

NSF Hydrologic Sciences Final Report

Collaborative research: Restricted plasticity of canopy stomatal conductance: Conceptual basis for simplified models of canopy transpiration

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Major Research and Education Activities

Summary of Overall Goals of the Project:

The overall goal of this project was to develop the conceptual model that intra and inter-species spatial variation of stomatal conductance could be explained by plant hydraulic responses to soil texture, atmospheric vapor pressure deficit, nutrient availability, temperature, and topographically controlled soil moisture. The implication of this work was that future models of forest transpiration could be made simple and yet be consistent with mechanistic plastic responses of plant hydraulic to environmental drivers. To accomplish our overall goal our efforts were directed at making spatially explicit sap flux measurements in trees arranged along different forest spatial gradients, combined with modeling activities aimed at synthesizing and interpreting this data.

Field Experiments:

A test of our strategy for sampling many sapflux trees simultaneously in space was conducted in June and July of 2004 in a subalpine forest near Laramie, WY to facilitate quick access to the Ewers laboratory. co-PI Ewers, graduate student Jonathan Adelman and technicians/undergraduates Sarah Adelman and Ian Abernathy field tested the data logging, cabling systems and solar power configurations under rigorous field conditions. We refined the technique of surveying, sampling and analyzing spatial data from forests which led to much more efficient work at the primary field sites in Wisconsin.

From late July to Early August, 2004 all three institutions (UB, Wyoming, Wisconsin) participated in an initial field campaign. The PIs (Mackay, Ewers, Kruger) helped survey in and set up field equipment to conduct spatial measurements of sap flux in a aspen stand at the study site. We set up a cyclic sampling consisting of 144 plots established on a 120m x 120m block (**Figure 1**), following the protocol detailed in our proposal. The plots spanned a gradient from relatively dry, upland aspen sites to wetland sites consisting of a mix of aspen, alder, and cedar. At each plot we measured continuous sap flux (using Granier-type sensors) for the dominant (largest basal area) tree for each species, for a total of about 180 trees. Soil moisture was measured in every plot at three times over a 10-day period. Vapor pressure deficit (VPD) was measured at every plot twice during the period and continuously at one fixed point in the upland. Tree basal areas were measured for every tree in which sap flux measurements were made. It took only a week for 8 people (3 from Buffalo, 3 from Wisconsin, 2 from Wyoming) to set up the site and one or two students to keep it running.

There were essentially four phases to the field experiments in summer 2005. In the first phase the aspen sapflux study (144 cyclically sampled plots in a 120 x 120m block, with a base lag

distance of 5m), which was installed in 2004, was turned back on in early May and run continuously for approximately 6 weeks. During this time soil moisture, VPD, and leaf water potential (LWP) measurements were made on a repeated basis every few days. A second phase of field experiments focused on leaf gas exchange. Canopy access scaffolding was installed in upland and wetland aspen plots, and measurements of leaf gas exchange were made for eight days. In a third phase of field work an intensive campaign (all PIs, all students) was conducted over a 10-day period to survey and install sap flux sensors in the sugar maple-red pine block. This second study also had 144 cyclically sampled plots, but in a 144 x 126 m block using a base lag distance of 6m (**Figure 2**). The fourth phase consisted of three types of intensive measurements. First, synoptic leaf gas exchange and midday leaf water potential measurements were made to test the hypothesis that aspen proximity to wetland altered leaf light response and stomatal conductance. Second, we harvested aspen from wetland and upland sites to characterize their canopy light environments and allometric relationships. Third, we conducted measurements of competition for light among sap flux trees and the 10 nearest neighboring trees. Subsequent analysis of this data suggested a need for competition data from every potential competitor, and consequently, additional field activities were added to the field campaigns for 2006.

There were essentially three primary components of the field work conducted in summer 2006. First, a subset of sapflux sensors were turned on for about a 3-week period in each of the sites, during which two intensive field campaigns were conducted aimed at gaining a mechanistic understanding of the spatial variability of transpiration in reference canopy stomatal conductance we conducted in parallel.

Second, an intensive campaign was conducted to collect soil data from each of the cyclically sampled plots in the aspen-wetland and a subset of sugar maple-red pine. The primary variables we obtained from this data were soil texture, root content, carbon, and nitrogen content. Bulk density samples were collected with a soil corer (10 x 3.4 cm) on a majority of plots in the Aspen stand (87 plots, Fig. 1) and in two transects (9 plots, Fig. 2) across the Maple stand. Soils were oven dried for 24 hours at 40 °C, and the bulk density calculated. Soil samples from below the layer were collected at every plot in the Aspen stand and at 18 plots in the Maple stand (Fig. 2); a subset of 38 plots in the Aspen stand and 9 plots in the Maple stand was analyzed for total carbon (C), total nitrogen (N) and C:N ratios using an Elementar Vario Analyzer (MACRO Elemental Analyzer, Germany). The same subset of plots in the Aspen stand and the Maple stand was also analyzed for soil texture (GLOBE 2005). All soil samples were collected in July of 2006. The subset of plots in the Aspen stand was chosen transects to represent the range of soil moisture across the stand (Figure 1). The soil samples transects in the Maple stand were also believed to be representative transects, and there was an expectation of less variability in the soil characteristics (Figure 1). During this time soil moisture and VPD measurements were made on a repeated basis every few days.

Third, two campaigns were conducted to quantify tree competition in the aspen site. For every sap flux tree we measured height, azimuth, crown depth, species, DBH, and distance to every competitor tree within a 5m radius. The purpose of this data is to examine competition for light as a mechanistic explanation of transpiration. This was conducted in two campaigns because of the laborious nature of measurements. This data has been analyzed as part of M. Loranty's dissertation.

As described later, our analysis showed that 1) spatial variability at a given set of environmental conditions, especially VPD, was driven by A_s and 2) spatial variability in time could be described by environmental drivers. Thus, we could determine seasonal spatial variability in transpiration

by just measuring a few trees in specific gradients in both the aspen and maple stands to quantify seasonal variability in spatial transpiration. In May 2007, we set up two transects of sap flux measurements going from the wet to dry locations in the aspen stand and from the red pine to the sugar maple dominated areas of the maple stand.

Data obtained from these field studies are summarized in **Table 1**. **Figures 3** and **4** show a sample of sap flux and environmental drivers of canopy transpiration, E_c , for the Wyoming test site, the aspen site, and the sugar maple site. All data is being archived once it is published. Details on these archived datasets are discussed in more detail later when we discuss the significance of the results and products for the broader scientific community.

Data Analysis:

Sap flux data cleaning, scaling, and analysis were conducted by Mike Loranty during the Fall 2004 semester. For our preliminary analysis we divided the aspen sap flux trees into three topographic positions (wetland, intermediate, and upland). We tested (using ANOVA) for significant differences in per unit xylem sap flux among topographic positions, and in whole tree sap flux among topographic positions. Semivariograms of synoptic soil moisture were generated for the purpose of kriging. Jonathan Adelman developed the basic filtering and graphical methods for spatial analysis. These analyses include construction and testing of spatial assumptions through the use of semivariograms and kriging. Results of these analyses are presented in **Figures 5-7** and discussed in more detail in the major results sections.

The TREES model was employed to examine the coupled carbon-hydraulic controls on canopy transpiration and stomatal conductance. The model was constrained using leaf gas exchange and leaf area data collected in the aspen site in 2005. Inverse modeling evaluated with sapflux data was employed to derive canopy parameters along a soil moisture transect in the aspen-wetland. One of the project objectives is to assess whether hydrologically significant transpiration is limited by hydraulic or photosynthetic controls. TREES was used to assimilate leaf level gas exchange data, micrometeorology data, and sap flux across this gradient.

The TREES model was employed to simulate canopy transpiration (E_c) and canopy stomatal conductance for every sap flux tree measured in the summer 2004 campaign. Both data and simulation results were analyzed using semivariogram analysis to examine how spatial and total variance varies with environmental drivers (radiation, vapor pressure deficit) (Loranty *et al.*, 2007). The geostatistical range, or maximum distance at which individuals are autocorrelated in space, exhibits a negative correlation with vapor pressure deficit. Analyses of observed and simulated data yielded similar relationships indicating that our model effectively captures spatial and temporal variations in E_c . A reduced semivariogram range at higher VPD demonstrates that E_c and canopy stomatal conductance are spatially more heterogeneous when flux rates are high. Our results show that although water cycling through the forest exhibits strong nonlinear behavior there is clear evidence that this behavior can be predicted in both time and space.

Work is nearing completion on using spatial covariate analysis on soil variables to find correlates with spatial tree E_c . We have found that soil N is inversely correlated with tree transpiration with the other soil variables having no significant correlation (**Figure 8**). In this case, soil N is acting as a proxy for wetland conditions because 1) anerobic conditions limit N cycling and maintain high soil N and 2) speckled alder, which dominates the wetland area, is an N-fixer. These results are being submitted to *Functional Ecology* (Traver *et al.*). We have also studied canopy self-shading as a mechanistic control of temporal variation in E_c . An extensive

inventory of canopy competition has been collected for the site with the intention of developing a 3-dimensional shade model for the canopy. Thus far, a combination of data analysis and modeling indicates a spatial autocorrelation in canopy competition and a negative correlation between the degree of competition and reference canopy stomatal conductance (G_{Sref}) (**Figure 9**). This analysis is part of M. Loranty's dissertation.

Because of some instrument issues, we were not able to sample the vulnerability to cavitation of roots during the spatial measurement campaigns of the project. The instrument issues have been resolved and an air injection system has now been extensively tested in the Ewers lab at Wyoming in preparation for sampling these stands in July 2008. The sampling will include 8 to 10 roots between 2 and 5 mm in diameter; previous work has shown these to be the most vulnerable to cavitation and thus most useful for describing plant hydraulic controls. In the aspen stand, roots from aspen will be sampled in the upland, transition and wetland zones, alder will be sampled in the transition and wetland zones and cedar will be sampled in the wetland zone. In the maple stand, maple and red pine will both be sampled from areas in which they are dominant and in areas in which the other species is dominant. The results of this dataset will allow us to test 1) how acclimation of roots to both edaphic and canopy conditions impacts spatial transpiration and 2) how much model complexity is required with respect to tree hydraulics to capture spatial variation in transpiration.

Simulations:

The initial setup of TREES to incorporate plant hydraulics was tested on an extensive database of sugar maple transpiration from around the western Great Lakes. The main goal was to determine if incorporating a simple plant hydraulic tradeoff between high canopy stomatal conductance and response to VPD would improve model performance. The plant hydraulic tradeoff uses a reference canopy stomatal conductance (G_{Sref}) and tests whether G_{Sref} is proportional to the rate of change in G_S with increase in VPD (sensitivity of stomatal conductance to VPD or m). Plant hydraulic theory predicts that G_{Sref} should be related to m with a 0.6 ratio when plants are isohydric, i.e. limiting minimum LWP to prevent excessive and catastrophic cavitation. Using a Monte Carlo approach, we found that incorporating this tradeoff did indeed improve the TREES model performance (Ewers et al. 2008). This result was used to constrain all future use of the TREES model in this project.

We initially applied the TREES model, with a simple three-parameter Jarvis-based model of canopy stomatal conductance, to the aggregated sap flux for aspen. Monte Carlo analysis was performed on the parameters in order to derive G_{Sref} using the procedures outlined in the proposal. M. Loranty has been in charge of running Monte Carlo simulations with TREES. He has conducted spatial simulations (tree by tree), and geostatistical analyses on the results of these simulations. Mackay has been conducting the intensive plot simulations, which are primarily focusing on the coupled carbon-water relations and canopy light environment of each intensively studied tree.

Presentations:

The primary findings from the project were reported in 14 invited presentations at conferences, universities, or other organizations, and 27 contributed presentations in conferences, workshops, or seminars. Presentations were made by graduate students, M. Loranty (10), J. Adelman (4), E. Traver (2), and S. Samanta (1); undergraduate student D. Roberts (1); and principal investigators, Mackay (13) and Ewers (10).

Major findings resulting from these activities

Major Conclusions

(1) Spatiotemporal Variability of Tree Transpiration

Data from 2004 at aspen, alder, cedar site showed that mean daily sap flux velocity, J_S , exhibited no spatial autocorrelation (Loranty *et al.*, 2008). Data from 2005, in which additional aspen trees were added to increase the number of point-pairs at shorter lag distances, showed a slight linear trend in the semivariogram of J_S , implying spatial autocorrelation beyond the spatial extent of the study site (Traver *et al.*, submitted to *Functional Ecology*). A similar pattern was observed at the maple-pine site. Moreover, at the pilot study in Wyoming J_S showed much less spatial variance in comparison to tree transpiration, E_C , and only showed autocorrelation at high vapor pressure deficit, D (Adelman *et al.*, 2008). Spatial autocorrelation in mean tree transpiration, E_{C-OBS} , a product of J_S and sapwood area, A_S , was attributed primarily to spatial autocorrelation in A_S at a given set of environmental conditions in all sites. Simulations with the TREES model reproduced the spatial structure of the mean daily tree transpiration, E_{C-SIM} . An important outcome of this result is that the primary scalar of transpiration may be A_S , a relatively easy parameter to obtain and the dynamics in the spatial autocorrelation can be explained with environmental drivers using a mechanistic foundation. The implication of this is that larger scale water flux studies in forests may be able to use a much smaller number of sap flux observations in each species and yet still have the robust spatial estimations found in our studies.

Further analysis of fluxes at sub-daily temporal scales showed that the spatial variability in E_C was driven by temporal changes in D but not changes in light, Q , and showed less dependence on time-of-day. At low D levels, spatial autocorrelation is high resulting in small sills and nuggets but large ranges from semivariogram analyses. At high D levels, spatial autocorrelation is low resulting in large sills and nuggets but smaller ranges from semivariogram analyses. These results indicate that spatial patterning can be predicted with environmental drivers (**Figures 5, 6, and 7**). Such clustering of E_C fluxes in space with increasing D was consistent across very different forests in Wyoming and Wisconsin. The implication of this result is that spatial variation of E_C is not fully explained by spatial variations in A_S , but the response to D suggests that differences in E_C in space and time can be explained by plant hydraulics, namely controls on stomatal conductance, G_S .

(2) Spatiotemporal variability of G_{Sref}

Explanations for the effects of plant hydraulics on spatial variability of E_C over time include acclimation to edaphic conditions such as soil texture changes, spatial variability of allometric relationships, spatial variability of leaf-level light response, differences in responses to inter-tree competition for light due to a coordinated response between plant hydraulics and photosynthesis, or genetic autocorrelation in space in response to disturbance or clonal propagation. Future studies might consider spatial genetics in such systems as genetic sequencing of species come online. In our study we examined edaphic conditions and competition for light as potential mechanisms underlying spatial variations in plant hydraulics, as well as allometry and leaf gas response data. In the aspen site there was evidence of plant hydraulics acclimating to edaphic conditions. In particular, there was an inverse relationship between aspen E_C and soil N content (**Figure 8**), reflecting a relatively large accumulation of total N, but not necessarily easily mineralized N, in the wetland in comparison to upland

positions. However, there was no correlation between edaphic conditions and E_c in the maple stand. While there was a lack of strong edaphic control on species at our sites, such a relationship may not hold in ecosystems where strong soil moisture gradients occur. Our findings are most directly applicable to mesic forest systems. However, the approach to quantifying and explain spatial patterns in water and other fluxes should be very broadly applicable to most ecosystems from arid- to wetlands. Further study is needed to ascertain how edaphic conditions affect spatial variability of plant hydraulics in these other systems, especially semi-arid systems with dynamic atmospheric and soil drought.

Aspen trees in the wetland and upland sites show no difference in allometric relationships and no significant differences in leaf-level light response. This has forced us to reject the hypothesis that differences in reference canopy stomatal conductance are determined in part by allometry and/or level-level gas exchange.

M. Loranty employed inverse modeling with TREES to estimate G_{Sref} spatially, which was then examined for correlations with A_s , soil moisture, and a competition index based on the tree competition data collected. Results for the aspen site (**Figure 9**) show no correlation between G_{Sref} and A_s , a weak parabolic relationship with soil moisture, and strong negative correlation with the competition for light index. In addition, the optimal models maintained proportionality between sensitivity of G_s to D , m , close to 0.6 times G_{Sref} indicating that the aspen remained isohydric at all times. Thus, G_{Sref} varies with crown closure yet conforms to our conceptual model of restricted plasticity. This result supports explaining spatial variability in plant hydraulics by competition for light. If this holds across ecosystems then it would be possible to use remotely sensed data and widely used canopy radiative transfer schemes to quantify competition for light, and in turn spatial variability of plant hydraulics. M. Loranty is examining this issue in much more detail for his dissertation using his competition data, the intensive plot photosynthesis data, and LiDAR data collected by the U. Minnesota (P. Bolstad). An important implication of this work for larger scale studies is that forest structure, and not just composition, needs to be incorporated into models.

One of our main project goals was to determine if incorporating a simple plant hydraulic tradeoff between high canopy stomatal conductance and response to VPD would improve model performance, regardless of the apparent need for model complexity as suggested by the role of forest structure. The plant hydraulic tradeoff uses G_{Sref} and tests whether G_{Sref} is proportional to the rate of change in G_s with increase in VPD (sensitivity of stomatal conductance to VPD or m). TREES simulations incorporating such simple plant hydraulics were successfully able to simulate canopy transpiration despite large differences in forest structure among sugar maple stands across the region around our study (Ewers *et al.*, 2008). Specifically, we examined this issue in more detail at a regional extent by comparing canopy transpiration from old growth, unthinned mature, and thinned mature sugar maple stands in the region around our study site. This comparison showed that transpiration per unit leaf area, E_L , varied by as much as a factor of 5 times. Inverse modeling with TREES showed clear inter-site and inter-annual changes in G_{Sref} , but all stands remained isohydric (**Figure 10**). This shows that across the full range of forest management conditions sugar maple, one of the core species for this study, followed our conceptual model. This has important implications for modeling regional and larger scale studies of land surface – atmosphere water and energy because it shows that parameterizations cannot ignore forest management effects on E_L . Ultimately, understanding such bottom up mechanisms will be required to predict regional changes in land surface responses to global change. Despite this additional complication in upscaling from stands to regions, our results show that the time series of transpiration can be adequately modeled and parameter uncertainty can be reduced using current knowledge of tree physiological mechanisms. Indeed, the

application of plant hydraulics in the selection of model parameters enables models to be grounded in mechanistic rigor while retaining the parsimony needed for regional scale modeling with relatively sparse knowledge of individual forest stands. If our hypotheses about plant hydraulics hold up with the root cavitation inclusion, then we ultimately have a simple yet mechanistically rigorous model.

The key drivers of evapotranspiration (E_T) differ between wetlands, where response is primarily to Q , and uplands where the response is primarily to D . These patterns are invariant among years, but differ seasonally in response to leaf phenology, with the upland forest in particular responding more to Q than D during the spring “greening-up” period. Parameters that define these responses also varied with time in response to freezing (upland and wetland), water table height (wetland), and soil moisture (upland) (**Figure 10**). However, in the case of the upland, the relationship between G_{Sref} and m showed that the trees remained isohydric at all times (Mackay *et al.*, 2007, *Water Resources Research*). Furthermore, the seasonal responses of G_{Sref} to drivers were evaluated using whole season (late April to mid-October) sap flux data for aspen and red pine. Our results show that leaf expansion alone cannot explain seasonal E_c dynamics. In particular, the red pine showed increasing G_{Sref} (per unit leaf area basis) up to mid-september even though its new needle cohort expanded in June (Mackay *et al.*, 2006, AGU presentation). These findings combined with large intra- and inter-specific differences in timing of leaf expansion found in another on-going project at the site (Mark Schwartz, personal communication), have important implications for predicting the dynamics of land surface – atmosphere water and other fluxes.

(3) Model Complexity

More detailed analysis of the combined information content of sap flux data and the TREES model were conducted with Bayesian analysis and sap flux data from sugar maple. Markov Chain convergence and relatively small spread of the posterior parameter estimates in comparison to the uninformed priors used to initialize the Markov Chain analysis (**Figure 11**) was evidence that parameters in the conceptual transpiration model can be accurately estimated (Samanta *et al.*, 2007). However, there was a considerable amount of uncertainty in the predictions. We expanded upon this analysis by considering alternative models of stomatal conductance with different levels of complexity. The results show that for predicting sap flux very simple stomatal conductance models are poor predictors, while very complex models have too much predictive uncertainty (**Tables 2&3**; Samanta *et al.* 2008).

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Non-Refereed Manuscripts

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