Understanding stomatal conductance responses to long-term environmental changes: a Bayesian framework that combines patterns and processes

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When stomata are open, the trade-off between water loss through transpiration and CO₂ uptake via photosynthesis is a result of the evolutionary history of land plants from green algae. To supply the up to 1000-fold higher flux of water leaving the leaf compared with CO₂ molecules entering the leaf during leaf gas exchange (Nobel 2009), plant hydraulics has evolved to be highly efficient. The intimate connection between plant water transport and photosynthesis has been explained elegantly with a theory of stomata themselves (Cowan and Farquhar 1977) and expanded to connect plant hydraulics and photosynthesis directly through an economic approach (Katul et al. 2009). This theory is well supported by data including correlations between plant hydraulic conductance and stomatal conductance (Meinzer and Grantz 1990), mesophyll conductance to CO₂ (Peguero-Pina et al. 2012) and the quantum yield of photosystem II (Brodribb and Feild 2000). These studies illustrate that the connections between plant hydraulics and photosynthesis include both biochemical and gas exchange components of photosynthesis. However, the main plant physiological regulation over the photosynthesis and transpiration compromise, stomatal conductance, is still without a full mechanistic basis from genes to environmental responses. As a result, our predictive understanding of plant hydraulic and photosynthetic responses to anthropogenic changes to climate and historical disturbance regimes is still hindered even in the most recent soil–plant–atmosphere models (Berry et al. 2010).

Modern models of stomatal conductance are, very often, still based on more than three decades old concepts of multiplicative constraints (Jarvis 1976) and semi-mechanistic parameterizations (Ball et al. 1987, Leuning 1995, Buckley et al. 2012). Such models require sufficient empirical data for appropriate calibration and thus cannot independently predict stomatal controls over water and carbon exchange without parameterization. Empirical estimates of stomatal conductance are divided into two types, gas exchange and sap flux. The benefits of gas exchange measurements are that they include both transpiration and photosynthesis, and they permit manipulation of some environmental conditions including light, temperature, CO₂, wind speed and humidity (Long and Bernacchi 2003); however, the disadvantage is that the measurements disturb the environment of the leaf, sample a small area of the canopy and are limited in time. In contrast, sap flux measurements are relatively continuous, sample a relatively large area of the xylem pipes supporting the canopy and do not disturb the environment of the leaves. The disadvantages of sap flux measurements include potentially biased measurements based on xylem anatomy and sensor type (Bush et al. 2010, Steppe et al. 2010), consideration of capacitance between the measurement point somewhere in the stem and the loss of water from the leaves (Phillips et al. 1997, Meinzer et al. 2003, Zweifel et al. 2007), and estimation of the environment of the whole canopy (Ewers et al. 2007). Both methods, neither of which are direct measurements of stomatal conductance, also require some type of scaling from the area of water loss estimated (i.e. part of the stem sapwood system or a subset of leaves) to the area of water loss under investigation (i.e. whole canopy, stands, watersheds or landscapes). Given the known issues in sap flux-based estimates of stomatal conductance (Ewers and Oren 2000) and still incomplete knowledge concerning environmental regulation over stomatal conductance...
investigates the contribution of measurement error and necess-
ary scalars to empirical estimates of stomatal conductance
is able to accommodate both missing data and the sensor
responses to climate change. Their hierarchical Bayesian model
over more than a decade—a time scale relevant to tree
measurement time steps representing millions of data points
largest sap flux data set ever published; more than 20,000
support of this method, these authors have assembled the
generally estimate stomatal conductance from empirical mea-
from both the patterns and processes simultaneously (white arrows). In
the face of incomplete knowledge of processes such as the mechanistic
basis of stomata responses to environmental regulators from genes to
whole plants and measurement errors, the Bayesian hierarchical model
provides new biological insights compared with commonly used meth-
ods that investigate the two black arrows independently.

First, the role of leaf vs. whole-plant regulation of stomatal conductance in response to elevated CO₂ levels and soil N changes with species. In the case of the angiosperm Liquidambar styryciflua L., the decline in stomatal conductance itself with elevated CO₂ levels is most important. In the case of the gymnosperm Pinus taeda L., the hydraulic regulation of stomatal conductance governed by changes in resources, especially those contributing to hydraulic supply, partitioning over the 11 years of the data is most important. Further, the hydraulic contribution to stomatal conductance in P. taeda includes changes in the capacitance of the stem in which the treatment and species differences are greater when soil moisture is high (Ward et al. 2013b). The hydraulic dynamics over the whole data set includes changes in both resources partitioning between the supply of water via roots and sapwood area and the demand for water via leaves. Such changes have been shown in shorter time scale studies (i.e. from a growing season to a few years) in which the rate of transpiration per unit leaf area is different from the rate of transpiration per sapwood area or per tree (Ewers et al. 2001, Angstmann et al. 2012).

Second, the response of stomatal conductance to environ-
mental regulators changes over the 11 years of the record. The

One application of this approach to statistics is a Bayesian
starvation analysis in which complex models are compared with simpler models to quantify which model explains data the most parsimoniously. In a recent example, 16 different models, ranging from a fully coupled photosynthesis and stomatal conductance process model with five parameters to single-parameter, big leaf models, were tested against sap flux data (Mackay et al. 2012). The priors were the maximum and minimum of the parameters of the models based on the literature. The most likely model based on a comparison of the posteriors with the means of data representing particular parameters was the model with four parameters, notably neither the most complex nor the least complex model. The work of Ward et al. (2013a) provides another approach to directly test models against data: hierarchical Bayesian modeling. This method investigates the contribution of measurement error and necessary scalars to empirical estimates of stomatal conductance and errors in the process model at any given time in the face of different plant species, soil nutrition and elevated CO₂ levels. In support of this method, these authors have assembled the largest sap flux data set ever published; more than 20,000 measurement time steps representing millions of data points over more than a decade—a time scale relevant to tree responses to climate change. Their hierarchical Bayesian model is able to accommodate both missing data and the sensor

Figure 1. The understanding of stomatal conductance at any point in time is a function of the measurements that provide estimates for the patterns and the processes that regulate those patterns. Measurements include both direct estimates as well as scalars (e.g. leaf area and sapwood area) needed to estimate stomatal conductance at different spatial scales. Processes include regulators operating in both external and internal plant conditions. The black arrows represent an independent means of understanding stomatal conductance either through direct empirical estimation or through current, yet limited understanding of the regulators of stomatal conductance. The hierarchical Bayesian model in Ward et al. (2013a) presents an approach that combines information from both the patterns and processes simultaneously (white arrows). In the face of incomplete knowledge of processes such as the mechanistic basis of stomata responses to environmental regulators from genes to whole plants and measurement errors, the Bayesian hierarchical model provides new biological insights compared with commonly used methods that investigate the two black arrows independently.
initial response to elevated $\text{CO}_2$ and soil nutrients in the first year is not the same as the long term. This shows that long-lived plant species should be studied with approaches that allow inferences at time scales that are relevant to the question. In the case of elevated $\text{CO}_2$ levels and soil nutrients, the study must last long enough for the plant to not only acclimate its stomatal conductance, but also its structural components such as leaf to sapwood or root area ratios. From the work of Ward et al. (2013a), this time scale would be shorter for $L. \text{styraciflua}$ than for $P. \text{taeda}$ because the former has responses to elevated $\text{CO}_2$ levels (i.e. lower stomatal conductance) that occur on shorter time scales than the changes in resource allocation that occur in the latter. Caution must also be taken if results are extrapolated from climate change studies in which a step function change is imposed. Changes in $\text{CO}_2$ levels and soil nutrient are not step changes but rather occur over time scales in which the trees can continue to acclimate.

The work of Ward et al. (2013a, 2013b) provides a framework for collecting and analyzing stomatal conductance patterns at time and spatial scales which are relevant for many pressing environmental problems. Forest die-off is a global phenomenon (Allen et al. 2010) that often takes years to develop; plant hydraulics plays a crucial—if partial—role in many of these die-offs (McDowell et al. 2011, Edburg et al. 2012). Studies must be designed that capture the relevant mechanisms over the appropriate times scales. In the case of drought, it may not be the acute driving condition, soil moisture, that kills the tree, but rather the length of time in which the tree is exposed to the drought and the antecedent condition as shown in seedlings (Resco et al. 2008). Long-term data sets combined with testable processes in a Bayesian framework like that of Mackay et al. (2012) or Ward et al. (2013a) will likely provide the best hope for improving our predictive understanding of forest responses to long time scale and large spatial scale anthropogenic climate changes and disturbance regimes.

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Conflict of interest

None declared.

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