

5-19-2010

On the Representativeness of Plot Size and Location for Scaling Transpiration from Trees to a Stand

D. S. Mackay

Brent E. Ewers

University of Wyoming, beewers@uwyo.edu

M. M. Loranty

E. L. Kruger

Follow this and additional works at: http://repository.uwyo.edu/botany_facpub



Part of the [Botany Commons](#)

Publication Information

Mackay, D. S.; Ewers, Brent E.; Loranty, M. M.; and Kruger, E. L. (2010). "On the Representativeness of Plot Size and Location for Scaling Transpiration from Trees to a Stand." *Journal of Geophysical Research-Biogeosciences* 115.2.

This Article is brought to you for free and open access by the Botany at Wyoming Scholars Repository. It has been accepted for inclusion in Botany Faculty Publications by an authorized administrator of Wyoming Scholars Repository. For more information, please contact scholcom@uwyo.edu.



On the representativeness of plot size and location for scaling transpiration from trees to a stand

D. Scott Mackay,¹ Brent E. Ewers,² Michael M. Loranty,³ and Eric L. Kruger⁴

Received 3 July 2009; revised 7 January 2010; accepted 21 January 2010; published 19 May 2010.

[1] Scaling transpiration from trees to larger areas is a fundamental problem in ecohydrology. For scaling stand transpiration from sap flux sensors we asked if plot representativeness depended on plot size and location, the magnitude of environmental drivers, parameter needs for ecosystem models, and whether the goal was to estimate transpiration per unit ground area (E_C), per unit leaf area (E_L), or canopy stomatal conductance (G_S). Sap flux data were collected in 108 trees with heat dissipation probes, and biometric properties were measured for 752 trees within a 1.44 ha *Populus tremuloides* stand along an upland-to-wetland gradient. E_C was estimated for the stand using eight different plot sizes spanning a radius of 2.0–12.0 m. Each estimate of E_C was derived from 200 plots placed randomly throughout the stand. We also derived leaf area index (L), canopy closure (P_{CC}), and the canopy average reference stomatal conductance (G_{Sref}), which are key parameters used in modeling transpiration and evapotranspiration. With increasing plot size, E_C declined monotonically but E_L and G_{Sref} were largely invariant. Interplot variance of E_C also declined with increasing plot size, at a rate that was independent of vapor pressure deficit. Plot representativeness was dependent on location within the stand. Scaling to the stand required three plots spanning the upland to wetland, with one to at most 10 trees instrumented for sap flux. Plots that were chosen to accurately reflect the spatial covariation of L , P_{CC} , and G_{Sref} were most representative of the stand.

Citation: Mackay, D. S., B. E. Ewers, M. M. Loranty, and E. L. Kruger (2010), On the representativeness of plot size and location for scaling transpiration from trees to a stand, *J. Geophys. Res.*, 115, G02016, doi:10.1029/2009JG001092.

1. Introduction

[2] Scaling up from plots to stands and from stands to larger areas is a fundamental problem in ecohydrology. It is an essential step in combining information from multiple spatial, temporal, and organizational scales at which systems are observed, or as a pragmatic solution to the problem of having limited observational data within a larger region. No single scale is always sufficient for characterizing a system, as each scale imposes a sampling bias [Levin, 1992]. For example, regional scale models of canopy transpiration (E_C) typically combine vegetation classification, leaf area index (L), and canopy stomatal conductance (G_S) [Bonan, 1991; Wood et al., 1992; Foley et al., 1996; Sellers et al., 1997; Baldocchi et al., 2002; Su et al., 2007]. Most of these models have the potential of blurring mechanisms when they consider

evapotranspiration (i.e., evaporation from soils and wet canopies as well as transpiration) rather than just E_C . However, a potentially bigger source of uncertainty lies with the current scaling logic where a set of representative stands is identified based on the composition of vegetation in a region, a measurement plot is identified within each stand, and flux and parameter values are obtained for the plot. The plot is assumed to be representative of its respective stand, which in turn is representative of all stands of a similar vegetation composition at the regional level. The information obtained from the plot is distributed onto the region by mapping the respective observations to their vegetation composition on the classification map [Mackay et al., 2002]. With respect to scaling to the stand, plot representativeness can be interpreted in different ways. One could consider a plot representative if its scaled flux values match those of the whole stand (i.e., absolutely representative), if fluxes of the plot and stand have similar dynamics with different scalar values (i.e., dynamically representative), or if parameters derived from the plot can be used to accurately simulate fluxes at the stand level (i.e., parametrically representative). Errors typically occur when scaling up from representative plots if the scaling process is nonlinear [Raupach and Finnigan, 1988; Baldocchi et al., 1991; Band et al., 1991; Norman, 1993]. Moreover, even scaling of

¹Department of Geography, State University of New York at Buffalo, Buffalo, New York, USA.

²Department of Botany and Program in Ecology, University of Wyoming, Laramie, Wyoming, USA.

³Woods Hole Research Center, Falmouth, Massachusetts, USA.

⁴Department of Forest and Wildlife Ecology, University of Wisconsin-Madison, Madison, Wisconsin, USA.

linear quantities can introduce error if a plot is not representative in the respective interpretation employed. Recent studies using sap flux to scale-up E_C in heterogeneous forests suggest that finding representative plots may be challenging with respect to quantifying absolute values and dynamics of E_C , and deriving G_S [Kumagai et al., 2005b; Tromp-van Meerveld and McDonnell, 2006; Adelman et al., 2008; Kumagai et al., 2008; Loranty et al., 2008; Traver et al., 2009]. The purpose of this paper is to examine the implications of a plot's size and location for its representativeness in scaling E_C from sap flux and quantifying L , G_S , and canopy closure inputs to stand or regional models.

[3] Measurement of xylem water transport using sap flux sensors and scaling to canopy transpiration at the level of whole tree, stand, or larger areas has matured over the past few decades. For example, methods for scaling from constant-heat type sensors to whole trees have an extensive set of protocols [Granier, 1987; Phillips et al., 1996; Clearwater et al., 1999; Ewers and Oren, 2000; Meinzer et al., 2001; James et al., 2002; Ford et al., 2004; Oishi et al., 2008]. Methods for scaling from individual trees to plots and then to stands differ with respect to plot size used for sampling, replication of plots, the number of trees sampled per species, and the scalar used to convert flux per tree to flux per plot. Table 1 presents a cross section of studies that have provided sufficient information for scaling from sap flux sensors to some ground area. In these studies the ground area to which sap flux sensor observations are scaled vary from 8 m² to 60,000 m² (or 6 ha), and include circular plots [Oren et al., 1998a; Ewers et al., 2002; Ewers et al., 2005; Pataki et al., 2005; Simonin et al., 2007], noncircular plots [Hatton et al., 1990; Cermak et al., 1995; Vertessy et al., 2001; Cienciala et al., 2002; Ewers et al., 2002; Herbst et al., 2007], transects [Kurpius et al., 2003], and whole stand or hillslope boundaries [Zimmermann et al., 2000; Tromp-van Meerveld and McDonnell, 2006]. In most of the studies in Table 1 the number of plots used to represent a larger area is quite small, and in two-thirds of the studies this is limited to 1 or 2 plots. The number of trees instrumented for sap flux per species per plot varied from 1 to 19, with approximately half the studies using 8 or fewer sap flux trees per species per plot. Stand heterogeneity is included in the scaling processes by weighting each sap flux sensor by a representative scalar [Hatton and Wu, 1995], such as sapwood area, basal area, leaf area, tree circumference, or some other weighting measures. The number of scalar measurements (e.g., basal area) made typically far exceeds the number of trees instrumented for flux, as the scalars are typically easier to obtain and can be the largest source of variability in E_C [Vertessy et al., 1997; Ford et al., 2007].

[4] A number of variables contribute to the spatial heterogeneity of transpiration within a single species, including sap flux density variations [Medhurst et al., 2002; Bovard et al., 2005; Ewers et al., 2005; Kumagai et al., 2005a; Pataki et al., 2005; Ewers et al., 2007; Herbst et al., 2007; Adelman et al., 2008], the influences of a scalar such as sapwood area [Vertessy et al., 1997; Bovard et al., 2005; Herbst et al., 2007; Kumagai et al., 2007; Loranty et al., 2008], and radial declines in sap flux density with increasing depth into the sapwood [Phillips et al., 1996; Pausch et al., 2000; Schafer et al., 2000; Ford et al., 2004; Hultine et al., 2007]. These variables

have been associated with spatial variations in edaphic properties [Schiller et al., 2002; Eberbach and Burrows, 2006; Tromp-van Meerveld and McDonnell, 2006; Wullschlegel and Hanson, 2006; Nadezhkina et al., 2007], stand structure [Cienciala et al., 2000; Taylor et al., 2001; Medhurst et al., 2002; Giambelluca et al., 2003; Simonin et al., 2006; Hultine et al., 2007], and age [Zimmermann et al., 2000; Phillips et al., 2002; Delzon and Loustau, 2005; Ewers et al., 2005], as these affect root extractable water, convective and radiative energy transfers, and plant water relations. Spatiotemporal analyses have shown temporal changes in the spatial heterogeneity of tree transpiration associated with tree-level responses to environmental drivers such as vapor pressure deficit [Adelman et al., 2008; Loranty et al., 2008; Traver et al., 2009].

[5] Given such sources of variability we asked the following questions: (1) How representative are plots of forest transpiration for a stand; (2) does plot representativeness change with the magnitude of environmental drivers and G_S ; and (3) does plot representativeness differ for estimates of E_C and canopy transpiration per unit leaf area (E_L)?

2. Methods and Materials

2.1. Study Site

[6] The study was conducted in the Chequamegon-Nicolet National Forest near the town of Park Falls (45.95°N, 90.27°W), Wisconsin, United States. The area represents the interface between northern temperate and southern boreal ecosystems and is part of the northern highlands physiographic province. The bedrock consists of Precambrian igneous and metamorphic rock, overlain by 8–90 m of glacial and glaciofluvial material. Geomorphic features in the area are outwash, pitted outwash, and moraines resulting in gently rolling topography. Climate is characterized by long winters and a short growing season with mean January and July temperatures of -12°C and 19°C , respectively [Fassnacht and Gower, 1997]. Data for the study were collected at a site located approximately 800 m southeast of the WLEF eddy flux tower [Bakwin et al., 1998; Davis et al., 2003]. Field observations for the study were collected in a 20 year old regenerating *P. tremuloides* stand during the summer of 2005. We selected *P. tremuloides* because it had the highest transpiration per unit leaf area of any species measured in northern Wisconsin [Ewers et al., 2002]. We chose the particular stand because it was spatially heterogeneous with respect to topography and basal area. The stand comprised a transition from forested wetland to upland forest over a 2–3 m variation in elevation, with the wetland dominated by speckled alder (*Alnus incana* (DuRoi) Spreng) and white cedar (*Thuja occidentalis*). The upland positions also had balsam fir (*Abies balsamea* (L.) Mill) in the overstory, and *Sphagnum* spp. covered all on hummocks in the wetland areas.

2.2. Measurements

[7] The study was conducted in 16 25 × 25 m substand blocks within a 1.7 ha stand (Figure 1). These blocks were a sampling construct, and there were no substantial differences in basal area between the sample areas and areas between the blocks. Two of the blocks had no *P. tremuloides*, as they were in a *T. occidentalis* wetland, and so

Table 1. Summary of Sap Flux Studies in Which Plot Size and Sap Flux Scaling Parameters Are Reported^a

Plot Area (m ²)	Number of Plots	Number of Species	Trees/Species (per Plot)	A _B (m ² ha ⁻¹)	A _S (cm ² m ⁻²)	Scalar ^b	IGBP ^c	Biome ^d	Reference
8	6	1	1	-	-	T	EN-P	TE	Hatton et al. [1990]
9	16	1	1	27.7, 13.9	19.9, 9.7	As	EB-P	TE	Taylor et al. [2001]
20	144	3	79, 41, 9 ^e	-	5.9, 3.5, 19.7	As	MF	TE	Lorantý et al. [2008]
20	144	2	93, 41 ^e	-	5.3-11.8, 2.7-4.8	As	MF	TE	Traver et al. [2009]
25	4	1	8	10.1-24.9	9.0-21.2	As	EN-P	TE	Ewers et al. [2000]
25	4	1	8	10.1-24.9	4.7-23.7	As	EN-P	TE	Ewers et al. [2001]
25	1	1	10	-	-	As	DB	TE	Roberts et al. [2005]
30	3	1	1	20.0	-	C	EN-P	BO	Mellander et al. [2006]
34	144	2	99, 41 ^e	-	33.6-47.4, 86.9-92.5	As	MF	TE	Traver et al. [2009]
50	48	4	54, 37, 11, 27 ^e	24.7, 7.4, 2.6, 4.9	11.0, 1.2, 2.1, 3.5	As	MF	TE	Adelman et al. [2008]
53	1	1	10	14.9	12.7	As	EN-P	TE	Oren et al. [1998a, 1998b]
60-80	4	1	10	9.4-26.0	4.7-23.7	As	EN-P	BO	Phillips et al. [2002] and Ewers et al. [2001]
60	9	1	2	-	-	-	DB-P	TE	Kang et al. [2002]
76	12	2	9, 3	15.0-30.0	-	As	DB-P	TE	Uddling et al. [2008]
78	2	1	8 or 10	73.3, 82.1	1.5-16.7	As	EN	TE	Simonin et al. [2006, 2007]
79	1	2	8	30.0, 3.7	15.8, 2.5	As	MF	TE	Ewers et al. [2002, 2007]
100	2	1	9, 6	38.0, 63.0	19.4, 32.1	As	DB	BO	Hogg et al. [1997]
100	2	1	12, 12	38.0, 63.0	19.4, 32.1	As	DB	BO	Hogg and Hurdle [1997]
100	3	2	3 or 13	-	-	B	OS	TE	Scott et al. [2006]
111	1	1	10	15.8	13.8	As	EN-P	TE	Oren et al. [1998a, 1998b]
113	1	1	8	51.6	39.3	As	EN-P	TE	Ewers et al. [2002, 2007]
113	1	3	12	3.4, 5.9, 1.1	0.3-1.8, 1.8-2.7, 0.3	As	MF	BO	Ewers et al. [2005]
113	1	1	12	49.9	3.0-24.0	As	EN	BO	Ewers et al. [2005]
113	2	1	18	66.2, 33.7	-	As	DB	TE	Pataki et al. [2005]
117	1	1	10	16.9	14.4	As	EN-P	TE	Oren et al. [1998a, 1998b]
154	1	2	5 or 7	2.4, 2.2	0.2, 0.8	As	DB	BO	Ewers et al. [2005]
166	12	1	9	15.0-30.0	-	As	DB-P	TE	Uddling et al. [2008]
198	1	1	6	56.4	-	N/A	EN	TE	Oliveras and Llorens [2001]
203	1	1	14	54.2	-	As	EN-P	TE	Ford et al. [2007]
207	1	1	14	3.9	-	As	EN-P	TE	Kumagai et al. [2005a]
289	1	1	12	68.1	-	As	EN-P	TE	Ford et al. [2007]
292	1	1	14	77.2	-	As	EN-P	TE	Ford et al. [2007]
314	1	3	8	24.4, 16.1, 1.1	6.1, 16.1, 0.6	As	PW	TE	Ewers et al. [2002, 2007]
314	1	6	1-4	21.7-34.9	-	As	EN-P	TE	Wilson et al. [2001]
318	1	1	23	71.7	36.3	As	EN-P	TE	Kumagai et al. [2007, 2008]
321	1	1	15	118.7	46.0	As	EN-P	TE	Kumagai et al. [2007, 2008]
365	1	1	7	31.6	-	As or Ac	EN-P	TE	Nadezhda et al. [2007]
500	2	4	2	52.3, 64.5	-	W	EB	TE	Eberbach and Burrows [2006]
530	1	1	12	45.3	3.5-42.0	As	EN	BO	Ewers et al. [2005]
600	2	1	9, 10	NA	-	As	EN	BO	Hatton and Wu [1995]
606	1	1	7	32.2	-	As	EN-P	TE	Nadezhda et al. [2007]
625	1	2	5, 8	up to 16.2 (As)	-	D	DB	TE	Vertessy et al. [2001]
633	1	1	7	77.7	-	As	EN	TE	Simonin et al. [2006, 2007]
707	4	3	8	8.2, 7.5, 5.4	1.5-16.7	As	MF	BO	Ewers et al. [2005]
750	3	1	11-13	14.0-68.0	-	As	DB-P	TE	Medhurst et al. [2002]
800	1	6	6, 6, 2, 1, 1, 1	1.4-11.3	1.0-5.1	As	DB	TE	Oren et al. [2001]
800	1	2	8	18.8, 9.7	12.6, 4.2	As	DB	TE	Ewers et al. [2002, 2007, 2008]
869	1	1	4	77.7	1.5-16.7	As	EN	TE	Simonin et al. [2006, 2007]
900	4	4	~4	35.6-47.6	-	As	DB	TE	Herbst et al. [2007]
960	1	1	14	24.8	-	As	MF	TE	Tromp-van Meerveld and McDonnell [2006]

Table 1. (continued)

Plot Area (m ²)	Number of Plots	Number of Species	Trees/Species (per Plot)	A _B (m ² ha ⁻¹)	A _S (cm ² m ⁻²)	Scalar ^b	IGBP ^c	Biome ^d	Reference
1,000	2	1	8	8.2–8.9	-	C	DB-P	TE	Schiller et al. [2007]
1,000	4	1	8	7.5	-	A _L	OS	TE	Schiller et al. [2002]
1,000	2	1	6	4.8, 10.3	0.9, 1.1	A _S	DB	TE	Engel et al. [2002]
1,100	1	1	5	28.2	-	A _S	DB	TE	Bernier et al. [2002]
1,200	2	2	12 per stand	17.8, 28.0	1.5, 1.4	A _S	EN	BO	Lundblad and Lindroth [2002]
1,212	1	3	19	87.5	13.8	A _S	DB	TE	Ewers et al. [2008]
1,256	1	4	5	43.0–91.1	24.1–48.8	A _B	MF	TE	Pataki et al. [2000]
1,256	1	3	5	15.4	12.2	A _S	DB	TE	Ewers et al. [2008]
1,600	1	1	5	73.2	4.2	A _S	EB	TE	Dunn and Connor [1993]
1,600	4	2	12 per stand	29.9, 44.0, 26.9, 39.5	2.3, 2.3, 0.8, 2.3	A _S	EN	BO	Lundblad and Lindroth [2002]
1,800	1	1	4	9.4	8.0	A _S	EN-P	TE	Kurpius et al. [2003]
1,963	1	6	2–6	-	0.6–6.1	A _S	DB	TE	Pataki and Oren [2003]
1,963	1	1	10	73.6	31.7	A _S	PW-P	TE	Oren et al. [2001]
1,965	1	3	3	21.4	10.6	A _S	EB	TR	Giambelluca et al. [2003]
2,500	3	1	19, 5, 8	56.6, 63.1, 78.6	6.7, 6.1, 4.0	A _S	EB	TE	Dunn and Connor [1993]
2,500	1	2	19, 7	21.4, 9.5	8.0, 4.2	A _S	DB	TE	Vertessy et al. [1995]
2,500	6 ^g	4	10–17	45.0 (A _S)	-	A _S	DB	TE	Hultine et al. [2007]
2,500	1	1	5	N/A	-	W	MF	TE	Bowman et al. [2005]
2,500	1	1	6	N/A	-	A _L	OS	TE	Yue et al. [2008]
2,550	1	3	3	21.2	10.5	A _S	EB	TR	Giambelluca et al. [2003]
3,000	2	6	1–4	46.0	-	W	MF	TE	Cech et al. [2003]
4,000	1	1	9	101.6	85.0	A _S	EN-P	TE	Teskey and Sheriff [1996]
4,000	1	1	10	20.0	-	C	EN	BO	Gienciala et al. [2002]
4,000	2	1	10, 6	18.6, 40.4	10.2, 12.4	C	EB-P	TR	Gienciala et al. [2000]
4,900	1	1	10	50.0	3.2	A _B or A _L	DB	TE	Vertessy et al. [1997]
6,000	1	1	10	15.6	-	C	DB	TE	Davi et al. [2005]
6,400	3	7	1 or 2	23.1–24.6	11.8–12.4	A _S	DB	TE	Wullschlegler and Hanson [2006]
10,000	1	3	14, 15, or 19	23.4, 4.9, 5.0	13.8, 2.9, 2.9	A _S	MF	TE	Tang et al. [2006]
10,000	2	2	12	27.9, 6.8	-	A _B	EN	TE	Cermak et al. [1995]
10,000	2	1	5	N/A	25.2, 17.3	A _S	EN-P	TE	Granier [1987]
10,000 ^h	3	1	9, 9, 6	46.9, 38.4, 35.6	23.9, 12.7, 4.5	A _L	EN	TE	Phillips et al. [2002]
10,000 ^h	4	1	6 or 7	up to 40.0	5.6–13.1	A _S	EN	TE	Delzon and Loustau [2005]
11,000	1	4	4	2.1–12.2	0.5–7.7	A _S	DB	TE	Bovard et al. [2005]
15,000	6	1	6–12	6.6, 22.0, 28.0, 30.4, 42.8, 10.6	4.7, 11.4, 5.7, 7.7, 6.8, 3.7	A _S	EN	BO	Zimmermann et al. [2000]
17,000	1	4	9 total trees	18.1, 32.6	9.7, 28.4	A _S	MF	TE	Iida et al. [2006]
19,200	1	6	9, 1, 1, 1, 1	22.5	11.9	A _S	DB	TE	Wullschlegler et al. [2001]
20,000	1	1	3	3.3, 6.0	2.3, 3.9	A _S	EB-P	TR	Oguntunde and van de Giesen [2005]
40,000	1	1	8	N/A	-	A _S	DB-P	TE	Williams et al. [2004]
40,000	1	3	6	-	4.6, 11.1, 1.4	A _S	EN	TE	Unsworth et al. [2004]
60,000	1	1	10	8.3	-	A _S	EB-P	TR	Roupsard et al. [2006]

^aStudies are sorted from lowest to highest plot size. Shown are the number of plots employed, the number of species in which sap flux measurements were made, the number of sap flux trees per species per plot, the basal area (A_B) and sapwood area (A_S) of the plot or stand, the scalar or variable employed to scale from individual trees to the plot, the International Geosphere-Biosphere Program (IGBP) vegetation classification, general biome, and cited work.

^bScalars: B, branch area; C, circumference; D, canopy diameter; T, Dericthlet tessellation; W, weighted averaging; A_S, sapwood area; A_B, basal area; A_L, leaf area.

^cIGBP global land cover classes: EN, evergreen needleleaf; EB, evergreen broadleaf; DB, deciduous broadleaf; MF, mixed forest; OS, open shrub; PW, permanent wetland; “-P” indicates plantation.

^dBiome types: BO, boreal; TE, temperate; TR, tropical.

^eShows total number of trees per species among all plots, selecting the dominant tree of each species in each plot.

^fFive scalars tested were leaf area, sapwood area, diameter, tessellation, and field theory.

^gSix plots established for sapwood area calculation.

^hStand size not reported, but measurements were given on a per hectare basis.

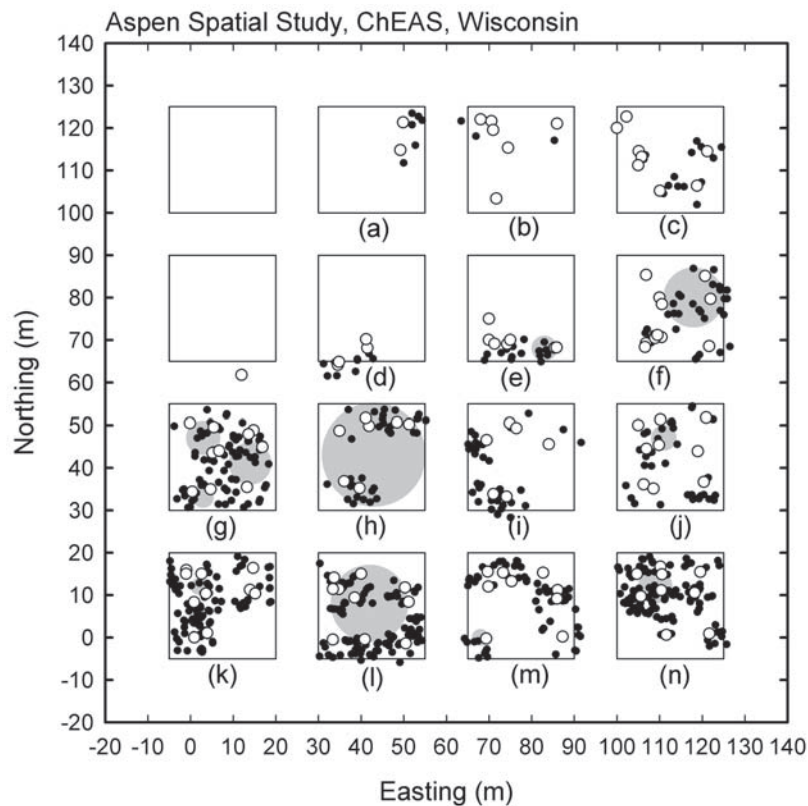


Figure 1. Map of study site showing distribution of *Populus tremuloides* (trembling aspen) sap flux trees (white circles) and all other *P. tremuloides* trees measured (black circles). Superimposed are 11 randomly located 2–12 m radius plots (gray circles). Shown also are 16 25 m \times 25 m blocks used in the cyclic sampling design. Blocks a–n contained one or more *P. tremuloides* trees.

the total effective stand area was 0.875 ha. The remaining 14 blocks consisted of forested wetland (blocks b, e, f, and i) and upland forest. In each block, 9 cyclic sampling plots with a 2.5 m radius were arranged using lags of 5 and 10 m in two dimensions [Loranty *et al.*, 2008]. The cyclic sampling scheme maximizes the efficiency with which a fixed number of samples is distributed in space, and optimizes the sampling for spatial analysis [Burrows *et al.*, 2002]. However, in each sampling plot we recorded the absolute (Easting, Northing) locations of the dominant *P. tremuloides* trees rather than sampling plot centers, and so measured fluxes were related to their absolute location in space. Dominant trees were selected for flux measurements as these were expected to be most representative of edaphic and other environmental characteristics limiting growth in the respective sampling plots. This is justified because tree size impacts on sap flux could still be investigated when many trees were sampled across the site [Adelman *et al.*, 2008; Loranty *et al.*, 2008; Traver *et al.*, 2009]. Moreover, recent work has shown that G_{Sref} as well as differences in E_C among individual trees can be explained by competition for light [Loranty, 2009; Loranty *et al.*, 2010; M. M. Loranty *et al.*, Competition for light between individual trees lowers reference canopy stomatal conductance: Results from a model, submitted to *Journal of Geophysical Research*, 2010], and so even the bias introduced by measuring sap flux in dominant individuals could be corrected with rela-

tively simple intertree competition data. We also recorded height and DBH for each dominant tree. In addition, we recorded the location, height, and DBH of every *P. tremuloides* individual within 5 m of each dominant tree. This resulted in an inventory of 109 dominant and 644 additional *P. tremuloides* trees, for a total of 752 trees distributed among the 14 0.06 ha blocks. One dominant tree was eliminated from the analysis, as it was a much older remnant of the previously clear-cut stand. Mean basal areas, on a per-tree basis, for the dominant and other *P. tremuloides* trees were 80.3 (± 5.3 standard error) cm^2 and 70.5 (± 2.1 standard error) cm^2 , respectively. Selection of the dominant tree in each sampling plot slightly biased the flux measurements toward higher mean basal area. However, this was not considered a problem for the scales in this study, as basal areas were spatially autocorrelated at up to 70 m lag distance [Loranty *et al.*, 2008] and the primary source of variability of reference G_S was competition among trees for light [Loranty, 2009; Loranty *et al.*, 2010, also submitted manuscript, 2010].

[8] In each dominant *P. tremuloides* we installed Granier-type 20 mm length constant-heat sap flux sensors [Granier, 1987]. One sensor pair was placed on the north side of each tree at breast height (1.3 m). Intra-tree scaling followed Ewers *et al.* [2002], which accounted for bark thickness, sapwood depth, and radial and circumferential trends in sap flux. We assumed the same relationships in this study. To

Table 2. Number of Sap Flux Trees per Plot and Mean Parameters for Plots at Each Plot Size and Respective Plot Area^a

Radius (m)	Trees (per Plot)	A_{plot} (m ²)	L^b (m ² m ⁻²)	G_{Sref}^b (mmol m ⁻² s ⁻¹)	m (mmol m ⁻² s ⁻¹)	P_{CC}^c (m ² m ⁻²)
2.0	1–3	12.6	5.96 (0.23)	87.3 (6.1)	51.4	1.08
2.5	1–4	19.6	4.92 (0.25)	82.5 (6.0)	49.4	0.84
3.0	1–4	28.3	3.83 (0.15)	86.4 (5.2)	52.0	0.75
4.0	1–5	50.3	3.28 (0.17)	81.1 (5.0)	46.6	0.58
5.0	1–5	78.5	2.81 (0.14)	82.8 (5.1)	48.3	0.49
7.0	1–7	153.9	2.13 (0.12)	77.7 (4.8)	42.6	0.39
9.0	2–8	254.5	1.86 (0.10)	79.9 (4.7)	47.4	0.34
12.0	2–10	452.4	1.48 (0.09)	95.9 (5.6)	56.2	0.25

^aHere A_{plot} is plot area. Leaf area index (L) and canopy closure (P_{CC}) were derived allometrically from site-specific data. Reference canopy average stomatal conductance (G_{Sref}) and sensitivity of stomatal closure to vapor pressure deficit (m) were derived from boundary line analysis of canopy average stomatal conductance versus vapor pressure deficit.

^bShows mean at each plot size with standard error in parentheses.

^cCanopy closure exceeding 1.0 occurred when total crown cross-sectional area at canopy base exceeded plot area.

include nighttime transpiration, baselines were determined from the maximum temperature difference over a week long period [Oishi *et al.*, 2008]. Sap flux measurements for the study were made from mid-June to mid-July 2005. The period 1–7 July was used for the present analyses, as it was the one contiguous period in which sensors in no trees were affected by power outages. Concurrently, air temperature (T_A) and relative humidity (R_H) (Vaisala HMP 45C, Vaisala Oyj, Helsinki, Finland) were measured at two-thirds canopy height (~7 m). Vapor pressure deficit (D) was calculated from T_A and R_H based on equations adapted from [Goff and Gratch, 1946]. Ewers *et al.* [2007, 2008] showed that *P. tremuloides* and other stands in this area are well coupled to the atmosphere because D measurements at 2/3 canopy height from six different stands are the same as D measurements at 30 m on the WLEF tower (regression analysis indicated that the slope of the two measurements was not different from 1 and the intercept was not different from zero). This also justifies an assumption of D being spatially unaffected by varying transpiration rates in each stand. Sap flux, temperature, and relative humidity measurements were recorded every 30 s (CR10X, Campbell Scientific, Logan, UT, United States) and aggregated to 30 min values. Wind speed, photosynthetically active radiation (Q_0), and precipitation measurements from the nearby WLEF (~1 km) [Davis *et al.*, 2003] and Lost Creek (~10 km) [Cook *et al.*, 2004] flux towers were used as model inputs.

[9] Total height was measured for each tree using a laser rangefinder and clinometer with triangulation methods outlined by the Eastern Native Tree Society [Bolzan, 2004]. Leaf area (A_L) (m²) and projected crown area (A_C) (m²) were determined for each tree through allometric relationships with tree basal area (A_{BT}) (cm²). These relationships were developed through destructive harvesting of 13 *P. tremuloides* trees spanning the wetland to upland. All harvested trees fit allometric relations, $A_L = 10.2 \ln A_{\text{BT}} - 24.9$ ($r^2 = 0.97$; $N = 13$) and $A_C = 1.74 \exp(A_{\text{BT}} * 0.0111)$ ($r^2 = 0.61$; $N = 13$). For each tree we used the allometric relationship for sapwood depth, $d_S = -1.91 + 7.159 * \text{DBH}^{0.7501}$, where d_S is given in mm and DBH in cm, derived from a *P. tremuloides* stand within 10 km of our site [Ewers *et al.*, 2002, 2007], from which heartwood area was calculated and then subtracted from A_{BT} to obtain sapwood area (A_S) (cm²).

2.3. Scaling From Plots to the Stand

[10] Circular scaling plots (hereafter called plots) were generated by randomly sampling, with replacement, using plot centers (Easting, Northings) from a uniform distribution bounded within the domain (Figure 1). Plot selection was subject to three constraints: (1) no part of a plot was allowed to fall outside one of the 0.06 ha blocks, (2) every plot was required to have a minimum of one sap flux tree, and (3) every plot had to have at least three total trees. The second constraint ensured that every plot met the minimum sap flux sensor sample size employed in previous studies (Table 1). The third constraint ensured that no plot represented a single, isolated tree. These constraints were intended to mimic sap flux plot selection. We note that for small plots the latter two constraints would ignore gaps in the canopy and overestimate canopy density. However, such bias is not inconsistent with sap flux studies in which plots are selected randomly [e.g., Kang *et al.*, 2002; Mellander *et al.*, 2006], based on site characteristics [e.g., Hogg and Hurdle, 1997; Roberts *et al.*, 2005], or using aggregate measures such as stand basal area or leaf area [e.g., Ewers *et al.*, 2002; Simonin *et al.*, 2006].

[11] To examine the effects of plot size on scaling E_C and G_S we generated 8 sets of 200 plots using uniform radii of 2 m, 2.5 m, 3 m, 4 m, 5 m, 7 m, 9 m, or 12 m, giving a range of plot areas from 12 to 450 m², respectively (Table 2). This bootstrapping method produced overlap of some plots, which meant that total variance declined and variance shifted from between plots to within plots with increasing plot size. In each plot we calculated L (m² leaf m⁻² ground area) by summing A_L of all *P. tremuloides* trees within the plot and dividing by plot area (A_{plot}) (m²). We note that these calculations include trees whose crowns extend beyond the plot boundary. This is necessary to ensure that total leaf area used to calculate E_L is consistent with the total sapwood area used to calculate E_C . While it could lead to overestimates of L and canopy cover, particularly for small plots, these parameters would also be consistent with the plot total E_C . The proportion of canopy cover (P_{CC}) was estimated by summing A_C for all trees in the plot, subtracting overlapping crown areas that were counted multiple times, and dividing by A_{plot} . Overlapping crown areas were quantified using a simple algorithm that estimates the area of the asymmetric

lens produced by the intersection of two circles [Weisstein, 2009].

[12] Canopy transpiration on a per unit ground area basis, E_C ($\text{mm H}_2\text{O s}^{-1}$), was calculated following the approach of Oren *et al.* [1998b]:

$$E_C = \frac{1}{A_{\text{plot}}} \sum_{i=1}^k \sum_{j=1}^l J_{i,j} \cdot A_{S,i,j} \quad (1)$$

where k is the number of bins of sapwood area (A_S) (m^2), l is the number of individuals within each bin, and J is sap flux velocity ($\text{m}^3 \text{s}^{-1}$). To include nighttime transpiration, baselines were determined from the maximum temperature difference over a weeklong period using the approach of Oishi *et al.* [2008]. Radial and circumferential trend information used data from Ewers *et al.* [2002] to set up ratios between the outer xylem measurements and inner or southern xylem. Sapwood area bins were obtained by sorting from lowest to highest A_S , all sap flux and the *P. tremuloides* not instrumented for sap flux trees (or nonflux trees) within the plot. Nonflux trees were then binned with flux trees with bins spanning from the midpoints between successive sap flux tree A_S values. In the degenerative case where a plot had only a single flux tree all trees in the plot were put in a single bin. We note that this method can lead to a systematic bias in plots with only one sap flux tree, if the chosen sap flux tree is always a dominant tree.

[13] First and second moments of the distribution of plot canopy transpiration were calculated at every half-hourly time step, with the mean and variance respectively calculated as

$$E[E_C(t)] = \frac{1}{n} \sum_{i=1}^n E_C(t)_i \quad (2)$$

and

$$\text{VAR}[E_C(t)] = \frac{1}{n} \sum_{i=1}^n \{E_C(t)_i - E[E_C(t)]\}^2 \quad (3)$$

where t is the time (30 min step) and n is the number of plots. In general, relationships between variability and areal sample size follow some form of power law [Levin, 1992]. Power law functions yield straight lines on log-log plots, and so we plotted variance of E_C versus plot area with log-log axes.

[14] G_S was calculated by inverting a form of the Penman-Monteith equation [Monteith and Unsworth, 1990]:

$$G_S(t) = \frac{K_G[T(t)] E[E_C(t)]}{D(t) L} \quad (4)$$

where D is vapor pressure deficit (kPa), L is mean leaf area index ($\text{m}^2 \text{leaf m}^{-2} \text{ground}$), and $K_G(T) = 115.8 + 0.4236T$ ($\text{kPa m}^3 \text{kg}^{-1}$) is the conductance coefficient at average canopy temperature T ($^{\circ}\text{C}$). $K_G(T)$ accounts for temperature effects on the psychrometric constant, latent heat of vaporization, specific heat of air at constant pressure, and density of air [Phillips and Oren, 1998].

2.4. Statistical Analysis and Evaluation of Goodness of Fit

[15] Curve fitting, regression analysis, ANOVAs, and t tests were performed in Sigmaplot (version 11.0 2008 Systat

Software, CA, United States). We used two criteria to evaluate the goodness of fit between individual plot E_C values and mean values for the whole stand. First, a regression analysis was conducted and the slope of the regression was used as a criterion for goodness of fit. In a subset of plots that had slopes between 0.97 and 1.03 we calculated the index of agreement (IOA) [Willmott, 1982] and sorted the results from highest (=1) to lowest (=0) IOA.

3. Results

3.1. Representativeness of Plots

[16] The actual number of sap flux trees per plot ranged from as low as 1 for the 13 m^2 plots to as high as 10 for some of the 452 m^2 plots (Table 2). The upper end of this range is comparable to most of the studies presented in Table 1, as 67 of the 90 studies had at most 10 sap flux trees per species per plot, and 48 had fewer than 8 trees per species per plot.

[17] E_C for any 12 m radius plot selected from block h (see Figure 1) was representative of stand E_C , as indicated absolutely by a slope of regression of 0.999 and dynamically by IOA of 0.991 between the plot and whole stand fluxes evaluated using all 30 min values for the 7 days. Block h had mean canopy structural parameters ($A_B = 5.7 \text{ m}^2 \text{ha}^{-1}$, $P_{CC} = 0.29$, $L = 1.24$) that were similar to those for the whole stand at the 12 m radius scale ($A_B = 6.3 \text{ m}^2 \text{ha}^{-1}$, $P_{CC} = 0.25$, $L = 1.48$). At the 12 m radius plot size the canopies in the other blocks were either denser or more open than the stand average with A_B ranging from 0.7 to 22.7 $\text{m}^2 \text{ha}^{-1}$. Using the same slope of regression and IOA criteria we also found representative plots at all sizes in different locations in the stand having similar values of L and P_{CC} as the stand. All plots shown in gray in Figure 1 had slopes between 0.97 and 1.03, and IOA values of 0.98 or higher. For instance, representative 7 and 9 m plots were located in the center of block i and representative 4 m plots were found centered at 5 m east, 50 m north in block g. No representative plots were found in areas of dense canopy, such as the west half of block k and west edge of block n, or in the low canopy density areas such as blocks a–d.

3.2. Representativeness and Environmental Drivers

[18] Figures 2–4 summarize the first two moments of E_C derived from the plots. Figure 2 shows scaled E_C for 2 m, 3 m and 12 m radius plots, along with environmental drivers. Although E_C values changed in an absolute sense as the size of the plot changed, the values showed the same dynamic responses to environmental drivers. To test whether or not this environmental driver affected the representativeness of plots we examined mean and variance of E_C in three bins of D representing low ($D \leq 0.5$ kPa), intermediate ($0.5 < D \leq 1.0$ kPa), and high levels ($D > 1.0$ kPa). E_C declined monotonically with increasing plot size, and the rate of change of flux per unit increase in plot size also declined with increasing plot size (Figure 3a). Moreover, L and P_{CC} also declined monotonically (Table 2), and so E_L was less variable among plot sizes (Figure 3b). The mean responses were similar among bins of D . The $\log[\text{VAR}(E_C)]$ versus $\log(A_{\text{plot}})$ all fit straight lines ($P < 0.0001$) (Figure 4). The absolute E_C variances increased

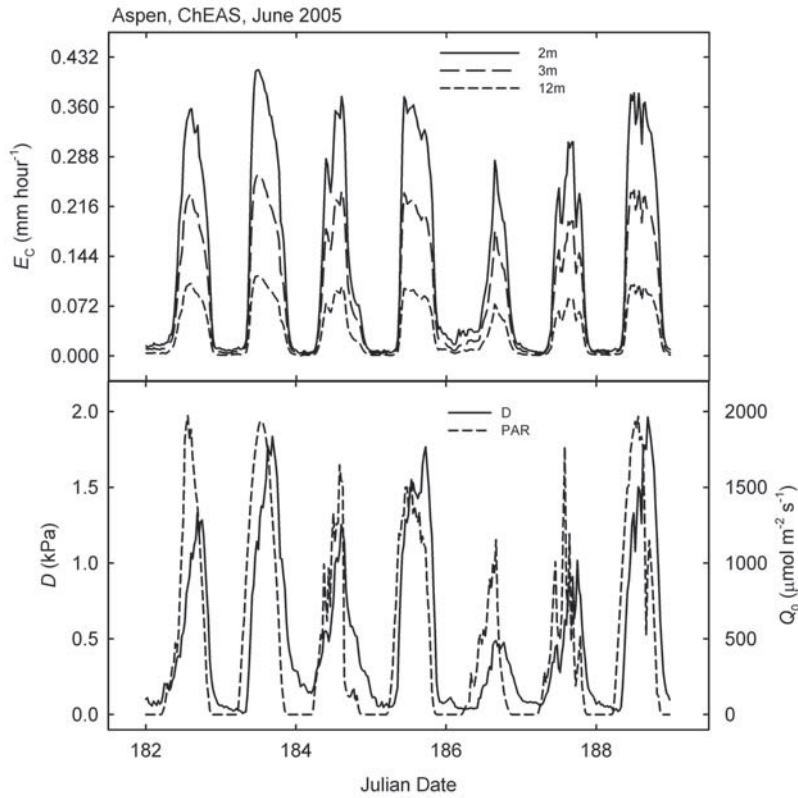


Figure 2. Mean diurnal canopy transpiration (E_C) for 2, 3, and 12 m radius plots, along with diurnals for vapor pressure deficit (D) and incident photosynthetically active radiation (Q_0).

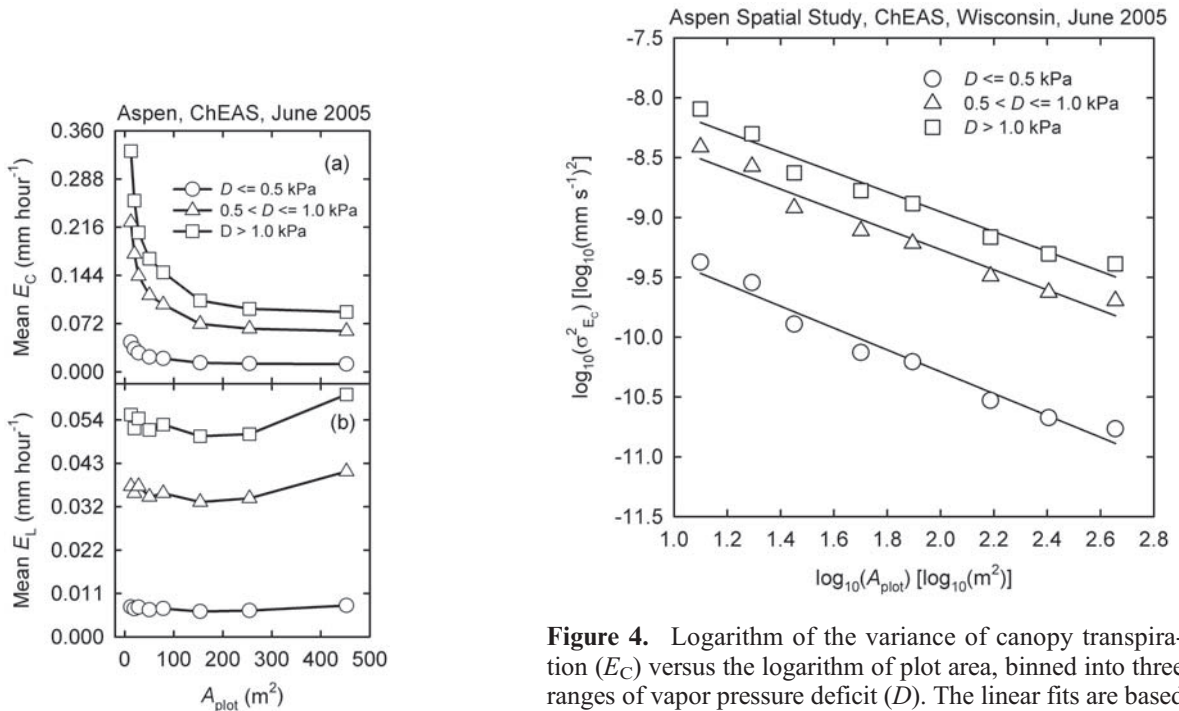


Figure 3. (a) Mean canopy transpiration (E_C) and (b) mean transpiration per unit leaf area (E_L) versus plot area (A_{plot}), into groups of low, intermediate, and high vapor pressure deficit (D).

Figure 4. Logarithm of the variance of canopy transpiration (E_C) versus the logarithm of plot area, binned into three ranges of vapor pressure deficit (D). The linear fits are based on $y = y_0 + ax$, where $y_0 = -8.4635$ and $a = -0.9131$ for low D , $y_0 = -7.5844$ and $a = -0.8423$ for intermediate D , and $y_0 = -7.2952$ and $a = -0.8291$ for high D . All regression lines are significant ($P < 0.0001$), and slopes are not significantly different ($P > 0.39$, $R^2 > 0.95$).

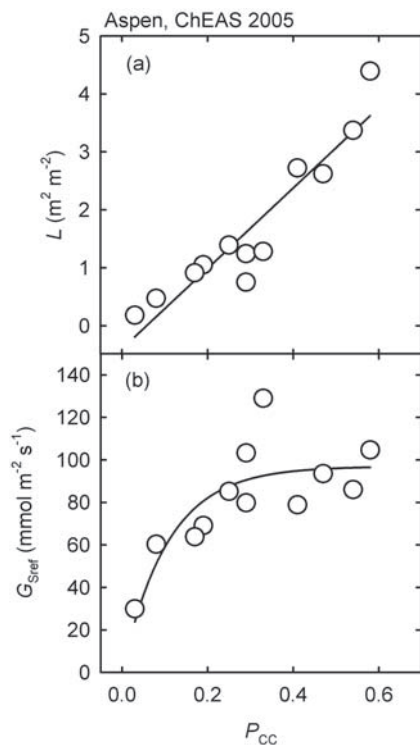


Figure 5. Block mean (a) leaf area index (L) and (b) reference canopy average stomatal conductance (G_{Sref}) versus canopy closure (P_{CC}). A linear equation ($L = -0.40 + 6.94 P_{CC}$) is fit for L versus P_{CC} ($r^2 = 0.86$, $P < 0.0001$), while an exponential rise to a maximum ($\{G_{Sref} = 96.9[1 - \exp(-9.36P_{CC})]\}$) is fit through G_{Sref} versus P_{CC} ($r^2 = 0.61$, $P = 0.0016$).

with D , but the rate of change of $\log[\text{VAR}(E_C)]$ with $\log(A_{plot})$ was independent of D ($P > 0.39$).

3.3. Representativeness of Parameters for Ecosystem Models

[19] G_{Sref} and m are given in Table 2. G_{Sref} varied from 77.7 to 95.9 $\text{mmol m}^{-2} \text{s}^{-1}$ and m varied in proportion to G_{Sref} , but there was no clear relationship between these parameters and plot size. However, across scales m was linearly related to G_{Sref} with a slope not statistically different from 0.6 ($P = 0.367$). Figure 5 shows L and G_{Sref} versus P_{CC} at the block level using one randomly chosen 12 m radius plot in each block. Blocks a and d (Figure 1) were excluded as their respective plots had near-zero E_C , and so only 12 blocks were included in Figure 5. P_{CC} ranged from 0.03 to 0.58, with values less than 0.2 all occurring in forested wetland blocks. A_B ranged from 0.7 to 3.9 $\text{m}^2 \text{ha}^{-1}$ in the wetland blocks and 4.3 to 22.7 $\text{m}^2 \text{ha}^{-1}$ in upland blocks. L varied from 0.13 to 1.03 $\text{m}^2 \text{m}^{-2}$ in the wetland and 0.76 to 4.39 $\text{m}^2 \text{m}^{-2}$ in the upland and was linearly related to P_{CC} , as would be expected given that both parameters were derived allometrically from A_{BT} . G_{Sref} also varied with P_{CC} , albeit nonlinearly. Indeed, there was a threshold response in which G_{Sref} increased with P_{CC} in the wetland, but showed little or no variation with P_{CC} in upland blocks. Moreover, the nonwetland G_{Sref} values closely cor-

responded to the values reported for the whole stand using any plot size (Table 2).

4. Discussion

4.1. Plot Representativeness

[20] The representativeness of plots depended upon on whether total stand average canopy transpiration, E_C , or transpiration per unit leaf area, E_L , was considered. Although mean E_C decreased when going from the smallest to largest plot sizes, when scaled to E_L there was little variation among plot sizes. All plots were required to have at least one flux tree and two additional trees for scaling from sap flux to E_C . This forced small plots to sample in relatively dense parts of the stand, which excluded gaps in the small plots. As plot size increased more gap areas were included. We note that the decline in E_C , L , and P_{CC} would not occur if randomly selected plots were permitted to occur in gaps where there were no flux measurements. However, including plots with no flux trees would be an unrealistic representation of traditional sap flux plot sampling methods. Moreover, both mean and variance of E_C showed a monotonic decline with plot size, supporting a predictable scaling behavior even at the canopy scale. It should be noted that the scaling behavior for the variance (Figure 4) would be expected to change among studies as a function of the amount of spatial autocorrelation in E_C . For example, a relatively homogeneous stand with respect to E_C would have less steep slopes of variance versus plot size. The slopes would be steepest in a stand where the individual fluxes were spatially independent. Alternatively, if one partitions a study area into non-overlapping areal units then beyond the correlation length the variance is expected to fall off as the inverse of the number of areal units [Levin, 1992]. Within the correlation length recent evidence that spatial heterogeneity of E_C is a function of the rate of water loss, as expressed through changes in D [Adelman et al., 2008; Loranty et al., 2008; Traver et al., 2009], suggest that through plant hydraulics one can increase the predictability and interpretation of E_C variance between studies.

[21] Plot representativeness was also independent of the magnitude of environmental drivers, as the rate of change in variance of E_C with plot size did not change with D . We suggest that it was time-invariant stand structural characteristics (i.e., L and P_{CC}), and by implication A_B and A_S , not spatial dynamics of flux rates that was key to scaling fluxes to the stand and extracting parameters such as L and G_{Sref} , as has been suggested by other studies [Ford et al., 2007; Adelman et al., 2008; Loranty et al., 2008].

4.2. Random or Biased Plot Selection

[22] Given our plot sampling criteria, smaller plot sizes were more likely to systematically overestimate E_C than larger plots. Similarly, systematic error could potentially have occurred in any of the studies shown in Table 1 had they not chosen plots representative of the stand density. Our plot sizes (13 to 452 m^2) spanned a range representing 40 percent of the sap flux studies presented in Table 1, and bounded all plot sizes of those studies conducted in *P. tremuloides* stands [Hogg et al., 1997; Hogg and Hurdle, 1997; Pataki et al., 2000; Ewers et al., 2002; Uddling et al., 2008]. The rate of change in mean stand values for E_C , L , and P_{CC}

declined with increasing plot size and was smallest for plots between 154 and 452 m². Randomly located plots at the 7–12 m radius plot sizes would therefore be expected to yield more representative canopy parameters than smaller plots. However, these plot areas are larger than those previously employed in sap flux studies conducted in *P. tremuloides* [Hogg et al., 1997; Hogg and Hurdle, 1997; Pataki et al., 2000; Ewers et al., 2002; Adelman et al., 2008], with the exception of a plantation study [Uddling et al., 2008]. Clearly either biased plot selection is preferred, our stand is anomalous, or the prior studies undersampled their respective stands. We considered the possibility that our stand was unusual in terms of structure or canopy transpiration. Evidence from the literature on *P. tremuloides* suggests that this is not the case. Mean basal area (A_B) (m² ha⁻¹) of our 20 year old stand was 6.3 m² ha⁻¹, but varied from 0.7 to 22.7 m² ha⁻¹ among 12 m radius plots. This range bounded A_B values reported for 30 year old Boreal (3.4 m² ha⁻¹) [Ewers et al., 2005] and subalpine Wyoming (4.9 m² ha⁻¹) [Adelman et al., 2008] stands, but our basal areas were smaller than values reported in northern Wisconsin (30.0 m² ha⁻¹) [Ewers et al., 2002; Uddling et al., 2008], 20 year old Boreal (38.0 to 63.0 m² ha⁻¹) [Hogg and Hurdle, 1997], and another subalpine stand in Wyoming (43.0 m² ha⁻¹) [Pataki et al., 2000].

[23] The range of L , 0.13 to 4.39 m² m⁻² among blocks, spanned the range of values among prior sap flux studies conducted on *P. tremuloides* stands in Boreal [Hogg et al., 1997; Hogg and Hurdle, 1997; Ewers et al., 2005], subalpine [Pataki et al., 2000; Adelman et al., 2008], and northern temperate [Ewers et al., 2002, 2007; Uddling et al., 2008] biomes. Our mean stand L of 1.48 m² m⁻² using 12 m radius plots was similar to the values reported by Hogg and Hurdle [1997], less than half the values reported for stands with higher A_B [Pataki et al., 2000; Ewers et al., 2002; Uddling et al., 2008], and higher than the values reported in studies that had smaller A_B [Ewers et al., 2005; Adelman et al., 2008]. Thus, the allometry of our stand (i.e., relationship between L and A_B) appears to be consistent with other *P. tremuloides* studies.

[24] The scale independence of E_L is important since ecosystem models typically require some parameter for G_S (or its reference parameter value, G_{Sref}), which is expressed on a per unit leaf area basis. While plot location had a large effect on L and P_{CC} , the effect was minimal for G_{Sref} . Plots located in the wetland ($P_{CC} < 0.2$) had low and variable G_{Sref} values, while other plots showed a limited range of G_{Sref} . Moreover, we derived a proportionality between m and G_{Sref} of 0.59, which is consistent with previous studies involving *P. tremuloides* [Hogg et al., 2000; Ewers et al., 2005, 2007; Uddling et al., 2008] and other species [Oren et al., 1999; Ewers et al., 2000; Ogle and Reynolds, 2002; Mackay et al., 2003; Addington et al., 2004; Fisher et al., 2006; David et al., 2007; Ewers et al., 2007]. Our estimates of G_{Sref} varied between 77.7 and 95.9 mmol m⁻² s⁻¹ among plot sizes, which were somewhat higher than the maximum value of 65 mmol m⁻² s⁻¹ reported by Ewers et al. [2005], but smaller than the values reported in other *P. tremuloides* studies [Hogg and Hurdle, 1997; Ewers et al., 2007]. Moreover, the range of G_{Sref} (77.7 to 95.9 mmol m⁻² s⁻¹) is quite small compared to intertree variability of G_{Sref} attributed to competition for light at our study site

[Loranty et al., 2010] or at another *P. tremuloides* stand within 10 km of the site [Ewers et al., 2007].

[25] If our stand is not an anomaly then the more likely alternative explanation for the apparent effectiveness of relatively smaller plot sizes employed in previous *P. tremuloides* studies is that they relied on biased selection of plot locations. This is clearly evidenced in the earlier Boreal studies [Hogg et al., 1997; Hogg and Hurdle, 1997] in which plots were chosen to distinguish among clones, or plantation plots [Uddling et al., 2008] that had experimental control on factors affecting growth rates. Pataki et al. [2000] chose 3 m radius plots centered on each sap flux tree on the assumption that these plots contained all the flux trees' competitors. Ewers et al. [2002, 2007] measured L optically and allometrically in an 804 m² stand. A 79 m² sap flux plot within the stand was chosen to closely match the mean L (=3.5 m² m⁻²) and to capture the range of DBH within the stand. Adelman et al. [2008] and Loranty et al. [2008] used initial surveys of A_B to determine the spatial extent and sample design for their plots. The logic behind this was that sapwood area would be related to A_B , and E_C would scale with sapwood area. The unit lag distance needed to adequately sample A_B at a stand scale while providing sufficient information to quantify spatial autocorrelation of tree transpiration determined the respective plot sizes. Our results from selecting the best fit plots at each of the radii, and these other *P. tremuloides* studies, support a scaling logic that exploits stand structural properties to find representative plots.

4.3. Implications for Scaling From Trees to Stands

[26] E_C scaling logic that relies on characterizing stand structure in space with relatively few flux measurement points is also generally supported by the literature spanning a range of species composition and biomes. Nonetheless, multiple sources of spatial variability in E_C have been implicated. Intertree variations in J_S have been cited as primary [Kumagai et al., 2005a; Pataki et al., 2005; Hultine et al., 2007; Nadezhdina et al., 2007] or secondary [Bovard et al., 2005; Herbst et al., 2007; Adelman et al., 2008] sources of heterogeneity in canopy transpiration. We cannot rule out the potential for spatial variability in J_S in our own study, but such heterogeneity was not expressed in such a way that it prevented us from scaling up from any plot size. Moreover, Loranty et al. [2008], using data from the same stand a year earlier, found no clear evidence of spatial autocorrelation in J_S . Oren et al. [1998a, 1998b] used a coefficient of variation of 20% as a guideline and said that the sample size thus changes with stand characteristics. Alternatively, Kumagai et al. [2005a] found up to a three-fold difference in sap flux velocity among trees, and so he argued that sap flux measurements should be made in as many trees per species as possible to accurately quantify scaled E_C . On the one hand, if such a requirement were indeed justified it could make scaling from a practical number of sap flux measurements to regional levels questionable. On the other hand, Ford et al. [2007] found that variations in sapwood area among plots was the greatest source of variability in canopy transpiration despite the relative homogeneity in species and age of their stand. The need for a large number of sap flux sensors per species was unwarranted for our stand because (1) single plots were

representative of stand mean E_C , (2) no single plot at any size had more than 10 sap flux trees, (3) G_{Sref} was insensitive to P_{CC} and, by implication, plot location in the upland forest areas of the stand, and (4) G_{Sref} was predictable from P_{CC} in the forested wetland areas of the stand. We suppose, based on Figure 5b, that three plots representing wetland, upland, and transitional between these end-members, with at most 10 sap flux trees per plot, would be sufficient for parameterizing models where each of these components of the stand were needed. Consequently, our analysis suggests a representative number of sap flux trees for our stand was somewhere between 3 and 30. However, to move toward the low end of this range, a tractable number of J_S measurements for studies requiring many species, requires mechanistic explanations for transpiration variability in space and time.

[27] Potential mechanistic explanations of such spatial heterogeneity implicate edaphic and topographic controls on vertical and lateral water flow, respectively, as well as stand structure. A number of studies have shown that spatial variability of transpiration attributed to soil moisture controls was predictable from edaphic or topographic properties [Schiller et al., 2002; Eberbach and Burrows, 2006; Tromp-van Meerveld and McDonnell, 2006; Nadezhdina et al., 2007]. Tromp-van Meerveld and McDonnell [2006] showed that topographic and edaphic controls affected growth rates of individual trees, which in turn modified the spatial distribution of transpiration. In northern Wisconsin, Traver et al. [2009] showed no impact of edaphic conditions, while Loranty et al. [2010, also submitted manuscript, 2010] showed that competition for light explained a significant amount of spatial variation of E_C and G_{Sref} . Higher flux rates have also been shown near stand edges in comparison to stand centers [Taylor et al., 2001; Cienciala et al., 2002; Giambelluca et al., 2003; Herbst et al., 2007]. Taylor et al. [2001] attributed higher transpiration rates in edge trees to advection, although considerable velocity variance along forest edges suggests they cannot be treated simply as edges [Detto et al., 2008]. Similarly, evidence of stand structure as a control on the variability of E_C among stands was shown when stand thinning led to increased soil moisture that in turn promoted greater transpiration during periods of intermediate soil moisture [Simonin et al., 2006, 2007]. Alternatively, some stand structural changes associated with age [Zimmermann et al., 2000; Phillips et al., 2002; Ewers et al., 2005], such as adjustments in leaf-to-sapwood area [Phillips et al., 2002] and root-shoot ratio [Ewers et al., 2005] appear to be more elusive qualities to obtain routinely.

[28] Most studies that account for spatial heterogeneity of E_C at the stand level employ a logic that is based on the scaling theory of Hatton and Wu [1995] relating tree water use to leaf area index. Numerous studies either use this approach explicitly [Vertessy et al., 1997; Medhurst et al., 2002; Phillips et al., 2002; Schiller et al., 2002] or modify it by using sapwood area as the primary scalar of E_C [Vertessy et al., 1995; Oren et al., 1998b; Bovard et al., 2005; Ford et al., 2007; Herbst et al., 2007; Kumagai et al., 2007]. However, this simplified scaling logic loses credibility when different scalars yield different flux values, as has been suggested by some studies [Vertessy et al., 1997; Ford et al., 2007]. This would seem distressing, as scalars such as sapwood area, leaf area, and stem diameter should be correlated

through allometric relationships. Our results and numerous others [Taylor et al., 2001; Cienciala et al., 2002; Giambelluca et al., 2003; Tromp-van Meerveld and McDonnell, 2006; Kumagai et al., 2007; Adelman et al., 2008] suggest that this problem would be avoided if plots were located in structurally representative areas within the stand, and not simply defined to include a wide range of DBH. So, this study and others suggest that to scale flux observations from trees to stand we should take into account the spatial arrangement of DBH and not just its moments. Our study differed from others in that we measured and directly analyzed both sap flux and transpiration scalars spatially with high density within the stand. Previous studies either examined just the sap flux trees using aggregate measures of spatial variability [e.g., Adelman et al., 2008; Loranty et al., 2008; Traver et al., 2009] or had representative measures of the scalars and a limited number of sap flux sensors [e.g., Hogg and Hurdle, 1997; Vertessy et al., 1997; Oren et al., 1998b; Wilson et al., 2001; Ewers et al., 2002; Giambelluca et al., 2003; Ewers et al., 2005; Simonin et al., 2006]. By employing a high density and spatially extensive set of both flux and scalar measurements in a heterogeneous stand our study provides a robust demonstration of how scaling transpiration from plots to stands should work. This study shows quantitatively, as other studies have suggested, that biased sampling would be preferred over random sampling for characterizing stand level water fluxes. We suggest that future scaling efforts take into consideration three spatially covarying parameters, G_{Sref} , L , and P_{CC} , which are needed to accurately scale canopy transpiration to the whole stand level or to larger spatial extents.

[29] **Acknowledgments.** Funding for this study was from the National Science Foundation, Hydrologic Sciences Program (EAR-0405306 to D.S.M., EAR-0405381 to B.E.E., and EAR-0405318 to E.L.K.). The NSF IGERT program also supported M.M.L. The statements made in this manuscript reflect the views of the authors and do not necessarily reflect the views of NSF. D.S.M. also acknowledges funding from the Department of Energy (DOE) Office of Biological and Environmental Research, National Institute for Climatic Change Research (NICCR) Midwestern region subagreement 050516Z20. We are grateful for the comments provided by the anonymous reviewers, associate editor, and editor, Dennis Baldocchi. We are also grateful to personnel at Kemp Natural Resources Station, and to Elizabeth Traver and David Roberts for their assistance with fieldwork.

References

- Addington, R. N., R. J. Mitchell, R. Oren, and L. A. Donovan (2004), Stomatal sensitivity to vapor pressure deficit and its relationship to hydraulic conductance in *Pinus palustris*, *Tree Physiol.*, 24(5), 561–569.
- Adelman, J. D., B. E. Ewers, and D. S. Mackay (2008), Use of temporal patterns in vapor pressure deficit to explain spatial autocorrelation dynamics in tree transpiration, *Tree Physiol.*, 28(4), 647–658.
- Bakwin, P. S., P. P. Tans, D. F. Hurst, and C. L. Zhao (1998), Measurements of carbon dioxide on very tall towers: Results of the NOAA/CMDL program, *Tellus, Ser. B*, 50(5), 401–415, doi:10.1034/j.1600-0889.1998.t014-00001.x.
- Baldocchi, D. D., R. J. Luxmoore, and J. L. Hatfield (1991), Discerning the forest from the trees - an essay on scaling canopy stomatal conductance, *Agric. For. Meteorol.*, 54(2–4), 197–226, doi:10.1016/0168-1923(91)90006-C.
- Baldocchi, D. D., K. B. Wilson, and L. H. Gu (2002), How the environment, canopy structure and canopy physiological functioning influence carbon, water and energy fluxes of a temperate broad-leaved deciduous forest—an assessment with the biophysical model CANOAK, *Tree Physiol.*, 22(15–16), 1065–1077.
- Band, L. E., D. L. Peterson, S. W. Running, J. Coughlan, R. Lammers, J. Dungan, and R. Nemani (1991), Forest ecosystem processes at the

- watershed scale—Basis for distributed simulation, *Ecol. Modell.*, 56(1–4), 171–196, doi:10.1016/0304-3800(91)90199-B.
- Bernier, P. Y., N. Breda, A. Granier, F. Raulier, and F. Mathieu (2002), Validation of a canopy gas exchange model and derivation of a soil water modifier for transpiration for sugar maple (*Acer saccharum* Marsh.) using sap flow density measurements, *For. Ecol. Manage.*, 163(1–3), 185–196, doi:10.1016/S0378-1127(01)00578-3.
- Bolzan, W. (2004), *Tree Measuring Guidelines of the Eastern Native Tree Society*, 11 pp., East. Native Tree Soc., Florence, Mass.
- Bonan, G. B. (1991), Atmosphere-biosphere exchange of carbon-dioxide in Boreal forests, *J. Geophys. Res.*, 96(D4), 7301–7312.
- Bovard, B. D., P. S. Curtis, C. S. Vogel, H. B. Su, and H. P. Schmid (2005), Environmental controls on sap flow in a northern hardwood forest, *Tree Physiol.*, 25(1), 31–38.
- Bowman, W. P., M. M. Barbour, M. H. Turnbull, D. T. Tissue, D. Whitehead, and K. L. Griffin (2005), Sap flow rates and sapwood density are critical factors in within- and between-tree variation in CO₂ efflux from stems of mature *Dacrydium cupressinum* trees, *New Phytol.*, 167(3), 815–828, doi:10.1111/j.1469-8137.2005.01478.x.
- Burrows, S. N., S. T. Gower, M. K. Clayton, D. S. Mackay, D. E. Ahl, J. M. Norman, and G. Diak (2002), Application of geostatistics to characterize leaf area index (LAI) from flux tower to landscape scales using a cyclic sampling design, *Ecosystems*, 5(7), 667–679.
- Cech, P. G., S. Pepin, and C. Korner (2003), Elevated CO₂ reduces sap flux in mature deciduous forest trees, *Oecologia*, 137(2), 258–268, doi:10.1007/s00442-003-1348-7.
- Cermak, J., E. Cienciala, J. Kucera, A. Lindroth, and E. Bednarova (1995), Individual variation of sap-flow rate in large pine and spruce trees and stand transpiration—A pilot-study at the Central NOPEX site, *J. Hydrol.*, 168(1–4), 17–27, doi:10.1016/0022-1694(94)02657-W.
- Cienciala, E., J. Kucera, and A. Malmer (2000), Tree sap flow and stand transpiration of two *Acacia mangium* plantations in Sabah, Borneo, *J. Hydrol.*, 236(1–2), 109–120, doi:10.1016/S0022-1694(00)00291-2.
- Cienciala, E., P. E. Mellander, J. Kucera, M. Oplustilova, M. Ottosson-Lofvenius, and K. Bishop (2002), The effect of a north-facing forest edge on tree water use in a boreal Scots pine stand, *Can. J. For. Res.*, 32(4), 693–702, doi:10.1139/x02-013.
- Clearwater, M. J., F. C. Meinzer, J. L. Andrade, G. Goldstein, and N. M. Holbrook (1999), Potential errors in measurement of nonuniform sap flow using heat dissipation probes, *Tree Physiol.*, 19(10), 681–687.
- Cook, B. D., et al. (2004), Carbon exchange and venting anomalies in an upland deciduous forest in northern Wisconsin, USA, *Agric. For. Meteorol.*, 126(3–4), 271–295, doi:10.1016/j.agrformet.2004.06.008.
- Davi, H., E. Duffrene, A. Granier, V. Le Dantec, C. Barbaroux, C. Francois, and N. Breda (2005), Modelling carbon and water cycles in a beech forest Part II: Validation of the main processes from organ to stand scale, *Ecol. Modell.*, 185(2–4), 387–405, doi:10.1016/j.ecolmodel.2005.01.003.
- David, T. S., et al. (2007), Water-use strategies in two co-occurring Mediterranean evergreen oaks: Surviving the summer drought, *Tree Physiol.*, 27(6), 793–803.
- Davis, K. J., P. S. Bakwin, C. X. Yi, B. W. Berger, C. L. Zhao, R. M. Teclaw, and J. G. Isebrands (2003), The annual cycles of CO₂ and H₂O exchange over a northern mixed forest as observed from a very tall tower, *Global Change Biol.*, 9(9), 1278–1293, doi:10.1046/j.1365-2486.2003.00672.x.
- Delzon, S., and D. Loustau (2005), Age-related decline in stand water use: Sap flow and transpiration in a pine forest chronosequence, *Agric. For. Meteorol.*, 129(3–4), 105–119, doi:10.1016/j.agrformet.2005.01.002.
- Detto, M., G. G. Katul, M. Siqueira, J. Y. Juang, and P. Stoy (2008), The structure of turbulence near a tall forest edge: The backward-facing step flow analogy revisited, *Ecol. Appl.*, 18(6), 1420–1435, doi:10.1890/06-0920.1.
- Dunn, G. M., and D. J. Connor (1993), An analysis of sap flow in mountain ash (*Eucalyptus regnans*) forests of different age, *Tree Physiol.*, 13(4), 321–336.
- Eberbach, P. L., and G. E. Burrows (2006), The transpiration response by four topographically distributed *Eucalyptus* species, to rainfall occurring during drought in south eastern Australia, *Physiol. Plant.*, 127(3), 483–493, doi:10.1111/j.1399-3054.2006.00762.x.
- Engel, V. C., M. Stieglitz, M. Williams, and K. L. Griffin (2002), Forest canopy hydraulic properties and catchment water balance: Observations and modeling, *Ecol. Model.*, 154(3), 263–288.
- Ewers, B. E., and R. Oren (2000), Analyses of assumptions and errors in the calculation of stomatal conductance from sap flux measurements, *Tree Physiol.*, 20(9), 579–589.
- Ewers, B. E., R. Oren, and J. S. Sperry (2000), Influence of nutrient versus water supply on hydraulic architecture and water balance in *Pinus taeda*, *Plant Cell Environ.*, 23(10), 1055–1066, doi:10.1046/j.1365-3040.2000.00625.x.
- Ewers, B. E., R. Oren, N. Phillips, M. Stromgren, and S. Linder (2001), Mean canopy stomatal conductance responses to water and nutrient availabilities in *Picea abies* and *Pinus taeda*, *Tree Physiol.*, 21(12–13), 841–850.
- Ewers, B. E., D. S. Mackay, S. T. Gower, D. E. Ahl, S. N. Burrows, and S. S. Samanta (2002), Tree species effects on stand transpiration in northern Wisconsin, *Water Resour. Res.*, 38(7), 1103, doi:10.1029/2001WR000830.
- Ewers, B. E., S. T. Gower, B. Bond-Lamberty, and C. K. Wang (2005), Effects of stand age and tree species on canopy transpiration and average stomatal conductance of Boreal forests, *Plant Cell Environ.*, 28(5), 660–678, doi:10.1111/j.1365-3040.2005.01312.x.
- Ewers, B. E., D. S. Mackay, and S. Samanta (2007), Interannual consistency in canopy stomatal conductance control of leaf water potential across seven tree species, *Tree Physiol.*, 27(1), 11–24.
- Ewers, B. E., D. S. Mackay, J. Tang, P. Bolstad, and S. Samanta (2008), Intercomparison of Sugar Maple (*Acer saccharum* Marsh.) stand transpiration responses to environmental conditions from the Western Great Lakes Region of the United States, *Agric. For. Meteorol.*, 148, 231–246, doi:10.1016/j.agrformet.2007.08.003.
- Fassnacht, K. S., and S. T. Gower (1997), Interrelationships among the edaphic and stand characteristics, leaf area index, and aboveground net primary production of upland forest ecosystems in north central Wisconsin, *Can. J. For. Res.*, 27(7), 1058–1067, doi:10.1139/cjfr-27-7-1058.
- Fisher, R. A., M. Williams, R. L. Do Vale, A. L. Da Costa, and P. Meir (2006), Evidence from Amazonian forests is consistent with isohydric control of leaf water potential, *Plant Cell Environ.*, 29(2), 151–165, doi:10.1111/j.1365-3040.2005.01407.x.
- Foley, J. A., I. C. Prentice, N. Ramankutty, S. Levis, D. Pollard, S. Sitch, and A. Haxeltine (1996), An integrated biosphere model of land surface processes, terrestrial carbon balance, and vegetation dynamics, *Global Biogeochem. Cycles*, 10(4), 603–628, doi:10.1029/96GB02692.
- Ford, C. R., M. A. McGuire, R. J. Mitchell, and R. O. Teskey (2004), Assessing variation in the radial profile of sap flux density in *Pinus* species and its effect on daily water use, *Tree Physiol.*, 24(3), 241–249.
- Ford, C. R., R. M. Hubbard, B. D. Kloeppel, and J. M. Vose (2007), A comparison of sap flux-based evapotranspiration estimates with catchment-scale water balance, *Agric. For. Meteorol.*, 145(3–4), 176–185, doi:10.1016/j.agrformet.2007.04.010.
- Giambelluca, T. W., A. D. Ziegler, M. A. Nullet, D. M. Truong, and L. T. Tran (2003), Transpiration in a small tropical forest patch, *Agric. For. Meteorol.*, 117(1–2), 1–22, doi:10.1016/S0168-1923(03)00041-8.
- Goff, J. A., and S. Gratch (1946), Smithsonian meteorological tables, *Trans. Am. Soc. Ventilation Eng.*, 52, 95.
- Granier, A. (1987), Evaluation of transpiration in a Douglas-fir stand by means of sap flow measurements, *Tree Physiol.*, 3(4), 309–319.
- Hatton, T. J., and H. I. Wu (1995), Scaling theory to extrapolate individual tree water-use to stand water-use, *Hydrol. Process.*, 9(5–6), 527–540, doi:10.1002/hyp.3360090505.
- Hatton, T. J., E. A. Catchpole, and R. A. Vertessy (1990), Integration of sapflow velocity to estimate plant water-use, *Tree Physiol.*, 6(2), 201–209.
- Herbst, M., J. M. Roberts, P. T. W. Rosier, M. E. Taylor, and D. J. Gowing (2007), Edge effects and forest water use: A field study in a mixed deciduous woodland, *For. Ecol. Manage.*, 250(3), 176–186, doi:10.1016/j.foreco.2007.05.013.
- Hogg, E. H., and P. A. Hurdle (1997), Sap flow in trembling aspen: Implications for stomatal responses to vapor pressure deficit, *Tree Physiol.*, 17(8–9), 501–509.
- Hogg, E. H., et al. (1997), A comparison of sap flow and eddy fluxes of water vapor from a Boreal deciduous forest, *J. Geophys. Res.*, 102(D24), 28,929–28,937.
- Hogg, E. H., B. Saugier, J. Y. Pontailleur, T. A. Black, W. Chen, P. A. Hurdle, and A. Wu (2000), Responses of trembling aspen and hazelnut to vapor pressure deficit in a Boreal deciduous forest, *Tree Physiol.*, 20(11), 725–734.
- Hultine, K. R., S. E. Bush, A. G. West, and J. R. Ehleringer (2007), Effect of gender on sap-flux-scaled transpiration in a dominant riparian tree species: Box elder (*Acer negundo*), *J. Geophys. Res.*, 112, G03S06, doi:10.1029/2006JG000232.
- Iida, S., T. Tanaka, and M. Sugita (2006), Change of evapotranspiration components due to the succession from Japanese red pine to evergreen oak, *J. Hydrol.*, 326(1–4), 166–180, doi:10.1016/j.jhydrol.2005.11.002.
- James, S. A., M. J. Clearwater, F. C. Meinzer, and G. Goldstein (2002), Heat dissipation sensors of variable length for the measurement of sap flow in trees with deep sapwood, *Tree Physiol.*, 22(4), 277–283.
- Kang, S. Y., S. Kim, and D. Lee (2002), Spatial and temporal patterns of solar radiation based on topography and air temperature, *Can. J. For. Res.*, 32(3), 487–497, doi:10.1139/x01-221.

- Kumagai, T., S. Aoki, H. Nagasawa, T. Mabuchi, K. Kubota, S. Inoue, Y. Utsumi, and K. Otsuki (2005a), Effects of tree-to-tree and radial variations on sap flow estimates of transpiration in Japanese cedar, *Agric. For. Meteorol.*, 135(1–4), 110–116, doi:10.1016/j.agrformet.2005.11.007.
- Kumagai, T., H. Nagasawa, T. Mabuchi, S. Ohsaki, K. Kubota, K. Kogi, Y. Utsumi, S. Koga, and K. Otsuki (2005b), Sources of error in estimating stand transpiration using allometric relationships between stem diameter and sapwood area for *Cryptomeria japonica* and *Chamaecyparis obtusa*, *For. Ecol. Manage.*, 206(1–3), 191–195, doi:10.1016/j.foreco.2004.10.066.
- Kumagai, T., S. Aoki, T. Shimizu, and K. Otsuki (2007), Sap flow estimates of stand transpiration at two slope positions in a Japanese cedar forest watershed, *Tree Physiol.*, 27(2), 161–168.
- Kumagai, T., M. Tateishi, T. Shimizu, and K. Otsuki (2008), Transpiration and canopy conductance at two slope positions in a Japanese cedar forest watershed, *Agric. For. Meteorol.*, 148(10), 1444–1455, doi:10.1016/j.agrformet.2008.04.010.
- Kurpius, M. R., J. A. Panek, N. T. Nikolov, M. McKay, and A. H. Goldstein (2003), Partitioning of water flux in a Sierra Nevada ponderosa pine plantation, *Agric. For. Meteorol.*, 117(3–4), 173–192, doi:10.1016/S0168-1923(03)00062-5.
- Levin, S. A. (1992), The problem of pattern and scale in ecology, *Ecology*, 73(6), 1943–1967, doi:10.2307/1941447.
- Loranty, M. M. (2009), Towards a mechanistic understanding of spatial patterns of forest transpiration, and its implications for scaling, Ph.D. dissertation, 155 pp., State Univ. of N. Y. at Buffalo, Buffalo.
- Loranty, M. M., D. S. Mackay, B. E. Ewers, J. D. Adelman, and E. L. Kruger (2008), Environmental drivers of spatial variation in whole-tree transpiration in an aspen-dominated upland-to-wetland forest gradient, *Water Resour. Res.*, 44, W02441, doi:10.1029/2007WR006272.
- Loranty, M. M., D. S. Mackay, B. E. Ewers, E. Traver, and E. L. Kruger (2010), Competition for light contributes to within-species variability in stomatal conductance, *Water Resour. Res.*, doi:10.1029/2009WR008125, in press.
- Lundblad, M., and A. Lindroth (2002), Stand transpiration and sapflow density in relation to weather, soil moisture and stand characteristics, *Basic Appl. Ecol.*, 3(3), 229–243, doi:10.1078/1439-1791-00099.
- Mackay, D. S., D. E. Ahl, B. E. Ewers, S. T. Gower, S. N. Burrows, S. Samanta, and K. J. Davis (2002), Effects of aggregated classifications of forest composition on estimates of evapotranspiration in a northern Wisconsin forest, *Global Change Biol.*, 8(12), 1253–1265, doi:10.1046/j.1365-2486.2002.00554.x.
- Mackay, D. S., D. E. Ahl, B. E. Ewers, S. Samanta, S. T. Gower, and S. N. Burrows (2003), Physiological tradeoffs in the parameterization of a model of canopy transpiration, *Adv. Water Resour.*, 26(2), 179–194, doi:10.1016/S0309-1708(02)00090-8.
- Medhurst, J. L., M. Battaglia, and C. L. Beadle (2002), Measured and predicted changes in tree and stand water use following high-intensity thinning of an 8-year-old *Eucalyptus nitens* plantation, *Tree Physiol.*, 22(11), 775–784.
- Meinzer, F. C., G. Goldstein, and J. L. Andrade (2001), Regulation of water flux through tropical forest canopy trees: Do universal rules apply?, *Tree Physiol.*, 21(1), 19–26.
- Mellander, P. E., M. Stahli, D. Gustafsson, and K. Bishop (2006), Modeling the effect of low soil temperatures on transpiration by Scots pine, *Hydrol. Process.*, 20(9), 1929–1944, doi:10.1002/hyp.6045.
- Monteith, J. L., and M. H. Unsworth (1990), *Principles of Environmental Physics*, 291 pp., Edward Arnold, London.
- Nadezhdina, N., J. Cermak, L. Meiresonne, and R. Ceulemans (2007), Transpiration of Scots pine in Flanders growing on soil with irregular substratum, *For. Ecol. Manage.*, 243(1), 1–9, doi:10.1016/j.foreco.2007.01.089.
- Norman, J. M. (1993), Scaling processes between leaf and canopy levels, in *Scaling Physiological Processes: Leaf to Globe*, edited by J. R. Ehleringer and C. B. Field, pp. 41–76, Academic, San Diego, Calif.
- Ogle, K., and J. F. Reynolds (2002), Desert dogma revisited: Coupling of stomatal conductance and photosynthesis in the desert shrub, *Larrea tridentata*, *Plant Cell Environ.*, 25(7), 909–921, doi:10.1046/j.1365-3040.2002.00876.x.
- Oguntunde, P. G., and N. van de Giesen (2005), Water flux measurement and prediction in young cashew trees using sap flow data, *Hydrol. Process.*, 19(16), 3235–3248, doi:10.1002/hyp.5831.
- Oishi, A. C., R. Oren, and P. C. Stoy (2008), Estimating components of forest evapotranspiration: A footprint approach for scaling sap flux measurements, *Agric. For. Meteorol.*, 148(11), 1719–1732, doi:10.1016/j.agrformet.2008.06.013.
- Oliveras, I., and P. Llorens (2001), Medium-term sap flux monitoring in a Scots pine stand: Analysis of the operability of the heat dissipation method for hydrological purposes, *Tree Physiol.*, 21(7), 473–480.
- Oren, R., B. E. Ewers, P. Todd, N. Phillips, and G. Katul (1998a), Water balance delineates the soil layer in which moisture affects canopy conductance, *Ecol. Appl.*, 8(4), 990–1002, doi:10.1890/1051-0761(1998)008[0990:WBDSL]2.0.CO;2.
- Oren, R., N. Phillips, G. Katul, B. E. Ewers, and D. E. Pataki (1998b), Scaling xylem sap flux and soil water balance and calculating variance: A method for partitioning water flux in forests, *Ann. Sci. For.*, 55(1–2), 191–216, doi:10.1051/forest:19980112.
- Oren, R., J. S. Sperry, G. G. Katul, D. E. Pataki, B. E. Ewers, N. Phillips, and K. V. R. Schafer (1999), Survey and synthesis of intra- and interspecific variation in stomatal sensitivity to vapour pressure deficit, *Plant Cell Environ.*, 22(12), 1515–1526, doi:10.1046/j.1365-3040.1999.00513.x.
- Oren, R., J. S. Sperry, B. E. Ewers, D. E. Pataki, N. Phillips, and J. P. Mezonigal (2001), Sensitivity of mean canopy stomatal conductance to vapor pressure deficit in a flooded *Taxodium distichum* L. forest: Hydraulic and non-hydraulic effects, *Oecologia*, 126(1), 21–29, doi:10.1007/s004420000497.
- Pataki, D. E., and R. Oren (2003), Species differences in stomatal control of water loss at the canopy scale in a mature bottomland deciduous forest, *Adv. Water Resour.*, 26(12), 1267–1278, doi:10.1016/j.advwatres.2003.08.001.
- Pataki, D. E., R. Oren, and W. K. Smith (2000), Sap flux of co-occurring species in a western subalpine forest during seasonal soil drought, *Ecology*, 81(9), 2557–2566.
- Pataki, D. E., S. E. Bush, P. Gardner, D. K. Solomon, and J. R. Ehleringer (2005), Ecohydrology in a Colorado River riparian forest: Implications for the decline of *Populus fremontii*, *Ecol. Appl.*, 15(3), 1009–1018, doi:10.1890/04-1272.
- Pausch, R. C., E. E. Grote, and T. E. Dawson (2000), Estimating water use by sugar maple trees: Considerations when using heat-pulse methods in trees with deep functional sapwood, *Tree Physiol.*, 20(4), 217–227.
- Phillips, N., and R. Oren (1998), A comparison of daily representations of canopy conductance based on two conditional time-averaging methods and the dependence of daily conductance on environmental factors, *Ann. Sci. For.*, 55(1–2), 217–235, doi:10.1051/forest:19980113.
- Phillips, N., R. Oren, and R. Zimmermann (1996), Radial patterns of xylem sap flow in non-, diffuse- and ring-porous tree species, *Plant Cell Environ.*, 19(8), 983–990, doi:10.1111/j.1365-3040.1996.tb00463.x.
- Phillips, N., B. J. Bond, N. G. McDowell, and M. G. Ryan (2002), Canopy and hydraulic conductance in young, mature and old Douglas-fir trees, *Tree Physiol.*, 22(2–3), 205–211.
- Raupach, M. R., and J. J. Finnigan (1988), Single-layer models of evaporation from plant canopies are incorrect but useful, whereas multilayer models are correct but useless: Discuss, *Aust. J. Plant Physiol.*, 15(6), 705–716, doi:10.1071/PP9880705.
- Roberts, J., P. Rosier, and D. M. Smith (2005), The impact of broadleaved woodland on water resources in lowland UK: II. Evaporation estimates from sensible heat flux measurements over beech woodland and grass on chalk sites in Hampshire, *Hydrol. Earth Syst. Sci.*, 9(6), 607–613.
- Roupsard, O., et al. (2006), Partitioning energy and evapo-transpiration above and below a tropical palm canopy, *Agric. For. Meteorol.*, 139(3–4), 252–268, doi:10.1016/j.agrformet.2006.07.006.
- Schafer, K. V. R., R. Oren, and J. D. Tenhunen (2000), The effect of tree height on crown level stomatal conductance, *Plant Cell Environ.*, 23(4), 365–375, doi:10.1046/j.1365-3040.2000.00553.x.
- Schiller, G., E. D. Ungar, and Y. Cohen (2002), Estimating the water use of a sclerophyllous species under an East-Mediterranean climate I. Response of transpiration of *Phillyrea latifolia* L. to site factors, *For. Ecol. Manage.*, 170(1–3), 117–126, doi:10.1016/S0378-1127(01)00785-X.
- Schiller, G., S. Cohen, E. D. Ungar, Y. Moshe, and N. Herr (2007), Estimating water use of sclerophyllous species under East-Mediterranean climate - III. Tabor oak forest sap flow distribution and transpiration, *For. Ecol. Manage.*, 238(1–3), 147–155, doi:10.1016/j.foreco.2006.10.007.
- Scott, R. L., T. E. Huxman, W. L. Cable, and W. E. Emmerich (2006), Partitioning of evapotranspiration and its relation to carbon dioxide exchange in a Chihuahuan Desert shrubland, *Hydrol. Process.*, 20(15), 3227–3243.
- Sellers, P. J., et al. (1997), Modeling the exchanges of energy, water, and carbon between continents and the atmosphere, *Science*, 275(5299), 502–509, doi:10.1126/science.275.5299.502.
- Simonin, K., T. E. Kolb, M. Montes-Helu, and G. W. Koch (2006), Restoration thinning and influence of tree size and leaf area to sapwood area ratio on water relations of *Pinus ponderosa*, *Tree Physiol.*, 26(4), 493–503.
- Simonin, K., T. E. Kolb, M. Montes-Helu, and G. W. Koch (2007), The influence of thinning on components of stand water balance in a ponderosa pine forest stand during and after extreme drought, *Agric. For. Meteorol.*, 143(3–4), 266–276, doi:10.1016/j.agrformet.2007.01.003.

- Su, H., E. F. Wood, M. F. McCabe, and Z. Su (2007), Evaluation of remotely sensed evapotranspiration over the CEOP EOP-1 reference sites, *J. Meteorol. Soc. Jpn.*, *85A*, 439–459, doi:10.2151/jmsj.85A.439.
- Tang, J. W., P. V. Bolstad, B. E. Ewers, A. R. Desai, K. J. Davis, and E. V. Carey (2006), Sap flux-upscaled canopy transpiration, stomatal conductance, and water use efficiency in an old growth forest in the Great Lakes region of the United States, *J. Geophys. Res.*, *111*, G02009, doi:10.1029/2005JG000083.
- Taylor, P. J., I. K. Nuberg, and T. J. Hatton (2001), Enhanced transpiration in response to wind effects at the edge of a blue gum (*Eucalyptus globulus*) plantation, *Tree Physiol.*, *21*(6), 403–408.
- Teskey, R. O., and D. W. Sheriff (1996), Water use by *Pinus radiata* trees in a plantation, *Tree Physiol.*, *16*(1–2), 273–279.
- Traver, E., B. E. Ewers, D. S. Mackay, and M. M. Loranty (2009), Tree transpiration varies spatially in response to atmospheric but not edaphic conditions, *Funct. Ecol.*, *24*(2), 272–282, doi:10.1111/j.1365-2435.2009.01657.x.
- Tromp-van Meerveld, H. J., and J. J. McDonnell (2006), On the interrelations between topography, soil depth, soil moisture, transpiration rates and species distribution at the hillslope scale, *Adv. Water Resour.*, *29*(2), 293–310, doi:10.1016/j.advwatres.2005.02.016.
- Uddling, J., R. M. Teclaw, M. E. Kubiske, K. S. Pregitzer, and D. S. Ellsworth (2008), Sap flux in pure aspen and mixed aspen-birch forests exposed to elevated concentrations of carbon dioxide and ozone, *Tree Physiol.*, *28*(8), 1231–1243.
- Unsworth, M. H., N. Phillips, T. Link, B. J. Bond, M. Falk, M. E. Harmon, T. M. Hinckley, D. Marks, and K. T. Paw U (2004), Components and controls of water flux in an old-growth Douglas-fir-western hemlock ecosystem, *Ecosystems*, *7*(5), 468–481, doi:10.1007/s10021-004-0138-3.
- Vertessy, R. A., R. G. Benyon, S. K. Osullivan, and P. R. Gribben (1995), Relationships between stem diameter, sapwood area, leaf-area and transpiration in a young mountain ash forest, *Tree Physiol.*, *15*(9), 559–567.
- Vertessy, R. A., T. J. Hatton, P. Reece, S. K. Osullivan, and R. G. Benyon (1997), Estimating stand water use of large mountain ash trees and validation of the sap flow measurement technique, *Tree Physiol.*, *17*(12), 747–756.
- Vertessy, R. A., F. G. R. Watson, and S. K. O’Sullivan (2001), Factors determining relations between stand age and catchment water balance in mountain ash forests, *For. Ecol. Manage.*, *143*(1–3), 13–26, doi:10.1016/S0378-1127(00)00501-6.
- Weisstein, E. W. (2009), Circle-circle intersection, in *MathWorld*, Wolfram Res., Inc., Champaign, Ill. (Available at <http://mathworld.wolfram.com/Circle-CircleIntersection.html>)
- Williams, D. G., et al. (2004), Evapotranspiration components determined by stable isotope, sap flow and eddy covariance techniques, *Agric. For. Meteorol.*, *125*(3–4), 241–258, doi:10.1016/j.agrformet.2004.04.008.
- Willmott, C. J. (1982), Some comments on the evaluation of model performance, *Bull. Am. Meteorol. Soc.*, *63*(11), 1309–1313, doi:10.1175/1520-0477(1982)063<1309:SCOTEO>2.0.CO;2.
- Wilson, K. B., P. J. Hanson, P. J. Mulholland, D. D. Baldocchi, and S. D. Wullschleger (2001), A comparison of methods for determining forest evapotranspiration and its components: Sap-flow, soil water budget, eddy covariance and catchment water balance, *Agric. For. Meteorol.*, *106*(2), 153–168, doi:10.1016/S0168-1923(00)00199-4.
- Wood, E. F., D. P. Lettenmaier, and V. G. Zartarian (1992), A land-surface hydrology parameterization with subgrid variability for general-circulation models, *J. Geophys. Res.*, *97*(D3), 2717–2728.
- Wullschleger, S. D., and P. J. Hanson (2006), Sensitivity of canopy transpiration to altered precipitation in an upland oak forest: Evidence from a long-term field manipulation study, *Global Change Biol.*, *12*(1), 97–109, doi:10.1111/j.1365-2486.2005.001082.x.
- Wullschleger, S. D., P. J. Hanson, and D. E. Todd (2001), Transpiration from a multi-species deciduous forest as estimated by xylem sap flow techniques, *For. Ecol. Manage.*, *143*(1–3), 205–213, doi:10.1016/S0378-1127(00)00518-1.
- Yue, G. Y., H. L. Zhao, T. H. Zhang, X. Y. Zhao, L. Niu, and S. Drake (2008), Evaluation of water use of *Caragana microphylla* with the stem heat-balance method in Horqin Sandy Land, Inner Mongolia, China, *Agric. For. Meteorol.*, *148*(11), 1668–1678, doi:10.1016/j.agrformet.2008.05.019.
- Zimmermann, R., E. D. Schulze, C. Wirth, E. E. Schulze, K. C. McDonald, N. N. Vygodskaya, and W. Ziegler (2000), Canopy transpiration in a chronosequence of Central Siberian pine forests, *Global Change Biol.*, *6*(1), 25–37, doi:10.1046/j.1365-2486.2000.00289.x.

B. E. Ewers, Department of Botany, University of Wyoming, 1000 E. University Ave., Laramie, WY 82071, USA.

E. L. Kruger, Department of Forest and Wildlife Ecology, University of Wisconsin-Madison, 1630 Linden Dr., Madison, WI 53706, USA.

M. M. Loranty, Woods Hole Research Center, 149 Woods Hole Rd., Falmouth, MA 02540, USA.

D. S. Mackay, Department of Geography, State University of New York at Buffalo, 105 Wilkeson Quadrangle, Buffalo, NY 14261, USA. (dsmackay@buffalo.edu)