Meetings

Improving representation of photosynthesis in Earth System Models

9th New Phytologist Workshop, Montauk, New York, USA, April 2014

Earth System Models (ESMs) provide the complex simulations of past, current and future climate that are required to inform policy decisions. Because climate change is driven principally by rising atmospheric carbon dioxide concentration ($[CO_2]$), model estimation of future $[CO_2]$ will strongly influence climate projections. The inability of ESMs to confidently simulate the enormous CO_2 fluxes associated with the global carbon cycle translates to greater uncertainty in projections of the onset, frequency and severity of the increasingly inevitable high impact consequences of our changing climate (IPCC, 2013). The CO_2 fluxes associated with the terrestrial biosphere – in comparison to the CO_2 fluxes between the atmosphere and oceans – are poorly constrained (Friedlingstein *et al.*, 2014). Current understanding and model representation of the terrestrial carbon cycle, and the response of the terrestrial carbon cycle to rising atmospheric $[CO_2]$ and temperature, and changing precipitation patterns, are among the greatest uncertainties in ESMs in terms of both scientific understanding and model representation (Booth *et al.*, 2012).

In July 2013, the 8th New Phytologist Workshop – 'Improving representation of leaf level respiration in large-scale predictive climate-vegetation models,' held in Canberra and Kioloa, Australia – addressed uncertainty in carbon cycle projections associated with model representation of plant respiration (Atkin *et al.*, 2014). The 9th New Phytologist Workshop complemented the preceding workshop on autotrophic respiration by addressing model uncertainty associated with the representation of photosynthesis in the terrestrial carbon cycle. Unlike respiration, photosynthetic CO_2 uptake is already well described by a model – the Farquhar, von Caemmerer and Berry model of photosynthesis (Farquhar *et al.*, 1980) – and many ESMs use a derivation of this formulation coupled to models of stomatal control (Ball *et al.*, 1987) to estimate gross primary production (GPP). However, ESMs differ in the way this model is implemented and parameterized, as well as how photosynthesis responds to temperature, with unclear consequences for ESM output.

A road map for new science

The workshop was organized by Alistair Rogers, Belinda Medlyn and Jeffrey Dukes, and was attended by a group with expertise in both Earth System Modeling and photosynthetic physiology: Gordon Bonan, Michael Dietze, Jens Kattge, Andrew Leakey, Lina Mercado, Ülo Niinemets, Colin Prentice, Shawn Serbin, Stephen Sitch, Susanne von Caemmerer, Danielle Way and Sönke Zaehle (Fig. 1). At the workshop, this group began to assemble a 'road map' for the new science required to advance understanding and representation of photosynthesis in ESMs. Specifically, the workshop had two goals: (1) identify areas of weakness in existing ESMs where current process knowledge and emerging data sets can be used to improve model skill; and (2) identify gaps in current knowledge of photosynthesis that directly impact model output.

The program began with an after dinner poster session at which the modeling community laid bare the model structure and constants that underlie the estimates of global GPP in their models. Posters covered a range of process models, including several of the land models currently used in ESMs: The Community Land Model (CLM), The Joint UK Land Environment Simulator (JULES), The Joint Scheme for Biosphere Atmosphere Coupling in Hamburg (JSBACH), and the Organizing Carbon and Hydrology in Dynamic Ecosystems – CN model (O-CN). This session highlighted some surprising differences in model representation of the response of photosynthesis to CO_2, temperature, vapor pressure deficit and soil moisture content. The modelers expressed a willingness to incorporate more physiological understanding into their models, and as the workshop progressed, the differences in parameterization underlying contrasting model responses began to emerge.

'. . .incorporating formulations for acclimation into models can have strong and counter-intuitive effects on projected carbon storage.'

The main part of the workshop was organized around four major themes: responses to CO_2, temperature, and water stress, and scaling of responses from leaves to the globe. For each theme, participants prepared one-slide presentations explaining their thinking about that theme; for example, demonstrating how a response is represented in their model, or highlighting the emerging evidence that they see as being important to accurately describe that

Fig. 1 Workshop participants and family members at Montauk Point, the eastern-most tip of Long Island. The lighthouse in background began service in 1796 and still serves as a navigational aid. Not pictured, Gordon Bonan.

response. This rapid round-table approach to presentations provoked fluid and constructive discussion, highlighting areas where participants were largely in agreement, areas of new research development, and areas of active debate and uncertainty.

Parameterization

One area of strong agreement was the need to use internally consistent equations and parameterizations. Model parameters are obtained by fitting equations to gas exchange data; if these parameters are then used with different equations without consideration of the assumptions underlying the original data, photosynthesis will be incorrectly estimated. An example discussed at the meeting is that the CO_2 response of photosynthesis is strongly dependent on the assumed $J_{max} : V_{c,max}$ ratio, the ratio between potential electron transport and maximum Rubisco activity. Two published values for this ratio are widely used in models: 1.97 (Wullschleger, 1993) and 1.67 (Medlyn et al., 2002). However, these two estimates differ because the parameterization of Rubisco kinetics used to derive them differs. Modelers therefore cannot choose freely between these values, but should choose a value that matches the Rubisco parameterization used in their model.

Participants also strongly supported the idea, proposed by Mike Dietze (Boston University, MA, USA), of a fully open database of raw gas exchange data that would make raw instrument data outputs available to investigators around the world. Having access to raw data would enable modelers to derive parameters to exactly match the equations used in their model, ensuring consistency between parameters and equations. Such a database would also create an opportunity to undertake powerful meta-analyses using the vast amounts of raw data that have been generated using similar methods on a handful of platforms. As scientific understanding and new temperature response functions emerge, the database would enable the recalculation of parameters from raw data, thus ensuring continued relevance of old measurements.

Process knowledge

An area of very active debate was the issue of whether, and how, to include mesophyll conductance (g_m) in models. Several participants demonstrated that mesophyll resistance to CO_2 is considerable and that it plays a strong role in determining responses of photosynthesis to temperature and [CO_2] (e.g. Niinemets et al., 2011; Evans & von Caemmerer, 2013). However, other participants argued that we should not include g_m in models yet, on the grounds that we still have relatively little information about g_m and its responses to environmental variables, that we have very few parameter values for models incorporating g_m, and that we have no evidence yet that models incorporating g_m perform better at projecting [CO_2] or temperature responses of canopy gas exchange than models that do not. This debate highlights the importance of continued research in this area and calls for thoughtful investigation of how inclusion of g_m into models would affect model projections and their associated uncertainty.

The theme related to water use and drought saw enthusiastic discussion due to several exciting new research developments in this area. The standard empirical models of stomatal conductance have recently been re-interpreted in terms of optimization theory (Medlyn et al., 2011; Prentice et al., 2014). Gordon Bonan (NCAR, Boulder, CO, USA), described how this approach to modeling stomatal conductance has been implemented in CLM, while Belinda Medlyn (Macquarie University, Australia) described new meta-analyses to identify stomatal trait values for use with this modeling approach. Andrew Leakey (University of Illinois at Urbana-Champaign, IL, USA) showed the importance of incorporating genetic variation in stomatal sensitivity to photosynthesis, relative humidity and CO_2 into model parameterization.

Acclimation

One major area of uncertainty, highlighted during the temperature theme, is that of acclimation to prevailing conditions. Many plants adjust the temperature sensitivity of photosynthesis to the temperatures they experience in the preceding days and weeks (e.g. Way & Yamori, 2014), but few land models include this process of acclimation (Smith & Dukes, 2013). Jeff Dukes (Purdue University, West Lafayette, IN, USA) and Lina Mercado (University of Exeter, UK) demonstrated that incorporating formulations for acclimation into models can have strong and counter-intuitive effects on projected carbon storage. However, there are relatively few data available to parameterize the acclimation process, and in particular to distinguish acclimation from interspecific differences. Measurement of the temperature responses of photosynthetic parameters (e.g. J_{max} as opposed to net photosynthesis) on a wide variety of plant functional types from around the globe would provide a more solid foundation for incorporating acclimation in large-scale models. In contrast to temperature acclimation, physiologists were pleasantly surprised to realize that the representation of CO_2 acclimation in the O-CN model is quite close to their understanding of this process (e.g. Ainsworth & Rogers, 2007).

Scaling

Many of the thorniest issues were raised during the discussion of scaling. The parameter values used in models do not directly correspond to leaf-level measurements, but rather are effective values reflecting the variability across landscapes. As a consequence, parameter values are often obtained by tuning to model output; one example given at the meeting was of a modeling group using $V_{c,max}$ to tune surface runoff! This approach can result in wildly different values of the same parameter for the same plant functional types (Rogers, 2014), and ignores the information available from leaf-level measurements. Large data sets, such as those available through TRY (Kattge *et al.*, 2011), and the promise of temporally and spatially resolved remotely sensed maps of leaf biochemical properties (Serbin *et al.*, 2012) can help to constrain these model inputs, and in new model frameworks – where parameters such as $V_{c,max}$ will be emergent model properties – offer the opportunity to validate projected parameters.

These were just some of the highlights of the discussion. Together with all workshop participants, we are currently working on a manuscript entitled 'A roadmap for improving the representation of photosynthesis in Earth System Models' and we hope to see the manuscript in *New Phytologist* in the coming months.

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