Measuring water fluxes in forests: the need for integrative platforms of analysis

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To understand the importance of analytical tools such as those provided by Berdanier et al. (2016) in this issue of Tree Physiology, one must understand both the grand challenges facing Earth system modelers, as well as the minutia of engaging in ecophysiological research in the field. It is between these two extremes of scale that many ecologists struggle to translate empirical research into useful conclusions that guide our understanding of how ecosystems currently function and how they are likely to change in the future. Likewise, modelers struggle to build complexity into their models that match this sophisticated understanding of how ecosystems function, so that necessary simplifications required by large scales do not themselves change the conclusions drawn from these simulations. As both monitoring technology and computational power increase, along with the continual effort in both empirical and modeling research, the gap between the scale of Earth system models and ecological observations continually closes. This creates a need for platforms of model–data interaction that incorporate uncertainties in both simulations and observations when scaling from one to the other, moving beyond simple comparisons of monthly or annual sums and means.

Global models of the Earth system are now approaching the complexity and resolution at which the dynamics of vegetation begin to play a crucial role. The next generation of dynamic global vegetation models (DGVMs) will not just include regional representations of typical ecosystems of different plant functional types (PFTs), but will take into account variation in important plant traits within them (Wullschleger et al. 2014), such as carbon allocation, stomatal regulation, xylem hydraulics, photosynthetic potential and respiration. Indeed, trait variability within PFTs has been shown to change projections of future terrestrial carbon sinks by up to 33% or more (Verheijen et al. 2015), while almost 70% of the variance in FLUXNET (a global database of ecosystem eddy-covariance observations) remain unexplained by classical PFT approach (Reichstein et al. 2014). This level of sophistication is understood as a prerequisite for predicting how ecosystems will adapt to a changing climate, including areas whose climate envelope is pushed beyond the range observed in recorded history. To achieve this, models must move beyond using aggregated observations of different PFTs to fully utilizing the complex record of observations acquired over decades of ecological field and laboratory research. Achieving such data–model interaction requires collaborations between empirical scientists and modelers, as well as those conversant in both types of research.

Approaches that harness model–data interaction can be useful in multi-model comparisons (McDowell et al. 2013, Walker et al. 2015), in the design of observational and experimental studies (Medlyn et al. 2016, Norby et al. 2016), and even in selecting the most valuable measurements to transmit to dataloggers (Clark et al. 2011). The software that translates ecophysiological measurements from electrical signals (e.g. millivolts measured by a sensor) to state variables found in DGVMs (e.g. millimeters per day of transpiration) forms an often-overlooked part of model–data interaction and represents a key platform for this integration between physiological ecologists and ecological modelers. It is important to realize that the vast majority of researchers lack formal training in software development yet they may devote 30% of their time to developing domain-specific software to address such issues (Wilson et al. 2014). The assumptions inherent within such software forms a crucial
part of our understanding of these systems. While it may not be feasible, or even desirable, for all researchers engaged in measurements across diverse ecosystems to adopt the same assumptions and analytical tools, open source code provides a common platform for discussing such assumptions and making them transparent to the larger scientific community. The research by Berdanier et al. (2016) in this issue of *Tree Physiology* represents the beginning of such a discussion and the accompanying code is an invitation to continue and expand upon it.

Of particular concern to many ecologists are observations of drought impacts on tree mortality and changes in vegetation cover (e.g. Allen et al. 2010, Anderegg et al. 2013, Zeppel et al. 2013) and our limited ability to predict such changes associated with water stress (Xu et al. 2013), as well as other aspects of global environmental change. Sap flux measurements have been a major contributor to estimates of water fluxes from forest ecosystems in recent decades. While the estimates made by aggregating many sensors over many measurement intervals into a monthly or annual estimate of canopy transpiration are useful, there is a great potential for detailed ecophysiological measurements such as these to inform next-generation trait-based DGVMs. In most cases, each sensor can be linked to an individual tree with a measured or estimated sapwood area and each measurement interval can be linked to a set of environmental conditions. Sapwood area, sap flux density and their responses to environmental variation are all plant traits that could be incorporated into these next-generation DGVMs. Fully utilizing the information contained in such databases of sap flux measurements requires careful thought about scaling of such measurements for each individual and species, as well as approaches for dealing with large volumes of data.

Sap flux databases can be very large indeed, with sub-hourly measurements from hundreds of sensors over many years resulting in millions of data points for some studies (e.g. Ward et al. 2013). The data collected from an individual sap flux sensor is rather limited in scope. For example, most sensors of the thermal dissipation probe type (Granier 1987, Lu et al. 2004) measure over a 10–20 mm sapwood depth interval with a somewhat ill-defined region of measurement on the order of a few centimeters in each direction of the cylindrical probe (Wuenschleger et al. 2011). While some guidance has been provided in recent years on sap flux measurements and their scaling (e.g. Ewers and Oren 2000, Poyatos et al. 2007, Oishi et al. 2008, Kume et al. 2010), there is no universal approach for scaling from individual sensor measurements to a tree or stand. As sapwood age increases with depth from the cambium, it is usually found that sap flux density declines with this depth, but the rate of this decline has been found to vary widely, depending on a tree’s xylem type (non-porous, diffuse-porous or ring-porous), size, species or growth rate.

While the radial variation of sap flux density may not seem like an issue of great importance, any errors in its assessment directly translate to errors in estimates of stand-level transpiration using this technique. If these stand-level estimates are used as a basis for DGVMs, then it is easy to see how an apparently small consideration can hinder our understanding of very large questions, such as the future distributions of forest species. As detailed by Berdanier et al. (2016), previous studies have adopted a wide variety of functions that have performed well for certain species, xylem types or stands. However, these authors’ work represents a significant step forward in clarifying which of these approaches performs best across a wide range of species of different xylem anatomies, as well as by providing the code necessary for other researchers to apply their findings or even recalibrate the functions using their own data. This is critical for the utility of their approach to new species and sites, as well as the possibility of it being incorporated into larger-scale models that are driven by or provide inference on such sap flux data, such as TREES (Mackay et al. 2003, Mackay et al. 2015) or StaCC (Bell et al. 2015).

Berdanier et al. (2016) find that a gamma function with parameters varying by xylem type provided the best predictions of radial sap flux profiles. The inclusion of xylem type in this approach is an important one. Given the vast number of possible plant traits that could be included in next-generation DGVMs, it is important to identify ways to group species that are physiologically meaningful. Xylem type may be one important trait to include in such DGVMs, as has been shown for hydraulic traits of xylem in modeling stand-level responses to drought (Mackay et al. 2015). If researchers test these findings with independent data and find them to be robust over a large number of species and climates, it would represent an important consensus in the interpretation of such measurements. If not, the authors have provided valuable tools to apply other functions and calibrate them using radial profile data for a given species or site. In addition, the authors find that non-porous (i.e. gymnosperm) species may have a sap flux density peak some distance from the cambium, a pattern noted in some—but far from all—previous studies on conifer species. Again, this is an intriguing finding, but the contribution of the paper is not dependent on other studies coming to the same conclusion. Simply providing the means to replicate the analysis with other data and continue the discussion of this finding is a worthy contribution in itself.

Questions of method may appear either arcane or uninteresting to those unfamiliar with a technique, but they may be as important to estimates of state variables of interest (e.g. stand transpiration) as the ecological factor that is the subject of a given study (e.g. climate, soils, species composition or atmospheric concentrations of CO₂). It is therefore crucial that the scientists employing a given measurement technique develop the analytic platforms necessary to integrate across disparate studies and help the larger scientific community responsibly use the data gathered with said measurement technique. For sap flux measurements, the efforts of Berdanier et al. (2016) represent an important step in this direction.
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