed great metabolism flexibility, with the highest sugar and amino acid concentrations in the spring. As elements do not actuate by themselves, but as molecular components, coupling the stoichiometric and metabolomic studies appears to be a challenge in the objective of testing ecological regularities.

23. Effect of dominating tree species upon stoichiometric relations in soil/litter invertebrates.

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Dominant tree species determine the chemical properties of forest litter and soil; it may be hypothesized that the whole detrital trophic web may also be affected. We compared stoichiometric characteristics of 17 taxons of litter and soil invertebrates, and their potential food, taking into account 10 elements (C, N, P, Fe, Mg, Cu, Zn, Mn, K, Ca), in five forest monocultures (The Siemianice Common Garden Experiment): *Picea abies, Pinus sylvestris, Larix decidua, Quercus robur* and *Tilia cordata*. Multivariate analysis of stoichiometric ratios grouped litter and detritus samples according to tree taxon (gymnosperms vs. angiosperms), but this pattern did not extend to fungi and invertebrates comprising the soil/litter trophic web. Invertebrates maintained within-taxon stoichiometric homeostasis; the major taxa grouped with little overlap on a PCA plot (Oligochaeta, Gastropoda, Isopoda, Diplopoda, Arachnida, Insecta-Coleoptera, with some additional taxonomic subdivisions). The effect of functional position (detritivores vs. herbivores vs. predators) is less clear because this division cannot be separated from taxonomy.

24. Stoichiometric relations in trophic groups of carabid beetles

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Life histories of species depend on stoichiometric relations between animals and their food. Most carabids are predators feeding on animal tissues, with varying shares of plant material, but the natural food composition of many species is poorly known. We compared stoichiometric relations of 10 elements (C, N, P, Fe, Mg, Cu, Zn, Mn, K, Ca) in 6 species of sympatric carabids: *Amara* sp. (mainly granivorous), *Cychrus caraboides* (specialized in snails), *Carabus nemoralis* (large, general predator, including snails), *Leistus ferrugineus*, *L. rufomarginatus* and *Notiophilus rufipes* (small predators, specialized in Collembola, possibly omnivorous). The species differed significantly in the body content of nitrogen and microelements; multivariate clustering grouped *C. nemoralis* with *Cychrus* and both *Leistus* sp., leaving *Amara* and *Notiophilus* apart. Predators can balance their requirements with other arthropods, but feeding exclusively on snails could cause Ca deficiency even in the specialized *C. caraboides*. Omni- and herbivores apparently cannot balance their stoichiometry without supplemental foraging on animals.

25. Stoichiometric limitation of litter and soil trophic web: the role of fungi.

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Heterotrophs can balance their nutritional budget when stoichiometric ratios between their growing tissues and their food do not exceed a certain threshold. Not much is known about terrestrial trophic web stoichiometry and particularly about elements other than the major macronutrients. We compared the body concentrations of elements (C, N, P, Fe, Mg, Cu, Zn, Mn, K, Ca) in soil and litter invertebrate taxa [Oligochaeta (Enchytraeidae and Lumbricidae), Gastropoda, Isopoda, Araneae, Opiliones, Diplopoda, Chilopoda, Collembola, Blattodea, Dermaptera, Hymenoptera (Formicidae), Coleoptera (Geotrupidae, Staphylinidae, Curculionidae, Carabidae, and larvae)] with their potential diet (plant material, detritus, fungi, other invertebrates). Taxa differed in stoichiometric strategies for balancing nutritional requirements with their food. Herbivores, omnivores and detritivores had highest threshold to surmount, particularly for N, P, Cu and Zn. We conclude that the necessary condition for a detrital trophic web to function is the action of fungi, which are the only providers of some essential macro- and microelements.

26. Differential responses of litter decomposition and microbial enzyme activities to warming and precipitation changes: Insights from the Boston-Area Climate Experiment.

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Litter decomposition, one of the most fundamental ecosystem processes, not only drives nutrient recycling but also releases carbon to the atmosphere that could feed back to climate change. We examined how warming and altered precipitation affected the decomposition of three litter types (the shrub-like *Polygonum cuspidatum*, at two stages - newly senesced litter and standing litter that has been decomposing for a year - and the grass *Poa trivialis*), at the Boston-Area Climate Experiment, in Massachusetts, USA. After 13 months, one year old *P. cuspidatum* litter had greater mass remaining in the drought treatment than that in the ambient and wet precipitation treatments. However, after 27 months, both drought and ambient had greater mass remaining compared to the wet treatment. Mass loss of newly senesced *P. cuspidatum* litter did not vary with warming and precipitation. *P. trivialis* litter decomposed faster in the wet treatment after 13 months and with warming (+4^{o}C) after 24 months. These responses will be further discussed in relation to the quality of litter analyzed using FTIR and 13C NMR and microbial enzyme activities. Our results suggest that the differential response of the three litter types to climate treatments could be due to the difference in litter quality.

27. Differential responses of two specialist insects to the fertilization of their host plant: the role of plant-insect N:P stoichiometric mismatch

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Nitrogen and phosphorus are believed to be the two most limiting elements for herbivores due to their higher body N and P concentrations compared to plants. Although the importance of N:P stoichiometry for herbivore performance has been demonstrated in aquatic systems, less evidence has been reported for terrestrial insects. Recently, anthropogenic nitrogen deposition has induced phosphorus limitation in some terrestrial plants, enhancing the possibility of P limitation in insects. Moreover, previous studies show that herbivores differ in response to N deposition, suggesting that they might experience different levels of P limitation. Therefore, we hypothesized that insect performance and response to N enrichments will be determined by the N:P stoichiometric mismatch between insect and host plant tissues.

We fertilized common milkweed (*Asclepias syriaca*) with 10 N levels within the range of N deposition, and 10 P levels observed in nature. The plants were fed to two specialist herbivores, monarch caterpillars (*Danaus plexippus*) and aphids (*Aphis asclepiadis*). *A.asclepiadis* exhibited higher body N:P ratios than did *D.plexippus*, and correspondingly, exhibited a greater response to N enrichment. Moreover, the growth rate of both species decreased as their body-plant N:P mismatch increased. Our results thus provide the first evidence that global change may affect terrestrial insect community composition via N:P stoichiometry.

28. An inter-comparison of nitrogen limitation in global land surface models with carbon and nitrogen cycles (CLM-CN and O-CN)

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Predictions of climate change depend on accurately modeling the feedbacks among the carbon cycle, nitrogen cycle, and climate system. Several global land surface models have shown that nitrogen limitation determines how land carbon fluxes respond to rising CO_2 and climate change, thereby influencing predictions of climate change. However, the magnitude of the carbon-nitrogen-climate feedbacks varies considerably by model, leading to critical and timely questions of why they differ and how they compare to field observations. To address these questions, a model inter-comparison of spatial patterns and drivers of nitrogen limitation was initiated. The experiment assesses the regional consequences of sustained nitrogen additions in a set of 25-year global nitrogen fertilization simulations. The model experiments were designed to cover effects from small changes in nitrogen inputs (associated with plausible increases in nitrogen deposition) to large changes (associated with field-based nitrogen fertilization experiments) to assess the geographical variation in the degree of nitrogen limitation on plant and soil carbon cycling. Here we present first results from two global land-surface models (CLM-CN and O-CN). The predictions from each model were compared to a set of observational data that include long-term monitoring sites and nitrogen fertilization experiments. These preliminary results will become part of a seven-model inter-comparison project.

29. The different effects of long term vs. short term N addition on foliar CO_2 exchange parameters in the Arctic

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In this study, we examined the effects of short (6 weeks and 4 years) and long term (>20 years) N addition on the foliar CO_2 exchange parameters of the common Arctic species *Betula nana* and *Eriophorum vaginatum* near the Toolik field station in Alaska. Variables that were measured included: the carboxylation efficiency of Rubisco (V_{cmax}), electron transport capacity (J_{max}), dark respiration (R_d), chlorophyll content and total foliar N. For both *B. nana* and *E. vaginatum,* no significant differences in V_{cmax} and J_{max} were observed after short and long term N addition, even though foliar N content increased by 20 to 50% as a consequence of 6 weeks to 21 years fertilisation, respectively. In contrast, R_d was significantly higher (>25%) in both species after 21 years of N addition, but not in the shorter term treatments. Chlorophyll content only increased in both species during the first year of fertilisation (i.e. after 6 weeks). These results suggest that under current (low) N availability, these Arctic species already optimize their photosynthetic capacity per leaf area. Furthermore, the results show that short term effects (1-4 years) of nutrient addition cannot always be extrapolated to a larger time scale, underlining the importance of long term ecological experiments.

30. FACE Modelling in Tennessee and North Carolina

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Free Air Carbon dioxide Enrichment (FACE) experiments enrich, with CO_2, the atmosphere of plants in their natural environment. Increased CO_2 stimulates photosynthesis causing increased drawdown of CO_2 from the atmosphere, leading to higher plant growth rates. In the Earth System, CO_2 fertilisation of plant growth creates negative feedback on increasing atmospheric CO_2 and has, to date, significantly damped the rate of CO_2 increase. However, predictions of CO_2 fertilisation for the coming century have been shown to be unrealistically high given the increased plant nitrogen required for the additional growth.

Data from FACE experiments provide us with an unprecedented opportunity to validate plant responses to CO_2 and to inform terrestrial carbon-cycle models. Results are presented from simulations of the Oak Ridge and Duke FACE experiments using SDGVM and JULES (Sheffield Dynamic Global Vegetation Model and Joint UK Land Environment Simulator). These simulations were improved using site specific data, not normally used as inputs to the models, highlighting areas for model development and the importance of nitrogen in the simulation of CO_2 fertilisation.

31. Ecological stoichiometric response of plantation to nitrogen and phosphorus fertilization in subtropical China

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Nitrogen (N) and phosphorus (P) availability can limit vegetation growth in most terrestrial ecosystems. It is widely acknowledged that N and P addition will modify ecosystem structure and function. We examined the effects of N and P additions (100kg N ha^{-1} $year^{-1}$, 100kg P ha^{-1} $year^{-1}$, 100kg N ha^{-1} $year^{-1}$+100kg P ha^{-1} $year^{-1}$) on foliar chemistry and stoichiometric ratios (C:N:P ratios) of four dominant species (*Pinus elliottii*, *Pinus massoniana*, *Cunninghamia lanceolata*, *Schima superba*) in a subtropical plantation in southern China. After three years of addition, we found that the plants sampled had responded in a variety of ways to the treatment. N addition increased litter C:N ratios, but this response was inverted in the P addition treatments. Fertilization generally lowered N:P ratios.

32. A comparison of leaf trait relationships in tropical versus temperate rainforest plant species

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In seeking to understand the impact of thermal origin on leaf trait scaling relationships, we quantified a range of traits [N concentration, mass:area ratios, and photosynthetic CO_2 assimilation (A) and respiratory CO_2 release (R_{dark})] in several contrasting Australian tropical and temperate rainforest species grown in a temperature-controlled glasshouse (25°C day, 20°C night). As expected, variations in A and R_{dark} scaled positively with increasing leaf N and negatively with increasing leaf mass:area ratios (LMA) in both tropical and temperate species. However, at any given LMA, leaf N concentration, A and R_{dark} were all higher in the temperate rainforest species than their tropical counterparts. Underpinning the higher A in the temperate species were higher rates of carboxylation capacity of Rubisco (V_{cmax}) and RuBP regeneration capacity (J_{max}), with the J_{max}:V_{cmax} ratio being greater in temperate rainforest species (indicating greater allocation of N to photosynthetic electron transport). No differences were found between the temperate and tropical species in terms of log-log scaling relationships linking A and R_{dark} to leaf N. In conclusion, our results suggest that as a consequence of greater N investment in metabolic capacity, cool-adapted temperate rainforest species exhibit higher photosynthetic and respiration rates than their warm-adapted tropical counterparts.

33. C:N:P stoichiometry in soil organic matter

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A growing interest in ecological stoichiometry has led to a broader use of carbon:nitrogen:phosphorus (C:N:P) in plants to infer nutrient limitation in terrestrial ecosystems. We investigate the C:N:P stoichiometry in soil organic matter (SOM) here by utilizing a recently expanded Hedley P database compiled from literature. This expanded Hedley P database, encompassing all US soil taxonomy major soil orders except for Gelisols, includes information on different forms of P (including soil organic P) along with soil organic C and N. Our analysis of the database shows that C and N in SOM are closely linked in all soil orders, but P is decoupled from C and N in highly weathered soils with larger variations of N:P ratio and higher mean values of N:P ratio in SOM, compared to slightly and intermediately weathered soils. The higher N:P ratio in SOM could be used as another indicator of P limitation in highly weathered tropical soils.

34. C:N:P stoichiometry and growth rate in vascular plants: a revision to the current growth-rate hypothesis

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The growth rate hypothesis (GRH) proposes that higher growth rate (μ) is associated with higher P concentration and lower C:P and N:P. However, the applicability of the GRH to vascular plants is not well-studied and no study has been done on belowground biomass. Here we showed that, for both aboveground and belowground biomass of three study species, μ was positively correlated with N:C and P:C, and positively correlated with N:P in N-limited treatments but negatively in P-limited treatments. The variation of μ was negatively correlated with homeostasis of C:N:P stoichiometry. Furthermore, opposite species ranks for μ, C:N:P, and CV of them were found for aboveground versus belowground biomass. We suggest a revised version of the GRH for vascular plants: 1) μ is positively associated with N and P concentrations. 2) N:P is positively correlated with μ when N is limiting but negatively correlated when P is limiting.

35. Nitrogen dependence of the organic matter accumulation in recalcitrant soil pool. Experiments with ROMUL model in climate-C cycle framework.

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Interconnection between C and N cycles in the soil has been recognized for a long time, however only a few C cycle models within climate models consider this interplay. Here we demonstrate the results from the ROMUL model that directly describe coupling between soil C and soil N and is incorporated in a climate model with a C cycle INMCM. First, the steady-state carbon amount in a mineral soil humus pool as a function of C/N ratio in litter and mean annual temperature was analyzed. In the group of grid cells with intermediate productivity N dependence of the mineral soil humus storage was persistent for the whole temperature range. In the group of grid cells with high productivity, N content in litter affected mineral soil humus storage more weakly, and temperature dependence was stronger. As for the future projections for the 21st-22nd centuries, the model predicts C uptake in the global soil pool due to higher litter input caused by CO_2 fertilization effect, but some grid cells act as C source or are C neutral. Nitrogen dependency of additional accumulation of C in the mineral soil humus pool in is seen only for the higher percentiles (grid cells that accumulated most C).

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