Expanding the use of plant trait observations and ecological theory in Earth system models

A Summary Report from the Terrestrial Ecosystem Science (TES) and Earth System Modeling (ESM) Workshop on Trait Methods for Representing Ecosystem Change
Rockville, MD, 18-19 November 2015

Expanding the use of plant trait observations and ecological theory in Earth system models

DOE Workshop Report

A Summary Report from the Terrestrial Ecosystem Science (TES)
and Earth System Modeling (ESM) Workshop on
Trait Methods for Representing Ecosystem Change;
Rockville, MD, 18-19 November 2015

Report Date: May 31, 2016

Organizing Committee:
Charles Koven[1], Lara Kueppers[1], Colleen Iversen[2], Peter Reich[3],
Peter Thornton[2]

1. Lawrence Berkeley National Laboratory
2. Oak Ridge National Laboratory
3. University of Minnesota

Cover Photo credit: Charlie Koven

1

Abstract

Plants show a wide array of functional diversity, as evidenced by the wide range of plant traits that are measured worldwide. This diversity in traits has important implications for the global carbon cycle and its feedbacks with climate change, as traits govern the key processes of plant growth, reproduction, and mortality that underlie the terrestrial carbon cycle. Most Earth system models (ESMs) do not currently allow for key ecological processes of functional community assembly that determine plant trait distributions, and as a result must either specify fixed plant traits, or use dynamic vegetation models that may not capture critical responses of plant traits to global change. Recent developments in synthesizing plant trait data via large collaborative databases have begun to identify key axes of plant trait variation, as well as the linkages between plant traits and environmental drivers, and the role of traits in ecosystem scale structure and function. These observations and relationships can be used to construct and test the next generation of ESMs that will better capture changes to plant trait distributions and their effects on the global carbon, water, nutrient, and energy cycles in a changing world. The Office of Biological and Environmental Research in the U.S. DOE's Office of Science hosted a workshop to bring together a wide range of scientists with expertise in the observations and theory of plant functional trait diversity and ecosystem function to discuss ways to better include plant trait dynamics in ESMs. Outcomes included a summarization of current and future research directions, identification of key observational and theoretical gaps, and an emphasis on the need to continue a range of diverse approaches for representing trait dynamics in ESMs.

1. Introduction

To be useful, Earth system models (ESMs) must capture important ecosystem processes including how these may feed back to environmental change. However, it remains a challenge for models to represent the wide variation in plant trait diversity within any given ecosystem (or model grid cell) as well as its sensitivity to, and influence on, the climate. Most ESMs use plant functional types (PFTs), which are lists of parameter values that govern plant processes represented in the models, differentiating plant physiology and growth form among groups such as needleleaf evergreen trees, broadleaf deciduous trees, shrubs, and grasses. Through PFTs, these ESMs already represent some diversity in plant traits—such as variation in maximum photosynthesis rates and phenology—that affect ecosystem processes. In November 2015, 36 scientists (participant list in Appendix) representing expertise in Earth system and ecosystem modeling, plant trait observations, and trait data synthesis and analysis met in Rockville, Md., to assess and expand the use of plant functional trait observations in ESMs.

Presentations and discussions addressed theory of plant trait variation and underlying drivers, current and future model treatments of plant traits, data availability for model parameterization, initialization, and validation, and consequences for ESM predictions.

The workshop brought overlapping communities of researchers together to share current thinking and approaches to this issue. It also provided a forum for new ideas useful for the ecological and Earth system research communities and for evolving the DOE strategies and approaches for field research, theory and land modeling in the Next Generation Ecosystem Experiments (NGEEs) in the Arctic and in the Tropics, as well as the Accelerated Climate Model for Energy (ACME).

2. Workshop overview

2.1. Plant functional traits and trait trade-offs across species, plant functional types, and biomes

Plant traits have long occupied a central role in ideas about plant physiological functioning. The large functional diversity of plants (Figure 1) is evident in looking across the world's ecosystems, which can be traced to the set of traits that govern this diversity. In particular, leaf traits such as its thickness, as expressed by the metric Leaf Mass per unit Area (LMA), or its reciprocal Specific Leaf Area (SLA), have long been a focus of studies on plant productivity (e.g. Blackman et al., 1919, West et al., 1920). Such traits govern a wide variety of plant process rates, and vary continuously across the enormous range of environments on Earth (Reich et al., 1997). Modern efforts to synthesize information on plant traits have led to the creation of large databases, such as TRY (Kattge et al., 2011), with which the relationships among plant traits, and between plant traits and the abiotic environment, may be identified. Such analyses led to a number of key insights into the role of plant traits in governing behavior, such as (a) the correlation among traits into specific axes of variability, known as 'economic spectra', including the leaf economic (Wright et al., 2004) and wood economic spectra (Chave et al., 2009); (b) that variability along these economic spectra is in many cases closely related to abiotic environments; (c) that variation across these spectra can

Figure 1. Variation in leaf size, shape, thickness and other properties. Credit: Jacek Oleksyn

generally be linked to the overall rate of resource acquisition and use by plants (Reich et al., 2014).

Key gaps and uncertainties remain in our understanding of plant traits. In particular, observations of plant traits are sparse in type and number, and those that exist are extremely heterogeneous spatially; with databases such as TRY having much more information on well-studied traits such as leaf SLA and photosynthetic rates or wood density than on less-well studied traits such as other wood traits, bark traits, root traits, life history and reproductive traits; and with observations lacking in less developed and populated parts of the globe. Additionally, the number of ways in which plants differ from each other in ways that could plausibly affect ecosystem-level responses to global change is large, and at present poorly defined.

A number of efforts are underway to fill these gaps. One key activity is to broaden the set of traits that are included in large-scale syntheses of plant trait variability, in order to better understand both the variability of key plant traits and the roles that these traits play in governing plant function. In particular, statistical approaches to estimating unobserved traits in large databases have the potential to more accurately extend our knowledge of well-observed traits to those that are less commonly observed. Furthermore, incorporating known relationships between plant traits and the abiotic environment may allow the creation of spatially-upscaled trait datasets.

Several other key uncertainties remain in understanding how plant trait variation may influence ecosystem functioning at the scale at which it may affect overall Earth system dynamics. One is the need to understand both the mechanistic basis and generality of observed trait correlations. Some tradeoffs result directly from basic principles such as mass conservation, whereas others arise from more complex interactions between strategy and form (Scheiter et al., 2013). The latter category may result in different relationships across different gradients. For example (Lusk et al 2008), the intra-specific correlation between SLA and leaf longevity across a vertical canopy gradient often has the opposite trend as the interspecific relationship among species (even for plants with canopies in similar canopy strata). Although this particular countergradient is understood, identifying and resolving variation among scales in trait tradeoffs may give clues to the nature of the trade-offs and assist in identifying which trade-offs are generally conserved (and at what scales), enabling their better utility in models.

2.2. Approaches to representing diversity and dynamism of plant traits in models

ESMs and dynamic global vegetation models (DGVMs) have historically included representation of plant functional traits through their use of the plant functional type (PFT) concept. PFTs can be defined simply as modeled vegetation entities with a given set of plant traits. Historically, the traits that have primarily distinguished PFTs have been phenological traits (e.g. evergreen versus deciduous), gross allocation or form traits (e.g. trees versus shrub versus grass), photosynthetic pathway (C3 versus C4) and
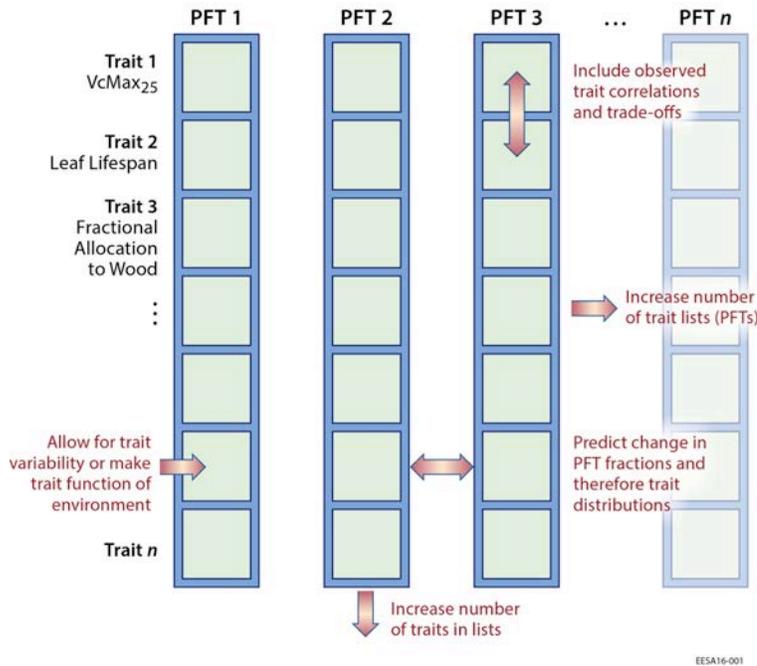
biome-specific types to separate trait values from different regions. Several other physiological traits are typically specified to covary with these types, including leaf properties (e.g., $V_{c,max}$, stomatal functioning traits), tissue turnover times, etc.

The appeal of this coarse level of PFT aggregation is that trait data for PFTs, let alone individual species, are scarce in many parts of the world; additionally coarse PFT distributions can be readily initialized from or compared to large-scale remotely sensed observations. However, many issues in this definition of traits have arisen. These include the observation that plant traits may vary more within a given PFT than among PFTs, that many more PFTs than are typically used are required to capture key gradients in plant functioning, such as along successional gradients, and that typical PFT definitions fail to include the observed correlations among multiple traits that define plant economic spectra. DGVMs—and those ESMs that include DGVMS—are quite diverse in construction, and use a wide variety of approaches for predicting PFT distributions. These approaches can be roughly ordered along a hierarchy of complexity, with bioclimatic rule-based models at the simple end, pseudo-competitive models (e.g. using Lotke-Volterra approaches) at the next level of complexity, and fully-resolved competitive models at the highest level of complexity. Many DGVMs and ESMs use combinations of these approaches, for example including some sorts of resolved competition while also using bioclimatic thresholds to substitute for unresolved processes that determine PFT distributions. The bioclimatic approach may be able to match historical and paleo records over which such bioclimatic thresholds have been trained but has a poor basis for prediction in emerging novel climates.

As a result of these issues, many new approaches are being developed to better include observed diversity of plant traits and better predict dynamic plant traits in ESM-scale DGVMs. Three broad categories of model approaches encompass many of the specific approaches developed for individual models: here we will call then "correlative", "optimizing", and "competitive" approaches. These are not necessarily exclusive, and in particular models may use one or another approach to define different suites of plant traits. Correlative approaches seek to enable dynamism and/or diversity in plant traits through the use of observed correlations between plant traits and abiotic environmental conditions. Optimizing approaches define a cost surface that defines the success of a given trait or traits contingent on a given set of environmental conditions, and then assumes that unresolved competitive processes will optimize the successful plants to have the optimal trait or traits for that condition. Competitive approaches seek to enable trait dynamism by explicitly allowing PFTs with differing plant traits to compete by resolving the processes of growth, reproduction, and mortality, in order to predict the successful strategies that will dominate in a given environmental condition.

These approaches are summarized in Figure 2, which shows possible ways in which trait dynamics may be included in PFT-based models. A key first principle is that correlations among traits should be respected in PFT models, as choosing a value for one particular trait may partially determine the possible range of values of a second trait.

Correlative or optimizing approaches may seek to set a given trait value for a given PFT directly either based on an observed relationship with an abiotic environment, or via optimizing a cost function as a consequence of that abiotic environment. Competitive approaches will require growth and mortality processes to determine the fractional coverage of a given PFT, such that filtering by trait values may occur and lead to emergent ecosystem-level changes in the trait distributions. The number of PFTs may need to be expanded to include variation along multiple axes, such as successional gradients and resistance to different agents of disturbance, as well as biome-level categories. Lastly, the number of plant traits may need to be expanded as the mechanistic basis for these traits is better resolved in models, to include traits that control processes such as hydraulic function, root nutrient acquisition, or mortality due to multiple agents.

Figure 2. Possible approaches to representing dynamic plant traits within the context of plant functional types (PFTs) in ESMs. PFTs in ESMs are essentially defined as a set of functional traits. In many ESMs, these PFTs are static. A key observation in trait databases is the correlation between plant traits, such that a range of values of one trait in a PFT imply a range of values in another trait. Possible approaches to including more dynamic PFTs in ESMs include: (a) correlative or optimizing approaches to allow individual trait values to vary within a given PFT; or (b) competitive approaches whereby the traits comprising individual PFTs remain static but the PFT fractional coverage is dynamically determined by competition, which leads to changes in the community trait distributions. A greater diversity of PFTs is required to move beyond PFT-biome correspondance, and at the same time, greater mechanistic fidelity will require more traits to be present in models. Credit: Charlie Koven and Diana Swantek

A key conceptual problem that has been encountered in the construction of trait-filtering models is the maintenance of functional diversity. The idealized ecosystems represented in models cannot

include the remarkable heterogeneity of environments that exist in the real world; thus the number of distinct niches that different plant types may occupy is substantially smaller. In the absence of heterogeneity, a single type of plant typically outcompetes others, giving rise to functionally non-diverse ecosystems. Approaches to increase the environmental heterogeneity in models, such as by including vertical gradients in light availability and in soil properties, allow some diversity to be maintained, and have a strong mechanistic basis for inclusion (e.g. Moorcroft et al., 2001). Other approaches that may act to maintain diversity in the real world, such as inclusion of density-dependent mortality due to pests, are in general poorly justified at the PFT level since such processes typically act on phylogenetic rather than functional categories as used in models, though they may be important and justified in low-diversity ecosystems.

The correlative, competitive, and optimizing approaches are quite distinct, with potential advantages and disadvantages to each. This implies that no single approach is likely to be objectively better or worse than the others, particularly at the current state of scientific understanding. There are both near-term and long-term opportunities with each type of approach, and the different approaches are likely to inform each other, e.g., as different levels of a hierarchy of complexity. Furthermore, the way in which observations are used to inform each type of model is distinct: e.g., a given dataset such as the geographic distribution of a given plant trait may be used as a model input for a purely correlative approach, such as trait-mapping, and as a benchmark to test emergent model behavior in another approach, such as a trait-filtering model.

2.3. Datasets to inform models representing diverse or dynamic plant traits

Dynamic Global Vegetation Models that project future plant community composition and ecosystem function across the world are built on an underlying foundation of observational data. As described above, plant trait data and associated geographic, edaphic, and environmental conditions are needed to inform model initialization, parameterization, and validation at scales both global and local. Scientists have been observing the world around them for millennia, but the digital age provides unprecedented opportunity to relate what empiricists observe in the natural world to the numerical hypotheses encoded in models. A number of global plant trait databases have been developed in recent years, each with different goals (e.g., BAAD (Falster et al., 2015), BettyDB (https://www.betydb.org/), BIEN (http://bien.nceas.ucsb.edu/bien/), *FRED* (http://roots.ornl.gov), TRY (www.try-db.org)). However, there are several challenges associated with interpreting and synthesizing plant trait data in way that is useful to inform models, and data are still lacking for many important processes and biomes.

Available data
The largest plant trait database in the world, the TRY database, contains 5.6 million plant trait records of from 100,000 species across the globe (Kattge et al., 2011).

However, the matrix of observations in TRY is more than 90% empty. Thus a major issue is whether the spatial and temporal coverage of available plant trait data can inform models operating at a global scale. The challenges faced by both current and future DGVMs are two-fold: (1) sparse observations of a given plant trait can preclude the estimation of trait values across the globe for model initialization and parameterization, and (2) a limited number of plant species for which two or more traits have been measured hinders estimates of trait-trait covariation necessary to inform competitive trait modeling approaches. These challenges can be addressed in part through statistical gap-filling methods, such as Bayesian hierarchical approaches, that can predict trait values to fill the missing data in the trait matrix across the globe (Schrodt et al. 2015). The predictive capacity of gap-filling trait values can be further improved by the incorporation of additional data on plant phylogeny, as well as trait-trait interactions and trait-environment relationships (Schrodt et al. 2015). Remote sensing data sets may prove particularly useful in this context, given a larger data coverage in space and time (Serbin et al. 2014).

Models also face the challenge of potential mismatches between observations of plant traits in large databases and model needs. For example, models may need continuous rather than categorical trait values that allow the representation of processes at the larger-scale of a plant functional type or a grid cell, as well as relevant ancillary data and metadata on site, edaphic, and environmental conditions. Unfortunately, these characteristics are often lacking for many of the observations included in the large trait databases available for model use, which can hinder the interpretation of these data and their usefulness in informing model parameterization and processes. For example, accurate georeferencing is required for understanding trait-climate relationships, but only 50% of data in TRY were georeferenced upon collection (Kattge et al. 2011). Moving forward, some of these challenges can be addressed in the way currently available observations are synthesized. For example, empiricists (and ultimately large plant trait databases) should include model-relevant metadata in their analyses, including the location and timing of trait data collection, but also the vegetation characteristics and edaphic and environmental conditions of the site. Furthermore, it would be most useful if these data were publically available in a single, publicly accessible data repository, or accessible via a data brokering portal. The release of observations to the broader community of empiricists and modelers can be stimulated by the development of improved agency data policies (e.g., U.S. DOE's Office of Science Statement on Digital Data Management, http://science.energy.gov/funding-opportunities/digital-data-management/). New model scaling methods can then be used to scale small-scale trait observations or processes to a larger temporal or spatial scale of land surface models, as can regional analyses of observations and syntheses of multiple experiments (Medlyn et al. 2016). At the same time, ongoing interactions among modelers, empiricists, and database managers can help to facilitate the collection of *new* model-inspired observations that help to fill some of the gaps in our understanding of plant traits across the globe.

Moving forward: Filling gaps in missing data

The next generation of observations should focus on processes or biomes that are highly uncertain or sensitive in models. Model uncertainty quantification and variance decomposition assessments could help to drive the collection of new measurements on poorly-understood traits where uncertainty is driven by lack of data rather than by model sensitivity. Evidence thus far indicates that undersampled biomes such as the Arctic and Tropics are a particularly important focus for the next generation of observations, especially given the importance of plant traits to climate feedbacks in the Arctic (Myers-Smith et al. 2015) and the high diversity of traits in tropical ecosystems (Negron-Juarez et al. 2015). Observations made at common sites by interdisciplinary teams that capture measurements of plant traits and trait-tradeoffs, relationships among traits and edaphic and environmental conditions, and relationships between traits and ecosystem process rates will be particularly useful.

Uncertainty quantification is only practical for parameters and processes that are included in the current generation of models; however, observations of traits that might make models more ecologically useful in the future are also needed. Belowground plant traits, particularly the distribution and dynamics of fine roots, are a particularly large gap in our observations and understanding of the natural world and are rather coarsely represented in the current generation of terrestrial biosphere models (Warren et al. 2015). However, the relationships between belowground plant traits and changing environmental conditions, as well as the linkages and tradeoffs among above- and belowground plant traits (Figure 3), will be necessary to inform the next generation of models using trait optimization and competitive approaches. To address this challenge, the Fine-Root Ecology Database (*FRED*; http://roots.ornl.gov*)* is being developed to fill gaps in our understanding and modeling of fine roots, and *FRED* will be submitted annually to the TRY database to facilitate above- and belowground linkages. However, *FRED* also indicates that more observations of fine root processes are needed across the globe. Furthermore, even physiological processes as well-understood as photosynthesis

Figure 3. Variation in leaf, stem and fine-root traits among arctic plants growing on polygonal ground at the Barrow Environmental Observatory (BEO). L to R *Eriophorum russeolum* (sedge), *Dupontia fisheri* (grass), and *Salix rotundifolia* (shrub). Photo credit: Victoria Sloan.

may be poorly-resolved in some large-scale models, especially with regard to the acclimation of plant physiology to environmental change, on multiple time scales (Rogers et al. 2014). Improved understanding and modeling of these important aspects of plant physiology will have consequences for the predictive power of ESMs.

2.4. Consequences of including diverse and dynamic plant traits in ESMs

Much of the rationale for including dynamic plant traits in coupled models of the Earth system is to better project the ways in which ecosystems will respond to global change. Early ESMs that included dynamic plant distributions based on simple bioclimatic or PFT interaction criteria identified the potential for abrupt transitions, such as forest loss in the Amazon, to dramatically alter the pace of global climate change (Cox et al., 2000). Such predictions may not have had a firm mechanistic basis, and a key goal in creating the next generation of ESMs with dynamic plant traits is to include both a more complete understanding of the possible ecosystem responses to global change as well as a more firm observational-based foundation for assessing the accuracy of these predictions.

Ecosystem models as represented in ESMs have become more complex in time, both through a richer representation of mechanistic processes that govern ecosystem function, and through increased structural complexity such as disaggregating vegetation into more highly resolved classes of size, age, and trait values. While such complexity may be required to accurately project key dynamics, it comes at the cost of requiring more robust metrics of model realism, more accurate assessments of initial conditions, and more finely-resolved parameterizations of processes that are not explicitly resolved (Luo et al., 2012).

The differing model strategies such as correlative, competitive, and optimizing approaches as described above will require different approaches to initialization, parameterization and benchmarking against datasets. Syntheses of trait observation data for testing against models must be aware of the assumptions used in a given approach, to avoid circularity in, for example, benchmarking a model against observations that were used to initialize or parameterize that model.

Finally, a key unresolved question is whether including dynamic plant traits acts over all to increase or decrease the magnitude of climate feedbacks arising from the terrestrial biosphere. The CMIP5 generation of ESMs predict that carbon feedbacks are almost entirely driven by leaf-level processes that govern productivity responses to global change (Koven et al., 2015); whereas next-generation models that achieve greater dynamism of traits via competitive mechanisms show that competitive processes exert a strong control (Ahlstrom et al., 2015; Friend et al., 2014). Observations across spatial gradients show a much greater decoupling of biomass from productivity, which is mediated by negative correlations between productivity and turnover time, both in soils

and biomass (Malhi et al., 2004); these relationships may also be observed in the temporal response to global change (Brienen et al., 2015). Thus the current models, by focusing on the productivity response, may be effectively missing compensatory responses that will dampen

Figure 4. Tropical forest canopy near Manaus, Brazil. Credit: Jeff Chambers

carbon responses to changing climate and CO_2 (Delbart et al., 2010). At the same time, the emergence of novel climate states, with effects that may not be well understood until they appear, may allow for destabilizing responses. It is certainly possible that inclusion of more complexity of plant trait dynamics in ESMs may increase rather than decrease the confidence intervals of future climate feedbacks, by more accurately including the wider range of possibilities that actually exist in the Earth system than the simplistic models currently in use permit.

3. Outcomes and priorities

The workshop discussions revealed priorities for future work to improve the use of plant traits in ESMs. Participants called for better understanding of which traits are conserved vs. responsive to a changing environment. Additionally, they identified a need to understand and represent (i) both trait correlations driven by physical constraints and those reflecting strategic plant trade-offs, and (ii) how plant traits mechanistically drive plant, community and ecosystem processes. Participants agreed that pursuit of multiple distinct modeling approaches will yield more rapid advances than a single approach at this early stage (Figure 2). Participants identified numerous gaps in the data available to inform new models. Data are sparse for belowground traits relevant to plant water and nutrient acquisition, and for undersampled but climatically important regions, such as biome transition zones, arctic tundra, and tropical forests (Figure 4), where trait diversity is highest. Participants seek to apply the tools of "big data" to assemble and interpret trait observations for the modeling community. Analytically tractable models and ensembles of stochastic models both may be required to understand the emergent behavior of real ecosystems.

A series of next steps and science needs are listed below. Some of these should be easy to address in the near term, including the application of statistical approaches that have been well developed in other fields to fill in gaps in existing databases, and in the upscaling of plant traits based on already-known trait-environment relationships. Others are longer-term, including the continued development of mechanistically and structurally complex ecosystem models in ESMs. Together, these steps will help the science community address the critical questions of how the wide diversity of plant traits will govern the terrestrial responses and feedbacks to global change.

4. Key Science Needs

- **Data and observational needs**
  - Methods for filling gaps in trait databases
  - Methods for scaling trait data from individual to species to community level
  - Synthesis and curation of plant trait observations into freely-available databases
  - Trait-trait correlations across measured environmental gradients at multiple scales
  - Trait measurements from climatically important ecosystems, e.g. high latitude, tropical, and semi-arid ecosystems
  - Better observations of carbon allocation, hydraulic, and plant life history traits
  - Remote-sensing approaches to linking site-scale measurements of traits to broader spatial scales
  - Better belowground trait measurements; understanding of relationships between above- and belowground plant traits; and traits that govern plant microbiomes
  - Better understanding of the degree of plasticity in trait values within individuals, populations, or species
  - Experiments to test predictions of plant traits and trait distributions in novel climates
  - Better linkages among observations of plant traits, demography, and ecosystem function
- **Model development and testing needs**
  - Improved workflows for testing models against plant trait information
  - Improved process resolution for mechanisms that determine plant trait distributions in ESMs
  - Development of models across a hierarchy of complexity levels for testing approaches to predicting plant traits via correlative, competitive, and optimizing approaches
  - Improved methods to attribute the causal tradeoff mechanisms behind observed trait correlations
  - Improved representation of disturbance processes in ESMs
  - Better incorporation of underrepresented processes in ESMs: e.g., belowground plant and microbiome processes, carbon allocation, hydraulic processes, plant life-history strategies
  - Better model representation of processes of community assembly in emerging novel climates
  - Better model representation of environmental heterogeneity to allow for improved coexistence of plant diversity
  - Better understanding of the implications of different choices in how PFTs are defined in ESMs

5. References

Ahlström, A., J. Xia, A. Arneth, Y. Luo, and B. Smith (2015), Importance of vegetation dynamics for future terrestrial carbon cycling, *Environmental Research Letters*, *10*(5), 054019.

Blackman, V. (1919), The compound interest law and plant growth, *Annals of Botany*, *33*(131), 353--360.

Brienen, R. J. W., et al. (2015), Long-term decline of the Amazon carbon sink, *Nature*, *519*(7543), 344--348.

Chave, J., D. Coomes, S. Jansen, S. L. Lewis, N. G. Swenson, and A. E. Zanne (2009), Towards a worldwide wood economics spectrum, *Ecology letters*, *12*(4), 351--366.

Cox, P., R. Betts, C. Jones, S. Spall, and I. Totterdell (2000), Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model, *Nature, 408*, 184-187.

Delbart, N., P. Ciais, J. Chave, N. Viovy, Y. Malhi, and T. Le Toan (2010), Mortality as a key driver of the spatial distribution of aboveground biomass in Amazonian forest: results from a dynamic vegetation model, *Biogeosciences*, *7*(10), 3027--3039, doi:10.5194/bg-7-3027-2010.

Falster, D. S., et al. (2015), BAAD: a Biomass And Allometry Database for woody plants, *Ecology*, *96*(5), 1445--1445, doi:10.1890/14-1889.1.

Kattge, J., et al. (2011), TRY --a global database of plant traits, *Global Change Biology*, *17*(9), 2905--2935.

Koven, C. D., J. Q. Chambers, K. Georgiou, R. Knox, R. Negron-Juarez, W. J. Riley, V. K. Arora, V. Brovkin, P. Friedlingstein, and C. D. Jones (2015), Controls on terrestrial carbon feedbacks by productivity versus turnover in the CMIP5 Earth System Models, *Biogeosciences*, *12*(17), 5211--5228, doi:10.5194/bg-12-5211-2015.

Luo, Y. Q., et al. (2012), A framework of benchmarking land models, *Biogeosciences*, *9*(2), 3857-3874, doi:10.5194/bg-9-3857-2012.

Lusk, C. H., Reich, P. B., Montgomery, R. A., Ackerly, D. D., & Cavender-Bares, J. (2008). Why are evergreen leaves so contrary about shade?. *Trends in Ecology & Evolution*, *23*(6), 299-303.

Malhi, Y., P. Meir, and S. Brown (2002), Forests, carbon and global climate, *Philosophical Transactions of the Royal Society of London. Series A: Mathematical, Physical and Engineering Sciences*, *360*(1797), 1567--1591.

Medlyn, B. E., et al. (2016), Using models to guide field experiments: a priori predictions for the CO2 response of a nutrient- and water-limited native Eucalypt woodland, *Global Change Biology*, n/a-n/a, doi:10.1111/gcb.13268.

Moorcroft, P., G. Hurtt, and S. Pacala (2001), A method for scaling vegetation dynamics: The ecosystem demography model (ED), *Ecological Monographs*, *71*(4), 557-585, doi:10.1890/0012-9615(2001)071[0557:AMFSVD]2.0.CO;2.

Myers-Smith, I. H., et al. (2015), Climate sensitivity of shrub growth across the tundra biome, *Nature Clim. Change, 5*(9), 887-891, doi:10.1038/nclimate2697.

Negrón-Juárez, R. I., C. D. Koven, W. J. Riley, R. G. Knox, and J. Q. Chambers (2015), Observed allocations of productivity and biomass, and turnover times in tropical forests are not accurately represented in CMIP5 Earth system models, *Environmental Research Letters*, *10*(6), 064017.

Reich, P. B. (2014), The world-wide `fast--slow'plant economics spectrum: a traits manifesto, *Journal of Ecology*, *102*(2), 275--301, doi:10.1111/1365-2745.12211.

Reich, P. B., M. B. Walters, and D. S. Ellsworth (1997), From tropics to tundra: Global convergence in plant functioning, *Proceedings of the National Academy of Sciences*, *94*(25), 13730-13734.

Rogers, A. (2014), The use and misuse of V c,max in Earth System Models, *Photosynthesis Research*, 1-15, doi:10.1007/s11120-013-9818-1.

Scheiter, S., L. Langan, and S. I. Higgins (2013), Next-generation dynamic global vegetation models: learning from community ecology, *New Phytologist*, *198*(3), 957--969, doi:10.1111/nph.12210.

Schrodt, F., et al. (2015), BHPMF – a hierarchical Bayesian approach to gap-filling and trait prediction for macroecology and functional biogeography, *Global Ecology and Biogeography*, *24*(12), 1510-1521, doi:10.1111/geb.12335.

Serbin, S. P., A. Singh, B. E. McNeil, C. C. Kingdon, and P. A. Townsend (2014), Spectroscopic determination of leaf morphological and biochemical traits for northern temperate and boreal tree species, *Ecological Applications*, *24*(7), 1651-1669, doi:10.1890/13-2110.1.

Warren, J. M., P. J. Hanson, C. M. Iversen, J. Kumar, A. P. Walker, and S. D. Wullschleger (2015), Root structural and functional dynamics in terrestrial biosphere models – evaluation and recommendations, *New Phytologist*, *205*(1), 59-78, doi:10.1111/nph.13034.

West, C., G. E. Briggs, and F. Kidd (1920), Methods and Significant Relations in the Quantitative Analysis of Plant Growth., *New Phytologist*, *19*(7-8), 200--207, doi:10.1111/j.1469-8137.1920.tb07327.x.

Wright, I. J., et al. (2004), The worldwide leaf economics spectrum, *Nature*, *428*(6985), 821--827.

6. Appendix: List of Workshop Participants

Arindam Banerjee, University of Minnesota
Ethan Butler, University of Minnesota
Ming Chen, University of Minnesota
Brad Christoffersen, Los Alamos National Laboratory
Mike Dietze, Boston University
Ray Dybzinski, Princeton University
Eugenie Euskirchen, University of Alaska, Fairbanks
Rosie Fisher, National Center for Atmospheric Research
Habacuc Flores, University of Minnesota
Bill Hoffmann, North Carolina State University
Colleen Iversen, Oak Ridge National Laboratory
Jens Kattge, Max Planck Institute
Charlie Koven, Lawrence Berkeley National Laboratory
Lara Kueppers, Lawrence Berkeley National Laboratory
Jeremy Lichstein, University of Florida
Yiqi Luo, University of Oklahoma
Luke McCormack, University of Minnesota
David Medvigy, Princeton University
Isla Myers-Smith, University of Edinburgh
Rich Norby, Oak Ridge National Laboratory
Ryan Pavlick, Jet Propulsion Laboratory
Adam Pellegrini, Princeton University
Ben Poulter, Montana State University
Peter Reich, University of Minnesota
Dan Ricciutto, Oak Ridge National Laboratory
Sahajpal Ritvik, University of Maryland
Alistair Rogers, Brookhaven National Laboratory
Elena Shevliakova, Princeton University
Peter Thornton, Oak Ridge National Laboratory
Ben Turner, Smithsonian Tropical Research Institute
Maria Uriarte, Columbia University
Dave Weston, Oak Ridge National Laboratory
Joe Wright, Smithsonian Tropical Research Institute
Kirk Wythers, University of Minnesota
Chonggang Xu, Los Alamos National Laboratory