*Meeting Report*

Terrestrial nitrogen cycling revisited

The degree to which nitrogen (N) availability limits land carbon (C) uptake under global environmental change represents a still-unresolved challenge. First-generation “C-only” vegetation models, lacking explicit representations of N cycling, projected a substantial and increasing land C sink under rising atmospheric CO2 concentrations. This prediction was questioned for not taking into account the potentially limiting effect of N availability, necessary for plant growth (Hungate et al., 2003). More recently developed global models of the coupled C and N cycles in land ecosystems (C-N models) are widely assumed to be more realistic, but may fail when confronted with diverse observations on the global C cycle (Wenzel et al., 2014; Zaehle et al., 2014). With the advent of a new generation of global models including coupled C, N and phosphorus (P) cycling, model complexity is sure to increase; but model reliability may not, unless greater attention is paid to the correspondence of model process representations and empirical evidence. It was in this context that the “Nitrogen Cycle Workshop” at Dartington Hall was held on 1-5 Feb 2016. Organised by I. Colin Prentice and Benjamin D. Stocker (Imperial College, UK), the workshop was funded by the ERC FP7 project *Earth system Model Bias Reduction and assessing Abrupt Climate changE* (EMBRACE). We gathered empirical ecologists and modellers to identify key uncertainties in terrestrial C-N cycling, and asked about processes that are missing or poorly represented in current models.

N cycle openness across the globe

We started by addressing how N cycling varies at large spatial scales. We focused on *N cycle openness*.This can be quantified as the ratio between “new N” inputs and total N cycling. Cleveland et al. (2013) inferred a strong latitudinal gradient of N cycle openness with high values in the tropics, particularly in savannahs, and values as low as 3% in temperate and boreal ecosystems. This is consistent with the prevalence of N limitation across biomes. Sönke Zaehle (MPI-BGC, Germany) noted that many models do not capture this gradient.

These quantifications hinge partly on estimates of biological N fixation, for which new measurements in tropical forests (ref) and a top-down analysis by Vitousek et al. (2013) suggest lower numbers than earlier estimates (Cleveland et al., 1999). However, remarkably large uncertainties remain. Sasha Reed (USGS, USA) emphasized the surprising variety of N-fixing organisms that have only recently been discovered in different habitats (Reed et al., 2011) and the high degree of variability in fixation rates with stand age in tropical forests (Batterman et al., 2013). Several participants pointed to the remaining challenges in measuring N fixation rates in the field and in particular the likely underestimation of free-living N fixation in current estimates. For example Elbert et al. (2012) estimated N fixation in biological crusts alone at 48 TgN/yr. T Davies-Barnard (University of Exeter, UK) and Andy Wiltshire (MetOffice, UK) and Karin Rebel (Utrecht University, Netherlands) noted that from a modelling perspective, it is essential not just to quantify the magnitude of this flux but also to understand its controls and its energetic (carbon) cost. Indeed, several mechanisms have been identified that imply a “nitrostat”, partly under plant control (Menge & Hedin, 2009; Hedin et al., 2009), including labile C export by plants to free-living N-fixing heterotrophs (ref). Finally, John Raven (Dundee University, UK) discussed insights of the physiological processes of N fixation.

Sarah Cornell (Stockholm Resilience Centre, Sweden) pointed out that the other major component of N inputs, atmospheric deposition, may also be underestimated. Deposition of organic N forms of N has generally been ignored, but can be substantial in remote areas due to their longer atmospheric lifetimes and transport ranges compared to NOx (ref). In view of the increasing appreciation of plant organic N nutrition, as noted by Torgny Näsholm (Umeå Plant Science Centre, Sweden), a re-assessment of N cycle openness in boreal systems may be required.

Adrien Finzi (Boston University, USA) presented a global compilation of denitrification rates and compared these with the fraction of total GPP allocated below ground. The derived pattern reveals a low apparent C cost of N acquisition in the tropics, consistent with “leaky” N cycling. But Ivan Janssens and Sara Vicca (University of Antwerp, Belgium) reported on their findings of low biomass production efficiency in tropical forests, suggesting high C costs of N acquisition. Further research will have to reconcile these apparently conflicting findings by investigating the contribution of autotrophic respiration and other non-structural C losses. Large-scale gradients of N cycle openness, total belowground allocation, and biomass production efficiency will be prime benchmarks for a new generation of C-N models.

N constraints on the CO2 response by plants

The positive effect of elevated CO2 on leaf-level photosynthesis implies a shift in the balance of supply and demand for C versus N. We went on to discuss effects on plant-soil interactions in response to this shift. Soenke Zaehle (MPI-BGC, Germany) reported that current C-N models, in contradiction with measurements in FACE experiments, achieve a positive NPP response primarily by increasing C:N at the tissue level (Zaehle et al., 2014) but fail to reproduce the actual observed shift towards belowground C allocation (De Kauwe et al., 2014). Ivan Janssens reported that leaf N content across European forests is primarily determined by a phylogenetic signal and has not responded to environmental change (Sardans et al., 2015). It became clear that stoichiometric flexibility in different plant tissues and effects on changes in CO2 and soil N availability on leaf-level photosynthetic capacity warrant special attention when designing and evaluating experiments, as well as in the formulation of models.

While overestimating the role of stoichiometric flexibility, current C-N models allow limited scope for shifts in C allocation when N acquisition falls short. Recent research has highlighted the importance of mycorrhizae (ref) and plant-controlled rhizosphere priming effects (ref). Oskar Franklin (IIASA, Laxenburg) pointed out that mycorrhizal associations may become parasitic under low N (Franklin et al., 2014). But Sara Vicca and César Terrer (Imperial College London) showed contrasting new results from a meta-analysis of experimental data. Under low N, a positive NPP response under elevated CO2 appears only in plants associated with ectomycorrhizal fungi. A similar mechanism may be at work for N-fixing species. Tuula Larmola (Natural Resources Institute, Finland) reported from an extreme case, where *Sphagnum*-associated N fixation far exceeded atmospheric N deposition, and thus enabled sustained C accumulation in notoriously nutrient-poor peatlands (Larmola et al., 2014). Sönke Zaehle showed results of a global modeling study indicating that assumptions regarding the controls on N fixation have major implications for its response to rising CO2. He posed the question “How do we put brakes on N fixation?” But interestingly, the implication of total N fixation for the global land C balance is limited (Meyerholt et al., 2015). This may be linked to the fact that C-N models that resolve the dynamics of a soil inorganic N pool, and simulate N loss as a function of its size, suggest that even in absence of any strong amplification of N fixation there is a progressive *release* from N limitationon a decadal time scale, thanks to an “automatic” adjustment towards improved N retention (Walker et al., 2015).

Adrien Finzi (Boston University, USA) asked the question: is N limitation just C limitation in disguise?  Plant C allocation has a central role in simulating the effects of environmental change and needs to be more realistically modelled. Simple models based on optimality principles have been proposed (Franklin et al., 2012) and may guide the development of a next generation of C-N models. Along the way, it will be important to make good use of data from manipulative experiments to test models at the level of individual processes. Conversely, future experiments should be specifically designed to identify constraints and tradeoffs.

The representation of soil N cycling in models

The CENTURY paradigm for modelling transformations of C and N in soils received a mixed response from participants. On the other hand, it was agreed that this modelling approach has stood the test of time, above all as a means for modelling the effects of land-use changes on the dynamics of soil C. On the other hand, it was found wanting in certain respects. Ivan Janssens noted that the observed response to N deposition is a reduction of heterotrophic respiration relative to NPP; this is opposite to what CENTURY predicts. Stefano Manzoni (Stockholm University, Sweden) drew attention to evidence that the carbon use efficiency of microbes adapts to changes in litter quality. These observations support an increasingly widespread view that a new generation of models should represent microbial processes more explicitly, taking into account adaptation of microbial communities to changes in their environment (refs).